Research Note

Are Pine Plantations "Inhospitable Seas" around Remnant Native Habitat within South-western Cape Forestry Areas?

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SYNOPSIS

Some areas of forestry estates, including unplantable ones, may be zoned and managed for nature conservation. This paper is an analysis of the results of studies of plants, birds and small mammals at Jonkershoek, Stellenbosch, to determine whether pine plantations are "inhospitable" to ecological and demographic processes required for the persistence of these biota in native habitat "islands" within forestry areas. The present study indicates that pine plantations are not unqualified "inhospitable seas". However, the human-assisted dominance of the pines over the indigenous vegetation eliminates many species of the original habitat and reduces the numbers, or the frequency of occurrence, of the remaining species. There were proportionally fewer vertebrate-pollinated, indigenous, plant species in the plantation sample than in the mountain fynbos one, and proportionally more vertebrate-dispersed, native, plant species. Vertebrate pollinators were infrequently recorded in, or absent from, mature pine plantations. These factors are likely to affect some ecological and demographic processes in the pine plantations, such as vertebrate-mediated pollination, and perhaps the continuity of these processes between large areas of original habitat and indigenous habitat patches in the forestry area. Therefore we suggest that areas of fynbos and riparian forest surrounded by plantations should be considered as "islands" in an "inhospitable sea" when considering the zonation and management of indigenous habitat for conservation on forestry estates.

Keywords: Pine plantations, plants, birds, small mammals, ecological processes.

INTRODUCTION

The equilibrium theory of island biogeography has been used to suggest designs for nature reserves. The theory, however, has been criticised by, *inter alia*, Gilbert (1980) who reviewed the evidence from studies relating to the theory and found almost no empirical support for the theory. No mainland insular studies provided unequivocal support for the theory. More recently the approach to the study of the fragmentation of habitats and the resultant proposition of measures to counteract these effects has changed from using the theory to studying each situation separately (e.g. Bennett, 1987; Bond *et al.*, 1988).

Bond *et al.* (1988) found that fynbos "islands" in a "sea" of Afrotropical forest had fewer species than comparably-sized areas of the fynbos "mainland" studied. The "sea" was inhospitable to fynbos plants because virtually no species were found common to both habitats. Fire is necessary for the regeneration of certain fynbos plants, but rarely occurs in the forest "sea". Therefore, the "islands" had fewer fires than the "mainland" and as a consequence apparently lost species dependent on frequent fires for regeneration. The forest is also an "inhospitable sea" for the rodent species, but not to all the ant species, recorded in the fynbos "islands" (Midgley and Bond, 1990). However, there appeared to be no major effects of insularisation on the ant and rodent faunas (Midgley and Bond, 1990). This is remarkable owing to the apparent long time since fragmentation of the fynbos occurred.

Cowling and Bond (1991) studied fynbos plants occurring on limestone outcrop "islands" in a "sea" of acid-sand fynbos. In contrast to the fynbos/forest situation reported in Bond *et al.* (1988), the "sea" was not inhospitable to the ecosystem processes occurring on the "islands" because myrmecochory, fire, ornithophilous pollination, etc., also occurred in the "sea". Some species on the "islands" were recruited from the "sea". Only small "islands" (<4 ha) had the expected reduced species richness when compared to comparable "mainland" areas. In general, the distribution of the species traits studied (eg. substrate specificity, dispersal method, and pollination syndrome) did not differ significantly between the "is-

lands" and the comparable "mainland" areas. Local endemic fynbos species were significantly underrepresented on small "islands", and so the critical factor is the amount of required habitat available for these habitat specialists rather than the total size of the "island".

Patches of indigenous vegetation in commercial timber plantations have been likened to habitat "islands" in an "inhospitable sea", i.e. the area planted to exotic timber trees. The species richness and abundance of plants, birds and small mammals are much greater in indigenous habitat than in mature pine plantations of similar area at Jonkershoek, near Stellenbosch (Scott, 1978; Richardson and van Wilgen, 1986; Armstrong and van Hensbergen, 1994). Some species present in the native habitat before afforestation are eliminated from the planted areas. There was approximately a 58 % reduction in the number of indigenous plant species over 35 years in the area planted to pines studied by Richardson and van Wilgen, (1986). The mean cover of the native vegetation was reduced from 75 % to 20 %, and mean native plant density was reduced to one third of its former value. Therefore remnant patches of native habitat are important for maintaining the presence of these species in forestry areas.

The question of whether ecological processes are disrupted by afforestation with pines should be asked when considering how best to manage remnant native habitat within plantations. Continuity of specific ecological processes between remnants and other nearby areas of the same habitat may be necessary for the persistence of some of the biota of the patches.

Are pine plantations inhospitable "seas" around indigenous habitat patches in the sense that ecological and demographic processes are disrupted in the plantations? Is the reduction in plant species richness and biomass with pine afforestation and with increasing age of pine plantations partly due to the disruption of important ecological processes or is it due solely to the human-assisted dominance of the pine trees when competing for light, water, nutrients and rooting space? Also, are certain avifaunal and mammalian guilds disproportionately affected by pine afforestation, thereby adversely affecting vertebrate-mediated ecological processes, and reducing or disrupting immigration to, and dispersal from, indigenous habitat patches?

This paper presents some analyses of the results of studies of plants, birds and small mammals in pine plantations and indigenous habitats at Jonkershoek, to provide some answers to these questions.

STUDY AREA

The Jonkershoek State Forest is in the south-western Cape region of South Africa (33°57' S, 18°15' E; *Figure 1*). The climate is mediterranean. By Köppen's (1931) system, the climate may be classified as mesothermal (Csb) with a warm dry summer (mean temperature of the hottest month ≤ 22 °C) and a relatively wet winter. More than 80 % of the rain falls between April and October (Wicht *et al.*, 1969) usually in long duration, low intensity, frontal events.

The indigenous vegetation of the area is fynbos, a sclerophyllous scrub dominated by species of Proteaceae, Ericaceae and Restionaceae, and along stream courses there are belts of native riparian forest. A total of 800 ha has been afforested with *Pinus radiata* which is managed as a saw-timber crop on a 35 to 40 year rotation.

The Peninsula Sandstone Formation of the Table Mountain Group underlies most of the Jonkershoek valley and outcrops as cliffs in the upper elevations. It is highly folded and faulted and contains occasional shale lenses. Beneath the sandstone, and outcropping occasionally in the lower parts of the valley, is deeply weathered Cape Granite which allows deep penetration of roots and water. Weathering, soil creep and colluviation have resulted in a complex and varied distribution pattern of soil parent materials derived from the two geological formations. The soils are mainly sandy loams (Versfeld, 1981).

METHODS

Plants

Fynbos data were collected from Biesievlei (Rycroft, 1950) and plantation data from Bosboukloof (Milton, 1976), situated along the south-westerly-facing side of the Jonkershoek Valley within 2 km of each other (*Figure 1*). The elevation at Biesievlei ranges from 290 to 580 m (Richardson and van Wilgen, 1986). Therefore only plant data collected within the elevation range of approximately 300 to 580 m by Milton (1976) at Bosboukloof were used in the comparison. The pine plantations studied by Milton (1976) were approximately 37 years old. Only the plants that were identified to species level in the studies of Rycroft (1950) and Milton (1976) were used in the analyses. Only one species was considered where two species on a list are subspecies of the same species.

Plants were classified according to the pollination system (Rebelo, 1987), the seed dispersal system (Bond and Slingsby, 1983; Knight, 1988; le Maitre and Midgley, 1992), and the persistence group of vital attributes (van der Merwe, 1966; Knight, 1988; Van Wilgen and Forsyth, 1992). The classes of these three characteristics are as follows.

Pollination system - wind, insect, insect and bird, bird, mammal.

Seed dispersal system - water, wind, other (gravity, ballistic, unknown), ant, vertebrate.

Method of persistence - dispersed propagules, dispersed propagules and vegetative regrowth, retained propagules, retained propagules and vegetative regrowth. These classes were modified from the scheme of Noble and Slatyer (1980).

Information was obtained from specimens at the Stellenbosch herbarium (STE) and from some field observations to supplement that in the literature. Plants were classified as having dispersed propagules if the possibility exists for the regular dispersal of the seeds more than a few metres from the parent plant. Plants classified into this category had wind-dispersed seeds, water-dispersed seeds or vertebrate-dispersed seeds (ectococho ry and endocochory). Other dispersal systems, eg. myrmechochory or ballisitic mechanisms, possibly do not result in seed dispersal in fynbos of more than a few metres from the parent plant (eg. Bond and Slingsby, 1983; Yeo, 1984). Plants falling into the latter group of dispersal systems have a restricted seed dispersal and were grouped with the plants with non-dispersed seeds. Seed dispersal systems are not mutually exclusive (eg. Dean *et al.*, 1990) and so seeds were classified according to their actual, or suspected, primary dispersal system.

Birds

The avifaunal data were obtained from four adjacent wooded habitats between Lambrechtsboskloof and Heuningkloof: three pine plantations (three, eight and 29 years old) and a riparian habitat (*Figure 1;* Armstrong and Van Hensbergen, 1994). All pine habitats were adjacent or close to riparian habitat corridors.

Birds were classified according to diet, foraging substratum, nest site and indigenous habitat. The classes of these four characteristics are as follows.

Diet - frugivore, granivore, herbivore, nectarivore, raptor, insectivore, insectivore and frugivore, insectivore and granivore, insectivore and herbivore, raptor and insectivore.

Foraging substratum - ground (includes still-hunting from a perch to the ground), "undergrowth" (in-

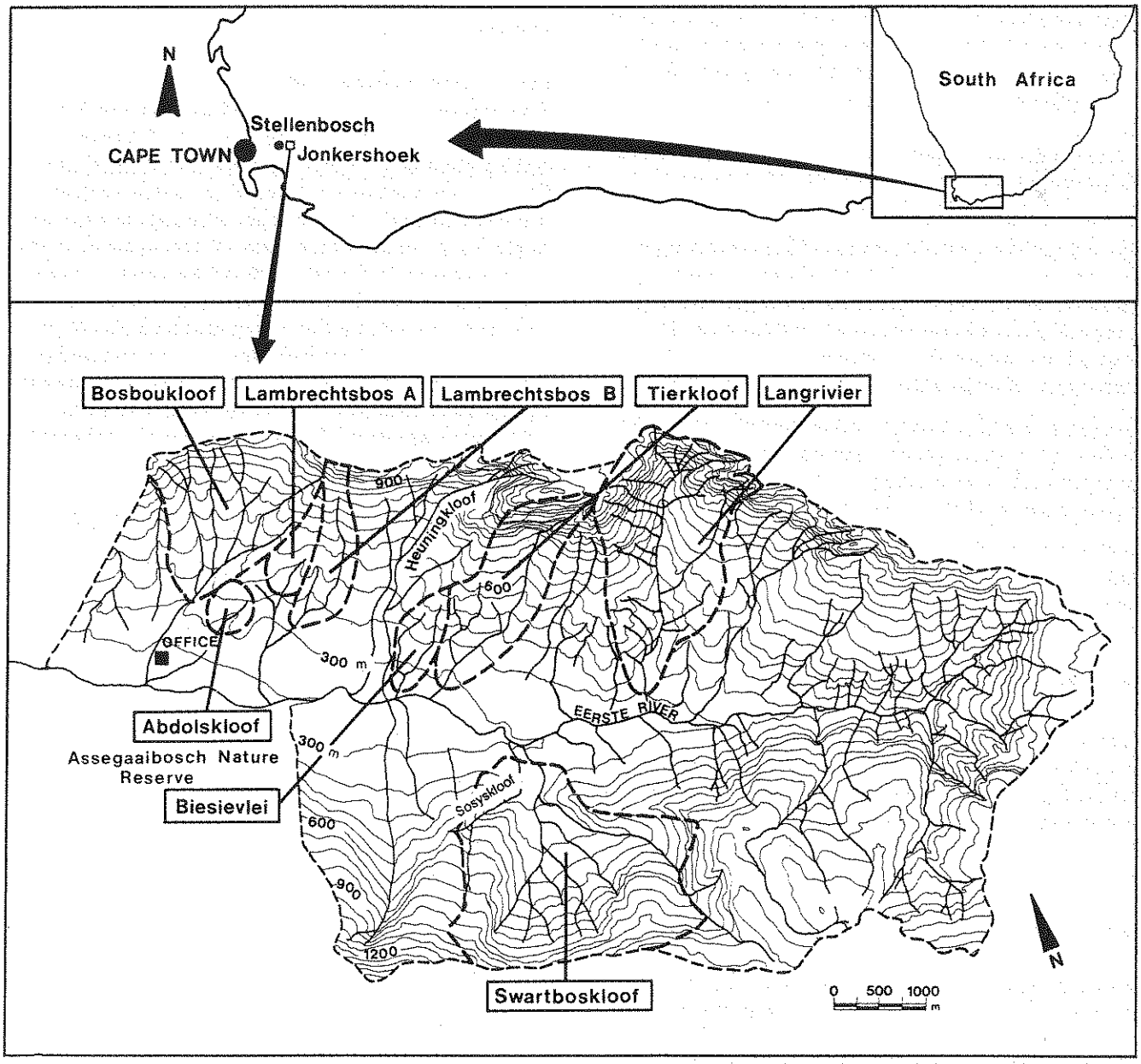

FIGURE 1. Location of Jonkershoek and the study areas.

cluding shrubs ≤1,5 m high), shrubs, bole and larger branches of trees, tree canopy, most or all substrata.

Nest site - ground (including ground holes), rock ledges and cavities, undergrowth, shrubs, tree-hole, tree canopy (forks of branches etc.).

Indigenous habitat - fynbos, riparian forest and scrub, both habitats.

Results were taken from Armstrong and van Hensbergen (1994).

Mammals

The species lists for pine plantations were collected at Bosboukloof (Scott, 1978), and the lists for the indigenous habitats were collected across the valley on the north-easterly-facing side of the Assegaaibosch Nature Reserve (*Figure 1;* Stuart, 1971). *Acomys subspinosus* was not recorded by Stuart (1971) but was captured by Toes (1974) in fynbos in nearby Swartboskloof. This species therefore was added to the fynbos list. The young pine plantation studied by Scott (1978) was approximately four years old and the middle-aged plantation approximately 13 years old.

Mammals were classified according to diet, foraging microhabitat and resting site. The classes of the characteristics are as follows.

Diet - "frugivore" (fruit, flowers, fungal fruiting bodies), granivore, "folivore" (herbivorous on vegetative parts of plants), herbivorous on underground organs of plants, generalist herbivore (combination of two or more of the above diet categories), insectivore (includes any invertebrates), carnivore, omnivore.

Foraging microhabitat - subterranean or ground surface in several microhabitats, amongst herbaceous growth, terrestrially amongst shrubby cover, water, most or all microhabitats.

Resting site - underground or on "bare" ground, among rocks in rocky open areas or on rock ledges, in rock hole or crevace, amongst herbaceous growth, among shrubs in shrubland or in thicket, in tree-hole.

Classification methods

Each species was assigned to the class of each characteristic that was predominant in the life history or the ecology of the species. A species was classified into a composite class if information enabling classification of the species into a predominant class was lacking.

Sampling intensity

Sampling intensity differed between the two plant studies and between the two mammal studies. This will not effect an analysis of the ratios between guild classes, on the assumption that the sampling methods used in these studies were not biased against the species of particular guilds. Similar results from other studies (plants: Richardson and van Wilgen, 1986; small mammals: Breytenbach, 1986; Armstrong and Van Hensbergen, 1995) give support to the validity of this assumption for the present study.

Statistical analysis

All statistical testing was done using BMDP statistical software (Dixon, 1988). *Chi*-square tests of association between habitat type and the different plant and animal guilds were done using species presence/absence data only, under the null hypothesis of no association. The resultant tables of adjusted standardised residuals were used to determine the significant associations (d_{ij}>1,86; p<0,05) between specific habitat and guild classes (Everitt, 1977).

RESULTS

Plants

(a) *Pollination system*

The plantation and fynbos habitats did not differ in the relative number of species in the different pollination classes (χ^2 = 5,831; df=4; p=0,212; *Table 1).* There were no bird-pollinated or rodent-pollinated plants in the plantation sample, although these plants made up a small proportion of the species in the fynbos sample (2,6 and 0,4 % of the species, respectively). However, when the vertebrate classes were combined (including the insect and bird class), pollination system and habitat type were associated (χ^2 = 6,648; df=2; p=0,036; *Table 1*). Vertebrate-pollinated plants were associated with the indigenous habitat and there was a lack of these species in the plantation habitat (d_j = 2,0; p<0,05).

TABLE 1. Number of plant species in each pollination class in the plantation and fynbos samples

Pollination system	Plantation	Fynbos
Vertebrate classes separate		
Bird and insect	1	7
Bird	0	7
Insect	82	212
Rodent	0	1
Wind	25	46
Vertebrate classes combined		
Vertebrate	1	15
Insect	82	212
Wind	25	46

(b) *Seed dispersal system*

Seed dispersal system and habitat type were associated ($\chi^2 = 14,19$; df=4; p=0,007; *Table 2*). The plantation habitat had a significantly greater proportion of vertebrate-dispersed plants than the fynbos habitat (26,1 and 11,7 % of the species, respectively; $d_{ij} = -3,5$; p<0,05).

(c) *Potential mode of persistence*

The plantation and fynbos habitats did not differ in the relative number of species in the different persistence mode classes (χ^2 = 1,632; df=3; p=0,652; *Table 3*).

TABLE 2. Number of plant species in each seed dispersal class in the plantation and fynbos samples

Seed dispersal system	Plantation	Fynbos
Ant	16	40
Other	34	101
Vertebrate	29	33
Water	1	9
Wind	31	99

Birds

(a) *Consistency of habitat occupation*

Birds were more regularly present in the indigenous riparian habitat than in any of the pine habitats. Birds were infrequently recorded in mature pine plantations.

(b) *Diet, foraging site and nest site*

There was no significant association between habitat type and diet, foraging site or nest site guilds (*Table 4*). However, there was a significant association between undergrowth-nesting species and the young pine habitat. Species nesting in the canopy were

TABLE 3. Number of plant species in each potential persistence class in the plantation and fynbos samples

Persistence mode	Plantation	Fynbos
Dispersed propagule	12	36
Retained propagule	49	105
Resprouting and dispersed propagule	11	32
Resprouting and retained propagule	39	109

TABLE 4. Number of bird species in each class of the various characteristics in the plantation and riparian habitat samples (from Armstrong & van Hensbergen, 1994)

Characteristic	Class	Habitat			
		Pine (years)			Riparian
		3	8	29	
Diet	Frugivore	1	2	1	3
	Frugivore/insectivore	1	1	1	2
	Granivore	2	2	3	4
	Granivore/insectivore	1	-	-	-
	Herbivore/insectivore	1	1	1	1
	Herbivore	1	-	-	1
	Insectivore	7	5	5	9
	Nectarivore	3	2	1	3
	Raptor/insectivore	2	-	-	-
Foraging substrate	Ground	4	2	2	3
	Undergrowth	6	4	3	4
	Shrubs	3	3	2	4
	Tree bole	-	-	-	1
	Tree canopy	2	2	3	6
	Aerial	1	-	-	-
	Most substrata	3	2	2	5
Nest site	Ground	1	-	-	-
	Rock	1	-	1	1
	Undergrowth	6	1	1	2
	Shrub	5	1	-	7
	Tree cavity	-	-	1	1
	Tree canopy	3	6	5	6
Indigenous habitat assemblage	Fynbos	7	2	2	4
	Riparian	5	6	7	14
	Both	7	5	3	5

significantly associated with the younger mature (eight year old) pine habitat, and predominated in the older mature pine habitat, but behaviour associated with nesting was not recorded.

Insectivorous species predominated in pine plantations. Avian pollinators, the malachite (*Nectarinia famosa*), orange-breasted *(N. violacea)* and lesser double-collared *(N. chalybea)* sunbirds, and some seed dispersers, the speckled mousebird *(Colius striatus)*, Cape *(Pycnonotus capensis)* and sombre *(Andropadus importunus)* bulbuls, and red-winged starling *(Onychognathus morio)*, were absent, or virtually so, from mature pine plantations. All the sunbirds and the mousebird and Cape bulbul were recorded in the young pine plantation. Birds that forage in the lower vegetation strata predominated in the pine habitats. Bole-foragers were only encountered in the riparian habitat.

(c) *Indigenous habitat assemblage*

Indigenous habitat bird assemblage and habitat type were not associated *(Table 4)*. Fynbos and widespread birds predominated in the young pine habitat, whereas riparian and widespread birds predominated in the younger mature pine habitat and riparian birds in the older one.

Mammals

There were no significant associations between diet guild, foraging site or resting site and habitat type (χ^2 = 90,421; df=21; p=0,985; *Table 5;* χ^2 = 13,565; df=12; p=0,329; *Table 6;* χ^2 = 10,053; df=15; p=0,816; *Table 7;* respectively). The only rodent pollinator recorded in the middle-aged (mature) pine plantation was the striped mouse *(Rhabdomys pumilio)*. The other rodent pollinators, the Cape spiny mouse *(Acomys subspinosus)*, namaqua rock mouse *(Aethomys namaquensis)* and Verreaux's mouse *(Myomyscus verreauxii)*, were either not recorded in pine plantations or were found in the young plantation.

DISCUSSION

Pine plantations are not unqualified "inhospitable seas". Ecological processes such as pollination and

TABLE 5. Number of mammal species in each diet class in the plantation and native habitat samples

Diet	Young plantation	Mature plantation	Fynbos	Riparian habitat
Carnivore	2	1	5	3
Folivore	1	1	4	0
Frugivore	1	0	1	1
Granivore	1	0	1	1
Herbivore	1	1	5	2
Insectivore	2	1	2	3
Omnivore	0	0	0	1
Herbivore (subterranean plant parts)	1	0	3	2

TABLE 6. Number of mammal species in each foraging microhabitat class in the plantation and native habitat samples

Foraging microhabitat	Young plantation	Mature plantation	Fynbos	Riparian habitat
Ground	1	0	5	4
Among herbs	5	2	8	4
Among shrubs	2	1	8	2
Water	0	0	0	2
Most microhabitats	1	1	0	1

TABLE 7. Number of mammal species in each resting site class in the plantation and native habitat samples

Resting site	Young plantation	Mature plantation	Fynbos	Riparian habitat
Ground	3	1	7	4
Open rocky area	0	0	2	1
Rock crevace	1	0	3	1
Among herbs	3	1	5	6
Among shrubs	1	1	4	0
Tree hole	1	1	0	1

seed dispersal are apparently not disrupted totally. The absence or scarcity of rodent and avian pollinators (Rebelo, 1987) and vertebrate-pollinated plants in mature pine plantations, however, may lead to disruption of vertebrate-mediated pollination in indigenous habitat patches isolated by these plantations. There may also be some disruption of wind-mediated and insect-medicated pollination. Plantations act as wind-breaks and perhaps flight barriers to insects (Saunders *et al.,* 1991; Wood and Samways, 1991). This subject requires further study.

Vertebrate-dispersed plants proportionately increased in pine plantations, perhaps because avian frugivores utilise pines as roosts and some mammalian species forage for mushrooms and insects in plantations, with the consequent opportunity for the deposition of seed there (Geertsema and Van den Berg, 1973; Oatley, 1984; Allen-Rowlandson, 1986; Dean, 1987). However, there is a danger that dispersal of indigenous fruits by birds to and from patches of native vegetation may be disrupted if the fruits of invasive plants growing in, or along the borders of, plantations become the preferred food of frugivores. This has happened in the case of the bugweed *Solanum mauritianum* and rameron pigeons *Columba arquatrix* in parts of Natal (Oatley, 1984).

The presence of plants with ant-dispersed seeds suggests that myrmecochory still occurs in pine plantations, but at considerably reduced rates. Ant species known to disperse seeds of fynbos plants were found in a *Pinus radiata* plantation at Jonkershoek (Slingsby and Bond, 1981; Donnelly and Giliomee, 1985). Ants were more scarce, and the ant diversity low, in the pine plantation in comparison with three fynbos vegetation sites (Donnelly and Giliomee, 1985).

Similarly, Richardson and Van Wilgen (1986) found that the proportion of bird-dispersed, larged-leaved sprouters had increased relative to the other reproductive and growth form guilds in a pine plantation at Jonkershoek over 35 years, owing to the pines providing perches for frugivorous birds. Serotinous non-sprouters, woody small-leaved sprouters, and woody small-leaved myrmecochorous species were eliminated. These authors suggested that myrmecochorous shrubs may re-establish from soil-stored seed after clear-felling or fire.

Wind dispersal of seeds to and from native remnants may be disrupted by the windbreak effect of the pines (Saunders *et al.,* 1991).

The replacement of mountain fynbos with pines changed the composition of the bird assemblage from predominantly fynbos species to an assemblage dominated by species of the riparian habitat, but of lower abundance and which lacked the specialist wooded-habitat species (olive woodpecker *Mesopicos griseocephalus,* sombre bulbul, paradise flycatcher *Terpsiphone viridis).* The fragmentation of the populations of fynbos species by the afforestation is expected to have increased the probability of extinction of the subpopulations in the native remnants (Merriam, 1991).

Avian frugivores and nectarivores, although consistently present in the riparian habitat, were present infrequently in the middle-aged and old plantations, and apparently used pines mainly for roosting and as song posts. Some of these species, and some habitat specialist birds which do not use pine plantations, e.g. sugarbirds and woodpeckers, may be prevented from dispersing to, or from, native habitat "islands", although nectarivores are known to disperse widely (Fraser *et al.,* 1989).

There was no statistically discernible impact of pine afforestation on the relative proportions of the different mammalian guilds. The negative impact of afforestation on the species richness and biomass of indigenous plants (Cowling *et al.,* 1976; Bigalke, 1980; Richardson and Van Wilgen, 1986; Richardson *et al.,* 1989), and therefore on the microhabitats, in pine plantations, appears to affect the different mammalian guilds similarly.

The results suggest that some vertebrate seed-dispersers are able to move between patches of indigenous habitats separated by relatively small pine plantations, although some vertebrate pollinators may not. However, vertebrate-mediated pollination and seed dispersal should not be totally disrupted. The results of Midgley and Bond (1990) suggest that if these habitat "islands" are managed well, rodent-mediated pollination (Wiens and Rourke, 1978), rodent-mediated seed dispersal (Vlok, 1995), and myrmecochory will continue because small mammals and ants should persist in the "islands". For example, burning of a native habitat patch should be done within the natural fire regime, and only one section of the patch at a time to prevent the elimination of species which do not disperse readily through pine plantations. Also, patches of riparian forest and scrub should be kept free of self-seeded plantation trees and other invader plants.

It appears that a contributing factor to the "inhospitable" nature of pine plantations is the management of them (removal of competing vegetation - Hinze, 1993), as opposed to the physical effects of the pine alone. Some small mammals survive in plantations where there is adequate undergrowth of indigenous plants. Such plantations are often, but not necessarily, young, and their small mammal inhabitants may include some species that feed on and disperse the seeds of fynbos plants, such as the Cape spiny mouse and Verreaux's mouse (Scott, 1978; Breytenbach, 1986; Armstrong and Van Hensbergen, 1995; Vlok, 1995).

Corridors between native vegetation remnants and other areas of native vegetation should provide flight pathways for insects, movement pathways for birds and mammals, and perhaps pathways for wind-blown pollen and seeds (e.g. Bennett, 1987; Newbey and Newbey, 1987; Merriam, 1991; Saunders and De Rebeira, 1991). Corridors would also at as habitat for certain species. Continuity of ecological and demographic processes should thereby be ensured. For some species, patches of native habitat close to each

other and to more extensive areas of the same habitat may act as "stepping stones", allowing movement between the areas of native vegetation (Date *et al.*, 1991).

Young pine plantations could be considered as "stepping stones" between areas of native vegetation due to the presence of native plants which attract nectar-feeding and fruit-eating birds.

When considering the zonation and management of indigenous habitat for conservation on forestry estates, should areas of fynbos and riparian forest surrounded by plantations be considered as "islands" in an "inhospitable sea"? The following all indicate that pine plantations are to varying degrees "inhospitable" to at least some indigenous plants, animals and ecologial processes: the large negative impact of afforestation with pines on the indigenous flora and fauna in terms of their abundance and species richness; the scarcity or absence of vertebrate pollinators in old plantations; the infrequent and non-permanent occupancy of pine plantations by birds, and; the change in the composition of bird assemblages with time as the pines mature. Therefore it is suggested that native remnants should be managed as if they were "islands" in an "inhospitable sea", and cognisance of this is important when zoning areas of indigenous vegetation for conservation in new forestry regions.

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REFERENCES

ALLEN-ROWLANDSON, T.S., 1986. An autecological study of bushbuck and common duiker in relation to forest management. Ph.D. thesis, University of Natal.

ARMSTRONG, A.J., and VAN HENSBERGEN, H.J., 1994. Comparison of avifaunas in *Pinus radiata* habitats and indigenous riparian habitat at Jonkershoek, Stellenbosch. *S. Afr. J. Wildl. Res.* 24: 48-55.

ARMSTRONG, A.J., and VAN HENSBERGEN, H.J., 1995. Effects of afforestation and clear-felling on birds and small mammals at Grootvadersbosch, South Africa. *S. Afr. J. For.* 174:17-21.

BENNETT, A.F., 1987. Conservation of mammals within a fragmented forest environment: the contributions of insular biogeography and autecology. In *Nature Conservation: the Role of Remnants of Natural Vegetation,* eds D.A. Saunders, G.W. Arnold, A.A. Burbidge & A.J.M. Hopkins, Surrey Beatty & Sons, Chipping Norton, pp. 41-52.

BIGALKE, R.C., 1980. Plantation forests as wildlife habitats in Southern Africa. In *Proceedings of the joint symposium on plantation forests as wildlife habitat and problems of damage,* 1, IUFRO, Athens, pp. 5-11.

BOND, W.J., MIDGELY, J., and VLOK, J., 1988. When is an island not an island? Insular effects and their causes in fynbos shrublands. *Oecologia* 77: 515-521.

BOND, W.J. and SLINGSBY, P., 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *S. Afr. J. Sci.* 79: 231-233.

BREYTENBACH, G.J., 1986. Impacts of alien organisms on terrestrial communities with emphasis on communities of the south-western Cape. In *The Ecology and Management of Biological Invasions in Southern Africa,* eds. I.A.W. Macdonald, F.J. Kruger & A.A. Ferrar, Oxford University Press, Cape Town, pp. 229-238.

COWLING, R.M., and BOND, W.J., 1991. How small can reserves be? An empirical approach in Cape fynbos, South Africa. *Biol. Conserv.* 58: 243-256.

COWLING, R.M., MOLL, E.J., and CAMPBELL, B.M., 1976. The ecological status of the understorey communities of pine forests on Table Mountain. *S. Afr. For. J.* 99: 13-23.

DATE, E.M., FORD, H.A., and RECHTER, H.F., 1991. Frugivorous pigeons, stepping stones, and weeds in northern New South Wales. In *Nature Conservation: the Role of corridors,* eds D.A. Saunders & R.J. Hobbs, Surrey Beatty & Sons, Chipping Norton, pp. 241-245.

DEAN, W.R.J., 1987. Rameron pigeons: some notes on food and foraging. *Bee-eater* 38:23.

DEAN, W.R.J., MILTON, S.J., and SIEGFRIED, W.R., 1990. Dispersal of seed as nest material by birds in semiarid Karoo shrubland. *Ecology* 71: 1299-1306.

DIXON, W.J. (ed.), 1988. *BMDP Statistical Software Manual.* University of California Press, Berkley.

DONNELLY, D., and GILIOMEE, J.H., 1985. Community structure of epigaeic ants in a pine plantation and in newly burnt fynbos. *J. Ent. Soc. Sth. Afr.* 48: 259-265.

FRASER, M.W., MACMAHON, L., UNDERHILL, L.G., UNDERHILL, G.D., and REBELO, A.G., 1989. Nectarivore ringing in the southwest Cape. *Safring News* 18: 3-18.

EVERITT, B.S., 1977. *The Analysis of Contingency Tables.* Chapman Hall, London.

GEERTSEMA, H., and VAN DEN BERG, M.A., 1973. A review of the more important forest pests of South Africa. *S. Afr. For. J.* 85: 29-34.

GILBERT, F.S., 1980. The equilibrium theory of island biogeography: fact or fiction? *J. Biogeogr.* 7: 209:235.

HINZE, W.H.F., 1993. Silviculture of pines. In *South African Forestry Handbook,* ed. H.A. van der Sijde, Southern African Institute of Forestry, Pretoria, pp. 161-170.

KÖPPEN, W., 1931. *Grundriss der Klimakunde.* Walter de Gruyter, Berlin.

KNIGHT, R.S., 1988. Aspects of plant dispersal in the southwestern Cape with particular reference to the roles of birds as dispersal agents. Ph.D. thesis, University of Cape Town.

LE MAITRE, D.C., and MIDGLEY, J.J., 1992. Plant reproductive ecology. In *The Ecology of Fynbos, Nutrients, Fire and Diversity,* ed. R.M. Cowling, Oxford University Press, Cape Town, pp. 135-174.

MERRIAM, G., 1991. Corridors and connectivity: animal populations in heterogeneous environments. In *Nature Conservation: the Role of Corridors,* eds D.A. Saunders & R.J. Hobbs, Surrey Beatty & Sons, Chipping Norton, pp. 133-142.

MIDGLEY, J.J., and BOND, W.J., 1990. Knysna fynbos "islands": origins and conservation. *S. Afr. For. J.* 153: 18-21.

MILTON, S.J., 1976. Understorey vegetation of a pine plantation, Bosboukloof, Jonkershoek, SW Cape. Department of Nature Conservation honours thesis, University of Stellenbosch.

NEWBEY, B.J., and NEWBEY, K.R., 1987. Bird dynamics of Foster Road reserve, near Ongerup, Western Australia. In *Nature Conservation: the Role of Remnants of Natural Vegetation,* eds D.A. Saunders, G.W. Arnold, A.A. Burbidge & A.J.M. Hopkins, Surrey Beatty & Sons, Chipping Norton, pp. 341-343.

NOBLE, I.R., and SLATYER, R.O., 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* 43: 5-21.

OATLEY, T.B., 1984. Exploitation of a new niche by the Rameron Pigeon *Columba arquatrix* in Natal. Proc. V Pan-Afr. orn. Congr.: 323-330.

REBELO, A.G. (ed.), 1987. A preliminary synthesis of pollination biology in the Cape flora. *S. Afr. Nat. Sci. Prog. Rpt.* 141: 1-255.

RICHARDSON, D.M., MACDONALD, I.A.W., and FORSYTH, G.G., 1989. Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. *S. Afr. For. J.* 149: 1-8.

RICHARDSON, D.M. and VAN WILGEN, B.W., 1986. Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *S. Afr. J. Bot.* 52: 309-315.

RYCROFT, H.B., 1950. A quantitative ecological study of the vegetation of Biesievlei catchment, Jonkershoek. Ph.D. thesis, University of Cape Town.
SAUNDERS, D.A., and DE REBEIRA, C.P., 1991. Values of corridors to avian populations in a fragmented landscape. In *Nature Conservation: the Role of Corridors*, eds D.A. Saunders & R.J. Hobbs, Surrey Beatty & Sons, Chipping Norton, pp. 221-240.
SCOTT, D.F., 1978. A study of the bird and mammal life of three age classes of *Pinus radiata* stands, Jonkershoek plantation. Department of Nature Conservation honours thesis, University of Stellenbosch.
SLINGSBY, P., and BOND, W., 1981. Ants - friends of the fynbos. *Veld & Flora* 67: 39-45.
STUART, C.T., 1971. Contributions to the biology and ecology of the rodents and insectivores of the Andries Venter Research Station, Jonkershoek Valley. Unpublished manuscript.
TOES, E., 1974. Tellingen van kleine zoogdieren en vogels in de Jonkershoek Vallei, Zuid Afrika. Unpublished report, Landbouwhogeschool, Nederland.
VAN DER MERWE, P., 1966. Die flora van Swartboskloof, Stellenbosch en die herstel van die soorte na 'n brand. *Ann. Univ. Stell.* 41(A): 691-736.
VAN WILGEN, B.W., and FORSYTH, G.G., 1992. Regeneration strategies in fynbos plants and their influence on the stability of community boundaries after fire. In *Fire in South African Mountain Fynbos*, eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen, Springer-Verlag, Berlin, pp. 54-80.
VERSFELD, D.B., 1981. Overland flow on small plots at Jonkershoek Forestry Research Station. *S. Afr. For. J.* 119:35-40.
VLOK, J., 1995. Fynbos and rodents. *Veld & Flora* 81: 105-107.
WICHT, C.L., MEYBURGH, J.C., and BOUSTEAD, P.G., 1969. Rainfall at the Jonkershoek Forest Hydrological Research Station. *Ann. Univ. Stell.* 44(A): 1-66.
WIENS, D., and ROURKE, J.P., 1978. Rodent pollination in southern African *Protea* spp. *Nature* 276: 71-73.
WOOD, P.A., and SAMWAYS, M.J., 1991. Landscape element pattern and continuity of butterfly flight paths in an ecologically landscaped botanic garden, Natal, South Africa. *Biol. Conserv.* 58: 149-166.
YEO, P.F., 1984. Fruit-discharge-type in *Geranium* (Geraniaceae): its use in classification and its evolutionary implications. *Bot. J. Linn. Soc.* 89: 1-36.