


Effects of alien pine plantations on small mammal community structure in a southern African biodiversity hotspot

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Abstract

Commercial plantations and alien tree invasions often have substantial negative impacts on local biodiversity. The effect of plantations on faunal communities in the fire-adapted fynbos vegetation of the Cape Floristic Region biodiversity hotspot is not yet well quantified. We studied small mammal community structure in alien *Pinus radiata* plantations and adjacent fynbos regenerating after clear-felling of plantations on the Cape Peninsula, South Africa. Small mammal sampling over 1,800 trap-nights resulted in 480 captures of 345 individuals (excluding recaptures) representing six species. Significantly more species, individuals (12 X) and biomasses (29 X) of small mammals occurred on recovering fynbos sites compared to plantations. This was commensurate with a higher diversity of plant growth forms, vegetation densities and live vegetation biomass. Only one small mammal species, the pygmy mouse (*Mus minutoides*), was consistently trapped within plantations. Fynbos sites were dominated by three small mammal species that are ecological generalists and early successional pioneer species, rendering the recovering fynbos slightly depauperate in terms of species richness and evenness relative to other studies done in pristine fynbos. We make three recommendations for forestry that would facilitate the restoration of more diverse natural plant communities and progressively more diverse and dynamic small mammal assemblages in a key biodiversity hotspot.

Résumé

Les plantations commerciales et les invasions d'arbres exotiques ont souvent des impacts négatifs importants sur la biodiversité locale. Les effets de plantations sur les communautés fauniques de la végétation de fynbos adaptées aux feux du point chaud de biodiversité de la région floristique du Cap ne sont pas encore quantifiés. Nous avons étudié la structure des communautés des petits mammifères dans les plantations exotiques de *Pinus radiata* et des fynbos adjacents régénérant après la coupe à blanc des plantations de la péninsule du Cap, en Afrique du Sud. L'échantillonnage de petits mammifères sur 1800 nuits-pièges a permis de capturer 345 individus sur les 480 captures (en excluant les recaptures) représentant six espèces. Considérablement plus d'espèces, d'individus (12 X) et de biomasses (29 X) du groupe des petits mammifères se sont produits de la récupération des sites de fynbos par rapport aux plantations. Cela correspondait avec une plus grande diversité de formes de croissance des plantes, de densités de végétation et de biomasse de végétation vivante. Seulement une petite espèce de mammifère, la souris pygmée

(*Mus minutoides*), était sans cesse piégée dans les plantations. Les sites de fynbos étaient dominés par trois petites espèces de mammifères qui sont écologiquement généralistes et à croissance rapide pionnières, permettant les fynbos légèrement appauvri de se rétablir en termes de richesse et de régularité des espèces par rapport à d'autres études menées sur des fynbos intacts. Nous formulons trois recommandations pour la foresterie qui faciliteraient la restauration de communautés de plantes naturelles plus diversifiées et d'assemblages de petits mammifères de plus en plus diversifiés et dynamiques dans un point chaud clé de la biodiversité

KEYWORDS

biodiversity hotspot, Cape Floristic Region, habitat heterogeneity, heathland, passive restoration, pine plantations

1 | INTRODUCTION

Worldwide there are 140 million hectares of exotic plantations, 1.3 million ha of which can be found in South Africa (FAO, 2001; Hawley, Taylor, & Dames, 2008). Pine plantations specifically make up 660 000 ha of this coverage in South Africa, and invasive pine stands cover an additional 2.9 million ha (van Wilgen, 2015). Alien pine plantations and invasions have been shown to modify local ecosystem properties and functioning, negatively impact local biodiversity and, in South Africa, consume large amounts of water and increase wildfire intensities (Richardson & Higgins, 1998; Richardson et al., 1996; Stephens & Wagner, 2007; Stock & Allsopp, 1992; van Wilgen, 2009, 2015). Pine plantations and invasions are particularly problematic in the fynbos-dominated mountains of the Cape Floristic Region (CFR), in the south-west of South Africa (van Wilgen, 2015). The CFR is one of the world's 35 biodiversity hotspots, noted for its exceptionally high plant species richness and endemism (Cowling et al., 2015; Mittermeier, Turner, Larsen, Brooks, & Gascon, 2011). Despite its inherent value, this biodiversity hotspot is threatened by the rapid expansion of the City of Cape Town metropole (population of approximately 4 million people), as well as the accompanying habitat transformation associated with agriculture, plantations and alien plant invasions (Rebelo, Holmes, Dorse, & Wood, 2011). Of the twelve fynbos vegetation types occurring within the greater Cape Town area, six are critically endangered, with only small, fragmented areas remaining (Rebelo et al., 2011).

Small mammals are good bio-indicators of the effects of habitat alteration on biodiversity, owing to their high reproductive outputs and fast population turnover rates, enabling them to respond rapidly to environmental changes (Avenant, 2011). Their small size and home ranges also allow them to persist in disturbed and fragmented habitats where larger-sized mammals are unable to survive (Merritt, 2010). Key environmental determinants of small mammal community structure are ground cover and vertical variation in habitat architecture (Bond, Ferguson, & Forsyth, 1980; Els & Kerley, 1996; Shanker, 2001; Twyford, 1997), habitat heterogeneity (Keller & Schradin, 2008), food availability (Merritt, 2010), fire regime

(Yarnell, Scott, Chimimba, & Metcalfe, 2007), proximity to waterbodies (Lyra-Jorge, Pivello, Meirelles, & Vivo, 2001), and rainfall and elevation (Bond et al., 1980; Yarnell et al., 2007). In fire-prone fynbos, small mammal succession follows vegetation recovery after disturbance (Breytenbach, 1987; Twyford, 1997; Willan & Bigalke, 1982), as has also been documented in other Mediterranean-climate heathlands (e.g. Fox, 1982).

Studies globally have documented how the establishment of plantations markedly reduces biodiversity (Stephens & Wagner, 2007) by reducing structural vegetation diversity, decreasing food resources, disrupting prevailing vegetation dynamics and changing nutrient cycling patterns (Armstrong, Hensbergen, Scott, & Milton, 1996; Richardson, 2008). Similarly in South Africa, plantations and alien tree invasions have been shown to reduce species richness and diversity of birds (Richardson & van Wilgen, 2004), small mammals (Armstrong et al., 1996; Ferguson et al., 2003) and invertebrates (Samways, Caldwell, & Osborn, 1996; Liu, Janion, & Chown, 2012; Uys, 2012). Studies of the effects of plantations on small mammal communities in the Grassland Biome (Ferguson et al., 2003; Johnson, Ferguson, Jaarsveld, Bronner, & Chimimba, 2002), different habitats in the Thicket Biome (Ramesh, Kalle, Rosenlund, & Downs, 2016) and Afromontane forest edges (Wilson, Stirnemann, Shaikh, & Scantlebury, 2010) have reported a general decrease in local population sizes and diversity with communities disappearing 5–8 years after grassland was transformed to plantations. Similarly, pine plantations in the Fynbos Biome were found to be "inhospitable seas" to plants, birds and small mammals, as many species were found to have been eliminated, or their numbers reduced, by plantations (Armstrong et al., 1996).

In 1980, Bond et al. wrote that despite its importance for planning and conservation management, there was very little published information on the ecology of small mammal communities in the mountains of the southern Cape. There has not been much research done since then, and the nature and extent of the impacts of invasive species on ecosystem structure and composition are also poorly documented (Richardson & van Wilgen, 2004). Furthermore, there is currently the public perception that plantations are environmentally

TABLE 1 Abiotic variables distinguishing the six sites at Tokai Park on the Cape Peninsula in 2009. Plantation age in years given in brackets indicates the age at the time of harvest

Site	Vegetation type	Soil category	Soil type	Plantation age (Years)	Soil fertility ^a	Fynbos age (years postharvesting)	Elevation (masl)	Co-ordinates (DMS)	Minimum distance to pristine fynbos (m)
A1	Sand Plain Fynbos	Sand	Acid sands of Tertiary origin	(60)	Low	4	50	34° 3'17.73"S 18°25'46.51"E	2,947
A2	Plantation (<i>P. radiata</i>)	Sand	Acid sands of Tertiary origin	14	Low	-	50	34° 3'23.34"S 18°25'59.98"E	3,369
B1	Silcrete Fynbos	Transitional	Acid sand over silcrete on fertile, sandy loams	(41)	Medium-low	5	70	34° 3'39.96"S 18°25'13.22"E	1,861
B2	Plantation (<i>P. radiata</i>)	Transitional	Acid sand over silcrete on fertile, sandy loams	14	Medium-low	-	70	34° 3'45.95"S 18°25'2.09"E	1,610
C1	Granite Fynbos	Granitic Loam	Fertile, sandy-loam soils (Cape Granite Suite)	(42)	Medium	4	150–200	34° 3'3.50"S 18°24'33.21"E	1,087
C2	Plantation (<i>P. radiata</i>)	Granitic Loam	Fertile, sandy-loam soils (Cape Granite Suite)	12	Medium	-	150–200	34° 3'4.69"S 18°24'18.75"E	598

^aBased on Cowling, Macdonald, and Simmons (1996) and Rebelo, Boucher, Helme, Mucina, and Rutherford (2006).

productivity, three pairs of sites were selected to represent these differences (Table 1). One pair of sites was sampled from each of the three soil types, with one in an existing plantation and the other in a fynbos site (Photographs of each of the six sites can be found in the Appendix S1: Plate 1).

The first pair of sites (A) was located on nutrient-poor alluvial sands and supports threatened Cape Flats Sand Fynbos, which is characterised by low vegetation biomass. The closest natural (undisturbed/unplanted) fynbos habitat was approximately 2,950–3,400 m from this pair of sites in the Table Mountain National Park. The second pair of sites (B) was located on silcrete soils along the geological transition from sand to granite. Silcrete soils have medium nutrient levels and sustain Silcrete Fynbos which is characterised by moderate vegetation biomass. The Silcrete Fynbos sites were approximately 1600–1800 m from the closest natural fynbos habitat. The third pair of sites (C) was located on deep, fertile, sandy-loam soils with relatively high nutrient levels. Granite soil supports endangered Granite Fynbos, which is characterised by high vegetation biomass (Rebelo et al., 2006). The Granite Fynbos sites were approximately 600–1,080 m from the closest natural fynbos habitat.

2.2 | Environmental and weather data

Environmental data were collected during the first sampling season, in 1 m² quadrats at six random locations along the small mammal traplines set at each site (i.e. twelve 1 m² quadrats for each pair of sites). The percentage cover of live vegetation, dead material (litter) and bare ground was estimated in each of these quadrats. The percentage live plant cover was estimated for each of four growth forms: graminoids (mostly alien grasses and restioids), proteoids (Proteaceae), ericoids (Ericaceae) and "other" plants (those that did not fall within the other three categories) to estimate horizontal vegetation heterogeneity (August, 1983). Vegetation density was estimated visually at three different heights (below 0.2 m; between 0.21–1 m; and between 1.1–1.5 m; August, 1983) using an index developed by Bond et al. (1980). This index is calculated by measuring the distance (m) at which an A5 screen became obscured from an observer by vegetation in four directions from the starting point (0°, 90°, 180°, 270°). This index is then expressed as a mean of the inverse of this distance (m) and, thus, a measure of vegetation density. Relative soil softness was compared using a metal fencing pole, 1 cm in diameter and 1.45 m in length weighing 0.73 kg, released from a height of 1 m and the depth of penetration was recorded with measuring tape. Aboveground plant biomass was determined by removing all live and dead (litter) plant material on the soil surface in a 400 cm² area, and drying it to constant mass at 40°C. Data for several weather variables were obtained for the sampling dates from the weather station at Cape Town International Airport (approximately 20 km away: 33° 58' S, 18° 35' E; from the South African Weather Service). These variables, minimum–maximum temperature, morning/night cloud cover, wind speed and rainfall, were used to test for possible small mammal sampling biases due to variation in weather among trapping sessions.

2.3 | Small mammal sampling

Small mammals (rodents and shrews) were caught during three trapping sessions spaced 10 days apart, in the austral autumn (March–May) of 2009, to minimise trap mortalities resulting from extreme temperatures during summer and winter. Each session consisted of five consecutive nights to ensure that trap-shy species would be captured (Bond et al., 1980). The traps used were Sherman livetraps (H.B. Sherman, Tallahassee, Florida, USA). A mixture of peanut butter, rolled oats, sunflower oil and raisins was used as bait. Traps were set each evening (16:00–20:00) and collected during processing in the mornings (06:30–10:00). This was done: to ensure that baboon troops that use the Tokai plantations for night roosting did not destroy traps during daylight hours; to minimise possible interference by cyclists and domestic dogs being walked; and to prevent diurnal heat-related trap mortalities. Wetlands and marshes were avoided, although some standing water occurred in the Silcrete site.

During each trapping session at each site, we set up one trapline consisting of 20 traps spaced 10 m apart to span a length of 190 m (Figure 1). Such traplines are relatively immune to sampling intensity differences and are more efficient in sampling large areas than grids (Pearson & Ruggiero, 2003). Small mammals captured were transferred from traps into mesh plastic bags, identified, weighed in-field (to the nearest 0.5 g) using a spring balance, their sex identified and given a general temporary mark (using a combination of fur clipping and ink dots unique to each of the three sessions) before being released at capture sites. Ethical clearance was granted by the University of Cape Town Science Faculty Animal Ethics Committee (reference number: 2009/V5/AR). Permission for trapping in Tokai Park was granted by SANParks (permit number CRC/2009--023/2009).

2.4 | Data analysis

To assess if trapping effort was sufficient to adequately sample the resident small mammal communities, species accumulation and individual-based (abundance) rarefaction curves were computed with EstimateS Ver 9.1.3 (Colwell, 2013). We used the non-parametric Chao 1 estimator. These rarefaction curves are adapted for mark–release–recapture data (Hughes, Hellmann, Ricketts, & Bohannon, 2001) and perform well even with small samples (Walter & Morand, 1998). This was done only for fynbos sites, as captures in plantations were too limited for analysis.

Before any univariate parametric analyses were used to test for differences among sites, data were screened for normality (Lilliefors or Kolmogorov–Smirnov test d -statistic) and homoscedasticity (homogeneity of variances Levene's test). Where results showed no unreasonable deviation from normality or homoscedasticity, parametric tests were done. The methodology of Nelson and Clark (1973) was used to correct for traps sprung in the catch per unit effort estimations. For statistical analyses, trapping effort was standardised by converting all data to values per 100 trap-nights for each site in each session, to account for any unsprung or faulty traps.

Schnabel and Jolly–Seber estimates (Krebs, 1999) calculated using our trapping data were often less than the number of individuals captured and showed such wide confidence intervals that these were deemed unreliable. Therefore, statistically estimated small mammal populations were not used and relative abundances (number of individuals per site) were used. Differences in relative abundance and biomass for each species and all species combined were compared between the fynbos and plantation sites using a mixed-model repeated-measures analysis of variance (ANOVA) in R (Chambers, Freeny & Heiberger, 1992).

Small mammal diversity was calculated using the Shannon–Wiener and Brillouin indices. The Shannon–Wiener index, although sensitive to unequal sample sizes, is widely used because of its high discriminatory power (Magurran, 2004). The Brillouin index, while having lower discriminatory power, is often more accurate in cases of non-random sampling that is the norm in small mammal trapping studies (Innes & Bendell, 1988; Magurran, 1988; Pielou, 1975). Both Shannon–Wiener and Brillouin methods were computed per site for each session using relative abundance data and compared using Pearson correlations. As Shannon–Wiener and the Brillouin diversity indices using relative abundance were strongly and significantly correlated ($r = 0.99$, $N = 18$, $p < 0.05$), only Shannon–Wiener indices are used in further analyses. Shannon–Wiener indices for each of the three trapping sessions at each site were computed from \log_e transformed species abundances using Multivariate Statistical Package (MVSP) v. 3.1 (Kovach, 2007), and sites were compared pairwise using a one-tailed Shannon t test.

Effects of weather on small mammal captures were tested using Pearson correlations over the 15 days of the study and chi-squared tests between the three sessions. Differences in *Mus minutoides* body mass between fynbos and plantations were compared using Welch's t test (Welch, 1947). Differences in body mass between male and female *M. minutoides* were not significantly different, and therefore, they were not separated in subsequent analyses. Differences in body mass between various reproductive stages of males and females were not investigated. Differences in environmental variables among sites were tested using a one-way ANOVA. To assess the environmental correlates of small mammal community compositions, we used canonical correspondence analysis (CCA) in MVSP. Relative abundance values were used as an index of small mammal species abundances. Plant cover percentages (Table 3) were arcsine-transformed prior to analysis. Given the differences in scale and magnitude of measurements, all data were \log_2 transformed. Axes extraction followed Kaiser's Rule, with the Hill reciprocal averaging algorithm used to scale eigenvectors. Overall the first two axes explained most of the variance among species and sites (89.9%), but there was significant multi-collinearity among environmental variables such that only five variables (litter biomass, % ericoids, % proteoids, % "other" plants and vegetation density 0–20 cm) were used for the final ordination (Table S1).

3 | RESULTS

3.1 | Small mammal communities

3.1.1 | Trapping

Three sessions, with each session representing 600 trap-nights for a total of 1800 trap-nights, resulted in 480 captures of 345 individuals representing six rodent and shrew species (Table 2), from among the 14 species that have historically been recorded on the Cape Peninsula (Child, Roxburgh, San, & E., Raimondo, D., Davies-Mostert, H.T., 2016; Appendix 2). Thus, despite the short duration and limited spatial scope of this study, we encountered 43% of the potentially resident species. Recapture rates were 23%–34%. Overall, two murid (Muridae) rodent species were dominant; *Mus minutoides* (Smith, 1834) with the highest number of individuals (206, total biomass =1,452 g) and four-striped mice (*Rhodomys pumilio* Sparrman, 1784) with the greatest biomass (201 individuals, total biomass =7,866 g). In terms of biomass, *R. pumilio* dominated the fynbos sites, whereas *M. minutoides* was the dominant species in the plantation sites, and the only species consistently caught in plantations (Table 2). *M. minutoides* body mass was significantly higher on plantation sites compared to fynbos sites (mean_{fynbos}:7.47 g, mean_{plantation}:8.78 g; $t = 2.93$, $df = 32.47$, $p < 0.01$), and there was no significant sexual dimorphism. The third most common species occurring in the fynbos was the forest shrew (*Myosorex varius* Smuts, 1832; Soricidae). There was only one capture of *M. varius* on a plantation site, suggesting the individual was not resident there. Of the other rodents captured, *Dendromus mesomelas* Brants, 1827 (Nesomyidae) and *Acomys subspinosus* Waterhouse, 1838 (Muridae) were only captured on the Granite Fynbos site, and only one individual of *Otomys irroratus* Brants, 1827 (Muridae) was captured during the study, on the Silcrete Fynbos site.

3.1.2 | Influence of weather

There were no significant differences in weather conditions (i.e. minimum and maximum temperature, rainfall and wind speed) during the three trapping sessions, though cloud cover was significantly higher in April ($52.5 \pm 23.33\%$) than either March ($15.0 \pm 8.49\%$) or May ($14.0 \pm 8.49\%$) ($\chi^2 = 63.20$, $df = 2$, $p < 0.05$). The only significant correlations between weather variables and captures of any species were for rainfall and the number of *M. minutoides* ($r^2 = 0.30$, $N = 15$, $p < 0.05$) and *M. varius* ($r^2 = 0.42$, $N = 15$, $p < 0.05$), and for captures of *A. subspinosus* with wind speed ($r^2 = 0.32$, $N = 15$, $p < 0.05$). Despite these weak trends, variation in weather conditions among sessions were negligible so it is unlikely that weather-related biases affected our trapping results significantly.

3.1.3 | Small mammal abundance and biomass

Small mammal abundance (numbers, all species combined) and biomasses were significantly higher on fynbos than plantation sites (Table 3). Of the most common species, numbers of *R. pumilio* and *M.*

minutoides differed significantly between the fynbos and plantations, whereas numbers of *M. varius* did not—though this can be ascribed to statistical error as only one individual was caught on plantation sites. When combining the relative abundances of the three most dominant species (*R. pumilio*, *M. minutoides* and *M. varius*), we found marked differences among the three fynbos sites. Relative abundances were highest on the Granite Fynbos site, intermediate on the Silcrete Fynbos site and lowest on the Sand Fynbos site. Three species (*R. pumilio*, *M. minutoides* and *M. varius*) dominated each of the fynbos sites. Small mammal biomasses showed the same trends as small mammal numbers.

3.1.4 | Species richness and diversity

Species accumulation and individual-based (abundance) Chao-1 rarefaction curves for the three fynbos sites converged asymptotically (Figure S1), indicating that sampling effort adequately reflected small mammal species richness (Magurran, 2004). Species richness was significantly lower on plantation sites compared to fynbos sites ($F = 33.88$, $df = 1$, $p < 0.01$). Granite Fynbos had the highest species richness ($n = 5$), followed by the Silcrete Fynbos ($n = 4$ species) and Sand Fynbos ($n = 3$). Shannon–Wiener (SW) diversity followed similar trends, being significantly higher on the Granite Fynbos site relative to the plantation (SW_{fynbos}:1.14, SW_{plantation}:0.53; $t_{5,1} = 3.1$, $p < 0.05$). Evenness indices for all fynbos sites were moderate (0.706–0.738), and differences were negligible.

3.2 | Environmental correlates of small mammal community structure

Fynbos and plantation sites differed markedly in terms of vegetation diversity and structure (Table 3). In the plantations, no ericoids or proteoids were present, and there were notably fewer graminoids (31x reduction) and “other” (non-proteoid, ericoid or graminoid) plants (8x reduction) compared to fynbos sites. The two most important environmental parameters determining small mammal community composition were percentage of “other plants” and vegetation densities at ground level (0–20 cm), which were significantly higher in the fynbos relative to the plantations (Figure 2, Table 3). These variables correlate strongly and positively with live plant biomass and negatively with percentage of dead plants, and therefore, the first axis of the CCA reflects a nutritional/habitat gradient from dead plant material on the right (plantation sites) to high live biomass and vegetation density on the left (fynbos sites). The second axis was strongly influenced by litter biomass as well as, in the opposite direction, the percentage of proteoids and ericoids. However given that proteoids and ericoids were restricted to single sites (Silcrete Fynbos and Sand Fynbos respectively; Table 3), and that litter biomass was inversely proportional to percentage of bare ground (Table S1), this axis can be interpreted as predominantly a litter biomass–bare ground gradient.

All three plantation sites plotted to the right of the fynbos sites along CCA1 and negatively along CCA2. The position of these sites reflects the significantly lower non-tree vegetation densities

TABLE 2 Summary of mean small mammal relative abundance (number of individuals) and biomass on the plantation and fynbos sites at Tokai Park and associated statistics testing significance of differences using a mixed-model repeated-measures ANOVA

Species	Plantations				Fynbos				Statistics		
	Sand	Silcrete	Granite	All	Sand	Silcrete	Granite	All	P versus F	Fynbos sites	
Relative abundance (mean)											
<i>Rhabdomys pumilio</i>	0	0	0	0	10.4 ± 5.2	16.7 ± 8.9	19.6 ± 5.0	15.6 ± 4.7	F = 32.95*	NS	
<i>Mus minutoides</i>	5.0 ± 6.2	2.2 ± 2.0	1.2 ± 0.8	2.8 ± 2	13.6 ± 8.7	16.4 ± 2.1	13.7 ± 6.0	14.6 ± 1.6	F = 64.39*	NS	
<i>Myosorex varius</i>	0	0	0.3 ± 0.6	0.1 ± 0.2	1.0 ± 0.6	5.4 ± 3.5	7.9 ± 5.1	4.8 ± 3.5	NS	NS	
<i>Otomys irroratus</i>	0	0	0	0	0	0.3 ± 0.6	0	0.1 ± 0.2	NS	NS	
<i>Acornys subspinosus</i>	0	0	0	0	0	0	0.5 ± 0.5	0.2 ± 0.3	NS	NS	
<i>Dendromus mesomelas</i>	0	0	0	0	0	0	0.8 ± 0.8	0.3 ± 0.5	NS	NS	
All species	5.0 ± 6.2	2.2 ± 2.0	1.5 ± 1.3	2.9 ± 1.9	25.0 ± 13.7	38.8 ± 12.5	42.5 ± 6.3	35.4 ± 9.2	F = 36.07*	NS	
Relative abundance (total)											
<i>Rhabdomys pumilio</i>	0	0	0	0	31	50	59	46.6 ± 14.3	-	-	
<i>Mus minutoides</i>	15	7	4	8.7 ± 5.7	41	49	41	43.7 ± 4.6	-	-	
<i>Myosorex varius</i>	0	0	1	0.3 ± 0.6	3	16	24	14.3 ± 10.6	-	-	
<i>Otomys irroratus</i>	0	0	0	0	0	1	0	0.3 ± 0.6	-	-	
<i>Acornys subspinosus</i>	0	0	0	0	0	0	1	0.3 ± 0.6	-	-	
<i>Dendromus mesomelas</i>	0	0	0	0	0	0	2	0.7 ± 1.2	-	-	
All species	15	7	5	9 ± 5.3	75	116	127	106.0 ± 27.4	-	-	
Biomass											
<i>Rhabdomys pumilio</i>	0	0	0	0	495.7 ± 264.5	590.9 ± 281.6	652 ± 190.7	579.5 ± 78.8	F = 162.37**	NS	
<i>Mus minutoides</i>	47.1 ± 61.8	18.4 ± 17.0	7.8 ± 6.0	24.4 ± 20.3	91.7 ± 53.8	121.4 ± 10.3	94.6 ± 39.1	102.6 ± 16.4	F = 26.89*	NS	
<i>Myosorex varius</i>	0	0	3.3 ± 5.8	1.1 ± 1.9	11.8 ± 6.3	57.6 ± 35.9	74.9 ± 50.4	48.1 ± 32.6	NS	NS	
<i>Otomys irroratus</i>	0	0	0	0	0	39.1 ± 67.7	0	13 ± 22.6	NS	NS	
<i>Acornys subspinosus</i>	0	0	0	0	0	0	3.4 ± 5.9	1.1 ± 2.0	NS	NS	
<i>Dendromus mesomelas</i>	0	0	0	0	0	0	6.4 ± 5.6	2.1 ± 3.7	NS	NS	
All species	47.1 ± 61.8	18.4 ± 17.0	11.2 ± 11.6	25.6 ± 19.0	599.2 ± 316.9	809.0 ± 372.9	831.3 ± 166.3	746.5 ± 128.1	F = 93.01*	NS	

TABLE 3 The mean (\pm standard deviation) of environmental variables and associated statistics for the plantation and fynbos sites at Tokai Park. Significance of differences was tested using a one-way ANOVA. VDI is the Vegetation Density Index which indicates the vegetation density per height class. Live plant biomass excludes trees

	Plantations				Fynbos				Statistics	
	Sand	Silcrete	Granite	All	Sand	Silcrete	Granite	All	P versus F	Fynbos Sites
Soil Softness (mm)	57.7 \pm 21.17	76.7 \pm 12.11	123.3 \pm 44.80	85.9 \pm 16.9	81.3 \pm 17.28	81.7 \pm 40.08	83.3 \pm 22.29	82.1 \pm 1.10	NS	F = 3.8*
Live plant biomass (g/m ²)	60.6 \pm 121.25	13.8 \pm 1,188.21	0.6 \pm 1,192.14	25.0 \pm 617.15	56.3 \pm 65.84	527.5 \pm 762.76	1,123.8 \pm 1,160.36	569.2 \pm 857.44	F = 4.80*	NS
Litter biomass (g/m ²)	1688.1 \pm 11.99	1,142.5 \pm 295.60	1,200.0 \pm 288.74	1,343.5 \pm 161.80	564.4 \pm 656.95	745.0 \pm 816.60	1,415.0 \pm 918.87	908.1 \pm 822.14	NS	NS
Total biomass (g/m ²)	1,748.8 \pm 1.25	1,156.3 \pm 475.95	1,200.6 \pm 476.86	1,368.5 \pm 274.33	620.6 \pm 619.30	1,272.5 \pm 712.84	2,538.8 \pm 1970.27	1,477.3 \pm 1,499.29	NS	NS
% Graminoids	0	0.8 \pm 2.04	0.3 \pm 0.82	0.4 \pm 0.40	3.5 \pm 3.94	4.8 \pm 6.21	29.2 \pm 36.39	12.5 \pm 14.50	F = 34.4*	NS
% Ericoids	0	0	0	0	3.3 \pm 8.16	0	0	1.1 \pm 1.90	NS	NS
% Proteoids	0	0	0	0	0	0.2 \pm 0.41	0	0.1 \pm 0.10	NS	NS
% Other plant species	3.3 \pm 8.16	3.7 \pm 8.04	6 \pm 10.10	4.3 \pm 1.50	26.5 \pm 34.34	35.5 \pm 28.28	37.0 \pm 31.59	33.0 \pm 5.70	F = 107.84**	NS
% dead plant material	96.7 \pm 8.16	95.5 \pm 7.84	93.7 \pm 9.89	95.3 \pm 1.50	51.7 \pm 32.96	45.8 \pm 40.18	29.7 \pm 43.18	42.4 \pm 11.40	F = 85.60*	NS
% Bare Ground	0	0	0	0	15.0 \pm 14.83	13.7 \pm 18.94	4.2 \pm 6.65	11.0 \pm 5.90	F = 10.37*	NS
VDI: <0.2 m (m)	0.3 \pm 0.05	0.3 \pm 0.07	0.2 \pm 0.03	0.3 \pm 0.01	0.4 \pm 0.08	0.8 \pm 0.38	1.3 \pm 0.86	0.8 \pm 0.47	F = 13.33**	F = 4.42*
VDI: 0.2-1 m (m)	0.2 \pm 0	0.2 \pm 0.03	0.2 \pm 0.02	0.2 \pm 0.02	0.2 \pm 0.03	0.5 \pm 0.20	0.8 \pm 0.64	0.5 \pm 0.27	F = 7.60*	NS
VDI: 1-2 m (m)	0.2 \pm 0	0.2 \pm 0.04	0.2 \pm 0.02	0.2 \pm 0.01	0.2 \pm 0.01	0.3 \pm 0.07	0.7 \pm 0.66	0.4 \pm 0.28	NS	NS

and biomass compared to the fynbos sites (Table 3), and a markedly greater litter biomass. Variation in live plant biomass was particularly pronounced among the fynbos sites, being an order of magnitude greater on the Silcrete sites compared to Sand Fynbos, and ~20 X higher on the Granite site. Granite Fynbos (C1) plotted furthestmost to the left along CCA1, with Silcrete Fynbos (B1) and Sand Fynbos (A1) plotting sequentially intermediate to the plantation sites, reflecting this decrease in vegetation density, live plant biomass and a concomitant increase in the incidence of dead plants (Figure 2). The presence of *D. mesomelas* and *Acomys subspinosus* correlated strongly with high percentages of graminoids and “other” plants, dense vegetation and high live plant biomass. *M. minutoides* plotted furthestmost to the right along CCA1 by virtue of it being the only species that was consistently trapped on plantation sites, suggesting a relatively broad ecological tolerance. *R. pumilio* and *M. varius* plotted together to the left along CCA1, but close to the origin, suggesting that both are ecological generalists that can persist in a variety of fynbos plant communities.

4 | DISCUSSION

4.1 | The effect of plantations on small mammal communities

There were stark differences in vegetation characteristics and small mammal communities on the fynbos compared to the plantation sites. Plantation sites were homogenous, consisting of *Pinus radiata* monocultures with regularly spaced, pruned tree trunks and a canopy several metres above the ground, with a litter carpet (95% of ground cover composed mostly of pine needles and a few cones or

branches from previous prunings) which was so continuous that no bare ground was evident. Understory vegetation was sparse, with no ericoids or proteoids, and notably fewer graminoids and other plant species compared to fynbos sites. Understory vegetation densities were only 25%–33% of those recorded on the fynbos stands, this being almost completely attributable to tree trunks. Thus vegetation composition and the horizontal and vertical stratification of the understory habitat were greatly simplified.

Despite the underlying soil fertility gradient and the differences in productivity among the three fynbos sites, there were no such differences in understory vegetation characteristics of the three plantation sites. This points to the homogenising effect of pine plantations on small mammal habitat heterogeneity, or that any substrate-related differences in plant diversity and productivity were probably neutralised by the management of plantations and subsequently *P. radiata* outcompeting and shading sub-canopy vegetation, as has been documented in other alien plantations (Ferguson et al., 2003; Majer & Recher, 1999; Recher, 1982). Nutrients cycles, especially of nitrogen and phosphorous, occur in tightly closed plant-litter-plant loops within *P. radiata* plantations (Dames, Scholes, & Straker, 2002), so nutrients are effectively “locked” in the trees rather than the understory vegetation, and are thus unavailable to most small vertebrate consumers (Golley, Ryszkowski, & Sokur, 1975). While litter production in plantations was about 48% higher than on fynbos sites, soil aridification and suppressed soil microbe activity, together with slow litter decomposition rates in plantations (Scholes & Nowicki, 1998), may further limit the availability of nutrients to small mammals, which rely on energy-rich resources to sustain their high mass-specific metabolic rates (Bourlière, 1975; Dames et al., 2002).

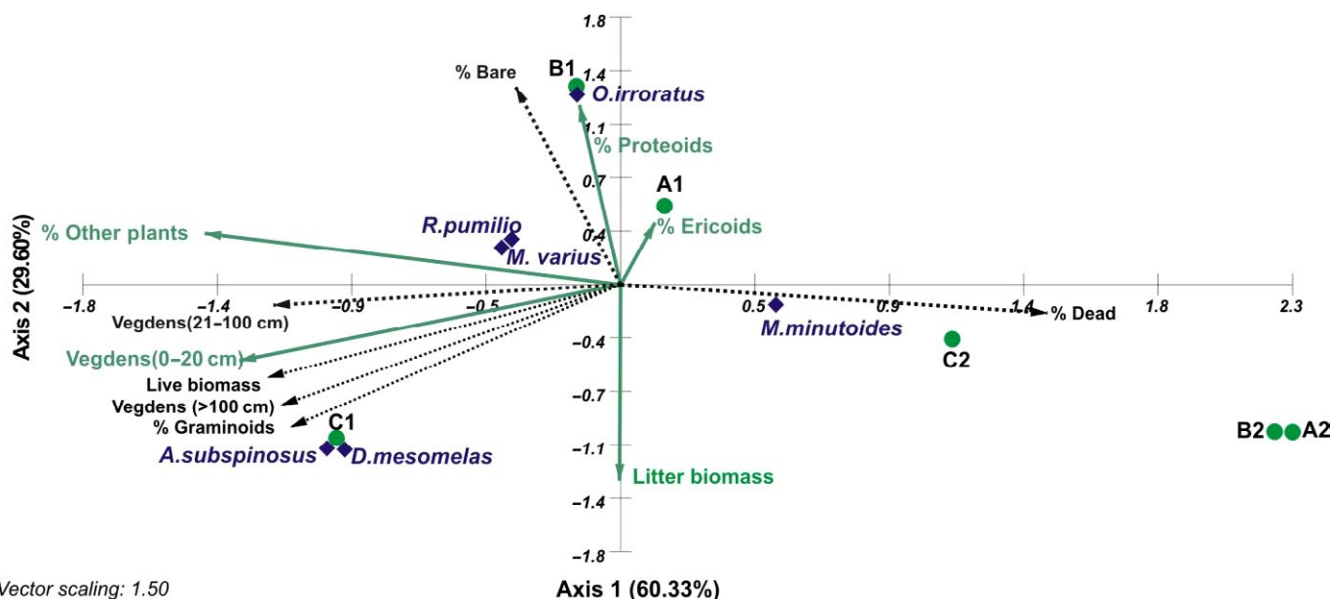


FIGURE 2 Canonical correspondence analysis biplot of the six study sites (●) and six species (◆) at Tokai Park, based on small mammal abundance (relative abundance; Table S1) and environmental data variables (Table 3). The most important vectors/environmental variables are indicated in grey; dotted vectors indicate variables omitted during analysis owing to multi-collinearity

The most important determinants of small mammal diversity and abundance—vegetation density, live plant biomass and vegetation composition (% ericoids, % proteoids and % other plants)—were much lower on plantation than fynbos sites. This, and the unavailability of accessible understory plant cover and food resources, likely accounts for the remarkably depauperate small mammal fauna recorded on the plantation sites, with only one species (*M. minutoides*) trapped consistently but with much lower (80%) numbers and biomass compared to fynbos. Small mammal abundances were also higher on fynbos sites, with overall numbers being 12 times higher and biomass 29 times greater.

The finding that small mammal abundances and diversity are lower in plantations relative to native fynbos sites corroborates results of other studies showing that traditionally managed alien plantations in South Africa are unsuitable habitats for small mammals soon (5–8 years) after planting (Armstrong et al., 1996; Ferguson et al., 2003). This is largely due to reduced habitat heterogeneity, plant species richness, vertical and horizontal habitat stratification (cover), food resources and an accompanying high risk of predation (Armstrong et al., 1996; Armstrong & van Hensbergen, 1995; Dames et al., 2002; Ferguson et al., 2003; Majer & Recher, 1999; Recher, 1982). The presence of only *M. minutoides* on the plantation sites, albeit in low numbers, can be attributed partly to its omnivorous habits and wide habitat tolerances (Monadjem, 2013), suggesting that it is an ecological generalist, as indicated by the CCA analyses. The diminutive body size (4–12 g) of *M. minutoides* may also allow it to better avoid detection by predators and also carries the corollary of lower overall daily metabolic needs, thereby facilitating its survival in cover- and resource-scarce plantations (Monadjem, 2013). Another reason why this species may persist in plantations is because it prefers to nest in rotten wood (Skinner & Chimimba, 2005).

4.2 | Mechanisms underlying patterns in small mammal community structure

Consistent with the gradient in soil fertility among sites, vegetation density in the lowest height class differed significantly among the fynbos sites, being highest in Granite Fynbos, intermediate in Silcrete Fynbos and lowest in Sand Fynbos. Small mammal numbers and biomasses (for all species combined, *R. pumilio* and *M. varius*), species richness and diversity showed the same trends. Thus, it appears in general that small mammal and plant community characteristics covary along the soil fertility gradient, supporting findings that small mammal succession tends to be largely determined by the structure of regenerating vegetation communities (van Hensbergen, Botha, Forsyth, & Matire, 1992).

Based on exhaustive literature searches on 3 major bibliographic engines (Science Direct, Web of Science, Google Scholar), there are no available long-term data on patterns of small mammal succession in regenerating austral Mediterranean shrubland habitats following deforestation, but several studies have documented micromammal community changes following major habitat disturbances caused by wildfires. Studies in the Mediterranean-climate ecosystems of Brazil

(Briani, Palma, & Vieira, 2004), South Africa (Bigalke & Willan, 1984; Kruger & Bigalke, 1984), Australia (Fox, 1982; Monamy & Fox, 2000) and Spain (Torre & Díaz, 2004) have similarly shown a general trend whereby small mammal succession and diversity tracks vegetation succession with time post-disturbance. Generalist species with broad feeding niches recolonise post-burn habitat patches rapidly, while more specialised species appear and reach peak abundance sequentially. Specialised species' diversity and abundance increase as vegetation density increases, as developing habitats fulfil their cover and food requirements and predation risks remain low. Thereafter, specialists' diversity and abundance decrease as fire-dependent vegetation communities become moribund and terrestrial predator populations increase. However, such a successional pattern was not yet evident at the Tokai Park sites.

Small mammal species richness (3–5) on the fynbos sites at Tokai Park was lower than recorded in similarly aged young (4–6 yr) post-fire fynbos sites, where 7–9 species have been sampled with more equitable distributions of numbers and biomass among species (Kruger & Bigalke, 1984). Of the six species we recorded, only two (*A. subspinosus* and *D. mesomelas*) are mid to late successional species, both of which were caught on only the more productive and vegetatively complex Granite Fynbos, owing (based on CCA analyses) to their predilection for abundant graminoids and “other” plants, dense vegetation (especially at ground level) and high live plant biomass. Three species (*R. pumilio*, *M. minutoides* and *M. varius*) dominated all the fynbos sites and collectively accounted for 97%–100% of the individuals sampled and 98%–100% of small mammal biomass. These early succession, pioneer species typically dominate young fynbos (4–6 years post-disturbance) after wildfires in the south-western Cape (Kruger & Bigalke, 1984; Willan & Bigalke, 1982).

Low species richness and diversity, with dominance by pioneer/generalist species, typify disturbed habitats (Brouat, Chevallier, Meusnier, Noblecourt, & Rasplus, 2004; Devictor, Julliard, & Jiguet, 2008). Thus, small mammal communities on the Tokai fynbos sites showed signs of impeded succession relative to other early post-disturbance (4–6 yr) fynbos habitats of a similar age, with three dominant generalist species that usually decline 2–4 years post-fire disturbance (Willan & Bigalke, 1982). This suggests that, in the regenerating fynbos patches, dominance by these pioneer species could exclude more specialised mid-successional species (such as *A. subspinosus*, *D. mesomelas* and *O. irroratus*). This could occur either directly, with ecological generalist outcompeting specialist; or, more likely, by changing the outcome of interspecific plant competition and successional dynamics through intensive herbivory/granivory (Bond, 1984; Quinn, 1986). Such an effect would be exacerbated by a lack of resources needed by more specialised species in the impoverished fynbos patches regenerating without active restoration.

Alternatively, the dominance of the generalist pioneer species, especially on the Silcrete and Sand fynbos sites, could reflect their greater ability to persist in disturbed urban-edge habitats adjoining plantations and/or their capacity to disperse through disturbed vegetation ecotopes and colonise regenerating fynbos patches. Reduced connectivity with nearby undisturbed fynbos

could also limit colonisation of regenerating fynbos patches by more specialised small mammals. A study of beetles in Oak Forests in Norway found that habitat connectivity affects specialist species richness more than generalists (Sverdrup-Thygeso, Skarpaasa, Blumentratha, Birkemoeb, & Evju, 2017). There is a clear trend whereby small mammal diversity declines with increasing distance from the nearest natural (undisturbed) fynbos habitats, commensurate with an altitudinal decline in soil fertility from the relatively "pristine" fynbos on higher elevation slopes towards the urban edge lower down. The roles of competition, resource availability and habitat disconnectivity on small mammal successional patterns in restored fynbos habitats at Tokai Park thus warrant further study. It is also important to consider that certain species are more prone to be trapped, whereas others are more trap-shy. It is possible that in some cases captures of the more common species precluded capture of the more rare ones in the fynbos sites in this study, though it is important to note that recapture rates did not differ significantly between sessions or sites.

5 | CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

Overall it is clear that the growth of mature plantations in the Mediterranean climate, shrub-dominated Fynbos biome impacts negatively on small mammal community structure by reducing both abundance and species richness when compared to restored fynbos sites. From our study, the full extent to which plantations impoverish small mammal communities in pristine fynbos is not apparent because there were no available reference fynbos sites available for comparison. As our study compared small mammals in regenerating shrub communities with mature pine plantations, the observed differences are likely due to the reduced light penetration, understory growth and low food/cover availability which typify even early- to mid-successional stage plantations (5–8 years old) in South Africa (Ferguson et al., 2003).

Although not applicable to the Tokai plantation (as forestry is withdrawing and the land ceded to Table Mountain National Park), there are some potential compromises between wood production and persistence of native flora and fauna available for the Fynbos biome. One recommendation is to identify patches at the landscape level that are likely to harbour high biodiversity, protect these from planting (or even actively restoring them), thereby restricting pine afforestation to less sensitive sites. A second recommendation is to ensure short cycles of plantations (30–40 years maximum), followed by restoration of the fynbos, including prescribed burns to activate long-lasting fynbos soil seed banks (Armstrong & van Hensbergen, 1996; Holmes, Richardson, Wilgen, & Gelderblom, 2000). Third, the establishment of corridors between plantation blocks and nearby undisturbed fynbos habitats could promote effective dispersal (during restoration) of species unable to persist in plantations. Implementation of these three recommendations would facilitate the restoration of more diverse natural plant communities and progressively more diverse and dynamic small

mammal assemblages in a key biodiversity hotspot (Petersen et al., 2007).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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APPENDIX 1

History of plantation compartments used in study

The pine plantations at Tokai were the first in southern Africa, founded in the 1890s. Initial plantings were unsuccessful and therefore a co-crop of wattles were established. This was not well documented. Initial clearing after 15–30 years was followed with a fire

and replanting, but since the 1980s burning has ceased and the new plants planted into the slash. Two to three cycles of pines, initially *Pinus pinaster*, later *Pinus radiata* were established in most compartments. Plantations were planted in situ by hand, and were not fertilized. Commercial products expected from these plantations are timber, pulp and poles. Canopy closure is by 5 to 6 years and thereafter there is no undergrowth. Clearing of all growth to 3 m is done so that the understorey is barren.

The three fynbos sites were under plantations of *Pinus radiata* until 2004–5. The fynbos site, A1, was first planted in 1896 with *Pinus pinaster*. Various fires burnt down sections of the compartment between 1932 and 1943 after which it was re-planted with *Pinus radiata* in 1944. It was clear-felled in 2004, not to be replanted (Compartment Register, 1885). The fynbos site, B1, was first planted in 1886 with mixed Eucalypt Species. It was clear-felled in 1928 and replanted the following year with *Pinus pinaster*. In 1963 it was again clear-felled and the next year *Pinus radiata* was planted. It was clear-felled in 2005, not to be replanted (Comp. Reg. 1885). The fynbos site, C1, was first planted in 1899 with *Pinus pinaster*. It was clear-felled in 1949 and replanted the following year with *Pinus canariensis*. In 1961, following a fire, it was again clear-felled and the next year *Pinus radiata* was planted. It was clear-felled in 2004, not to be replanted (Comp. Reg. 1885). Fynbos recovered naturally at each of the three fynbos sites with no active restoration or management. The recovered fynbos is severely impoverished with many alien shrubs and grasses. This habitat has not been burnt with the result that the seed banks have not been activated.

All existing plantations are due to be removed by MTO by 2024 under the supervision of SANParks. The lower plantation site (A2) was first planted in 1889 with *Pinus pinaster* after which it was

repeatedly replanted with different species. In 1995, *Pinus radiata* was planted and at present is 14 years old (Comp. Reg. 1885). The middle plantation site B2 was first planted in 1887 with *Eucalyptus obliqua* after which it was repeatedly replanted with different species. In 1995, it was replanted with *Pinus radiata* which still exists at present, 14 years old (Comp. Reg. 1885). The upper plantation site C2 was first planted in 1901 with *Pinus pinaster* after which it was repeatedly replanted with different species. In 1997, it was replanted, again with *Pinus radiata* which at present is 12 years old (Comp. Reg. 1885).

This information was compiled from personal communication with Mr Chris Botes (Park Manager) in 2009, using the Compartment Registers of Tokai Park (1885–2009).

APPENDIX 2

List of another 8 indigenous, non-fossorial small mammal (rodent and shrew) species that potentially occur on the Cape Peninsula (and in Tokai Park) according to distribution maps based on historical records (from the 2016 Red List of Mammals of South Africa, Swaziland and Lesotho - <https://www.ewt.org.za/Reddata/reddata.html>) and species habitat preferences.

- Cape Gerbil - *Gerbilliscus afra* (Gray, 1830)
- Hairy-footed gerbil - *Gerbilliscus paeba* (A. Smith, 1936)
- Kreb's fat mouse - *Steatomys krebsii* (Peters, 1852)
- Verreaux's mouse - *Myomyscus verreauxii* (Smith, 1834)
- Namaqua rock rat - *Micaelamys namaquensis* (Smith, 1834)
- Robert's vlei rat - *Otomys karoensis* Roberts, 1931
- Greater Musk Shrew - *Crocidura flavescens* (Geoffroy, 1827)
- Lesser Dwarf Shrew - *Suncus varilla* (Thomas, 1895)