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Composition and biogeography of forest patches on the inland mountains of the southern Cape

C. J. GELDENHUYS*

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ABSTRACT

Patterns in species richness of 23 small, isolated forests on the inland mountains of the southern Cape were studied. Species richness of woody plants and vines of the Kouga-Baviaanskloof Forests was higher than in the western mountain complexes, where species richness in the more southern Rooiberg and Kamanassie Mountains was higher than in the Swartberg range. The Rooiberg, a dry mountain with small forests far away from the coastal source area, had more species than, and contained many species which are absent from, the larger, moister forests of the Kamanassie which are closest to the coastal source areas. Neither altitude nor distance from the source area, the forests south of the coastal mountains, nor long-distance dispersal, adequately explained the variation in species richness. The variations are best explained in terms of dispersal corridors along the Gouritz and Gamtoos River systems which connect the coastal forests with the inland mountains. The distribution patterns of four species groups in relation to the geomorphological history of the two river systems provide relative dates for the expansion and contraction of temperate forest, subtropical forest and subtropical transitional thicket in the southern Cape.

CONTENTS

* Division of Water, Environment and Forestry Technology, CSIR, P. O. Box 395, Pretoria 0001.
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1 INTRODUCTION

In the southern Cape several mountain complexes occur north (inland) of the coastal mountains. These inland mountains are surrounded by semi-arid to arid valleys and lowland. Two river systems, however, connect the inland areas with the coast. A third river system almost breaks through the coastal mountains near one of the inland mountains. Forests on the inland mountains are very small and isolated and are in sharp contrast to the large and widespread forests along the coast (Anon. 1987). Their distribution, composition and conservation status are poorly known.

Axelrod & Raven (1978) and Deacon (1983) reconstructed the palaeofloras of Africa. They speculated that the temperate forest which covered the southern tip of Africa during the Palaeocene (65 to 55 My BP) was replaced by subtropical forest during the Oligocene-Miocene (37 to 5 My BP) and subsequently by fynbos and arid shrublands during the Late Pleistocene (125 000 to 10 000 yBP). The general increasing aridity in the southern Cape region since the beginning of the Miocene (24 My BP) (Deacon 1983) suggests further that over time the inland forest patches became increasingly isolated. Hypothetically the current flora of the isolated inland forests would therefore consist of species which have survived in suitable refuge sites, species with tolerance ranges which would enable them to survive in the changed environment, and species which have colonized from suitable forest source areas. Geldenhuys (1986; 1992a, b; 1994) studied several aspects of the distribution, fragmentation and biogeography of the South African forests in general and the southern Cape coastal forests in particular. The question was raised: how do the inland forests relate to the coastal forests in the southern Cape? Several studies have successfully used geomorphological evidence to reconstruct the biogeography of floras and taxa (Kaul *et al.* 1988; Moore 1988) and the phylogeny of families and genera, e.g. of freshwater fishes (Skelton 1986). Smith (1981) considered the geological and palaeogeographical

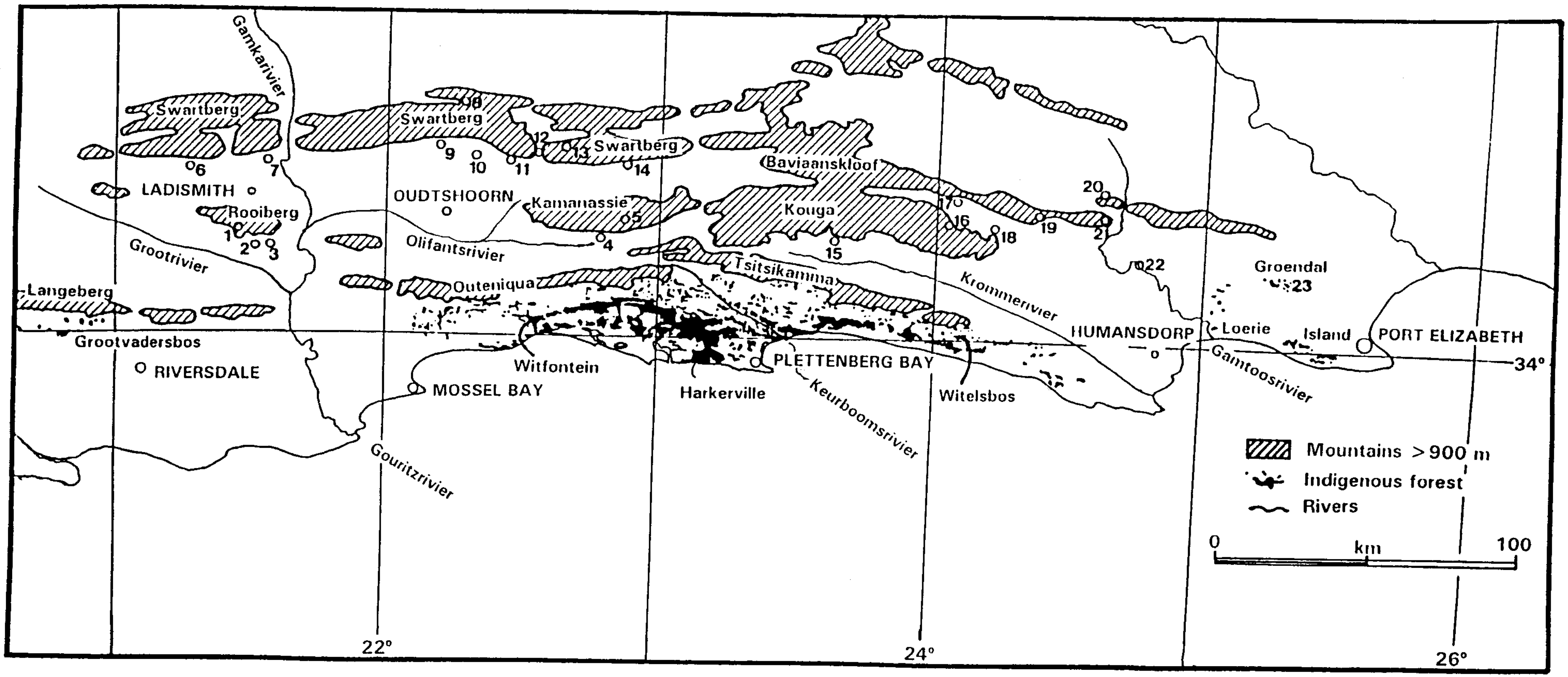

FIGURE 1.—The study area of the southern Cape inland mountains in relation to the widespread forests south of the coastal ranges. The numbers represent the following study sites in the respective mountain complexes (the forests are too small to be indicated on the map): **Rooiberg**: 1, Bosrivier upper; 2, Bosrivier lower; 3, Assegaaibosrivier. **Kamanassie**: 4, Kluesrivier; 5, Meulrivier upper. **Swartberg**: 6, Waterkloof; 7, Seweweekspoort; 8, Swartbergpoort; 9, Swartberg Pass; 10, Rust-en-Vrede; 11, Huisrivier upper; 12, Meiringspoort; 13, Tierkloof; 14, Cheridouwspoort. **Kouga**: 15, Sapreerivier. **Baviaanskloof**: 16, Doringkloof; 17, Diepnekkloof; 18, Geelhoutbos; 19, Assegaaikloof; 20, Witrivierkloof upper; 21, Witrivierkloof lower; 22, Grootrivierpoort. **Groendal**: 23, Zungarivier.

history of the landmasses around Tasmania as well as colonizing ability and altitudinal range of species in a study of the origin of the Tasmanian high mountain flora.

Taxa move from source areas along different pathways (corridors, filters or sweepstake routes) to colonize new sites (Brown & Gibson 1983). If they move along a corridor (which contains a wide variety of suitable sites or habitats), the composition of the community in the new site will be very similar to the community at the source. If they move through a filter (which contains a limited variety of suitable sites or habitats), the community at the new site will contain a limited component of the source community. If they move along a sweepstake route (which cuts across areas with totally different environments), the community in the new site will contain only species which will survive long distance dispersal across unsuitable areas. Island biogeographic theory was evoked to explain the extinction and colonization of animal species on oceanic islands of different size and distance away from the source areas (MacArthur & Wilson 1967), and more recently for plants in islands of fynbos in the southern Cape forests (Bond *et al.* 1988). Dispersal is only of significance if the organism can establish a viable population upon arrival in the new area (Brown & Gibson 1983). Physical and biological barriers to successful colonization by forest plants are insufficient moisture (arid valleys), extreme temperature (mountain tops, frost in valleys), disturbance patterns (fire in fynbos) and absence of long distance dispersal agents (migrant frugivorous birds). However, man-induced changes in the vegetation and environment during historical times may eliminate or confuse the evidence required to elucidate the biogeographical patterns.

The objectives of this study were:

- to determine the patterns in species composition and richness of forest communities in different inland mountain complexes of the southern Cape.
- to explain the observed patterns in terms of habitat preferences of species; species-area and species-distance relationships; long-distance dispersal; dispersal corridors in relation to the geomorphological history of the landscapes in the region.
- to aid interpretation of vegetation changes in the coastal forests from the dating of forest expansion and contraction on the inland mountains.

2 STUDY AREA

The study covers the Cape Folded Belt in the southern Cape of South Africa, between Ladismith and Riversdale in the west and Humansdorp in the east (Figure 1). A site in the Groendal Wilderness Area northwest of Port Elizabeth was included as a riverine site in the coastal mountains which appeared to be similar to the sites in the inland mountains. The dominant physiographic feature of the main study area are the subparallel mountain ranges and the intermontane lowland belts which run approximately east-west (Lenz 1957). In the west the Swartberg range, the highest range in the study area (up to 2 250 m) forms the northern boundary. The Kouga-Baviaanskloof Mountain complex forms the northern boundary to the east. It consists of several parallel ranges with relatively narrow east-trending valleys. The coastal Langeberg-Outeniqua-Tsitsikamma ranges form the southern boundary. A number of smaller, almost isolated mountains occur between the Swartberg and the Langeberg-Outeniqua ranges: Rooiberg-Gamka Hill between Calitzdorp and Ladismith, and Kamanassie Mountain between Oudtshoorn and Uniondale. The Oudtshoorn basin is a large semi-arid lowland between the Swartberg, Rooiberg, Outeniqua and Kamanassie Mountains which comprises hills of Cretaceous conglomerates (Lenz 1957). The relatively narrow Langkloof valley separates the Tsitsikamma Mountains from the Kouga Mountains. Groendal is a hilly landscape between the Great Winterhoek and Elandsberg Mountains. A relatively dry coastal plain occurs to the southeast of Groendal.

Three river systems link, or partially link, the coastal area with the inland mountains and are important for the interpretation of the forest flora. The Gouritz River breaches the Langeberg-Outeniqua ranges west of Mossel Bay through the Gouritzpoort. Inland it is formed by the confluence south of the Rooiberg of the Olifants River which drains the Oudtshoorn basin, the Gamka River which flows through the Swartberg north of Calitzdorp and which drains the Karoo west of Beaufort West, and the Groot River which drains the area to the west of the Rooiberg. Tributaries of these rivers breach the Swartberg range through several poorts such as, from west to east, Seweweekspoort, Gamkapoort, Meiringspoort and Cheridouwspoort. A poort is a relatively narrow, steep-walled opening, cutting almost perpendicularly across a topographic barrier, through which the open areas on either side are connected, usually by a river (Lenz 1957). The Keurbooms River which runs between the Kamanassie Mountain and Plettenberg Bay, does not fully breach the gap between the Outeniqua and Tsitsikamma ranges south of the Kamanassie Mountain. A low, narrow ridge separates its origin from the Kamanassie River which drains the southern slopes of the Kamanassie Mountain and runs in a northwesterly direction to join the Olifants River. The Gamtoos River east of Humansdorp is formed by the confluence of the Baviaanskloof and Groot Rivers. The Witrivier is a small stream which joins the Groot River north of the Grootrivierpoort at Cambria. The Zunga (or Swartkops) River runs from Groendal towards the coast at Port Elizabeth.

Geologically the mountains owe their existence to their heavily folded structure and the resistance of the quartzitic Table Mountain Sandstones to weathering. Softer sandstones and shales of the Bokkeveld Series eroded more readily to form the syncline valleys (Lenz 1957; Theron 1962; Toerien 1979).

The few weather stations in the area all occur in the lowlands. Data are available for short periods for a number of rain gauges across the Swartberg (along the Pass and in the east) and Kamanassie Mountains. Rainfall increases linearly with increase in elevation, and rain shadow effects are apparent on north slopes. In the Swartberg Pass area annual rainfall declines rapidly from 725 mm at 1 600 m to 210 mm at 884 m on the northern foothills and to 182 mm at 686 m in Prince Albert on the edge of the Great Karoo (Bond 1981). Annual rainfall on the southern foothills is 411 mm at 640 m (Cango Caves) and 570 mm at 762 m (Rust-en-Vrede, forest site No. 10, Figure 1, Table 1) (Weather Bureau 1986 unpubl.). In Swartberg East, near Blesberg between the Tierkloof and Cheridouwspoort sites (Nos 13 & 14 respectively), annual rainfall ranged from 766 mm on the northern midslope, to 847 mm on the crest, 798 mm on the upper south slope and 572 mm on the southern foothills (unpublished data). In the Kamanassie annual rainfall near the crest ranged between 815 mm on the southern side and 682 mm on the northern side, and declined to 239 mm on the southern foothill and 169 mm on the northern foothill (Kamanassie Policy Memorandum, Department of Nature Conservation). Rainfall data for Rooiberg are unreliable but appear to be lower than for the Kamanassie, also as judged from the appearance of the fynbos vegetation on the southern slopes. Rainfall in the lowlands ranges between 220 mm at Van Wyksdorp (305 m) on the southern footslopes of the Rooiberg, 244 mm at Oudtshoorn (335 m), 482 mm at Joubertina (544 m) in the Langkloof, 321 mm at Studtis (760 m) in the western end of Baviaanskloof, and 536 mm on the southern foothills of Groendal (229 m; forest site No. 23) (Weather Bureau 1986 unpubl.).

Reliable information on temperature regimes is less available. Diurnal and seasonal temperature variation is large. Mean maximum temperature for the warmest month is 31.8°C for Oudtshoorn and 27.8°C for Uitenhage and the mean minimum temperature for the coldest month is 3.5°C and 5.8°C for the two towns respectively. The mean number of days per annum with frost is 7.3 and 1.4 for the two towns (Weather Bureau 1986). Snow occurs five or six times per annum on the Swartberg and may lie for more than two weeks (Bond 1981).

The main vegetation types of the area have been described by Acocks (1988), Taylor (1979), Bond (1981) and Cowling (1984), and in unpublished reports. Mountain fynbos and grassy fynbos cover most of the mountains and are interspersed with small patches of evergreen forest in protected gullies and valleys. Karroid broken veld covers the low-lying valleys of the Little Karoo, and subtropical transitional thicket extends south of Groendal and occurs in parts of Baviaanskloof.

3 METHODS

Twenty-three forested gorges, gullies and riverine sites were visited to represent the variety of sites with forest species encountered on the inland mountains (Figure 1; Table 1). In this study the definition of a forest (Geldenhuys *et al.* 1988) was extended to accommodate scattered bush clumps and isolated trees of species which are usually associated with forest, as observed in Seweweekspoort, Meiringspoort and Cheridouwspoort. For each study site a list was compiled of all plant species which were associated with the forest communities. Emphasis was placed on recording all tree and shrub species, but taxa of other growth forms were also recorded as completely as possible.

The size of each forest (Table 1) was estimated in the field. Most forests consisted of a long, narrow stand along a stream or river. The length of the stream which was covered in the survey was estimated from 1 : 50 000 topographic maps and the mean width of the forest was estimated in the field. Altitude was read from the relevant 1 : 50 000 topographic maps.

Obvious or important disturbance factors affecting the forest communities were recorded. These included fire, flooding of rivers, landslides and wind.

TABLE 1.—List of forested sites visited in the inland mountains of the southern Cape

No.	Mountain	Forest site	Grid reference	Altitude, m	Forest area, ha	Forest habitat
1	Rooiberg	Bosrivier upper	33°41'S 21°30'E	500	20	Closed/open gorge, riverine/slopes, south
2	Rooiberg	Bosrivier lower	33°43'S 21°30'E	330	10	Closed/open gorge, riverine, south
3	Rooiberg	Assegaaibosrivier	33°43'S 21°34'E	300	40	Closed/open gorge, riverine, south
4	Kamanassie	Kluesrivier	33°39'S 22°48'E	980	120	Closed/open gorge, riverine/slopes, south
5	Kamanassie	Meulrivier upper	33°38'S 22°53'E	1 100	80	Closed/open gorge, riverine/slopes, south
6	Swartberg	Waterkloof	33°27'S 21°17'E	700	10	Closed/open gorge, riverine, south
7	Swartberg	Seweweekspoort	33°25'S 21°24'E	650	20	Open gorge, riverine
8	Swartberg	Swartbergpoort	33°19'S 22°04'E	950	5	Open/closed gorge, riverine, north
9	Swartberg	Swartberg Pass	33°21'S 22°05'E	1 300	3	Closed gorge, riverine, south
10	Swartberg	Rust-en-Vrede	33°24'S 22°21'E	850	15	Closed gorge, riverine/slopes, south
11	Swartberg	Huisrivier upper	33°25'S 22°29'E	1 170	10	Closed valley, riverine, south
12	Swartberg	Meiringspoort	33°25'S 22°34'E	600	30	Open gorge, riverine/slopes
13	Swartberg	Tierkloof	33°24'S 22°39'E	1 200	2	Closed/open gorge, riverine, north
14	Swartberg	Cheridouwspoort	33°27'S 22°54'E	720	10	Closed valley, open gorge, riverine
15	Kouga	Sapreerivier	33°40'S 23°36'E	580	30	Closed valley, open gorge, riverine/slopes
16	Baviaanskloof	Doringkloof	33°37'S 24°03'E	650	80	Closed gorge, riverine, north
17	Baviaanskloof	Diepnekkloof (Bosrug)	33°33'S 24°04'E	600	40	Closed/open gorge, riverine, south
18	Baviaanskloof	Geelhoutbos	33°38'S 24°15'E	300	20	Closed/open gorge, riverine/slopes, north
19	Baviaanskloof	Assegaaikloof	33°39'S 24°22'E	280	20	Closed/open gorge, riverine, south
20	Baviaanskloof	Witrivierkloof upper	33°36'S 24°31'E	1 170	2	Closed gorge, riverine, south
21	Baviaanskloof	Witrivierkloof lower	33°39'S 24°31'E	240	40	Closed/open gorge, riverine/slopes, south
22	Baviaanskloof	Grootrivierpoort	33°43'S 24°38'E	140	10	Open gorge, riverine/slopes, west
23	Groendal	Zungarivier (Chase's kloof)	33°41'S 25°14'E	150	150	Open valley, alluvial/slopes, west

TABLE 2.—Number of species by growth forms for the forest sites on the inland mountains of the southern Cape

Site no.	Mountain range and study area	Number of species: Trees & shrubs	Lianes & vines	Ferns	Geophytes & graminoids	Forbs & soft shrubs	Total
	Rooiberg (mean spp/site)	27.7	6.0	10.3	4.3	5.7	54.0
1.	Bosrivier upper	21	4	12	3	3	43
2.	Bosrivier lower	30	6	7	5	6	54
3.	Assegaaibosrivier	32	8	12	5	8	65
	Kamanassie (mean spp/site)	18.5	5.5	11.5	5.0	8.0	48.5
4.	Kluesrivier	24	7	15	5	13	64
5.	Meulrivier upper	13	4	8	5	3	33
	Swartberg (mean spp/site)	15.1	3.0	6.9	2.1	3.3	30.4
6.	Waterkloof	13	5	12	5	7	42
7.	Seweweekspoort	16	3	4	0	3	26
8.	Swartbergpoort	15	4	7	2	4	32
9.	Swartberg Pass	10	1	13	4	1	29
10.	Rust-en-Vrede	18	4	10	3	6	41
11.	Huisrivier upper	11	1	5	1	2	20
12.	Meiringspoort	21	4	2	2	2	31
13.	Tierkloof	14	1	4	1	2	22
14.	Cheridouwspoort	18	4	5	1	3	31
	Kouga-Baviaanskloof (mean spp/site)	35.4	7.0	9.0	5.3	5.3	62.0
15.	Sapreerivier	35	7	12	3	4	61
16.	Doringkloof	42	10	10	2	8	72
17.	Diepnekkloof (Bosrug)	31	5	7	5	6	54
18.	Geelhoutbos	27	6	6	7	1	47
19.	Assegaaikloof	35	7	4	4	5	55
20	Witrivierkloof upper	8	1	10	3	2	24
21	Witrivierkloof lower	53	7	16	10	10	96
22	Grootrivierpoort	52	13	7	8	6	86
	Groendal						
23	Zungarivier (Chase's kloof)	76	15	12	12	12	127
	Mean spp/site	26.7	5.5	8.7	4.2	5.1	50.2
	Total	118	29	38	22	43	250

The relationship between the number of woody species (plus vines) or the number of herbaceous species in a forest and the altitude, forest area and direct distance (km) to the nearest source area was determined by means of stepwise multiple regression (STSC 1986). Log transformations were used for all variables because of the highly skew nature of the observations, a procedure usually followed in such studies (Bond *et al.* 1988). The southern Cape forests (Geldenhuys 1993a), marked in black as 'indigenous forest', and 'island' coastal forest west of Port Elizabeth (Figure 1) were considered to be the nearest source areas.

The distribution of taxa, mainly woody species, on the inland mountains was represented by means of tables which indicate the frequency of species on each particular mountain range or in similar sites within a range. The sites were grouped on the basis of assumed dispersal barriers and corridors, as follows: Swartberg sites in three subgroups, i.e. on the northern slopes, at high altitudes and on the southern slopes; Rooiberg; Kamanassie; Kouga-Baviaanskloof; Grootrivierpoort, including the lower site of the Witrivierkloof; and the Groendal site (see Tables 5–8). The most likely dispersal mechanisms for the species are indicated and are based on Coates Palgrave (1977) and my own observations (Geldenhuys 1993a).

The plant nomenclature follows Arnold & De Wet (1993) and the plant author names are according to Brummitt & Powell (1992).

4 RESULTS

4.1 *Species richness*

The species are listed in the Appendix and summarized by growth forms for the different sites (Table 2). Woody plants and vines form the bulk of the species.

Species numbers vary greatly between sites. In general there is a decline in species richness from east to west and from south to north. The mean number of species per site in the Kouga-Baviaanskloof complex is double the number in the Swartberg range. Note however that the mean number of species, particularly woody species, in the Rooiberg forests tends to be higher than the number in the Kamanassie forests.

4.2 *Relationship between species richness and altitude, forest area and distance from source*

The number of woody species (plus vines) is significantly correlated with altitude and forest area (Table 3), but not with distance to source area. Altitude alone ex-

TABLE 3.—Analysis of variance for the stepwise multiple regression of the dependence of the (log) number of woody species and vines in a forest on its altitude and area

Independent variable	Coefficient	Standard error	t-value	Significance level
Constant	3.132426	0.221281	14.1559	0.0000
Log Altitude, m	−0.635723	0.078427	−8.1059	0.0000
Log Area, ha	0.195371	0.043653	4.4756	0.0002

R^2 (adjusted for Df) = 0.8582; standard error of the estimate = 0.09751.

plains 74% of the variation in number of woody species. The number of herbaceous species is significantly correlated only with forest size, but this regression model explains only 18% of the observed variation.

4.3 *Distribution of taxa on different mountain complexes*

Only 10% of the species occur in more than 50% of the sites and these are mostly tree and shrub species (Table 4). For example, 48 of the 118 tree and shrub species occurred in one or two sites only, i.e. 10% or less of the sites. The pattern of occurrence of species on the different mountain ranges became clearer when the pattern was considered in relation to the distribution range of species in both the inland and coastal forests.

4.3.1 Widespread species on the inland mountains

Species which occur in more than 50% of the sites occur in most sites of all the mountain groups (Table 5). Site preferences of the species are based on their occurrence in the coastal forests (Geldenhuys 1993a). The Kamanassie sites lack several species which have a preference for drier habitats although these species occur in the high altitude sites of the Swartberg. Those which do occur in the Kamanassie are confined to the lower end of Kluesrivier.

4.3.2 Species widespread in coastal forests but with limited spread in study area

Very few of the widespread species of the coastal forests which have a limited spread on the inland mountains do occur in the Swartberg range (Table 6). Those which do occur there are confined to the southern sites. Note again that very few of these species occur in the Kamanassie. However, two of the Kamanassie species are absent from the Rooiberg, i.e. *Rapanea melanophloeos* and *Diospyros whyteana*. *Ocotea bullata* is confined to the Kamanassie and one site in the Rooiberg. Many of the Rooiberg species are absent from the Kamanassie. The majority of the species occur in Groendal and Grootrivierpoort and in one or more sites of the Kouga-Baviaanskloof, and many of these are absent from the Kamanassie or Rooiberg. Note the decrease in number of species from Groendal through Grootrivierpoort to the Baviaanskloof.

4.3.3 Species with limited/disjunct distribution in, or absent from, the coastal forests

These species fall in two groups: those which are confined to the western ranges, i.e. Swartberg, Rooiberg and Kamanassie; and those which are confined to the eastern ranges (Table 7). Note again the decrease in number of species from Groendal through Grootrivierpoort to the Baviaanskloof.

4.3.4 Endemic species of the region

Nine woody species are endemic to the study area, or have their main distribution in the southern Cape. Of these only *Virgilia divaricata* is widespread in the study area (Table 8). *Laurophyllus capensis*, which has a wide distribution in the coastal areas, is confined to a few sites in the Groendal area where it grows in association with *V. divaricata*. *Strelitzia alba*, not recorded during this study, has since been recorded from one locality in the Kouga Mountains (M. Yates pers. comm. 1991; see Geldenhuys 1992a for its distribution in the coastal forests).

TABLE 4.—Absolute and relative frequencies by which species of different growth forms occur in the 23 forested study sites in the inland mountains of the southern Cape

Frequency of occurrence		Number of species				
Absolute number of sites	Relative % of all sites	Trees & shrubs	Climbers	Ferns	Herbs	
					Monocots	Dicots
1–2	1–10	48	14	16	6	28
3–4	11–20	20	6	7	9	9
5–7	21–30	24	4	4	4	3
8–9	31–40	9	1	4	1	1
10–11	41–50	2	1	3	1	1
12–13	51–60	4	-	-	-	1
14–16	61–70	6	2	2	1	-
17–18	71–80	1	1	2	-	-
19–20	81–90	4	-	-	-	-
Total number of species		118	29	38	22	43

TABLE 5.—Distribution and fruit/seed dispersal of species widespread in forested sites on the inland mountain ranges of the southern Cape

Species[1]	Mountain range[2]							
	SB[3]			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites[4]							
	3	2	4	3	2	6	2	1
Moist sites								
• *Ilex mitis*	2	2	4	3	2	4	1	1
• *Halleria lucida*	3	2	3	3	2	4	1	1
• *Kiggelaria africana*	2	2	3	2	2	5	2	1
• *Maytenus acuminata*	3	1	2	3	2	6	1	1
+ *Cunonia capensis*	2	1	3	3	2	4	1	1
• *Myrsine africana*	3	2	3	2	1	1	1	-
• *Pterocelastrus tricuspidatus*	1	-	1	3	2	5	2	1
# *Secamone alpini*	1	-	2	3	2	4	2	1
• *Zantedeschia aethiopica*	3	2	2	3	-	3	1	-
# *Blechnum australe*	2	2	4	2	2	4	1	1
# *Blechnum capense*	2	1	3	2	2	3	1	1
# *Blechnum punctulatum*	3	-	4	3	2	4	2	-
# *Todea barbara*	1	1	3	2	2	4	1	1
Dry sites								
• *Olea europaea* subsp. *africana*	2	1	4	3	-	4	2	1
• *Maytenus heterophylla*	1	1	3	2	-	5	2	1
• *Cussonia spicata*	2	-	4	3	-	3	1	1
+ *Buddleja salviifolia*	3	1	3	1	-	3	-	1
• *Rhus rehmanniana*	2	2	1	2	2	5	-	1
• *Rhus lucida*	3	1	3	3	1	1	-	-
+ *Dipogon lignosus*	2	1	2	3	1	6	1	1
• *Colpoon compressum*	2	-	4	2	1	2	2	1
• *Diospyros dichrophylla*	-	-	3	3	1	3	2	1
• *Asparagus aethiopicus*	2	-	4	3	1	3	-	1
+ *Pelargonium zonale*	2	-	4	3	1	3	-	-

[1] Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind; #, wind dispersal.
[2] Mountain range: SB, Swartberg (see [3] below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
[3] N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
[4] Maximum number of sites per range for comparison with number of sites in which a species is present.

4.4 *Seed dispersal mechanisms*

The majority of woody species (Tables 5–8) have fleshy fruits or seeds which are dispersed by frugivorous birds and/or mammals. Among the plants with dry propagules, only the ferns, the liane *Secamone alpini* and the two *Brachylaena* species are readily dispersed by wind. *Cunonia capensis, Nuxia floribunda, Buddleja saligna* and *B. salviifolia* produce small seeds in capsules which may be blown over short distances in strong wind. *Gonioma kamassi, Ptaeroxylon obliquum* and some of the other species have winged seeds which are not well suited for wind dispersal. Note that the majority of endemic species (Table 8) have dry seeds which are not particularly adapted for dispersal over longer distances.

5 DISCUSSION

5.1 *Species richness*

The forests on the inland mountains of the southern Cape contain 118 tree and woody shrub species, 24 of which are not included in the 140 tree and shrub species of the coastal forests (Geldenhuys 1993a). The difference in number of species of the herbaceous growth forms between the two areas is much larger. It has been assumed that woody species are more persistent in suitable habitats because the majority of them can resprout after fire, and that they create the micro-habitat for forest understorey plants. In this discussion interpretation of the patterns in species richness and composition is almost confined to the woody species.

5.2 *Habitat preferences of species*

Habitat preferences of species along an altitudinal gradient do not explain the major differences in species composition of forests in different parts of the inland mountains. The decrease in species richness of woody plants and vines with increasing altitude suggests that many species cannot grow at high altitude. The majority of the widespread species of the coastal forests which have a limited distribution in the inland sites are indeed confined to the low-lying mountain valleys and riverine sites. However, these species are also absent from similar sites on the northern side of the Swartberg range, and many are absent from similar sites on the southern Swartberg, the Kamanassie and the Rooiberg (Table 6).

TABLE 6.—Distribution and fruit/seed dispersal of species widespread in the coastal forests of the southern Cape but with a limited spread in the study area

Species[1]	Mountain range[2]							
	SB[3]			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites[4]							
	3	2	4	3	2	6	2	1
• *Ocotea bullata*	-	-	-	1	2	-	-	-
• *Olinia ventosa*	-	-	-	3	2	3	2	1
• *Cassine peragua*	-	-	-	3	2	2	2	1
• *Rapanea melanophloeos*	-	-	1	-	2	2	2	1
• *Diospyros whyteana*	-	-	-	-	2	1	2	1
• *Carissa bispinosa*	-	-	-	3	-	3	2	1
+ *Nuxia floribunda*	-	-	-	3	-	4	2	1
• *Curtisia dentata*	-	-	-	3	-	1	2	1
• *Allophylus decipiens*	-	-	-	2	-	4	2	1
• *Scutia myrtina*	-	-	-	3	-	-	1	1
• *Grewia occidentalis*	-	-	-	2	-	4	2	1
+ *Buddleja saligna*	-	-	1	2	-	2	1	1
• *Canthium inerme*	-	-	-	2	-	1	2	1
• *Olea capensis* subsp. *capensis*	-	-	-	1	-	1	2	-
• *Sideroxylon inerme*	-	-	-	1	-	3	2	1
• *Pittosporum viridiflorum*	-	-	-	-	-	5	2	1
• *Ficus burtt-davyi*	-	-	2	-	-	5	2	1
• *Celtis africana*	-	-	-	-	-	4	2	1
• *Ficus sur*	-	-	-	-	-	4	2	1
+ *Gonioma kamassi*	-	-	-	-	-	3	2	1
• *Podocarpus falcatus*	-	-	-	-	-	1	2	1
• *Apodytes dimidiata*	-	-	-	-	-	1	2	1
• *Vepris lanceolata*	-	-	-	-	-	2	1	1
• *Dovyalis rhamnoides*	-	-	-	-	-	1	1	1
• *Clausena anisata*	-	-	-	-	-	1	1	1
• *Ekebergia capensis*	-	-	-	-	-	1	1	1
• *Capparis sepiaria*	-	-	-	-	-	1	2	1
• *Cassine aethiopica*	-	-	-	-	-	1	2	1
• *Canthium mundianum*	-	-	-	-	-	1	1	-
• *Putterlickia pyracantha*	-	-	-	-	-	4	2	-
+ *Calodendrum capense*	-	-	-	-	-	-	1	1
• *Podocarpus latifolius*	-	-	-	-	-	-	1	1
• *Rothmannia capensis*	-	-	-	-	-	-	1	1
• *Psydrax obovata* & others[5]	-	-	-	-	-	-	1	1
• *Ochna arborea*	-	-	-	-	-	-	-	1
• *Olea capensis* subsp. *macrocarpa*	-	-	-	-	-	-	-	1
• *Cassine papillosa* & others[6]	-	-	-	-	-	-	-	1

[1] Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind.
[2] Mountain range: SB, Swartberg (see [3] below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
[3] N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6,7, 10 & 12).
[4] Maximum number of sites per range for comparison with number of sites in which a species is present.
[5] Species which occur in only the GR & GD sites.
[6] Species which occur only in Groendal.

Where habitat preferences have been attached to some species (Table 5), their demonstrated wide tolerances do not explain their absence from certain forests. The widespread species associated with moist coastal sites, occur on the inland sites both at high and low altitudes and in sites which are relatively dry. In several sites they are not confined to the moist, cool sites along the streams, but grow on steep, exposed slopes and often shallow, rocky sites far above the streams, for example in the Kamanassie, the upper Bosrivier, Meiringspoort and Sapreerivier sites. Only widespread inland species which are associated with both dry and moist coastal sites, grow in the northern Swartberg sites (Table 5), often where the stream courses open up to the north into the arid Great Karoo.

5.3 *Species-area relationships and long-distance dispersal*

Area is a significant variable in the regression models; this explains the richness of both woody and herbaceous species but in both cases accounts for a relatively small

TABLE 7.—Distribution and fruit/seed dispersal of species which have a limited or disjunct distribution in, or which are absent from the coastal forests of the southern Cape

Species[1]	Mountain range[2]							
	SB[3]			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites[4]							
	3	2	4	3	2	6	2	1
Species of coastal forest								
• *Pterocelastrus rostratus*	-	1	2	2	-	-	-	-
• *Diospyros glabra*	1	-	2	-	-	-	-	-
# *Brachylaena neriifolia*	1	1	3	2	2	-	-	-
• *Hippobromus pauciflorus*	-	-	-	-	-	2	2	1
+ *Schotia latifolia*	-	-	-	-	-	4	2	1
# *Brachylaena glabra*	-	-	-	-	-	2	1	1
+ *Plumbago auriculata*	-	-	-	-	-	2	2	1
• *Ochna serrulata*	-	-	-	-	-	-	2	1
• *Canthium ciliatum*	-	-	-	-	-	-	1	1
• *Canthium pauciflorum*	-	-	-	-	-	-	-	1
• *Strychnos decussata*	-	-	-	-	-	-	-	1
+ *Trichocladus ellipticus*	-	-	-	-	-	-	-	1
Species outside coastal forest								
• *Diospyros scabrida*	-	-	-	-	-	4	1	1
• *Pavetta lanceolata*	-	-	-	-	-	-	1	1
• *Teclea natalensis*	-	-	-	-	-	-	2	-
+ *Ptaeroxylon obliquum*	-	-	-	-	-	-	-	1
• *Pleurostylia capensis*	-	-	-	-	-	-	-	1
• *Eugenia zeyheri*	-	-	-	-	-	-	-	1
• *Chaetacme aristata*	-	-	-	-	-	-	-	1

1 Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind; #, wind dispersal.
2 Mountain range: SB, Swartberg (see 3 below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
3 N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
4 Maximum number of sites per range for comparison with number of sites in which a species is present.

TABLE 8.—Distribution and fruit/seed dispersal in the study area of endemic species of the region

Species[1]	Mountain range[2]							
	SB[3]			RB	KN	BK	GR	GD
	N	U	S					
	Number of sites[4]							
	3	2	4	3	2	6	2	1
+ *Lachnostylis bilocularis*	-	-	1	2	-	-	-	-
+ *Virgilia divaricata*	-	-	1	-	2	2	1	1
+ *Calpurnia villosa*	-	-	1	-	-	-	1	-
+ *Widdringtonia schwarzii*	-	-	-	-	-	2	-	-
• *Smelophyllum capense*	-	-	-	-	-	4	2	1
+ *Loxostylis alata*	-	-	-	-	-	1	2	1
+ *Atalaya capensis*	-	-	-	-	-	-	1	-
+ *Sterculia alexandri*	-	-	-	-	-	-	-	1
+ *Laurophyllus capensis*	-	-	-	-	-	-	-	1

1 Fruit/seed dispersal mechanisms: •, bird/mammal; +, small/large dry seed not dispersed by wind.
2 Mountain range: SB, Swartberg (see 3 below); RB, Rooiberg (sites 1–3); KN, Kamanassie (sites 4, 5); BK, Baviaanskloof (sites 15–20); GR, Grootrivier (sites 21, 22); GD, Groendal (site 23).
3 N, north (sites 8, 13 & 14); U, upper (sites 9 & 11); S, south (sites 6, 7, 10 & 12).
4 Maximum number of sites per range for comparison with number of sites in which a species is present.

portion of the variation. Direct distance from the source areas ranges from 30 to 80 km but is an insignificant variable in the regression models. For example, the Kamanassie Forests are some of the largest in the study area, are the closest to the coastal forests, particularly the large forests north of Knysna, and represent the moistest sites; yet they contain fewer species than the Rooiberg Forests and lack several species which are present in the Rooiberg. The Rooiberg is a drier mountain, has small forests and its closest source areas are scattered forests between Mossel Bay and George to the southeast and some Langeberg forests west of Riversdale.

The distribution patterns of very few species support claims of long-distance dispersal despite the fact that the majority of tree and shrub species have fleshy fruits or seeds, many of which I have observed being eaten by birds in the coastal forests.

- *Rapanea melanophloeos* and *Ficus burtt-davyi* occur in one and two sites respectively in the Swartberg range which could be attributed to long-distance dispersal. *Ocotea bullata* may have been dispersed into the Rooiberg and Kamanassie from relatively nearby forests with *O. bullata* which exist on the northern slopes of the Langeberg (Garcia Pass near Riversdale) and Outeniqua Mountains (Robinson Pass near Mossel Bay and near Noll west of Uniondale).
- Most of the species which are present in the Rooiberg but absent from the Kamanassie are generally readily dispersed by birds. Their absence from the Kamanassie and the limited distribution in the study area of other similarly readily dispersed species of the coastal forests such as *Apodytes dimidiata*, the two *Podocarpus* species, the two *Olea capensis* subspecies, *Psydrax obovata* and *Canthium mundianum* casts doubt on the relevance of long-distance dispersal in the study area.
- Several species which release minute dry seeds from dry capsules, but which are not effectively dispersed by wind, show distribution patterns which are similar to the patterns of frugivorous species. Examples are *Cunonia capensis, Nuxia floribunda, Buddleja saligna* and *B. salviifolia*. Their dispersal by birds or mammals is very unlikely.
- The absence of suitable dispersal vectors may be the reason for the insignificance of long-distance dispersal. The sites were visited during different seasons over several years but only one Rameron pigeon (*Columba arquatrix*) was seen in the Swartberg Pass Forest. No studies exist to indicate the migration patterns of frugivorous birds in the southern Cape. It has been suggested that the Rameron pigeon migrates up and down the coast (Phillips 1927). That Rameron pigeons would fly from the coast where food sources are more readily available to the inland mountain forests where their food sources are more limited and possibly irregularly available seems highly unlikely. Small flocks of Red-winged starlings (*Onychognathus morio*) were often seen in the vicinity of the inland forests, but rarely seen along the coast.

5.4 *Dispersal barriers and corridors*

The parallel mountain ranges are obvious barriers to the dispersal of forest taxa from the coast to the inland forests. The mountain ridges experience strong, cold winds and extreme temperatures. Ice often forms in the sheltered gullies near the top (pers. obs.). Frequent controlled and natural fires in the fynbos on the mountain slopes prevent the establishment of forest species in the exposed sites and confine or eliminate existing forests. This was observed in most of the sites or was evident in the small sizes of trees near the forest edge in more protected sites.

Dry lowlands and valleys of the Little Karoo minimize the number of species which are able to cross them by means of establishment in small bush clumps in a stepping-stone fashion.

The obvious dispersal corridors are the Zunga River, the Gamtoos River through the Grootrivierpoort and Baviaanskloof, the Keurbooms River and the Gouritzpoort. The first two river systems are effective corridors for stepping-stone dispersal. The sites along the Zunga River the end constitute of the subtropical transitional thicket and riverine forests which are connected with the Alexandria and other coastal forests. Many streams run into the Baviaanskloof River from the mountain ridges to its north and south and provide refuge sites for forest species. The Baviaanskloof shares many of the species which occur in the Grootrivierpoort and Witrivierkloof and at Groendal. The remaining two rivers are not effective corridors. The Keurbooms River does not breach the relatively low Outeniqua-Tsitsikamma mountain ridge to provide direct and easy access for dispersal of forest species from the large Knysna forests to the Kamanassie Mountains. The Gouritzpoort contains no sheltered sites for forest establishment and north of the poort is an arid lowland. It is not connected with any nearby forests to the south of the poort. It may have been an effective dispersal corridor in earlier, moister periods, but not under the present climate.

5.5 *Forest migration in relation to climatic change*

Following on from the earlier discussion, it is therefore suggested that the variation in species richness on the inland mountains is mainly the result of different degrees of intermingling during the contraction and expansion of the different floras due to climatic and landscape changes since the Palaeocene. Only tree and woody shrub species have been considered for this interpretation because it has been assumed they are the key elements which create the specific micro-habitats for herbaceous elements of the understorey of particular vegetation units. Certain understorey species should therefore correlate with the distribution pattern of particular groups of tree species. Factors such as the altitudinal gradient, forest size, site preferences and dispersal corridors and mechanisms are merely contributing to this variation within a particular mountain range. In this study at least four floras can be recognized from the distribution patterns of the species as listed in Tables 5 to 8, namely: temperate or austral forest relicts; subtropical forest; subtropical transitional thicket and karroid riverine woodland.

5.5.1 Temperate forest

It is suggested that most of the widespread inland species characteristic of moist sites (Table 5) represent relicts of the temperate austral forests (such as *Cunonia capensis*) or high-altitude forests of tropical latitudes (such as *Ilex mitis, Halleria lucida* and *Kiggelaria africana*) which covered the southern tip of Africa during the Palaeocene, rather than recent dispersal events. These temperate forests were eliminated with changes toward warmer and more humid climates associated with the northward drift of the African continent (Axelrod & Raven 1978; Deacon 1983). These constituent species grow in forests on all the mountain complexes in the study area, and are the only species which grow in sheltered sites on the northern slopes of the Swartberg range. They are also the main species of the forests in the cool, sheltered kloofs and gorges of the inland mountain ranges in the southwestern Cape (pers. obs.). Many of them occur in the isolated Afromontane forests of southern and eastern Africa (Killick 1963; Chapman & White 1970; Dowsett-Lemaire 1988). The poorts through the Swartberg range had breached the ranges by the early Tertiary (Lenz 1957) and would have allowed dispersal of other readily dispersed species through the poorts from south to north, if they were present by that time. Even if it is argued that in more recent times the fleshy-fruited tree species may have been dispersed to the northern side of the Swartberg by birds, the argument does not account for the presence of *Cunonia capensis* with its small, dry seeds. The wide habitat tolerances of these species enabled them to survive and to occur widespread in the study area, and in southern Africa (Geldenhuys 1992b).

Species which could be added to the list of temperate forest species are *Pterocelastrus rostratus, Diospyros glabra* and *Brachylaena neriifolia*. Their eastern distribution limits in the study area (Table 7) coincide with the longitude of their eastern limits in the coastal forests (Geldenhuys 1992a). Their distribution patterns suggest a more continuous distribution at some early period which was later fragmented into their present pattern.

5.5.2 Subtropical forest

It is suggested that the widespread coastal forest species with limited spread in the inland sites (Table 6) represent elements of the subtropical forest which replaced the temperate forests since the Oligocene-Miocene (Axelrod & Raven 1978; Deacon 1983). Most of these species occur also in the coastal forests of the southern and southwestern Cape (Geldenhuys 1993a; McKenzie 1978). These forests have expanded from the east. The easterly orientation of the Zunga and Gamtoos Rivers and the Kouga-Baviaanskloof valleys suggests that they would have been more readily colonized by the expanding subtropical forests. The Gouritz River breached the Langeberg-Outeniqua range during the late Cretaceous as a subsequent poort, i.e. it developed along a relatively weaker part of the range by a headward eroding stream (Lenz 1957). With widespread forest along the coast south of the Outeniqua-Langeberg Mountains and with a more humid climate (Hendey 1983) the Gouritz River could have been a suitable dispersal corridor for some species to enter the southern sides of the Rooiberg. The Rooiberg-Gamka mountain range forms a loose connection to the southeast with the Outeniqua range and may have had sheltered sites on the southwestern side. Today several species of the western fynbos element, e.g. *Mimetes cucullatus*, that are characteristic of the wetter coastal ranges, also occur on the Rooiberg-Gamka range and the adjacent Outeniqua range (Taylor 1979; J.H.J. Vlok pers. comm. 1988). They support the dispersal route suggested for the forest species, although the fynbos migration relates to Late Pleistocene times and different environmental conditions which would not support forest.

The nature of the deposits in the Oudtshoorn Basin suggests that the climate during the Late Cretaceous was similar to the present semi-arid climate and the Olifants River portion of the breach between Rooiberg and Gamka Hill occurred as late as Plio-Pleistocene (Lenz 1957). This semi-arid climate and the late breach would have prevented the spread of subtropical forest towards the Swartberg. The absence of a direct corridor between the Keurbooms River and the Kamanassie accounts for the absence from the Kamanassie of several Knysna forest species, which are present in the Rooiberg (Table 6).

Some of the widespread as well as disjunctly distributed coastal species are confined to the Groendal, Grootrivierpoort and lower Witrivierkloof sites (Tables 6 & 7; Appendix). Two possible explanations for this pattern are: 1, most of these species have relatively large fruits or seeds which require specialized dispersal vectors. The seeds of some species such as *Podocarpus latifolius* and *Calodendrum capense* loose viability fast when they dry out, and those of other species such as *Olea capensis* subsp. *macrocarpa* and *Cassine papillosa* have long germination periods due to woody seed coats (Geldenhuys 1975, 1996) and are then liable to predation by rodents (pers. obs.). However, others with similar seed types occur further into the Kouga-Baviaanskloof complex such as *Ekebergia capensis* and *Podocarpus falcatus* (both are dispersed by bats; see Geldenhuys 1993b for *P. falcatus*); 2, a more likely explanation is that the subtropical forests expanded in different waves and that each wave contained a different set of species. The expansion and contraction could be related to successive periods of high and low sea levels respectively, which in turn were associated with humid and arid periods respectively (Hendey 1983). During later periods of forest expansion along the coast, some areas, particularly the more arid inland areas, may not have been suitable for the colonization by forest species.

For example, *Podocarpus falcatus* occurs as far west as Swellendam, and *P. latifolius* as far west as the Cape Peninsula (Von Breitenbach 1986). Both grow in small forest patches near the southern exit of the Gouritz River through the Langeberg-Outeniqua ranges. Both are readily dispersed in the southern Cape coastal forests (Geldenhuys 1980, 1993a, b) but have a limited entry in the Baviaanskloof and are absent from the Rooiberg and Kamanassie. It is suggested that they represent a relatively late southwestern expansion of the subtropical forests when barriers of semi-arid lowlands inland of the coastal mountains prevented their spread inland. This implies that the two *Podocarpus* species have a tropical origin and are not part of the austral flora as has often been suggested (e.g. Levyns 1964). Their large fruit size indicates a tropical affinity (Givnish 1980), in contrast to the small fruit size of austral podocarps of Australia, New Zealand and Chili (pers. obs.). It is suggested that the fossil podocarp pollens from some southwestern Cape sites (e.g. Coetzee 1986) may represent austral podocarps which became extinct with the regression of the early temperate forests and before the present species arrived in the area.

Some species represent the spread of subtropical transitional thicket (Cowling 1984; Everard 1987). Species such as *Ptaeroxylon obliquum, Diospyros scabrida* and *Pavetta lanceolata* have not yet reached the southern Cape coastal forests. Others have reached the southern Cape but were cut off by the Late Pleistocene-Holocene marine transgression, e.g. *Hippobromus pauciflorus, Schotia latifolia* and *Plumbago auriculata* (Geldenhuys 1992a).

Some coastal dune forest species, such as *Strychnos decussata* and *Eugenia zeyheri*, require specialized sites which prevented their spread inland. For example, *S. decussata* grows on a terrace along the Zunga River in a site similar to that in which the species grows in Nature's Valley along the southern Cape coast (Geldenhuys 1986). *Strelitzia alba* also falls in this category.

Some species, such as *Trichocladus ellipticus*, represent relicts of a retreating forest flora (Geldenhuys 1992a).

5.5.3 Subtropical transitional thicket and karroid woodland

The widespread inland species of drier sites (Table 5) are generally associated with subtropical transitional thicket (Cowling 1984; Everard 1987). They have probably become mixed with the more tolerant moist forest elements with the increasing aridity since the beginning of the Miocene-Pliocene (Deacon 1983). They occur in few of the sites at higher altitudes. They are more prominent in the bush clumps and subtropical transitional thicket of the more arid lowlands and riverine sites in the drier, open valleys of the Baviaanskloof and Karoo. They occur in the drier parts of moist sites as they are found where streams from the mountains open up into the dry valleys, or on the drier slopes above the streams, or along open valleys or gorges such as Meiringspoort. Seeds of several of the species were found along the krantzes above the study sites and it is assumed that Red-winged starlings (*O. morio*) dispersed the seeds from the lowlands or other nearby sites. Many of these species are, however, absent from the Kamanassie sites although they are present in the lowlands further away from the mountain. The higher (Eo-Oligocene) and lower (Mio-Pliocene) surfaces on the southern side of the Kamanassie (Lenz 1957) could account for this absence. At Boomplaas Cave, between the Swartberg Pass and Rust-en-Vrede sites, charcoal assemblages indicate that *A. karroo* only became dominant in the late Holocene during more mesic conditions (Scholtz 1986). This species was absent from charcoal layers older than 12 000 years although it was apparently a much preferred firewood. It became a major component of woodland in the valley near the cave after 5 000 yBP, after an initial spread into the valley during the early Holocene (Deacon *et al.* 1983).

5.6 *Endemic species*

The endemic species represent two major groups: forest margin species such as *Virgilia divaricata* (Phillips 1926), *Laurophyllus capensis* (Phillips 1931; Geldenhuys 1993a) and *Widdringtonia schwarzii* (Lückhoff 1963); and species of drier sites such as *Lachnostylis bilocularis* and *Loxostylis alata* (Palmer & Pitman 1972). The sites in which the forest margin species mature suggest that they can only persist with less frequent fires than under which fynbos persists. This has been shown for *L. capensis* (Vlok & De Ronde 1989). Trees of *V. divaricata* (Phillips 1926) and *Widdringtonia schwarzii* (Lückhoff 1963) are killed by fires and depend on reseeding for regeneration. All except *Smelophyllum capense* have dry seeds which do not appear to be readily dispersed. It is assumed that these species have evolved in this region. It is suspected that they formed part of specific vegetation units but became separated and isolated to a lesser or greater degree as a result of their poor dispersability and sensitivity to frequent fires.

The distribution of *Virgilia* (Van Wyk 1986) corresponds with the distribution pattern of the subtropical forest species which expanded during the Oligocene-Miocene. It is suggested that *V. divaricata* was the parent species from which the other species evolved because of its presence in both the inland and coastal forests. Its absence from Rooiberg but presence in Kamanassie suggests that the species became established at a relatively late stage of expansion of subtropical forest. Its crossing of the gap north of the Keurbooms River towards the Kamanassie can perhaps be explained by dispersal of the resistant seeds by primates, particularly the baboon (*Papio ursinus*) and Vervet monkey (*Cercopithecus aethiops*). Both these primates have been seen in stands of *Acacia karroo* and the alien wattle *A. mearnsii* which have seeds very similar to *V. divaricata*. Seeds of *V. divaricata* have been found in the faeces of the baboon in the coastal mountains. Van Wyk (1986) mentioned two forms of the species: a form of drier localities such as in Seweweekspoort, Baviaanskloof and Groendal; and the form of the coastal forests between Humansdorp and George. In the context of the spread of the species I consider the form of drier localities as the first stage and the form of the coastal forest as the second stage.

Lachnostylis bilocularis was recorded in the Rooiberg and Meiringspoort but it also occurs in various localities between Ladismith and Uniondale (Palmer & Pitman 1972). In Meiringspoort the tree grows in the southern part of the gorge up to a particularly narrow part of the gorge but does not occur north of it. Its distribution suggests that it was more widespread before. The related *L. hirta* occurs in the coastal forests over a somewhat wider range (Palmer & Pitman 1972). It is suggested that *L. hirta* spanned the Gouritz River valley during less arid periods of the Oligocene-Miocene with a wider distribution in the dry, forested coastal areas. *L. bilocularis* evolved inland as an adaptation to dry, open sites and eventually became limited to the present localities when the lowlands became even drier. Both species have dry seeds in dry capsules and are poorly dispersed. *Calpurnia villosa* has a similar but more restricted distribution than *L. bilocularis,* which also centres on the Gouritz River and its tributaries in the Oudtshoorn basin (Palmer & Pitman 1972). The record of *C. villosa* from Grootrivierpoort could be based on my misidentification in the field of *C. aurea*, a species which has a disjunct distribution along the coast (Geldenhuys 1992a).

6 CONCLUSIONS

The systematic survey of forests in the inland mountain ranges in relation to the geomorphological evolution of dispersal corridors which link them with the coastal forests has provided a means to postulate relative dates for the expansion and contraction of floristic elements of both the inland and coastal forests. However, certain assumptions made in this study require to be verified, such as the following:

• Dispersal distances by wind of the small, dry seeds of *Cunonia capensis* and *Nuxia floribunda*.

• Flight patterns of frugivorous birds between the coastal and inland forests, and the feeding behaviour of these birds.

• The phylogenetic relationships of species of genera such as *Lachnostylis* and *Virgilia*, and of provenances of several other species such as *Ilex mitis* and the *Podocarpus* species.

Disturbance regimes in the study area have changed over time. The current man-induced disturbances of the vegetation exert extreme pressures on the forests which persisted in refuge sites in marginal environments. The forest patches should be treated as rare 'species' to allow the natural processes of population migration, settlement and adaptation to continue. The following examples of changed management could provide the required protection to these forests:

• Burning patterns during controlled block burns in catchments which contain forest patches should be reconsidered. The forests should not be used as fire breaks as has been done in several cases. Fires should be burnt down the slopes as would occur with natural fires (Geldenhuys 1994) and not from the bottom of the valleys upwards.

• Smaller alluvial sites along the rivers and the area surrounding the exit of streams from the mountains should not be cultivated, grazed or burnt.

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APPENDIX. SPECIES LIST FOR FORESTS IN INLAND MOUNTAINS OF THE SOUTHERN CAPE

The forest sites are as follows:

Rooiberg: 1, Bosrivier upper; 2, Bosrivier lower; 3, Assegaaibosrivier

Kamanassie: 4, Kluesrivier; 5, Meulrivier upper

Swartberg: 6, Waterkloof; 7, Seweweekspoort; 8, Swartbergpoort (Prins Albert); 9, Swartberg Pass (hotel site); 10, Rust-en-Vrede; 11, Huisrivier upper; 12, Meiringspoort; 13, Tierkloof; 14, Cheridouwspoort

Kouga-Baviaanskloof: 15, Sapreerivier; 16, Doringkloof; 17, Bosrug; 18, Geelhoutbos; 19, Assegaaikloof; 20, Witrivier upper; 21, Witrivier lower; 22, Grootrivierpoort

Groendal: 23, Zungarivier (Chase's kloof)

Species	Forest site																							Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Canopy and subcanopy tree species																								
Acacia karroo *Hayne*	-	-	-	-	-	-	•	-	-	-	-	•	-	-	-	•	-	-	•	•	-	•	-	6
Allophylus decipiens *(Sond.) Radlk.*	•	•	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	•	-	•	•	•	-	9
Apodytes dimidiata *E.Mey. ex Arn.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	4
Atalaya capensis *R.A.Dyer*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Brachylaena glabra *(L.f.) Druce*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	•	-	•	4
Buddleja saligna *Willd.*	•	•	-	-	-	•	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	•	•	7
Calodendrum capense *(L.f.) Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
Canthium																								
ciliatum *(Klotzsch) Kuntze*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
inerme *(L.f.) Kuntze*	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	6
mundianum *Cham. & Schlechtd.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	-	2
pauciflorum *(Klotzsch) Kuntze*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Cassine																								
aethiopica *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	3
eucleiformis *(Eckl. & Zeyh.) Kuntze*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
papillosa *(Hochst.) Kuntze*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
peragua *L.*	•	•	•	•	•	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	•	•	-	9
Celtis africana *Burm.f.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	7
Chionanthus foveolata *(E.Mey.) Stearn*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
Clausena anisata *(Willd.) Hook.f. ex Benth.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	•	3
Cunonia capensis *L.*	•	•	•	•	•	-	-	-	-	•	•	•	•	•	•	•	-	•	-	•	•	-	•	16
Curtisia dentata *(Burm.f.) C.A.Sm.*	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	7
Cussonia																								
paniculata *Eckl. & Zeyh.*	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	•	-	-	-	-	-	-	-	4
spicata *Thunb.*	•	•	•	-	-	•	•	•	-	•	-	•	-	•	•	•	•	-	-	-	-	•	•	14
Diospyros																								
dichrophylla *(Gand.) De Winter*	•	•	•	•	-	-	•	-	-	•	-	•	-	-	•	-	-	•	•	-	•	•	•	13
whyteana *(Hiern) F.White*	-	-	-	•	•	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	•	•	•	6
Ekebergia capensis *Sparrm.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	•	•	3
Euclea																								
racemosa *Murray*	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	-	-	-	-	-	-	2
schimperi *(A.DC.) Dandy* var. schimperi	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
undulata *Thunb.*	-	-	-	•	-	-	-	•	-	•	-	•	-	-	•	-	-	•	-	-	•	-	-	7

Species	Forest site 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
Eugenia zeyheri *Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Ficus sur *Forssk.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	7
Gonioma kamassi *E.Mey.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	•	•	•	6
Halleria lucida *L.*	•	•	•	•	•	•	-	•	•	•	•	•	•	•	•	•	•	-	-	•	•	-	•	19
Heteromorpha trifoliata *(Wendl.) Eckl. & Zeyh.*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Hippobromus pauciflorus *(L.f.) Radlk.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	•	•	5
Ilex mitis *(L.) Radlk.*	•	•	•	•	•	•	•	•	•	•	•	•	•	-	•	•	-	•	-	•	•	-	•	19
Kiggelaria africana *L.*	•	-	•	•	•	•	-	•	•	•	•	•	-	•	•	•	•	•	-	•	•	•	•	19
Loxostylis alata *Spreng.f. ex Rchb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	4
Maytenus																								
acuminata *(L.f.) Loes.*	•	•	•	•	•	-	-	•	-	•	•	•	•	•	•	•	•	•	•	•	-	•	•	19
nemorosa *(Eckl. & Zeyh.) Marais*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
oleoides *(Lam.) Loes.*	-	•	-	-	-	-	•	•	-	-	-	-	•	•	•	-	-	-	-	-	-	-	-	6
peduncularis *(Sond.) Loes.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
undata *(Thunb.) Blakelock*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	2
Nuxia floribunda *Benth.*	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	10
Ochna arborea *Burch. ex DC.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Ocotea bullata *(Burch.) Baill.*	•	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Olea																								
capensis *L.*																								
subsp. capensis	•	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	•	•	-	4
subsp. macrocarpa *(C.H.Wr.) I.Verd.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
europaea *L.* subsp. africana *(Mill.) P.S.Green*	•	•	•	-	-	•	•	•	•	•	-	•	-	•	•	•	•	•	-	-	•	•	•	17
Olinia ventosa *(L.) Cufod.*	•	•	•	•	•	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	•	•	•	11
Pappea capensis *Eckl. & Zeyh.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	-	-	-	2
Pittosporum viridiflorum *Sims*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	•	-	•	•	•	8
Pleurostylia capensis *(Turcz.) Oliv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Podocarpus																								
falcatus *(Thunb.) R.Br. ex Mirb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	•	4
latifolius *(Thunb.) R.Br. ex Mirb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
Psydrax obovata *(Eckl. & Zeyh.) Bridson*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
Ptaeroxylon obliquum *(Thunb.) Radlk.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Pterocelastrus																								
rostratus *Walp.*	-	•	-	•	-	-	•	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	5
tricuspidatus *(Lam.) Sond.*	•	•	•	•	•	-	•	•	-	-	-	-	-	-	•	•	•	•	•	-	•	•	•	15
Rapanea melanophloeos *(L.) Mez*	-	-	-	•	•	-	-	-	-	•	-	-	-	-	•	•	-	-	-	-	•	•	•	8
Rhus																								
chirindensis *Baker f.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
lancea *L.f.*	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	2
lucida *L.*	•	•	•	•	-	•	-	•	•	•	-	•	•	•	•	-	-	-	-	-	-	-	-	12
Rothmannia capensis *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
Schotia latifolia *Jacq.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	7
Scolopia																								
mundii *(Eckl. & Zeyh.) Warb.*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	2
zeyheri *(Nees) Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Sideroxylon inerme *L.*	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	•	-	•	7
Smelophyllum capense *(Sond.) Radlk.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	-	•	7
Sterculia alexandri *Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Strychnos decussata *(Pappe) Gilg*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Tarchonanthus camphoratus *L.*	-	•	-	-	-	-	-	-	-	-	-	•	-	•	•	-	-	-	-	-	-	-	•	5
Teclea natalensis *(Sond.) Engl.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	2
Vepris lanceolata *(Lam.) G.Don*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	•	4
Virgilia divaricata *Adamson*	-	-	-	-	-	•	-	-	-	-	-	-	-	-	•	•	-	-	-	-	•	-	•	7
Widdringtonia schwarzii *(Marloth) Mast.*	-	-	•	•	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	-	2
Zanthoxylum capense *(Thunb.) Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Shrubs																								
Acokanthera oppositifolia *(Lam.) Codd*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	3
Azima tetracantha *Lam.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	-	-	-	•	•	5
Brachylaena neriifolia *(L.) R.Br.*	-	-	•	•	•	•	•	-	-	-	•	•	•	•	-	-	-	-	-	-	-	-	-	9
Buddleja																								
salviifolia *(L.) Lam.*	-	-	•	-	-	-	•	•	•	•	-	•	•	•	•	•	•	-	-	-	-	-	•	12
sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	-	-	-	-	2
Calpurnia villosa *Harv.*	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	2
Capparis sepiaria *L.* var. citrifolia *(Lam.) Toelken*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	-	3
Carissa																								
bispinosa *(L.) Desf. ex Brenan*	•	•	•	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	•	-	•	•	•	9
haematocarpa *(Eckl.) A.DC.*	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Cassine																								
parvifolia *Sond.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
reticulata *(Eckl. & Zeyh.) Codd*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	-	-	-	3
tetragona *(L.f.) Loes.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
Chaetacme aristata *Planch.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Chrysanthemoides monilifera *(L.) Norl.*	-	-	•	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Colpoon compressum *P.J.Bergius*	-	•	•	•	-	•	•	-	-	•	-	•	•	•	•	•	-	-	-	-	•	•	•	14

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
Crotalaria capensis *Jacq.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
Diospyros																								
glabra (L.) De Winter	-	-	-	-	-	-	•	•	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	3
scabrida *(Harv. ex Hiern) De Winter*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	-	•	6
Dovyalis rhamnoides *(Burch. ex DC.) Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	3
Ehretia amoena *Klotzsch*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	1
Euclea schimperi *(A.DC.) Dandy* var. daphnoides *(Hiern) De Winter*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	-	-	•	•	6
Ficus burtt-davyi *Hutch.*	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	•	•	•	•	-	•	•	-	9
Grewia occidentalis *L.*	•	•	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	•	-	9
Lachnostylis bilocularis *R.A.Dyer*	-	-	•	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	3
Laurophyllus capensis *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Maytenus																								
heterophylla *(Eckl. & Zeyh.) N.Robson*	-	•	•	-	-	-	•	-	•	•	-	•	-	•	•	•	•	•	•	-	•	•	•	15
mossambicensis *(Klotzsch) Blakelock*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Myrica serrata *Lam.*	•	•	•	-	•	•	•	-	-	-	-	-	•	•	-	-	-	-	-	-	•	-	-	9
Myrsine africana *L.*	•	•	-	•	-	•	-	•	•	•	•	•	•	•	•	-	-	-	-	-	-	-	•	13
Ochna serrulata *(Hochst.) Walp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	3
Pavetta lanceolata *Eckl.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
Plumbago auriculata *Lam.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	•	•	5
Psoralea sp. cf. pinnata	-	-	-	•	-	-	•	•	-	-	•	-	•	•	•	-	-	-	-	-	-	-	-	7
Putterlickia pyracantha *(L.) Szyszyl.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	-	•	•	-	6
Rhamnus prinoides *L'Hér.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	•	2
Rhus																								
glauca *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	1
longispina *Eckl. & Zeyh.*	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	3
rehmanniana *Engl.*	-	•	•	•	•	•	-	-	•	-	•	-	•	•	•	•	•	•	•	-	-	-	•	15
sp. cf. refracta	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	1
Scutia myrtina *(Burm.f.) Kurz*	•	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	5
Trichocladus ellipticus *Eckl. & Zeyh. ex Walp.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Widdringtonia nodiflora *(L.) Powrie*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	2
Lianes and vines																								
Adenocline acuta *(Thunb.) Baill.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
Cissampelos torulosa *E.Mey. ex Harv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Clematis brachiata *Thunb.*	-	-	•	-	-	-	•	-	-	-	-	-	•	•	•	•	•	•	•	-	-	-	•	10
Coccinea palmata *(Sond.) Cogn.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	2
Cynanchum ellipticum *(Harv.) R.A.Dyer*	-	-	•	•	-	•	-	-	-	-	-	-	-	-	•	•	-	•	-	-	-	•	•	8
Dipogon lignosus *(L.) Verdc.*	•	•	•	•	-	•	-	•	-	-	•	•	-	•	•	•	•	•	•	•	•	-	•	17
Kedrostis nana *(Lam.) Cogn.* var. schlechteri *(Cogn.) A.Meeuse*	-	•	•	-	-	•	-	•	-	-	-	-	-	-	•	•	-	-	-	-	-	-	•	7
Microglossa mespilifolia *(Less.) B.L.Rob.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	2
Myrsiphyllum scandens *(Thunb.) Oberm.*	-	•	•	•	-	-	•	-	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	6
Oncinema lineare *(L.f.) Bullock*	-	-	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Pelargonium sp.	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	3
Protasparagus																								
aethiopicus *(L.) Oberm.*	•	•	•	•	-	•	•	•	-	•	-	•	-	•	•	•	•	-	-	-	-	-	•	14
setaceus *(Kunth) Oberm.*	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	•	•	•	6
sp.	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Rhoicissus																								
digitata *(L.f.) Gilg & Brandt*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	•	•	•	4
tomentosa *(Lam.) Wild & R.B.Drumm.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Rhynchosia caribaea *(Jacq.) DC.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	•	-	4
Rubus pinnatus *Willd.*	-	-	-	-	-	•	-	•	-	•	•	-	•	-	-	-	-	-	-	-	-	-	-	5
Rumex sagittatus *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	-	-	2
Secamone																								
alpini *Schult.*	•	•	•	•	•	-	-	-	-	•	-	•	-	•	•	•	-	•	•	-	•	•	•	15
filiformis *(L.f.) J.H.Ross*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	3
Senecio																								
angulatus *L.f.*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	3
deltoideus *Less.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
quinquelobus *(Thunb.) DC.*	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Thunbergia dregeana *Nees*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
Tylophora lycioides *(E.Mey.) Decne.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	1
Zehneria scabra *(L.f.) Sond.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	-	3
Ferns																								
Adiantum capillus-veneris *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	-	•	-	-	4
Asplenium																								
adiantum-nigrum *L.* var. solidum *(Kunze) J.P.Roux*	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
aethiopicum *(Burm.f.) Bech.*	-	•	-	•	•	-	•	-	•	•	-	-	-	-	-	-	•	-	-	-	•	-	-	8
lunulatum *Sw.*	•	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	•	4

Species	Forest site																						Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Asplenium (cont.)																								
monanthes *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	1
protensum *Schrad.*	-	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
rutifolium *(P.J.Bergius) Kunze*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	2
splendens *Kunze*	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	2
Blechnum																								
australe *L.*	•	-	•	•	•	•	•	•	•	•	•	•	•	-	•	•	•	•	-	-	•	-	•	18
capense *Burm.f.*	-	•	•	•	•	•	•	•	-	•	•	-	•	-	•	•	-	-	-	•	•	-	•	15
attenuatum *(Sw.)* var. giganteum *(Kaulf.) Bonap.*	-	-	•	•	-	•	-	-	•	•	•	-	-	-	-	-	•	•	-	•	•	-	-	10
inflexum *(Kunze) Kuhn*	-	-	-	-	-	•	-	-	•	•	-	•	-	-	•	-	-	-	-	-	-	-	-	5
punctulatum *Sw.*	•	•	•	•	•	•	•	•	-	•	-	•	•	•	•	•	•	-	-	•	•	•	-	18
tabulare *(Thunb.) Kuhn*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	-	-	-	-	2
Ceterach cordatum *(Thunb.) Desv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	•	•	-	4
Cheilanthes																								
capensis *(Thunb.) Sw.*	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
hirta *Sw.*	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	3
multifida (Sw.) Sw.	-	-	•	-	-	•	-	•	-	-	-	-	-	•	•	•	•	-	•	-	•	•	-	10
viridis *(Forssk.) Sw.*	-	-	•	-	-	•	-	-	-	•	-	-	-	-	-	•	-	-	•	-	•	•	•	8
parviloba *(Sw.) Sw.*	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ctenitis lanuginosa *(Willd. ex Kaulf.) Copel.*	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	1
Cyathea capensis *(L.f.) J.E.Sm.*	-	-	-	•	•	•	-	-	•	•	-	-	-	-	-	-	-	-	-	•	-	-	-	6
Dryopteris callolepis *C.Chr.*	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Elaphoglossum acrostichoides *(Hook. & Grev.) Schelpe*	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	-	2
Gleichenia polypodioides *(L.) J.E.Sm.*	-	-	•	•	-	•	-	-	-	-	-	-	•	•	•	-	-	-	-	•	•	•	-	9
Histiopteris incisa *(Thunb.) J.Sm.*	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	•	3
Hypolepis sparsisora *(Schrad.) Kuhn*	-	•	•	•	-	•	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	•	6
Lycopodium gnidioides *L.f.*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Microsorium ensiforme *(Thunb.) Schelpe*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Osmunda regalis *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	1
Pellaea pteroides *(L.) Prantl*	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Pleopeltis macrocarpa *(Bory ex Willd.) Kaulf.*	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Polystichum pungens *(Kaulf.) Presl*	•	-	-	•	•	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Pteris dentata *Forssk.*	•	•	•	-	-	•	-	-	-	-	•	-	-	-	•	•	•	•	-	-	•	-	•	11
Rumohra adiantiformis *(G.Forst.) Ching*	•	-	-	•	•	-	-	-	•	•	-	-	-	-	•	-	-	-	-	-	•	-	•	8
Thelypteris																								
bergiana *(Schlechtd.) Ching*	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	-	•	6
interrupta *(Willd.) K.Iwats.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	-	•	•	4
Todea barbara *(L.) T.Moore*	-	•	•	•	•	•	•	•	•	•	-	-	-	-	•	•	•	-	-	•	•	-	•	15
Geophytes and graminoids																								
Agapanthus sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Aristea ensifolia *J.Muir*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	3
Carex aethiopica *Schkuhr*	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	•	•	5
Chlorophytum comosum *(Thunb.) Jacq.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	•	-	•	4
Commelina africana *L.* var. lancispatha *C.B.Clarke*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	•	•	4
Cyperus albostriatus *Schrad.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	2
Dietes iridioides *(L.) Sweet ex Klatt*	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	•	•	-	-	•	•	5
Disperis lindleyana *Rchb.f.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Ehrharta																								
sp. cf. ramosa/gigantea	-	-	-	-	•	•	-	-	•	-	-	•	-	-	-	-	-	-	-	-	•	-	-	4
sp. 1	-	-	•	•	•	-	-	-	•	•	-	-	-	-	-	•	•	•	-	-	-	•	•	10
sp. 2	•	•	-	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	4
Ficinia sylvatica *Kunth*	-	•	•	•	-	•	-	-	•	-	-	-	-	-	-	•	•	-	-	•	•	-	-	9
Gladiolus robustus *Goldblatt*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Haemanthus albiflos *Jacq.*	-	•	•	-	-	-	-	•	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	4
Oplismenus hirtellus *(L.) P.Beauv.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Ornithogalum longibracteata *Jacq.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	-	•	3
Panicum deustum *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	•	•	4
Scadoxus puniceus *(L.) Friis & Nordal*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Schoenoxiphium																								
lanceum *(Thunb.) Kük.*	-	-	•	•	•	•	•	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	7
lehmannii *(Nees) Steud.*	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	•	4
Stipa dregeana *Steud.*	-	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	•	5
Zantedeschia aethiopica *(L.) Spreng.*	•	•	•	-	-	-	-	•	•	•	•	•	•	•	•	-	•	•	-	-	•	-	-	14
Soft shrubs and forbs																								
Abutilon sonneratianum *(Cav.) Sweet*	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Aloe sp.	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Asparagus macowanii *Baker*	-	-	-	•	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	4
Cardamine africana *L.*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Centella erianthe *(Rich.) Drude*	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ceropegia sp.	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total
	Forest site																							
Clutia																								
natalensis *Bernh.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	1
pulchella *L.*	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	-	4
Crassula																								
nemorosa *(Eckl. & Zeyh.) Endl. ex Walp.*	-	•	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	2
pellucida *L.* subsp. marginalis *(Dryand. in Aiton) Toelken*	-	-	-	•	-	•	-	•	-	•	-	-	-	-	-	•	•	-	-	-	•	•	-	8
Cyrtorchis arcuata *(Lindl.) Schltr.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Didymodoxa caffra *(Thunb.) Friis & Wilmot-Dear*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Euphorbia kraussiana *Bernh.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	•	•	3
Galium thunbergianum *Eckl. & Zeyh.*	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Galopina circaeoides *Thunb.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	-	•	3
Gerbera cordata *(Thunb.) Less.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	3
Helichrysum petiolare *Hilliard & B.L.Burtt*	-	-	-	•	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Hypoestes sp. cf. verticillatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	-	•	•	-	4
Isoglossa prolixa *(Nees) Lindau*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	•	2
Jatropha capensis *(L.f.) Sond.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	1
Knowltonia vesicatoria *(L.f.) Sims* subsp. humilis *H.Rasm.*	•	•	•	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	6
Leidesia procumbens *(L.) Prain*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
Leonotis ocymifolia *(Burm.f.) Iwarsson*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Lobelia sp.	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Nemesia mellissifolia *Benth.*	-	-	-	•	-	-	-	•	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	3
Oxalis incarnata *L.*	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	•	3
Pavonia praemorsa *(L.f.) Cav.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	1
Pelargonium																								
ribifolia *Jacq.*	-	•	•	•	-	•	-	-	-	-	-	-	•	•	•	-	-	-	-	-	-	-	-	7
scabroide *Knuth*	-	-	-	-	-	-	-	-	-	•	•	•	•	•	-	-	-	-	-	-	-	-	-	5
zonale *(L.) L'Hér.*	•	•	•	•	-	•	•	•	-	•	-	•	-	•	•	•	•	-	-	-	-	-	-	13
Peperomia																								
retusa *(L.f.) A.Dietr.*	•	-	•	-	-	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	•	-	-	4
tetraphylla *(G.Forst.) Hook. & Arn.*	-	-	-	•	-	-	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Peucedanum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
Plectranthus verticillatus *(L.f.) Druce*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	1
Polygala myrtifolia *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
Solanum																								
giganteum *Jacq.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	1
retroflexum *Dunal*	-	-	-	-	-	•	-	-	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
tomentosum *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1
Sp. cf. Acalypha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	•	2
Stachys																								
aethiopica *L.*	-	•	•	•	-	-	-	•	•	-	-	-	-	-	•	-	•	-	•	-	•	•	-	10
grandifolia *E.Mey. ex Benth.*	-	-	-	•	•	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Streptocarpus rexii *(Hook.) Lindl.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	•	2
Zygophyllum morgsana *L.*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	-	-	-	-	-	-	-	1