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Large trees, fertile islands, and birds in arid savanna

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Large *Acacia erioloba* trees scattered through the sparse grassy vegetation of arid oligotrophic savanna are focal points for animal activity because they supply nest sites, shade and scarce food resources. Faeces, fallen nest material and carcass remains left below trees elevate levels of nutrients available to plants in the soil beneath large trees. Soil concentrations of N and K were two times greater, and P concentrations 2·5 times greater under canopies of *A. erioloba* trees than in surrounding grassy shrubland.

Plant species with fleshy fruits (*Boscia, Grewia, Lycium* and *Solanum* spp.) occurred in 8% of treeless plots and beneath 17% of *A. erioloba* saplings, but their frequency increased to 90% beneath large trees. Dead *A. erioloba* trees were replaced by matrix vegetation (54%) and large shrubs with fleshy fruits (28%) rather than by conspecifics (17%). The distribution of fleshy-fruited plants in the Kalahari is thus dynamic and tied to the distribution of large trees such as *Acacia erioloba*.

The shade beneath the canopies of large spreading trees was used by birds (particularly Kori Bustards *Ardeotis kori*) and mammals (mainly Springbok *Antidorcas marsupialis,* Gemsbok *Oryx gazella*, Blue Wildebeest *Connochaetes taurinus* and Bat-eared Fox *Otocyon megalotis*) as a resting place during the heat of the day. Large raptors (> 1·5 kg) and vultures (> 5 kg) seldom perched on saplings, and more frugivorous bird species and individuals were seen on mature than sapling or dead trees. Nests of raptors, and the large communal nests of Sociable Weavers *Philetarius socius* were found mainly in large trees, and the nests of the Tree Rat *Thallomys paedulcus* were found in cavities in the stems of large trees.

Acacia erioloba and the only other large tree, *Acacia haematoxylon*, apparently structure plant and animal communities and determine pattern and patch dynamics in this arid savanna. We suggest that their role in maintaining biodiversity in the Kalahari cannot be served by the homogeneous thickets of stunted acacias that develop where the vegetation is overgrazed.

Keywords: *Acacia erioloba*; Kalahari; fleshy fruits; patch dynamics; seed dispersal; raptors

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Figure 1. Gemsbok *Oryx gazella* resting in the shade of a large *Acacia erioloba* tree during the heat of the day. The increased density of vegetation limited to the area around the tree can be clearly seen.

Introduction

Patchy nutrient accumulations in oligotrophic savannas tend to be maintained and reinforced because their enhanced productivity attracts animals which import additional nutrients (Scholes, 1990). Large isolated trees increase soil fertility beneath their canopies and are the foci for animal activity (Belsky & Canham, 1994) (Figs 1 & 2). Avifaunal species richness is correlated with plant height diversity in the Kalahari (Pianka & Huey, 1971), being dependent on horizontal and vertical structuring of the habitat by scattered trees.

In the arid savannas of the Kalahari Desert of southern Africa, where radiation levels are high and the sandy soils are poor in cations (Leistner, 1967), shaded fertile islands beneath trees are likely to support distinctive plant assemblages (Belsky & Canham, 1994). Plant species with a high probability of reaching subcanopy sites are bird- and mammal-dispersed species with barbed or edible fruits (Leistner, 1967). Shade and enhanced soil nutrient levels improve seedling survival of some fleshy-fruited trees (Manders & Richardson, 1992). Moreover, distribution of fleshy-fruited plants is thought to be correlated with soil fertility, more specifically with the availability of potassium, and to be correlated with soil fertility, or more specifically with the availability of potassium and nitrogen (Milewski, 1982; Hughes *et al.*, 1993). Frugivore-dispersed plants are therefore likely colonizers of subcanopy sites.

The development of a nutrient-rich patch beneath a tree in open savanna has been compared with the formation of a tree-fall gap in a forest. Belsky & Canham (1994) point out that the dynamics of these patches differ: a tree-fall gap in forest develops suddenly and closes gradually, whereas a subcanopy patch develops slowly and its duration is linked to the life-span of the tree. Subcanopy soil chemistry and the composition of subcanopy plant assemblages should therefore vary with tree age.

Figure 2. White-backed Vultures *Gyps africanus* and a lone Lappet-faced Vulture *Torgos tracheliotus* resting in the shade of a large *Acacia erioloba* tree, and feeding on the remains of a Gemsbok killed by lions the previous night.

In arid Kalahari savanna (Fig. 3) we hypothesized that: (1) subcanopy soils beneath the leguminous tree *Acacia erioloba* are nutrient enriched; (2) subcanopy sites are

Figure 3. Arid Kalahari savanna along the Nossob River, Kalahari Gemsbok National Park, South Africa, showing scattered large *Acacia erioloba* trees.

Figure 4. The remains of a large *Acacia erioloba* showing colonization of the area around the base of the tree by grasses, annual forbs (*Cleome* sp.) and a single large individual *Boscia albitrunca* (a tree with bird-dispersed fruits).

colonized primarily by plants with animal-dispersed fruits (Fig. 4); and (3) that soil fertility, and bird and plant assemblages vary with the developmental stage of the tree.

Study site and methods

Study site

The study was carried out in the Nossob River valley (approximately 25° 20′ S, 20° 30′ E) in the Kalahari Gemsbok National Park (KGNP) along the border between South Africa and Botswana. Rainfall in this semi-arid region (200–250 mm year^{-1}) occurs in mid to late summer (January to March). Mean maximum and minimum temperatures are 37·4°C and 19·5°C in January, and 22·2°C and 1·2°C in July (van Rooyen, 1984). Total nitrogen and available phosphorus are generally low in all soils of the KGNP but are higher in alluvial than dune soils (van Rooyen, 1984).

The vegetation is very open savanna with grasses (*Schmidtia kalihariensis*, *Stipagrostis* spp.) and occasional small trees (*Acacia erioloba*, *A. haematoxylon*, *A. mellifera*) on the dunes, and larger *A. erioloba* trees and fleshy-fruited shrubs (*Boscia albitrunca*, *Grewia* spp.) scattered in a matrix of grass and low shrubs (*Rhigozum trichotomum* and *Monechma* spp.) along the major river valleys (Leistner, 1967).

Soil nutrient status and fertility

In February 1993, one soil core (70 mm diameter × 100 mm deep) was taken from the A-horizon beneath the canopies of each of three isolated mature *A. erioloba* trees, within the canopy area of three dead *A. erioloba* trees, and at three sites in the corresponding matrix vegetation. These nine sample sites were subjectively selected. Samples were assayed for total nitrogen (N) (Kjeldahl method), organic carbon (C) (Walkey Black method) and for citric acid soluble phosphorus (P), potassium (K) and sodium (Na) (Bray number 2 method). One-way ANOVAs followed by Tukey multiple range tests were used to compare the soil data. However, high variances and small sample sizes necessitated increased confidence limits for statistical testing.

Subcanopy and matrix plant assemblages

Surveys of perennial plants were made in February 1993 in the Nossob River valley between Kwang (*c*. 20 km north of Nossob rest camp) and Kaspers Draai (*c*. 30 km south of Nossob rest camp). We drove 13 1-km road transects at 3-km intervals, and stopped at every individual or group of *A. erioloba* trees encountered within 20 m of the road on each transect. At each stop, vegetation beneath *A. erioloba* canopies and in matrix (between-tree) vegetation was assessed by recording all perennial plant species visible within one field of a spotting scope at a distance of 20 m from the road (sample area approximately 20 m^2). Groups of *Acacia erioloba* trees were not matched in all cases by a matrix sample. All *A. erioloba* trees within the sample field were classified on the basis of estimated height and basal diameter as either saplings (<5 m high, erect canopy, <20 cm basal diameter (b.d.), $N = 129$), mature living trees (>20 cm b.d., spreading canopy, $N = 153$) or dead trees (no foliage, $N = 69$). Vegetation composition in matrix vegetation ($N = 210$) was sampled at sites that were a minimum of 30 m from the nearest tree or group of trees. For the purposes of analysis of establishment sites for *Acacia erioloba*, sites containing saplings ($N = 129$) were also considered to be matrix vegetation. All plants recorded were allocated to one of four dispersal guilds on the basis of their fruit and seed morphology: wind-dispersed (seeds with large wings or plumes), autochorous (explosively dehiscent capsules), herbivore-dispersed (indehiscent, hard seeds enclosed in greenery, *sensu* Janzen, 1984), and frugivore-dispersed (seeds encased in fleshy fruits). Contingency table tests were used to compare observed and expected frequencies of dispersal guilds.

Use of trees by birds and mammals

A single observer recorded all birds and large nests seen on *A. erioloba* trees along a 166 km road transect between Nossob and Twee Rivieren on 10–11 March 1994. Each tree occupied by a bird or nest was classified as a sapling, mature tree or dead tree using the definitions given above. Bird species were allocated to food guilds: (1) insectivore, (2) granivore, (3) insectivore–granivore, (4) frugivore, (5) carnivore and (6) scavenger. Mammals and large birds resting in the shade of *A. erioloba* trees in the KGNP were noted on 3 days in February 1993 and on 2 days during March 1994. Contingency tables were used to compare the distribution of avifaunal feeding guilds in each of the tree stages.

Nomenclature follows Maclean (1993) for birds, Skinner & Smithers (1990) for mammals and Arnold & de Wet (1993) for plants.

Results

Soil nutrient status and fertility

In the nine soil samples from the Nossob valley, N ($r = 0{\cdot}96$, $p < 0{\cdot}01$) and P concentrations ($r = 0{\cdot}79$, $p < 0{\cdot}05$) were correlated with total organic carbon, and K was correlated with Na ($r = 0{\cdot}93$, $p < 0{\cdot}01$). Concentrations of N, P and K were greater in samples from beneath live *A. erioloba* trees than in soils from matrix vegetation (Table 1). Concentrations of these elements were at intermediate levels beneath dead trees.

Subcanopy and matrix plant assemblages

None of the dispersal guilds were randomly distributed ($p < 0{\cdot}0001$) among plots in the four sampled habitats (matrix, sapling, live tree, dead tree). Most wind-dispersed perennials were in matrix samples and were lower in frequency and abundance beneath tree canopies (Table 2). Herbivore-dispersed perennials were more evenly distributed between habitats, but fleshy-fruited plants increased in frequency and abundance from the matrix vegetation to beneath saplings, reaching a maximum under mature trees and decreasing again beneath dead trees. Within a dispersal guild, individual species (Appendix 1) showed similar patterns of frequency and abundance.

Acacia erioloba saplings were not randomly distributed with respect to tree canopies. Of 165 saplings, 129 (78%) were in 339 (matrix plus sapling) open sites, 19 (11%) under 282 living conspecifics, and 17 (10%) under 69 dead conspecifics. Significantly fewer saplings than expected occurred beneath living conspecifics ($\chi^2 = 225$, $p < 0{\cdot}001$). Dead *A. erioloba* trees were replaced by matrix vegetation in 42% of cases (29 of 69 trees). The remaining 40 dead trees had subcanopies with one or more woody plant species: conspecific saplings (11), *Acacia mellifera* trees (3), *Boscia* spp (15) or *Grewia flava* (17).

Use of trees by birds and mammals

The number of sightings of individual birds in each guild differed significantly between saplings and larger dead or live trees ($\chi^2 = 151$, df. = 10, $p < 0{\cdot}001$; Fig 5), although the relative abundance of bird species in each feeding guild did not differ between trees of different developmental stages ($\chi^2 = 12$, df. = 10). Large raptors (> 1·5 kg) and vultures (> 5 kg) seldom perched on saplings (Appendix 2). More frugivore species and individuals were seen on mature than sapling or dead trees. Nests of raptors, and the large communal nests of Sociable Weavers *Philetarius socius* were found mainly in large spreading trees (Table 3), and the nests of the Tree Rat *Thallomys paedulcus* were found in cavities in large tree trunks.

The shade beneath the canopies of spreading trees was used by birds (particularly Kori Bustards *Ardeotis kori*) and mammals (mainly Springbok *Antidorcas marsupialis*, Gemsbok *Oryx gazella*, Blue Wildebeest *Connochaetes taurinus* and Bat-eared Fox *Otocyon megalotis*) as a resting place during the heat of the day (Table 4; Figs 1 & 2).

Discussion

A conceptual model of patch dynamics of large trees and subcanopy plant assemblages and their relationships with animals and soil nutrients is shown in Fig. 6. The cycle starts with the dispersal of *Acacia erioloba* seeds to open vegetation in dung (Fig. 6: Step 1) by ruminants that consume the seed pods during the winter months (Leistner, 1961; Coe & Coe, 1987; Barnes *et al*., 1997).

Endozoochoric dispersal moves seeds away from tree canopies that support high densities of seed-feeding bruchid beetles, scarifies the seeds preparing them for

Table 1. *Concentrations (± S.D.) of organic carbon and nutrients in topsoils from beneath live and dead* Acacia erioloba *trees and from the adjacent grassland matrix. Different superscripts indicate means that differ significantly (Tukey test) at the 80% confidence level*

Parameter	Live tree	Dead tree	Grassy matrix	ANOVA F	Confidence level (p)
Carbon (%)	$0{\cdot}41 \pm 0{\cdot}30^a$	$0{\cdot}28 \pm 0{\cdot}21^a$	$0{\cdot}11 \pm 0{\cdot}11^a$	2·24	0·356
Nitrogen (%)	$0{\cdot}06 \pm 0{\cdot}05^a$	$0{\cdot}04 \pm 0{\cdot}03^{ab}$	$0{\cdot}01 \pm 0{\cdot}02^b$	2·77	0·141
Phosphorus (p.p.m.)	197 ± 172^a	159 ± 83^{ab}	82 ± 9^b	3·35	0·105
Potassium (p.p.m.)	517 ± 389^a	297 ± 123^{ab}	229 ± 56^b	2·68	0·147
Sodium (p.p.m.)	45 ± 43^a	37 ± 8^a	36 ± 9^a	1·23	0·356

Table 2. *Relative frequency (percentage of plots in which plant dispersal guild occurred), percentages of observed plants and average densities (± S.D.) of plants per 20* m^2 *plot, for four plant dispersal guilds in open matrix vegetation and beneath canopies of* Acacia erioloba *saplings, and mature and dead trees*

Dispersal guild	Matrix	Sapling tree	Live tree	Dead tree	Guild total all sites
Total plots	210	129	153	69	561
Total plants	1013	183	687	264	2147
Wind-dispersed					
% Frequency	89	43	14	10	48
% Plants	86	58	5	12	49
Average density	4·16 ± 2·61	0·83 ± 1·25	0·25 ± 0·71	0·46 ± 1·80	1·87 ± 2·57
Autochorous					
% Frequency	17	5	5	3	9
% Plants	11	5	2	3	7
Average density	0·51 ± 1·37	0·07 ± 0·36	0·09 ± 0·53	0·13 ± 0·96	0·25 ± 0·98
Herbivore-dispersed					
% Frequency	5	19	26	38	18
% Plants	1	15	8	23	7
Average density	0·06 ± 0·32	0·21 ± 0·40	0·35 ± 0·70	0·87 ± 1·39	0·28 ± 0·72
Frugivore-dispersed					
% Frequency	8	17	91	86	42
% Plants	2	22	84	62	37
Average density	0·08 ± 0·27	0·31 ± 0·98	3·79 ± 3·68	2·36 ± 2·12	1·43 ± 2·66

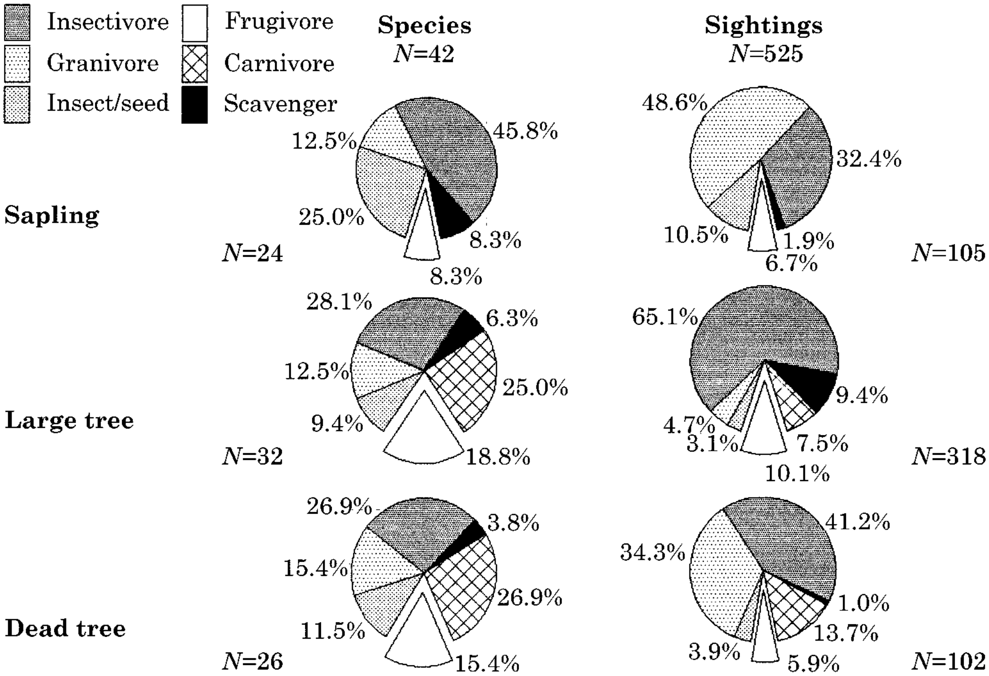

Figure 5. Food guild composition of avian species and individuals (sightings) in *Acacia erioloba* saplings, and live and dead trees.

germination, and often directs dispersal to disturbed sites with limited herbaceous cover (Coe & Coe, 1987; Hoffman *et al.*, 1989; Barnes *et al.*, 1997). Ruminant dung tends to be clumped in places where the animals sleep, shelter, drink or maintain territories (Leistner, 1967; Dean & Milton, 1991; Milton *et al.*, 1992; Jackson *et al.*, 1993). Although such sites include the shade beneath tree canopies, which is unsuitable for the establishment of *Acacia* seedlings (Smith & Shackleton, 1988), open disturbed sites may provide ideal establishment sites, particularly in wet years, because they

Table 3. *Nests of birds and small mammals in* Acacia erioloba *trees at three stages of development between Nossob Rest Camp and Twee Rivieren on 10–11 March 1994 (species arranged by nest size)*

Species	Sapling tree	Large tree	Dead tree
Sociable Weaver *Philetairius socius*	4	155	33
Raptor (unidentified)	0	4	0
White-backed Vulture *Gyps africanus*	0	1	0
Secretary Bird *Sagittarius serpentarius* (Miller)	1	0	0
Tree Rat *Thallomys paedulcus* (Sundevall)	0	8	0
Wattled Starling *Creatophora cinerea*	33	47	0
White-browed Sparrow-weaver *Plocepasser mahali*	1	7	0
Scaly-feathered Finch *Sporopipes squamifrons*	49	2	4
Masked Weaver *Ploceus velatus*	4	2	0

Table 4. *Animals seen resting in the shade of live* Acacia erioloba *trees during February 1993 and March 1994*

Species	Number seen in 5 days
Birds	
Ostrich *Struthio camelus* Linnaeus	1
Secretary Bird *Sagittarius serpentarius*	2
Crowned Plover *Vanellus coronatus* (Boddaert)	2
Kori Bustard *Ardeotis kori* (Burchell)	> 10
Mammalian herbivores	
Gemsbok *Oryx gazella* (Linnaeus)	> 50
Blue Wildebeest *Connochaetes taurinus* (Burchell)	> 50
Red Hartebeest *Alcephalus bucelaphus* (Pallas)	6
Springbok *Antidorcas marsupialis* (Zimmerman)	> 100
Steenbok *Raphicerus campestris* (Thunberg)	1
Mammalian carnivores and omnivores	
Leopard *Panthera pardus* (Linnaeus)	1
Lion *Panthera leo* (Linnaeus)	8
Bar-eared Fox *Otocyon megalotis* (Desmarest)	> 10
Black-backed Jackal *Canis mesomelas* Schreber	5

provide refuges from herbaceous competitors and fires that occasionally sweep through the Kalahari Gemsbok National Park (van der Walt & le Riche, 1984).

Acacis erioloba trees take about 20 years to reach 7 m in height (Fig. 6: Step 2), another 15–20 years to develop the typical spreading canopy (Fig. 6: Step 3), and can attain a height of 12 m and live to 300 years (Barnes *et al.*, 1997). Microclimate beneath the canopies of large savanna trees differs from that of unshaded sites. Shade reduces soil temperatures and evaporation so that soil moisture levels remain higher beneath canopies for most of the wet and dry season in surrounding grassland (Belsky *et al.*, 1989, 1993; Belsky & Canham, 1994). Shading changes vegetation composition by reducing the survival of plants typical of open habitats, and improving the survival of shade-tolerant species (Kennard & Walker, 1973; Smith & Goodman, 1986; Manders and Richardson, 1992).

Our data supports the notion that large trees also elevate plant nutrient concentrations beneath their canopies. Nutrient enrichment, reduced soil bulk densities and improved water infiltration rates have been reported from beneath large savanna trees elsewhere in Africa (Belsky *et al.*, 1989, 1993; Griffioen & O'Connor, 1990; Roos & Alsopp, 1997). Although trees may act as pumps which bring nutrients from deep soil layers and distribute it on the surface in the form of litter (Campbell *et al.*, 1988), or accumulate nutrients through persistence (Kellmann, 1979), we suggest that much of the nutrient enrichment of soils beneath trees is the result of animal activity (Fig. 6: Step 3) that is concentrated in and around large trees in open savannas. Just as the use of Kalahari water points by cattle increases the base status of topsoil (Perkins & Thomas, 1993), so soils beneath old trees are enriched by fallen nests, bird droppings and dung deposition by resting antelope, and subcanopy soils are enriched by the remains of prey regurgitated or discarded beneath trees by vultures, raptors, owls, Leopard *Panthera pardus* and Lion *P. leo* (Dean, 1975; Dean & Milton, 1988; Skinner & Smithers, 1990). Isolated trees attract animals, and greater isolation of trees, as

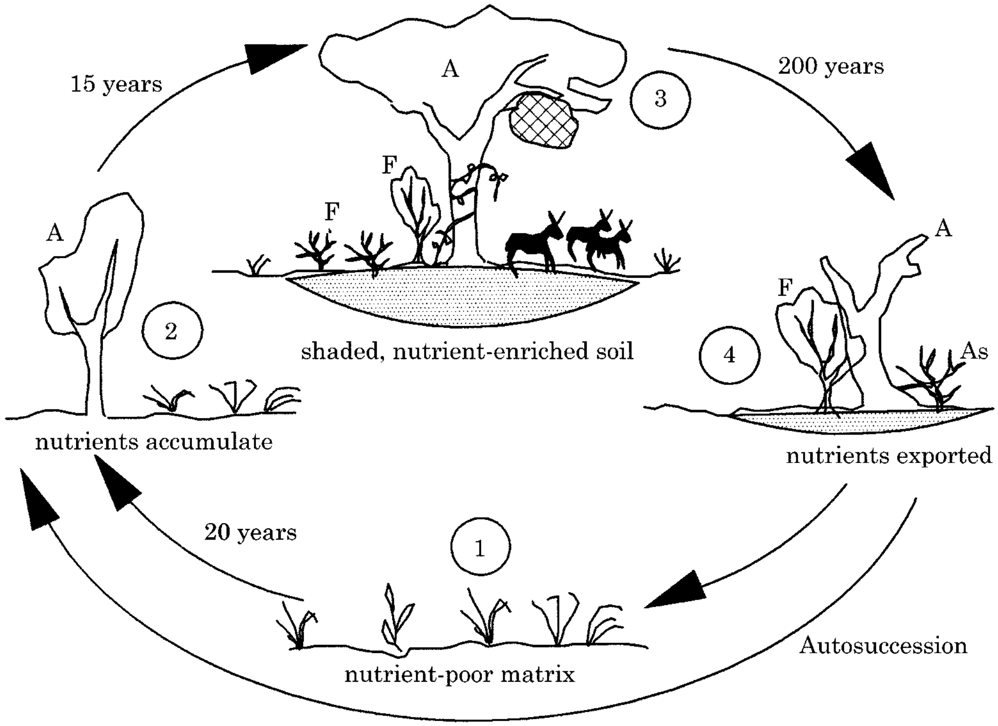

Figure 6. *Acacia erioloba* and the patch dynamics of subcanopy plant assemblages. (1) An *Acacia* seedling establishes in a small disturbance among wind-dispersed grasses and shrubs on the nutrient-poor sand; (2) *Acacia* (A) grows, excluding species of open habitat, attracting birds and accumulating nutrients; (3) frugivore-dispersed species (F) or an *Acacia* sapling (As) become established as nutrient accumulation is enhanced by mammals and the nutrient rain from bird nests; (4) *Acacia* dies, radiation increases, animal activity decreases, and there is a net export of nutrients in the form of leaves, fruits and soil leachate. Fruiting shrubs (e.g. *Boscia*) that outlive the *Acacia* are eventually replaced by matrix vegetation.

shown by Maclean (1973) for Sociable Weavers, may be associated with greater intensity of tree utilization.

Directed dispersal may be an essential process for ensuring that the seeds of relatively small populations of fleshy-fruited shrubs reach scattered sites that are suitable for their germination and survival. Our study suggests that potential dispersers to subcanopy sites in the Kalahari include mammals that use the shade, and frugivorous birds that perch or nest preferentially on large trees (Fig 6: Step 3). Humans, antelope, Black-backed Jackal *Canis mesomelas* and Bat-eared Fox all eat fruit, disperse viable seeds and are very mobile (Bothma, 1966; Leistner, 1967; Nel, 1978). The nitrophilous annuals (*Setaria verticillata*, *Amaranthus*, *Chenopodium*, *Cleome* spp.) that colonize subcanopy islands in the Kalahari all have barbed or typically herbivore-dispersed seeds and are probably moved to these sites by antelope and other mammals that rest in the shade (Leistner, 1996).

Plants that bear fleshy fruits were more abundant beneath large living *A. erioloba* trees than in other sites (Leistner, 1996; this study), a pattern predicted from the association of frugivore-dispersed plants with base-rich soils in Australia and South Africa (Milewski, 1982; Hughes *et al.*, 1993). The vegetation that develops on base-rich African termitaria within nutrient-poor ecosystems is similarly dominated by fleshy-fruited trees and palatable grasses (Bews, 1917; Tinley, 1973; Coetzee *et al.*, 1976;

Griffioen & O'Connor, 1990). It may therefore be hypothesized that in oligotrophic landscapes fleshy-fruited plants would be limited to relatively fertile sites.

Plants growing on nutrient-rich soils are often more productive or nutritious than plants in surrounding habitats (Leistner, 1967; Scholes, 1990; Huntly, 1991; Belsky *et al.*, 1993). Productive, nutritious plants would tend to attract herbivorous animals to patches near trees, reinforcing nutrient enrichment in these sites (Scholes, 1990). The combination of shade, nutrient enrichment and disturbance that occurs beneath isolated trees reduces the frequency of species common in open habitats but favours plant assemblages dominated by nitrophilous annuals and fleshy-fruited perennials (Story, 1952; Leistner, 1967; Smith & Goodman, 1986; Griffioen & O'Connor, 1990; Dean & Milton, 1991; Manders & Richardson, 1992; Leistner, 1996).

Following the death of a tree (Fig. 6: Step 4), either through senescence or fire (van der Walt & le Riche, 1984; Skarpe, 1991*a*), there is a rapid change in radiation intensity and soil temperature (Belsky & Canham, 1994). Leaching of salts, Ca, Mg, K and Na occurs early in the decay process (Muoghalu *et al.*, 1994), and since fewer birds nest and roost in dead trees and large mammals do not use dead trees for shelter from the sun, there is a net export of nutrients from the patch through removal of leaves and fruit. Fleshy-fruited shrubs, particularly *Boscia albitrunca* and *Grewia* spp. in the Kalahari (Leistner, 1996; this study), and *Zizyphus* sp. in mesic savannas (Barnes *et al.*, 1997) apparently persist long after the host *Acacia* tree has disintegrated. However, because they are low, compact, smooth-stemmed and do not produce pods, these species do not appear to attract as many birds and mammals as do *Acacia* trees. We therefore expect that the patches occupied by fleshy-fruited trees will return to matrix-type vegetation as the nutrients in the patch are expanded (Fig. 6: Step 4). Our data supported Skarpe's (1991*a*) observation that *A. erioloba* saplings seldom establish beneath conspecifics. However, where this does occur, the nutrient-enriched patch is expected to persist until the dying *Acacia* tree is replaced by a fleshy-fruited tree (Fig. 6: alternative pathway). The dynamics are comparable with the replacement of *Acacia* spp. by *Opuntia* spp. in the Chihuahuan Desert of Mexico (Yeaton & Manzanares, 1986) except that the fleshy-fruited plants of African subcanopy islands do not appear to cause the deaths of their *Acacia* hosts, but merely outlive and succeed them.

Trees and biodiversity

Large *A. erioloba* trees and their shrub islands provide resources and services that are scarce in the Kalahari. These include shade, shelter, nest sites, observation posts for raptorial birds, and specialized food or prey items. For example, large isolated trees provide shade and shelter for herds of antelope such as Eland *Taurotragus oryx* and Gemsbok (Eloff, 1959), canids and large ground-foraging birds (this study), while also providing an unrestricted view of the surrounding area. Leopards need large, rather than small trees to rest in during the day and to hang their prey out of reach of scavengers (Skinner & Smithers, 1990). Our observations support Maclean's (1970) conclusions that owls, raptors and vultures use large, rather than small *A. erioloba* trees for perch-hunting, roosting or nesting. Large senescent trees provide the natural cavities for hole-nesting birds and mammals (Leistner, 1967; Maclean, 1970) and the fissured bark used for foraging and sheltering by the Striped Skink *Mabuya striata* (Fitzsimons & Brain, 1958) and other lizards. Only mature *Acacia erioloba* trees, and exceptionally large individuals of *Boscia albitrunca* and *Acacia haematoxylon*, are robust enough to support the exceptionally large communal nests of the southern African endemic Sociable Weaver (Maclean, 1973, 1993). Trees which harbour weaver nests also provide food and shelter to commensals of the weaver, including Pygmy Falcons *Polihierax semitorquatus*, Barn Owls *Tyto alba*, Giant Eagle Owls *Bubo lacteus* and Redheaded Finch *Amadina erythrocephala* that breed in or on top of their nests (Maclean, 1973, 1993), and predators such as snakes (*Naja* spp.) and the Honey Badger *Mellivora capensis* which prey on eggs, young and adult birds.

In the cold dry winter, when other protein-rich foods are scarce, *A. erioloba* pods ripen and fall to the ground (van Wyk *et al.*, 1985) providing a major food supplement for Gemsbok, Eland, Karoo Rat *Parotomys brantsii*, Tree Rat and Striped Mouse *Rhabdomys pumilio* (Eloff, 1959; Leistner, 1967). The Kalahari sandveld is notably depauperate in frugivorous birds (Maclean, 1970), as are other vegetation types on sandy soils in southern Africa (Brooke, 1992). However six fruit-and-insect feeding species are resident in the area and the frugivorous Pied Barbet *Tricholaema leucomelas* and Red-eyed Bulbul *Pycnonotus nigricans* move into the area after rain (Maclean, 1970), presumably to feed on *Grewia* spp., *Lycium* spp. and other fruits that grow beneath *Acacia* trees.

Effects of land use on tree population structure and animal communities

Our data indicate that *Acacia erioloba* trees increase biodiversity because they structure the habitat vertically and horizontally, and generate resource-rich islands in an impoverished sand sea. Large isolated trees in arid and semi-arid regions of the world likewise generate habitat diversity (Roos & Allsopp, 1997), thereby maintaining species richness (Pianka & Huey, 1971; Archer *et al.*, 1988; Belsky & Canham, 1994). Such trees, and the species-rich 'green islands' associated with them, allow frugivorous, nectarivorous and tree-nesting birds to colonize and persist in deserts (Ward & Rohner, 1997). However, the effect that trees have on the spatial pattern of plant and animal assemblages depends on the spacing and size of trees (Smith & Goodman, 1986; Archer *et al.*, 1988; Skarpe, 1991*a*), and on processes that lead to development of distinct assemblages beneath the trees (Belsky *et al.*, 1993).

Bush encroachment is a well-known phenomenon in overgrazed savannas worldwide (Skarpe, 1991*b*), and appears to be the result of efficient seed dispersal by cattle (Tietema *et al.*, 1991) and improved tree seedling establishment in the absence of grass and fire (Bond & van Wilgen, 1996). High densities (5000–15,000 ha^{-1}) of *A. erioloba* and *A. mellifera* saplings establish in the Kalahari where intensive grazing by cattle has reduced the ability of grasses to compete for light and water (Skarpe, 1991*a*). On Kalahari cattle ranches, both bush encroachment and the removal of woody species by aerial application of herbicides (Moore *et al.*, 1985) are likely to change the pattern (Skarpe, 1991*a*) and dynamics of this ecosystem. It is likely that large birds, frugivores and habitat-specific plants will be lost once scattered trees are replaced by uniform grassland or thicket.

Conclusion

Our study supports our hypotheses that: (1) subcanopy soils beneath the leguminous tree *Acacia erioloba* are nutrient enriched; (2) subcanopy sites are colonized primarily by plants with animal-dispersed fruits; and (3) soil fertility, and bird and plant assemblages vary with the developmental stage of the tree. It is therefore apparent that large and small trees do not play identical roles in maintaining biodiversity in an arid savanna. Large individual trees are disproportionately important in providing shade, shelter and resting places. Tree species conservation is not the only issue for the conservation of biodiversity. It is clearly important to manage the population structure of a key tree species so as to maintain its role in generating spatial heterogeneity. The character of an arid savanna depends on such patchiness (nutrient-rich shaded islands) which increases biodiversity in an otherwise exposed and oligotrophic system. In this respect, the continued existence of such protected areas as the South African Kalahari Gemsbok National Park, and the contiguous Gemsbok National Park in Botswana are important, not only for the maintenance of biodiversity, but also for the preservations of key processes and the essential attributes of arid savanna.

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Appendix 1. *Approximate densities (plants ha^{-1}) of perennial plants in matrix vegetation and beneath the canopies of immature, mature and dead* Acacia erioloba *trees*

Species and dispersal type	Matrix	Sapling tree	Live tree	Dead tree
Autochorous (explosive dehiscence)				
Monechma spp.*	260	4	49	65
Winged seed coat (wind-dispersed)				
Rhigozum trichotomum Burch.	1783	306	101	94
Stipagrostis spp.†	292	109	23	138
Hard seeds (herbivore-dispersed)				
Acacia erioloba E. Mey.	304	7	55	123
Acacia mellifera Benth.	33	0	16	22
Galenia africana L.	0	98	104	290
Fleshy fruits (frugivore-dispersed)				
Boscia albitrunca (Burch.) Gilg. & Ben.	14	0	144	210
Cucurbitaceae‡	0	8	69	14
Ehretia rigida (Thunb.) Druce	0	0	29	0
Grewia flava D.C.	17	27	193	210
Lycium spp.§	5	112	1408	732
Asparagus spp.¶	5	4	26	14
Solanum spp.‖	2	0	26	0

**Monechma incanum* (Nees) C. B. Cl., *M. genistifolium* (Engl.) C. B. Cl.

†*Stipagrostis ciliata* (Desf.) de Winter, *S. obtusa* (Del.) Nees, *S. uniplumis* (Licht.) de Winter.

‡*Citrullus lanatus* (Thunb.) Matsumura & Nakai, *Coccinia rehmannii* Cogn., *Corallocarpus bainesii* (Hook. f.) A. Meeuse, *Kedrostis africana* (L.) Cogn.

§*Lycium cinereum* Thunb., *L. hirsutum* Dun., *L. oxycarpum* Dun.

¶*Asparagus africanus* (Lam.) Oberm., *A. laricinus* (Burch.) Oberm.

‖ *Solanum capense* L., *S. incanum* L.

Appendix 2. *Bird sightings on* Acacia erioloba *trees at three stages of growth: saplings (< 5 m high, erect canopy), large live trees (> 5 m high, spreading canopy) and dead trees. Observations were made between Nossob and Twee Rivieren on 11 March 1994. Species arranged systematically and by food guild (Maclean, 1993)*

Species (by feeding guild)	Weight (g)*	Sapling tree	Large tree	Dead tree
Insectivores				
Abdim's Stork *Ciconi abdimii* Lichtenstein	1500	0	0	1
Lesser Kestrel *Falco naumanni* Fleischer	134	1	1	0
Pygmy Falcon *Poliherax semitorquatus* (Smith)	60	3	2	0
Lilac-breasted Roller *Coracias caudata* Linnaeus	101	1	2	2
Scimitar-billed Woodhoopoe *Rhinopomastus cyanomelas* (Vieillot)	31	0	1	0
Fork-tailed Drongo *Dicrurus adsimilis* (Bechstein)	50	8	34	1
Capped Wheatear *Oenanthe pileata* (Gmelin)	32	1	0	2
Black-chested Prinia *Prinia flavicans* (Vieillot)	9	1	0	0
Marico Flycatcher *Melaenornis mariquensis* (Smith)	24	2	4	0
Chat Flycatcher *Melaenornis infuscatus* (Smith)	37	1	0	0
Lesser Grey Shrike *Lanius minor* Gmelin	48	8	5	2
Fiscal Shrike *Lanius collaris* Linnaeus	41	4	3	1
Sociable Weaver *Philetairius socius* (Latham)	27	4	155	33
Granivores				
Cape Turtle Dove *Streptopelia capicola* (Sundevall)	152	1	10	0
Namaqua Dove *Oena capensis* (Linnaeus)	40	1	1	22
Scaly-feathered Finch *Sporopipes squamifrons* (Smith)	11	49	2	4
Red-headed Finch *Amadina erythrocephala* (Linnaeus)	23	0	0	8
Shaft-tailed Whydah *Vidua regia* (Linnaeus)	15	0	2	1

Appendix 2—*continued*

Mixed seed and insect feeders				
Fawn-colored Lark *Mirafra africanoides* Smith	23	2	0	0
Sabota Lark *Mirafra sabota* Smith	25	1	0	0
Titbabbler *Parisoma subcaeruleum* (Vieillot)	15	0	0	1
White-browed Sparrow-weaver *Plocepasser mahali* Smith	47	1	7	0
Cape Sparrow *Passer melanurus* (Statius Müller)	27	2	0	2
Grey-headed Sparrow *Passer diffusus* (Smith)	24	1	1	1
Masked Weaver *Ploceus velatus* Vieillot	26	4	2	0
Frugivores				
Rosy-faced Lovebird *Agapornis roseicollis* (Vieillot)	54	0	1	0
Yellow-billed Hornbill *Tockus leucomelas* (Lichtenstein)	168	0	1	1
Black-Crow *Corvus capensis* Lichtenstein	500	0	11	1
Wattled Starling *Creatophora cinerea* (Meuschen)	67	1	10	1
Burchell's Starling *Lamprotornis australis* (Smith)	130	0	1	0
Glossy Starling *Lamprotornis nitens* (Linnaeus)	83	6	8	3
Vertebrate-eaters				
Yellow-billed (Black) Kite *Milvus migrans* (Boddaert)	805	0	2	1
Black-shouldered Kite *Elanus caeruleus* (Desfontaines)	251	0	1	0
Tawny Eagle *Aquila rapax* (Temminck)	2352	0	5	1
Black-breasted Snake Eagle *Circaetus pectoralis* Smith	1502	0	1	2
Bateleur *Terathopius ecaudatus* (Daudin)	2242	0	2	3
Gabar Goshawk *Micronisus gabar* (Daudin)	154	0	1	0
Pale Chanting Goshawk *Melierax canorus* (Thunberg)	750	0	11	3
Lanner Falcon *Falco biarmicus* Temminck	590	0	0	1
Greater Kestrel *Falco rupicoloides* Smith	261	0	1	3
Carrion-eaters				
White-backed Vulture *Gyps africanus* Salvadori	5400	1	25	1
Lappet-faced Vulture *Torgos tracheliotus* (Forster)	6600	1	5	0
Total sightings		105	318	102
Total species		24	32	26

[a] Bird weights as given in Maclean (1993).