



## Ants, altitude and change in the northern Cape Floristic Region

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### ABSTRACT

**Aim** Climate-modelling exercises have demonstrated that the Cape Floristic Region is highly sensitive to climate change and will apparently lose much of its northern limits over the next few decades. Because there is little monitoring of diversity in this area, ant assemblage structure was investigated within the main vegetation types in the Greater Cederberg Biodiversity Corridor. In particular, we sought to determine how ant assemblage structure differs between the main vegetation types, how restricted ants – and in particular the major myrmecochores – are to the major vegetation types, and which environmental variables might underlie differences in the ant assemblages and in the specificity of species to particular areas.

**Location** Northern Cape Floristic Region, Western Cape, South Africa.

**Methods** Sampling was undertaken during October 2002 and March 2003 across an altitudinal gradient ranging from sea level (Lambert's Bay) to c. 2000 m a.s.l. (Sneeukop, Cederberg) and down again to 500 m a.s.l. (Wupperthal) in the Western Cape, South Africa. Pitfall traps were used to sample ants at 17 altitudinal bands, stretching over three vegetation types (Strandveld, Mountain Fynbos and Succulent Karoo). Biotic and abiotic environmental variables were collected at each sampling site. Generalized linear models were used to determine the relationships between species richness, density, abundance and the abundance of the major myrmecochores, and the environmental variables. Redundancy analysis was used to determine the relationship between ant assemblage structure and the environmental variables. The Indicator Value Method was used to identify characteristic ant species for each vegetation type and altitudinal site.

**Results** Temperature explained significant proportions of the variation in species density and abundance, and, together with area and several vegetation variables, contributed significantly to the separation of the assemblages in the major vegetation types and biomes. Four major myrmecochores were identified [*Anoplolepis* sp. (cf. *custodiens*), *Anoplolepis* sp. (cf. *steinergroeveri*), *Camponotus niveosetosus*, *Tetramorium quadrispinosum*]. The abundances of the two *Anoplolepis* species were related to vegetation variables, while the abundance of the other two species showed opposite relationships with temperature variables. Fourteen ant species were characteristic of certain vegetation types and altitudes. Several of these species contributed to the differences between the assemblages.

**Main conclusions** There are likely to be substantial and complex changes to ant assemblages as climates change in the northern Cape Floristic Region. Moreover, the importance of ants for ecosystem functioning suggests that these responses are not only likely to be a response solely to vegetation changes, but might also precipitate vegetation changes. The changes that are predicted to take place in the next 50 years in the Cape Floristic Region could be substantially exacerbated by such synergistic effects, which have major implications for

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long-term conservation plans. Ongoing monitoring of this transect will reveal the nature and pace of the change as it unfolds.

### Keywords

Ants, climate change, conservation, myrmecochores, spatial autocorrelation, species–environment relationships, South Africa, species richness.

## INTRODUCTION

The Cape Floristic Region (CFR) is a major biodiversity hotspot of global significance (Myers, 1990; Cowling & Richardson, 1995; Mittermeier *et al.*, 1998). It is both the smallest and richest floral kingdom with c. 8700 plant species (Low & Rebelo, 1996), of which 68% are endemic (Bond & Goldblatt, 1984). The region has a high concentration of Red Data Book plant species (i.e. 1406 species: Cowling & Hilton-Taylor, 1994), and is listed as a Centre of Plant Diversity (WWF and IUCN 1994) and a Global 200 Ecoregion (Olson & Dinerstein, 1998). It is also home to several endemic vertebrate species and is an Endemic Bird Area (Stattersfield *et al.*, 1998). The CFR includes five biomes (Nama- and Succulent Karoo, Thicket, Forest and Fynbos) of which the dominant and most characteristic biome is the Fynbos (Low & Rebelo, 1996). However, the Succulent Karoo is also a biome of considerable significance. It has the richest succulent flora (c. 1000 sp.) globally, like Fynbos is extremely species rich at both regional and local scales, and is the only semi-arid region that qualifies as a biodiversity hotspot of global significance (Cowling & Hilton-Taylor, 1994; Cowling *et al.*, 1999).

The considerable biodiversity of the CFR is threatened by land transformation for agriculture and urban development, and by alien plant invasions (Todd & Hoffman, 1999; Rouget *et al.*, 2003b). At present, c. 30% of the area is transformed by agriculture (25.9%), urbanization (1.6%) and alien vegetation (1.6%) (Rouget *et al.*, 2003b). Some of the lowland habitats have been reduced by as much as 90% (Rouget *et al.*, 2003a), and it is predicted that at least 30% of the remaining natural vegetation will be transformed within the next 20 years (Rouget *et al.*, 2003b). Moreover, climate-modelling exercises have demonstrated that the Fynbos in the Cape Floristic Region (CFR) is likely to be highly sensitive to climate change (Midgley *et al.*, 2003; Hannah *et al.*, 2005). It is thought that within 50 years Fynbos will be largely replaced with a different, unknown vegetation type. Climate change models predict that, over this period, the CFR will experience a 1.8 °C increase in mean annual regional temperature and that this area will be faced with significantly more arid conditions (Midgley *et al.*, 2003). The Fynbos biome will apparently lose large areas near its northern limits (retaining less than 10%, Midgley *et al.*, 2002), especially those along the west coast and in the Cederberg mountains (Midgley *et al.*, 2002, 2003). Biome loss will occur at all altitudes, and will only be less than 50% at altitudes between 1800 and 2100 m. Slopes at lower altitudes along the northern borders of the Cape Fold Belt will also

become unsuitable for this biome and it is predicted that the range of Fynbos will contract southwards into this mountain range (see Midgley *et al.*, 2003). In addition, the Nama- and Succulent Karoo are also under threat and it is predicted that between 0.3% and 42.4% of species will become extinct within protected areas in these biomes (Rutherford *et al.*, 1999).

Given the predictions of significant loss of biodiversity in the CFR, conservation planning strategies for a future of change in the area are in place [including Cape Action for People and the Environment (CAPE) and the Succulent Karoo Ecosystem Plan (SKEP): see Cowling & Pressey (2003); Younge & Fowkes (2003) and Driver *et al.* (2003) for extensive overviews of aims and progress]. These ecoregional conservation planning strategies not only incorporate current richness assessments, but also processes such as migration, major areas of evolution such as ecotones and expected local-scale range shifts in response to climate change (Pressey *et al.*, 2003). Furthermore, the plans include consideration of ecosystem functioning aspects such as specialist pollination relationships, plant–herbivore interactions and fire regimes (Pressey *et al.*, 2003). The strategic plans have largely been based on information on plants (especially the Proteaceae), as well as expert knowledge regarding medium- and large-sized mammal, freshwater fish, amphibian and reptile distributions (Cowling & Pressey, 2003; Cowling *et al.*, 2003; Kerley *et al.*, 2003). However, other groups will also be affected by landscape transformations and climate change (e.g. Erasmus *et al.*, 2000), and the processes included in the strategies are a subset of those that need to be taken into consideration if conservation is to be successful over the longer term (see e.g. Rodrigues *et al.*, 2000). Nevertheless, their absence in these plans and the planning processes that gave rise to them is not a consequence of lack of concern, but rather the absence of adequate information (Cowling *et al.*, 2003). A prime example is ant diversity, and one of the most significant processes in which ants are involved, myrmecochory.

Myrmecochory (seed dispersal by ants) is an important ecological process in the Fynbos biome (Le Maitre & Midgley, 1992). Indeed, c. 20% of the 6500 strictly Fynbos plant species (i.e. 1300 species) are dependent on myrmecochory for their survival (Johnson, 1992). The only other comparable area is Australia with 1500 ant-dispersed plants, with the rest of the world containing a mere 300 species (Berg, 1975). In South Africa, myrmecochorous plants are mainly restricted to the Fynbos biome. A total of 29 families and 78 genera of Fynbos plants has been identified as containing species that are ant-dispersed (see Table 1 in Bond & Slingsby, 1983).

**Table 1** Species density and abundance of ants collected in the different vegetation types

Vegetation	<i>n</i>	<i>S</i>	<i>N</i>	Species density (mean $\pm$ SE)	Abundance (mean $\pm$ SE)
Strandveld	8	14	6490	6.63 $\pm$ 0.26	811.25 $\pm$ 199.93
Restioid Fynbos	24	47	13,155	12.08 $\pm$ 0.38	548.13 $\pm$ 106.12
Proteoid Fynbos	24	48	32,203	14.38 $\pm$ 0.47	1341.80 $\pm$ 137.45
Ericaceous Fynbos	64	58	16,824	10.13 $\pm$ 0.32	262.88 $\pm$ 57.32
Alpine Fynbos	8	23	707	5.88 $\pm$ 1.22	88.38 $\pm$ 39.84
Succulent Karoo	8	14	3000	7.50 $\pm$ 0.33	375.00 $\pm$ 55.940

*n*, number of sampling grids; *S*, total species density; *N*, total abundance.

Myrmecochory occurs only in two plant families outside Fynbos, the Euphorbiaceae and Zygophyllaceae (Bond & Slingsby, 1983).

Myrmecochorous ants belong to four subfamilies: Dolichoderinae, Formicinae, Myrmicinae and Ponerinae (Gómez & Espadaler, 1998). In the CFR the dominant myrmecochorous ants are *Pheidole capensis*, *Anoplolepis* sp. (cf. *custodiens*), *Anoplolepis* sp. (cf. *steinergeroeveri*), *Tetramorium quadrispinosum* and *Camponotus niveosetosus* (Bond & Slingsby, 1983, 1984). However, information on the extent of the habitat specificity of myrmecochorous ants is not widely available, especially for the areas in the CFR predicted to change rapidly in the next few years. Slingsby & Bond (1985) concluded that *Anoplolepis* sp. (cf. *custodiens*), *Anoplolepis* sp. (cf. *steinergeroeveri*) and *P. capensis* are ubiquitous in both mesic and arid areas of Fynbos, and the presence of *Anoplolepis* sp. (cf. *custodiens*) has been reported throughout Africa (Prins, 1963; Breytenbach, 1988). Moreover, no myrmecochorous ant species have been studied in terms of their likely direct and indirect (via vegetation change) responses to climate change. If they were to be substantially influenced by such change, thus also affecting the plant species with which they interact, then conservation plans that are based partially on plant data might prove to be inadequate for capturing likely change. To date only the influences of invasive ant species such as the Argentine ant, *Linepithema humile* (e.g. Bond & Slingsby, 1984; Midgley & Bond, 1995; Gómez & Oliveras, 2003), and exotic plant species, such as Australian *Acacia* (French & Major, 2001), on seed dispersal by ants have been investigated. Indeed, no monitoring systems exist for insect assemblages in the CFR.

Here we address these issues by investigating ant assemblage structure within the main vegetation types in a northern CFR area, the Cederberg. In particular, we determine if and how ant assemblage structure differs between the main vegetation types in the Greater Cederberg Biodiversity Corridor (GCBC), how restricted ants, and in particular the major myrmecochores, are to specific vegetation types, and which environmental variables might underlie differences in the ant assemblages and in the specificity of species to particular areas.

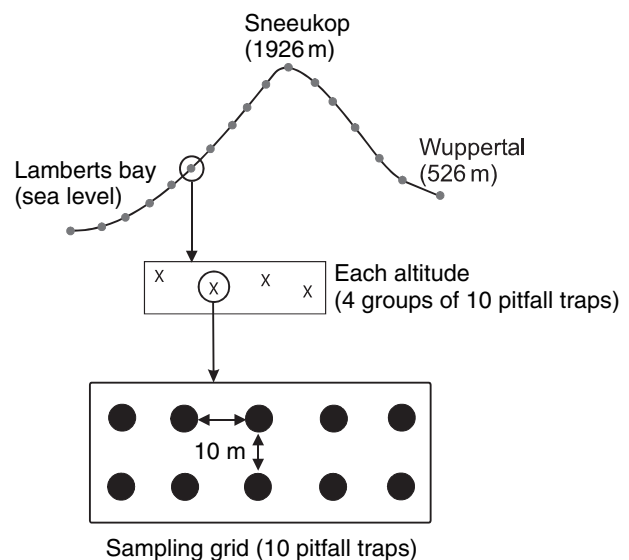
## MATERIAL AND METHODS

### Study site

This study took place in the Greater Cederberg Biodiversity Corridor. This mega-reserve spans a west–east gradient from

coastal lowlands, Mountain Fynbos to Succulent Karoo, and includes the northern most extremity of the CFR with the Cederberg Wilderness Area forming the core (Anonymous, 2004). Specifically, this study was conducted across an altitudinal transect covering the major vegetation types on both aspects of the Cederberg, encompassing the full range of vegetation. The transect ranged from sea level at Lambert's Bay to Sneeuksop (1926 m a.s.l.) then down the eastern slopes to Wupperthal (c. 500 m a.s.l.) (Fig. 1). A total of seventeen altitudinal bands was sampled at 200-m altitudinal intervals across the transect (see Appendix S1 in Supplementary Material) representing Strandveld Succulent Karoo (one site), Mountain Fynbos (15 sites) and Lowland Succulent Karoo (one site).

Strandveld Succulent Karoo is characterized by low, scattered succulent shrubs such as *Zygophyllum morganii* (Tortoisebush), *Euphorbia mauritanica* (Fragmenting Milkbrush) and *E. burmannii* (Poison Milkbrush) and stretches from the Berg River Mouth in the south to Alexander Bay in the north (Hoffman, 1996). Rainfall is generally low (50–300 mm: Hoffman, 1996) and the geology of this biome is characterized by dune sand with highly calcareous areas.



**Figure 1** Sampling layout of the transect ranging from Lambert's Bay, over the Cederberg and down to Wupperthal. Sampling was conducted in October 2002 and again during March 2003 in the same areas.

Three main plant families characterize Mountain Fynbos: Restionaceae (restios), Ericaceae (heaths) and Proteaceae (proteas) (Rebello, 1996). In the Cederberg district the Proteaceae constitutes the dominant overstorey in Fynbos (63 species of which seven are endemic to the area) and the majority of species are confined to the Fynbos biome (Rebello, 1996). The geology of these areas is mostly quartzitic sandstone with shale and conglomerate lenses. Rainfall varies from 200 to over 2000 mm year<sup>-1</sup> (Low & Rebello, 1996).

The Mountain Fynbos can be further classified into structural units (or types) based on the dominant plant families at each of the sites (following Campbell, 1985; see also Cowling & Holmes, 1992). These structural units are Restioid, Proteoid and Ericaceous Fynbos. Three sampling sites were located in Restioid Fynbos along the transect, at 200 and 900 m a.s.l. in the western slope and at 900 m a.s.l. on the eastern slope (see Appendix S1). At these sites the vegetation is dominated by a high cover (> 60%) of Restionaceae, or restios and sedges (900-m site on the western slope). *Protea nitida* and *Leucadendron salignum* occur at the 200-m site but constitute less than 10% of the cover. This site could thus still be classified as Restioid Fynbos (see Campbell, 1985). All three sites have gentle slopes (see Appendix S1).

Proteoid Fynbos only occurs on the western slope of the transect at the 300-, 500- and 700-m sites (see Appendix S1). At the 300-m site (Sawadee), the vegetation type is ecotonal, with both Fynbos and Succulent Shrubland elements, such as non-ericaceous, ericoid-leaved shrubs (e.g. *Passerina* and *Phyllica*) (L. Agenbag, pers. comm.). However, the dominant vegetation is proteoid and this site was thus included in the Proteoid Fynbos structural unit (Campbell, 1985). The 500- and 700-m sites are dominated by dense protea-dominated vegetation with restioids in the mid- to understorey. The sites in this vegetation type have steeper slopes than those sites in Restioid Fynbos (see Appendix S1).

The vegetation turns to Ericaceous Mountain Fynbos above 900 m along the transect on both western and eastern slopes (see Appendix S1) (Campbell, 1985). Eight sites were located in this structural unit, four on the western slope and four on the eastern slope (Table 1). The western and eastern slope Ericaceous Fynbos are very similar, both with a high restioid component. The two sites at 1700 m just below Sneekop were placed on very steep slopes compared with the other sampling sites (see Appendix S1).

In drier areas (e.g. between the Cederberg mountain range and Wupperthal) Mountain Fynbos is replaced by Lowland Succulent Karoo (Low & Rebello, 1996), which is dominated by small, scattered shrubs such as Mesembryanthemaceae (vygies), Crassulaceae (stonecrops) and Asteraceae (daisies). This biome is extremely arid and one sampling area was located in this habitat type on top of Singkop in Wupperthal (see Appendix S1). The geology of this area is dominated by siltstone and shale. Rainfall ranges between 50 and 200 mm year<sup>-1</sup> (Low & Rebello, 1996).

## Vegetation sampling

Vegetation structure was recorded at each sampling grid in October 2002 and March 2003 to determine the horizontal and vertical distribution of the vegetation. The horizontal distribution of vegetation was determined by estimating the coverage of the soil surface by vegetation, leaf litter, exposed rock and bare ground following the methods outlined by Rotenberry & Wiens (1980), Bestelmeyer & Wiens (1996) and Parr *et al.* (2004). A 1-m<sup>2</sup> grid was placed over each pitfall trap (see Ant sampling below) and the percentage of ground covered by the four categories within the grid was estimated. Mean ground cover was calculated for each sampling grid (i.e. each group of 10 pitfall traps).

The vertical distribution (relative vertical complexity) of the vegetation was measured by determining foliage height profiles using techniques similar to those of Rotenberry & Wiens (1980) and Bestelmeyer & Wiens (1996). Vegetation height was measured at four points located at 90° angles on a 1.5-m radius centred on each pitfall trap. At each of these sampling points a 1.5-m rod was placed vertically through the vegetation and the number of contacts with vegetation (hits) was recorded at 25-cm height increments (0–25, 26–50, 51–75, 76–100, 101–125, 125–150, 150+ cm). The average total number of hits per sample point was calculated as a measure of the changing vertical distribution of vegetation (Rotenberry & Wiens, 1980). The maximum height at each sampling point was taken as the highest 25-cm height interval where vegetation contacts were recorded (Rotenberry & Wiens, 1980).

One soil sample of 20 cm<sup>3</sup> (see Tan, 1996) was taken during October 2002 at each sampling grid to ascertain soil characteristics. At each sampling grid 20 subsamples were taken randomly and then mixed to make up one sample from which the 20 cm<sup>3</sup> was taken. The soil samples were air-dried in the laboratory for at least 10 days. The soil samples were analysed for composition (sand, silt, clay and rock), pH (McLean, 1982), K, Na, Ca and Mg (Chapman, 1965), P (Bray & Kurtz, 1945), C (Nelson & Sommers, 1982), NO<sub>3</sub>, H and conductivity (United States Salinity Laboratory Staff, 1954) by BemLab (Pty Ltd.), Somerset West, South Africa.

Two Thermocron iButtons (Semiconductor Corporation, Dallas/Maxim, TX, USA) were buried 10 mm beneath the soil surface at each sampling site (in an area where vegetation cover was low to ensure minimum shade cover) to measure soil temperature. This was done in June 2002 and data recordings are currently ongoing. The iButtons were set to record temperature at 1-h intervals. The data collected from June 2002 to October 2003 were used to calculate the following temperature parameters for each altitudinal band across the 16-month period: mean monthly temperature; mean monthly maximum and minimum temperatures; mean monthly temperature range; and absolute maximum and minimum temperature.

## Ant sampling

Epigaeic ants were sampled along the altitudinal gradient during October 2002 and March 2003 by pitfall trapping. A

total of forty pitfall traps, divided into four groups of 10 pitfalls each was placed at each site during each sampling event (Fig. 1). The four groups of pitfall traps were placed in such a way that they were at least 300 m apart. GPS readings were taken of the location of each group of 10 pitfalls for spatial analyses. The 10 traps were laid out in a grid ( $2 \times 5$ ) with traps spaced at 10-m intervals (Fig. 1). The disturbance caused by placing the pitfall traps was minimized and the vegetation around the traps was not cleared. The 'digging-in' effect (Greenslade, 1973) was thus considered negligible and the traps were set immediately. The traps contained 50 mL of a 50% propylene glycol solution as preservative, which does not significantly attract or repel ants (Adis, 1979). All pitfall traps were left open for a period of 5 days per sampling event. The samples were washed and placed in 70% ethanol in the laboratory and then sorted for ants. Ants were identified to species where possible or assigned to morphospecies. Voucher specimens of each species collected are held at the University of Stellenbosch and will be placed in the Iziko Museums of Cape Town.

### Data analysis

Sample-based rarefaction curves for the ants were compiled separately for the sites to determine the degree of sampling representivity (EstimateS V5, Colwell, 2000, <http://vice-roy.eeb.uconn.edu/estimates>; see also Gotelli & Colwell, 2001). The nonparametric Incidence Coverage Estimator (ICE) and Michaelis–Menten richness estimate provided by EstimateS were used to evaluate sample-size adequacy (Colwell & Coddington, 1994). Sampling may be considered adequate when the sample-based rarefaction curves and the two estimators converge closely at the highest observed values (Longino *et al.*, 2002). The ICE is a robust measure indicating sampling completeness because it stabilizes well and is independent of sample size (Longino *et al.*, 2002).

When sample-based rarefaction curves are used to compare different data sets, the comparison made is one of species density (the number of species per unit area) and not species richness (Gotelli & Colwell, 2001). To compare the species richness values of sites, individual-based rarefaction must be used (Gotelli & Colwell, 2001). These curves standardize different data sets on the basis of number of individuals and not on number of samples. Individual-based rarefaction curves were computed in EstimateS using the Coleman method (Coleman, 1981). Thereafter, the curves were rarefied to the lowest number of individuals recorded at a site to ensure valid comparisons of species richness between different sites (Gotelli & Colwell, 2001).

Because of the influence that available area has on species richness patterns (Rosenzweig, 1995), the species–area relationship was determined for both species richness and density across the altitudinal gradient using Generalized Linear Models assuming a Poisson error distribution (log link function, Type III model: Dobson, 2002). The available area was calculated across the Cederberg region ( $18^{\circ}15'–19^{\circ}45' \text{ E}$ ;  $32^{\circ}00'–$

$32^{\circ}45' \text{ S}$ ). The range of altitudes was divided into 200-m bands (each site was situated in an altitudinal band) and the total area in each altitudinal band within the Cederberg region was calculated using ArcVIEW GIS 3.3 (see Appendix S1). This was done separately for the eastern and the western slopes.

Collinearity in the abiotic variables (six temperature and 15 soil parameters, available area, altitude) and biotic variables (six vegetation parameters and post-fire vegetation age in Mountain Fynbos) was determined using Pearson's product–moment correlations. This was done separately for the abiotic and biotic variables. When variables were significantly correlated (and with  $r > 0.50$ ) one of them was excluded from further analyses, based on a consideration of its likely biological relevance. The structure of the correlograms (see below) of the independent variables was also compared to assist in decisions about which variables to exclude. This approach did not alter the final choice of variables and therefore the full set of correlograms is not shown. The relationships between the abiotic and biotic variables chosen for analyses were then determined, again using Pearson's product–moment correlations, to refine the selection of variables by excluding collinear variables. When abiotic and biotic variables were significantly correlated (and with  $r > 0.50$ ), one of the variables was excluded using the above protocol. These and the following analyses were performed for both the full transect and for a subset thereof in Mountain Fynbos. Mountain Fynbos constituted over 85% of the transect, and the climate change predictions for the region are for this biome (Midgley *et al.*, 2002, 2003). Differences in ant assemblage structure between the within (the dominant biome only) and across biome predictors were also examined.

The proportion of the variation explained in ant species density and abundance by spatial position and the environmental variables (abiotic and biotic) was determined using trend surface analysis and partial regression approaches (Legendre & Legendre, 1998). This was done for total species density and total abundance per site across the whole transect, then for total species density and total abundance in each site in Mountain Fynbos, and finally for the total abundance of the dominant myrmecochorous species separately collected at each site across the whole transect. Generalized Linear Models assuming a Poisson error distribution with a log link function (Type III model corrected for overdispersion) were used.

Following Legendre & Legendre (1998), trend surface analysis was first applied to determine the best-fit combination of spatial variables that contributed significantly to explaining the variation in the dependent variables. The spatial component of the variation in species density and abundance was modelled using a third-order polynomial that extracts linear and more complex spatial features (e.g. patches and gaps) from the data:

$$f(x, y) = b_0 + b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3,$$

where  $x$  and  $y$  are longitude and latitude respectively (Borcard *et al.*, 1992; Legendre, 1993). Generalized linear models were

then performed for the environmental variables on species density and abundance, and the best-fit model including only significant terms obtained [Legendre & Legendre, 1998; the only difference to the method was that we used generalized, rather than general, linear regression to accommodate the distribution of the dependent variables (see also McGeoch & Price, 2004)].

Thereafter, partial linear regression analyses were conducted in which the terms from the best-fit trend surface (spatial component) and environmental models were combined. Thus, the final model included both spatial and environmental terms, and was used to partition the explained variance (deviance) in species density and abundance into four components: (1) non-environmental spatial (the proportion of the variance explained by purely spatial components); (2) spatially structured environmental (the proportion of the variance explained by both spatial and environmental components); (3) non-spatial environmental (the proportion of the variance explained by environmental variables independent of any spatial structure); and (4) unexplained or residual variation (Legendre & Legendre, 1998). This procedure identifies the relative contribution of the environmental variables and spatial components to the explained variation in ant density and abundance, but it does not quantify the importance of individual variables (Legendre & Legendre, 1998; see also Lobo *et al.*, 2002; van Rensburg *et al.*, 2002).

To further understand the spatial structure in the selected environmental variables, spatial autocorrelation analysis (Moran's *I*: see Legendre & Fortin, 1989; Legendre & Legendre, 1998) and specifically SAAP V4.3 (Wartenberg, 1989) was used. Spatial correlograms based on 12 equal-frequency classes (i.e. same number of point pairs = 764) were used to graphically present the changes in the Moran's *I* coefficients (Legendre & Legendre, 1998). Overall significance of each correlogram was assessed with progressive Bonferroni correction and used to correct individual distance class *I* values for multiple comparisons (Wartenberg, 1989).

Canonical Community Ordination was used to relate the species composition of the assemblages to the environmental variables (CANOCO V4.5: ter Braak & Šmilauer, 2002). The relationship between ant assemblage structure within the different vegetation types and environmental variables was examined using redundancy analysis (RDA: ter Braak, 1994). The analysis was first conducted for assemblages in all six vegetation types together and then separately for those occurring in Mountain Fynbos. The species data were log<sub>10</sub>-transformed prior to analysis (Lepš & Šmilauer, 2003). A forward selection procedure of environmental variables was used to initially determine which of the variables significantly explained ant assemblage structure. The significance of each variable was judged using a Monte-Carlo permutation test (ter Braak, 1994). The model was then rerun with only significant explanatory variables to determine the percentage of assemblage variation accounted for by these variables. The results were displayed as biplots in which environmental variables are depicted as arrows and samples as symbols (Lepš & Šmilauer,

2003). Based on sample scaling, the length of the arrows indicates the relative importance of the environmental variables in explaining species composition of the samples and the arrows point in the expected direction of the steepest increase thereof (Lepš & Šmilauer, 2003). Species-sample relationships were also displayed as biplots to determine which species contribute to the differences between assemblages. Only those species with more than 30% of their variability explained by the ordination subspace were included in the biplots (Lepš & Šmilauer, 2003). Species are depicted as arrows with arrows pointing in the direction of steepest increase in abundance (Lepš & Šmilauer, 2003).

Dufrène & Legendre's (1997) Indicator Value Method was used to identify characteristic ant species for each vegetation type (based on hierarchical clustering) and altitudinal site (non-hierarchical clustering) (see McGeoch & Chown, 1998, for discussion). Using this method, measures of specificity (uniqueness to a site) and fidelity (frequency within that site) are combined for each ant species independently. An Indicator Value (IndVal) is then provided, as a percentage, for each species. A high indicator value indicates that a species has high fidelity and specificity to the site(s) within which it occurs and that it can be regarded as characteristic of that particular area. The significance of the IndVal measures for each species was tested using a random reallocation procedure of sites among site groups (Dufrène & Legendre, 1997). Species with significant IndVals greater than 70% (subjective benchmark, see van Rensburg *et al.*, 1999; McGeoch *et al.*, 2002) were then regarded as indicators of a particular site.

## RESULTS

### Species density, richness and abundance

In total, 85 ant species, representing 24 genera (72,379 individuals), were collected during the two sampling periods (see Appendix S2). Thirteen ant species were collected only in October 2002 while seven species were collected only during March 2003. Most species and genera belonged to the subfamily Myrmicinae (48 and 12 respectively), followed by the Formicinae (28 and 4 respectively) (see Appendix S1). The most speciose genera were *Camponotus* (20 species), *Tetramorium* (13 species) and *Monomorium* (12 species). Four myrmecochore species were sampled (see Appendix S2), although the ecological roles of species that could not be identified to the species level are not known.

Ericaceous Fynbos had the highest total species density, while the highest total abundance was found in Proteoid Fynbos (Table 1). Proteoid Fynbos also had the highest mean species density and abundance (Table 1). Strandveld and Alpine Fynbos had the lowest mean species density, and Alpine Fynbos had the lowest mean abundance (Table 1).

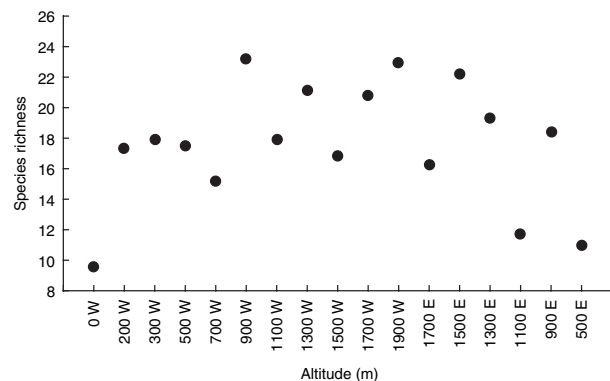
Sample-based species rarefaction curves approximated asymptotes for the two sampling periods indicating that most of the species at the different sites were collected (see Appendix S3). In most cases the rarefaction curves and

**Table 2** The number of species observed in the pooled samples ( $S_{\text{obs}}$ ), Incidence-based Coverage Estimator of species density (ICE) and the Michaelis–Menten richness estimator ( $MM_{\text{mean}}$ ) of the sample-based rarefaction curves

Sites (m a.s.l.)	$S_{\text{obs}}$	ICE ( $\pm$ SD)	$MM_{\text{mean}}$
Western slope			
0	14	15.56 $\pm$ 0.00	14.04
200	23	24.94 $\pm$ 0.01	23.17
300	35	41.74 $\pm$ 0.02	35.07
500	14	15.75 $\pm$ 0.02	13.23
700	28	29.29 $\pm$ 0.01	28.88
900	24	25.55 $\pm$ 0.01	24.84
1100	22	26.26 $\pm$ 0.01	21.62
1300	27	29.64 $\pm$ 0.01	28.46
1500	19	19.57 $\pm$ 0.00	20.44
1700	21	21.35 $\pm$ 0.00	22.48
1900	23	26.79 $\pm$ 0.01	27.94
Eastern slope			
1700	19	29.96 $\pm$ 0.02	18.23
1500	25	36.21 $\pm$ 0.01	25.47
1300	21	22.24 $\pm$ 0.00	23.87
1100	21	25.40 $\pm$ 0.02	21.15
900	24	25.55 $\pm$ 0.00	24.84
500	14	15.75 $\pm$ 0.02	13.23

estimators converged closely at the highest observed species density for each site. Species density estimates for each of the sites are thus considered representative (Table 2). However, this was not the case for the 300-m site on the western slope and the 1500-m site on the eastern slope. The reason for the substantial difference between the observed and ICE values was the relatively high number of singletons and doubletons. Although we have no explanation for these exceptions, they should be kept in mind throughout.

Individual-based rarefaction curves showed that, when the curves of the different altitudinal bands are rarefied to the lowest number of individuals collected at a site (1900 m, 670 individuals), the highest species richness (23 species) was recorded at 900 m on the western slope and at the summit (Fig. 2). The lowest number of species was recorded at sea level

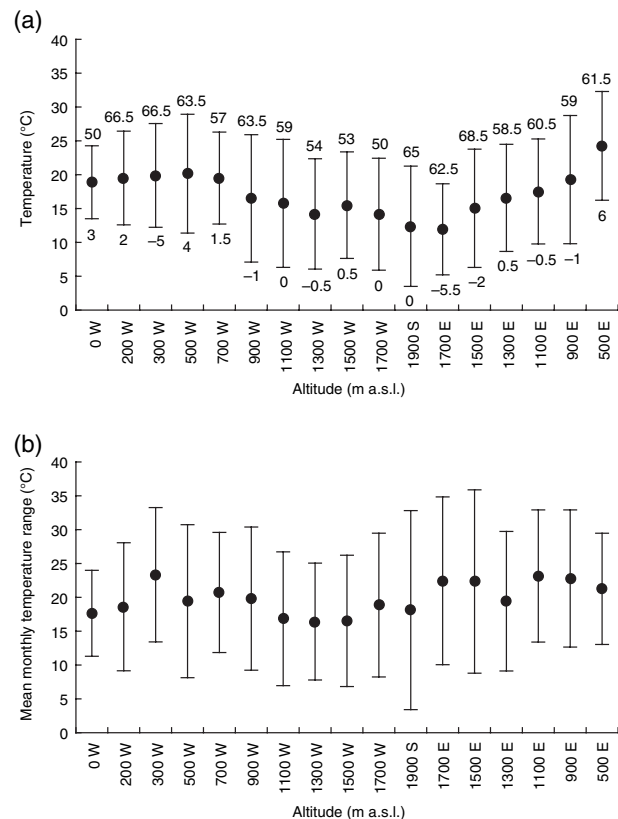


**Figure 2** Species richness values derived from individual-based species accumulation curves of ant assemblages across the different altitudinal bands.

(10 species), followed by the 500- and 1100-m altitudinal bands on the eastern slope (11 species) (Fig. 2).

Species richness across the entire transect was significantly related to available area ( $\chi^2 = 9.86$ ,  $P = 0.001$ ,  $R^2 = 38.72$ , scaled deviance = 15.53, d.f. = 16, estimate =  $+0.0002 \pm 6.5 \times 10^{-5}$ ). There was no relationship between species density across the whole transect and the available area ( $\chi^2 = 0.28$ ,  $P = 0.60$ ,  $R^2 = 1.38$ ; scaled deviance = 20.45, d.f. = 16). Within Mountain Fynbos, species density was significantly related to area ( $\chi^2 = 14.03$ ,  $P < 0.001$ ,  $R^2 = 51.99$ ; scaled deviance = 12.21, d.f. = 14), but with a negligible slope. There was no relationship between species richness and available area ( $\chi^2 = 0.67$ ,  $P = 0.41$ ,  $R^2 = 4.70$ , scaled deviance = 7.47, d.f. = 14).

The set of abiotic variables (six temperature and 15 soil parameters, altitude and available area) was reduced to 12 that were used in all subsequent analyses (see Appendix S4). Four of the six temperature variables were selected: mean monthly temperature, mean monthly temperature range, absolute monthly maximum and absolute monthly minimum temperature. The highest mean temperature was found at Wupperthal (500 m on the Eastern slope) and the lowest on the summit (Fig. 3a). The highest absolute maximum temperature was 68.5 °C (1500 m on the eastern slope) and the absolute minimum was –5.5 °C (1700 m on the eastern slope)



**Figure 3** (a) Mean monthly temperature, absolute maximum and absolute minimum temperatures and (b) mean temperature range for the different sites.

(Fig. 3a). The mean monthly temperature range was lowest between 1100 and 1500 m on the western slope (Fig. 3b).

Seven soil parameters were selected for analyses of which five were chemical (pH, conductivity, P, C, NO<sub>3</sub>; Appendix S5) and two were structural (proportion of clay and silt; see Appendix S5) components. Available area was included in the set of abiotic variables, but the abiotic variables were highly correlated with altitude and this variable was thus not used in further analyses (see Appendix S4).

Collinearity in the biotic variables was removed by excluding two variables (proportion of exposed rock and maximum vegetation height) (see Appendix S4). The vegetation variables that were used in all subsequent analyses were therefore: proportion of ground covered by litter and vegetation; proportion of bare ground; and the average total number of hits per sample point (TOTHTS) (see Appendix S5). Post-fire vegetation age in Mountain Fynbos was added as a biotic variable to the analyses of the species density and abundance of ants within Mountain Fynbos.

Total species density of ants per site across the whole transect was significantly related to six environmental variables (Table 3). However, after controlling for spatial position, no environmental variables remained significant in the model. A similar result was found for species density of ants in Mountain Fynbos (Table 3). This outcome is a consequence of considerable spatial structure in the environmental variables, as is indicated by the relatively high proportion of variance explained by the spatially structured environmental component (Table 3) and the autocorrelation structure of the environmental variables (Fig. 4). In other words, the high degree of spatial structure shared by species density and the environmental component suggests in this case that the environmental variables might be responsible for variation in species density. By contrast, several of the environmental variables remained significant in the models for variation in total abundance per site, across the whole transect and for Mountain Fynbos (Table 3). Thus, the proportion of variance explained by the pure environmental components was higher than the variance explained by pure spatial components in the case of the abundance of ants occurring in Mountain Fynbos (Table 3). Nonetheless, a large proportion of the explained variance in abundance was again due to the spatially structured environmental component (Table 3). The abundance of ants across the whole transect was positively related to mean monthly temperature range and negatively to absolute maximum monthly temperature (Table 3). The abundance of Mountain Fynbos ants was negatively related to absolute maximum monthly temperature and vertical complexity of the vegetation, and positively related to the proportion of litter (Table 3). Neither the density nor the abundance of ants in Mountain Fynbos was significantly related to post-fire vegetation age.

### Myrmecochores

The abundances of the four myrmecochorous ant species were related to different spatial and environmental variables in each

case, and the overall variance explained varied considerably between the species. Generally, the spatially structured environmental component did not explain the largest proportion of the variance in the abundance of these species, and large proportions of the variance in abundance were explained by pure environmental components (Table 3). The abundance of *Anoplolepis* sp. (cf. *custodiens*) was negatively related to the proportion of bare ground, while the abundance of *Anoplolepis* sp. (cf. *steinergroeveri*) was negatively related to clay and positively to litter (Table 3). The abundance of *C. niveosetosus* was positively related to area, but declined with increasing mean monthly temperature range and absolute maximum temperature, as well as with increasing pH and vegetation complexity. By contrast, the abundance of *T. quadrispinosum* increased with area, mean monthly temperature range, and maximum temperature, but declined with increasing absolute minimum temperature (Table 3).

### Assemblages

The first canonical axis in the RDA biplot (Fig. 5a) explained 29.7% of the sample–environment relation across the whole transect ( $F = 9.585$ ,  $P = 0.002$ ) and the first and second axes together explained 41.8%. Twelve of the environmental variables contributed significantly to the variance explained in the ant assemblages (Table 4). The first axis represents an environmental gradient of increasing mean monthly temperature, absolute maximum monthly temperature, mean monthly temperature range, percentage bare ground and vertical complexity of the vegetation, and decreasing carbon content, nitrogen content and vegetation cover (Table 4, Fig. 5a). The second axis represents increasing absolute minimum monthly temperature and area (Table 4, Fig. 5a). Mean monthly temperature was the most important environmental variable explaining variance in assemblage structures (Table 4, Fig. 5a). Eight species had more than 30% of their variability explained by the ordination subspace across the whole transect (Fig. 5b). Five of these species were identified as species that are characteristic of particular vegetation types (see Table 5). One of these (*Myrmecaria* sp. 1) explained the difference between assemblages in Strandveld and the other vegetation types, even though this species was not identified as characteristic of this biome (see Discussion below). Two species that were characteristic of Restioid and Proteoid Fynbos (*Camponotus mystaceus* and *Pheidole* sp. 2), contributed substantially to the differences between these two vegetation types and the other vegetation types.

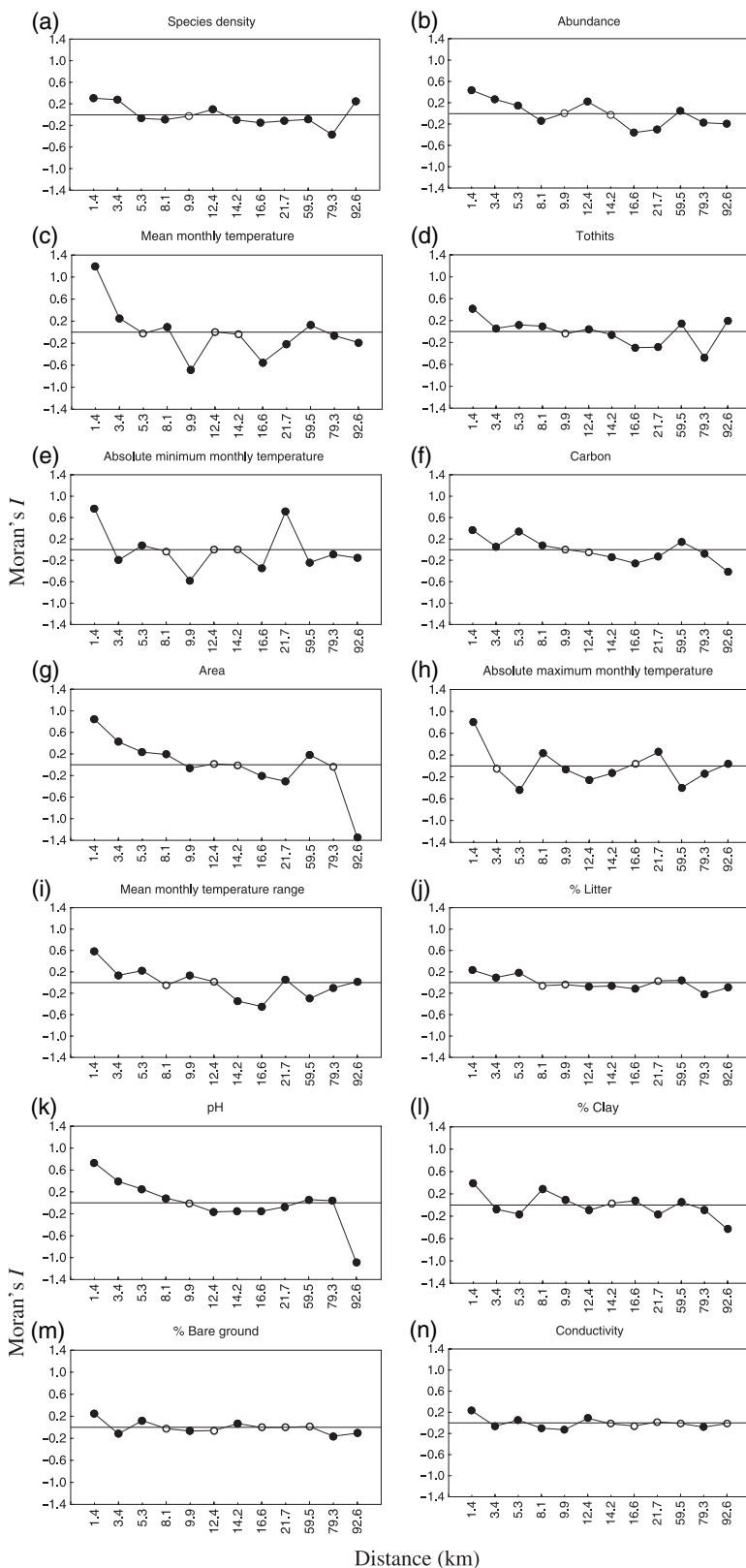
Within Mountain Fynbos, the first canonical axis in the RDA biplot (Fig. 6a) explained 36.5% of the relationship between assemblages and the environmental variables ( $F = 10.002$ ,  $P = 0.002$ ), and the first and second axes together explained 51.6%. Ten environmental variables significantly explained the variation in assemblage structure of ants occurring in Mountain Fynbos (Table 4). Available area was the environmental variable that explained most of the variance in assemblage structure (Table 4). The first axis of the RDA



**Table 3** Generalized linear model (Poisson error distribution, log link function, Type III model corrected for overdispersion) outcomes for the relationships between spatial terms plus environmental variables on species density and abundance of ant assemblages across the transect and within Mountain Fynbos, and on the abundance of myrmecochorous ants. Estimates are given in brackets. (a) Non-environmental spatial component, (b) spatially structured environmental component and (c) non-spatial environmental component

Model	d.f.	Dev	Selected environmental terms	Spatial terms	Percentage deviance explained		
					(a)	(b)	(c) Total
Species density							
Whole transect	123	136.57	Area (+0.0002), MM <sub>temp</sub> (+0.038), A <sub>min</sub> (−0.0002), MM <sub>range</sub> (−0.0007), P (−0.004), TOTHTS (+0.006)	$x$ (−0.654), $x^2$ (+25.359**), $y^2$ (+183.589*), $xy$ (−44.283), $x^2y$ (+591.665**), $xy^2$ (−1897.87**), $x$ (−1.414), $x^3$ (+12.494), $y^2$ (+128.909*), $y^3$ (−1383.730**), $y$ (−6.223), $x$ (−15.932**), $x^2$ (−52.818), $x^3$ (−111.928), $y^2$ (−493.514), $y^3$ (−2969.520), $x^2y$ (+632.357)	8.26	27.31	2.50 38.07
Mountain Fynbos	111	103.16	MM <sub>temp</sub> (+0.011), pH (+0.219), P (−0.004), BG (−0.284)	$x$ (−1.414), $x^3$ (+12.494), $y^2$ (+128.909*), $y^3$ (−1383.730**), $x$ (−16.335), $x^2$ (+140.292), $y^2$ (+891.478), $y^3$ (+3404.883), $xy$ (−319.695), $x^2y$ (+3278.270), $xy^2$ (−10421.800)	6.37	24.66	5.18 36.21
Total abundance							
Whole transect	115	97.23	MM <sub>temp</sub> (−0.174), MM <sub>range</sub> (+0.338*), A <sub>min</sub> (+0.140), A <sub>max</sub> (−0.104*), pH (+0.156), Cond (+0.005), P (+0.003), C (−6.341), Clay (+7.467), Silt (+6.061), Litter (+1.170), Vegcover (+0.266), TOTHTS (−0.021)	$y$ (−6.223), $x$ (−15.932**), $x^2$ (−52.818), $x^3$ (−111.928), $y^2$ (−493.514), $y^3$ (−2969.520), $x^2y$ (+632.357)	13.46	42.61	7.68 63.75
Mountain Fynbos	97	84.00	Area (+0.001), MM <sub>temp</sub> (−0.168), MM <sub>range</sub> (+0.342), A <sub>min</sub> (+0.229), A <sub>max</sub> (−0.146*), pH (−0.091), P (+0.002), C (−14.557), NO <sub>3</sub> (−0.016), Clay (+8.430), Silt (+7.970), Litter (+3.295**), Vegcover (+1.324), TOTHTS (−0.054*), Age (−0.006)	$x$ (−16.335), $x^2$ (+140.292), $y^2$ (+891.478), $y^3$ (+3404.883), $xy$ (−319.695), $x^2y$ (+3278.270), $xy^2$ (−10421.800)	6.86	49.86	12.97 69.69
Myrmecochores							
<i>Anoplolepis</i> sp. (cf. <i>custodiens</i> )	78	66.79	BG (−3.454**)	$y$ (−2043.890*), $x$ (−4503.426*), $x^2$ (−48464.000*), $x^3$ (−170927.500*), $y^2$ (−7554.100), $xy$ (+42677.060), $x^2y$ (−216134.000*), $xy^2$ (+65857.380)	22.79	6.48	10.94 40.21
<i>Anoplolepis</i> sp. (cf. <i>steinergroeveri</i> )	39	15.13	A <sub>max</sub> (−0.682), pH (−3.587), C (−210.753), Clay (−205.990**), Litter (+6.642*)	$y^3$ (−29548.100), $xy$ (+547.597), $xy^2$ (+11568.820)	2.93	31.57	41.70 76.20
<i>Camponotus nivosus</i>	65	92.69	Area (+0.006***), MM <sub>temp</sub> (−1.221***), A <sub>max</sub> (−0.115*), pH (−3.004***), TOTHTS (−0.228**)	$y$ (+7.726)	2.20	3.58	24.82 30.60
<i>Tetramorium quadrispinosum</i>	91	87.94	Area (+0.003**), MM <sub>temp</sub> (+0.849**), A <sub>max</sub> (+0.124*), A <sub>min</sub> (−0.349***), Cond (−0.001***), P (+0.011), C (−56.324**)	$y$ (−15.687), $x^2$ (−53.962), $xy$ (+177.411), $x^2y$ (−513.919), $xy^2$ (+1258.633)	3.53	32.34	20.97 56.84

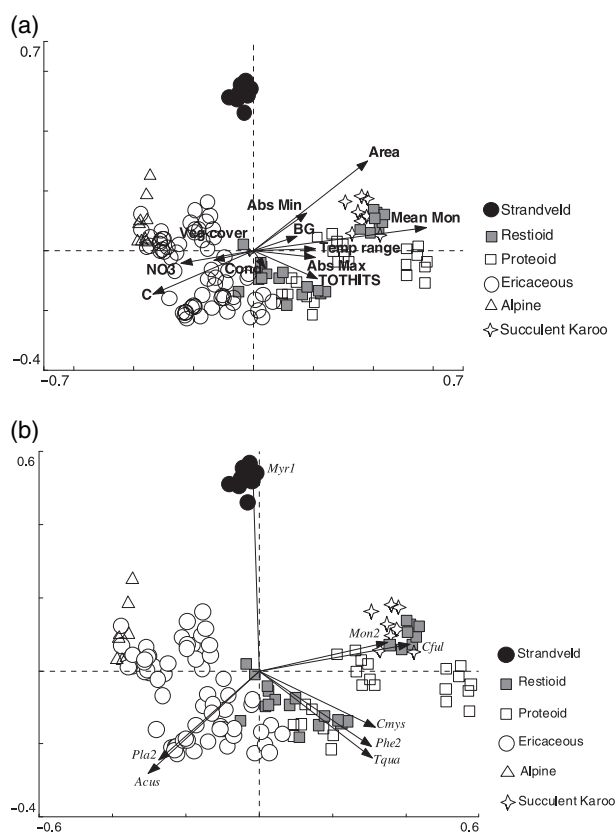
Dev, Deviance; A<sub>min</sub>, absolute minimum monthly temperature; A<sub>max</sub>, absolute maximum monthly temperature; BG, bare ground; Cond, conductivity; MM<sub>temp</sub>, mean monthly temperature; MM<sub>range</sub>, mean monthly temperature range; Vegcover, percentage vegetation cover; TOTHTS, vertical complexity of vegetation. \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.01$ .



**Figure 4** Spatial structure in species density and abundance, and the environmental variables that significantly explain the variance in species density and abundance. The correlograms were based on 12 equal-frequency classes (i.e. same number of point pairs = 764). Overall significance of each correlogram was assessed with progressive Bonferroni correction and used to correct individual distance class  $I$  values for multiple comparisons (Wartenberg, 1989). Significant Moran's  $I$  values (coefficient of autocorrelation) are indicated by closed circles.

biplot of samples vs. environmental variables represents an environmental gradient of increasing pH, mean monthly temperature, mean monthly temperature range, area and post-fire vegetation age. It further represented decreasing

carbon content and percentage silt in the soil (Table 4, Fig. 6a). The second axis represents increasing absolute minimum monthly temperature and percentage clay in the soil (Table 4, Fig. 6a). Ten species had more than 30% of their



**Figure 5** RDA ordination (biplot, sample scaling) of (a) the ant assemblages occurring in the different vegetation types across the whole transect in relation to the environmental variables and (b) the ant assemblages and species with more than 30% of their variability explained by the ordination subspace. *Acus* = *Anoplolepis* sp. (cf. *custodiens*), *Phe2* = *Pheidole* sp. 2, *Plagiopolepis* sp. 1, *Tqua* = *Tetramorium quadrispinosum*, *Mon2* = *Monomorium* sp. 2, *Myr1* = *Myrmecaria* sp. 1, *Cful* = *Camponotus fulvopilosus*, *Cmys* = *C. mystaceus*.

variability explained by the ordination subspace within Mountain Fynbos (Fig. 6b). Three of these species were identified as characteristic of Fynbos vegetation types (*Monomorium fridae*, *Pheidole* sp. 2 and *Camponotus mystaceus* – Restioid and Proteoid Fynbos) and three were characteristic of Succulent Karoo (*Tetramorium quadrispinosum*, *Ocymyrmex* sp. 1 and *Monomorium* sp. 2) (see Table 5).

### Indicator species

The IndVal analyses revealed that nine species were characteristic of certain vegetation types, of which six were specific to Succulent Karoo and one to Strandveld (Table 5). There were no species that could be regarded as characteristic of any of the four Mountain Fynbos vegetation types (Table 5), however two species were identified as characteristic of both Proteoid and Restioid Fynbos (Table 5). One species (*Myrmecaria* sp. 1) was restricted to Strandveld, but was not identified as specific to the biome. This species had a patchy distribution and was found in relatively low abundance, which translates into a low

**Table 4** Significant species–environment correlation coefficients ( $R$ -values, ter Braak & Šmilauer, 2002) from redundancy analysis (RDA). The significance of the  $R$ -values was determined using Monte Carlo permutation tests ( $P$  = significance and  $F$  = test statistic). Eigenvalues indicate the additional variance explained by each variable. Axes 1 and 2 are the first two ordination axes of the biplots of samples and environmental variables. A negative  $R$ -value reflects gradient direction in the RDA ordination

Variable	Eigenvalues	<i>P</i>	<i>F</i>	<i>R</i>	
				Axis 1	Axis 2
<b>Whole transect</b>					
MM <sub>temp</sub>	0.06	0.002	8.32	0.852*	0.176*
Area	0.03	0.002	3.92	0.564*	0.678*
<i>A</i> <sub>max</sub>	0.02	0.002	3.45	0.304*	−0.054
TOTHITS	0.02	0.002	3.40	0.315*	−0.218*
<i>A</i> <sub>min</sub>	0.02	0.002	2.92	0.264*	0.289*
Temperature range	0.03	0.002	3.85	0.306*	0.012
Bare ground	0.01	0.002	2.69	0.215*	0.109
Conductivity	0.02	0.002	2.09	0.057	−0.138
C	0.01	0.002	1.78	−0.497*	−0.338*
NO <sub>3</sub>	0.01	0.014	1.56	−0.359*	−0.104
Vegetation cover (%)	0.01	0.012	1.45	−0.197*	−0.081
Sum of all canonical eigenvalues: 0.24					
<b>Mountain Fynbos</b>					
Area	0.08	0.002	9.66	0.926*	−0.262*
MM <sub>temp</sub>	0.02	0.002	3.75	0.884*	0.145
pH	0.03	0.002	3.39	0.648*	0.225*
Temperature range	0.02	0.002	2.37	0.256*	−0.214*
Vegetation age	0.01	0.002	2.29	0.256*	0.061
<i>A</i> <sub>min</sub>	0.02	0.002	1.91	0.159*	0.254*
C	0.01	0.002	2.13	−0.501*	−0.024
Vegetation cover (%)	0.02	0.002	2.19	−0.115	−0.060
Clay	0.01	0.008	1.48	−0.178*	0.354*
Silt	0.01	0.016	1.51	−0.566*	0.478*
Sum of all canonical eigenvalues: 0.23					

A<sub>min</sub>, absolute minimum monthly temperature; A<sub>max</sub>, absolute maximum monthly temperature; MM<sub>temp</sub>, mean monthly temperature.

\* $R$ -values that are significant at the table-wide level of  $\alpha = 0.05$ .

fidelity of the species to the biome (see Dufrène & Legendre, 1997). Therefore the species was not identified as specific to the biome using Dufrène & Legendre's (1997) Indicator Value Method.

Furthermore, nine species were identified as characteristic of certain altitudes, and three of these were characteristic of a range of altitudes spanning more than one vegetation type (Table 5). Two species identified as characteristic of particular altitudes and vegetation types [*Anoplolepis* sp. (cf. *custodiens*) and *T. quadrispinosum*] are myrmecochores.

### DISCUSSION

The number of ant species collected in Proteoid Fynbos here (48 species) is comparable to that of other studies conducted in the same vegetation type (Donnelly & Giliomee, 1985;

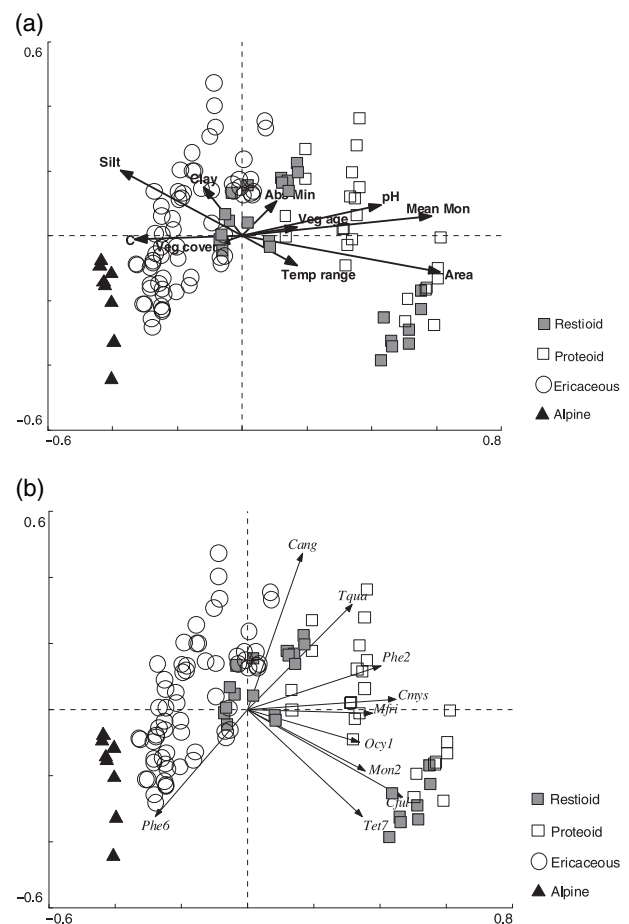
**Table 5** Percentage indicator values (IndVal > 70%) of ant species for each vegetation type (hierarchical clustering) and altitudinal band (non-hierarchical clustering)

Vegetation type/altitude	Species	% IndVal
<b>Vegetation type</b>		
Succulent Karoo	<i>Pheidole</i> sp. 1	98.66*
	<i>Monomorium</i> sp. 2	95.31*
	<i>Tetramorium quadrispinosum</i>	80.39*
	<i>Tetramorium</i> sp. 6	72.82*
	<i>Messor</i> sp. 1	72.29*
	<i>Ocymyrmex</i> sp. 1	71.73
Strandveld	<i>Technomyrmex</i> sp. 1	79.99*
Proteoid and Restioid	<i>Camponotus mystaceus</i>	81.63*
Fynbos	<i>Pheidole</i> sp. 2	80.33*
<b>Altitude</b>		
0–900 (W) m	<i>Monomorium fridae</i>	87.27*
	<i>Lepisiota</i> sp. 1	72.05
1100 (W)–1700 (W) and 900 (E)–1700 (E) m	<i>Anoplolepis</i> sp. (cf. <i>custodiens</i> )	73.75*
1900 m (Summit)	<i>Camponotus</i> sp. 1	96.37*
	<i>Meranoplus</i> sp. 1	90.00*
500 m (E)	<i>Pheidole</i> sp. 1	98.61*
	<i>Monomorium</i> sp. 2	95.17*
	<i>Tetramorium quadrispinosum</i>	79.89*
	<i>Ocymyrmex</i> sp. 1	71.08

\*Maximum IndVal values. W, western slope; E, eastern slope.

Schlettwein & Giliomee, 1987; Koen & Breytenbach, 1988). However, by comparison with ant assemblages in many other Southern African regions, with the exception of the arid Nama Karoo, total species (85) and generic (24) richness recorded in this study were low (Samways, 1983, 1990; Milton *et al.*, 1992; Swart *et al.*, 1999; Lindsey & Skinner, 2001; Parr *et al.*, 2002, 2004). These results suggest that ant species richness in the Cederberg (and in the Fynbos biome in particular) is intermediate between that of high-energy savanna environments and lower energy arid ecosystems in southern Africa. This would appear to be in keeping with large-scale patterns of variation in richness of other animals in southern Africa such as birds (van Rensburg *et al.*, 2002) and frogs (Minter *et al.*, 2004). It also suggests that ants are responding to energy availability in this region, as has been recorded elsewhere (Kaspari *et al.*, 2004), though broader scale studies will be necessary to confirm this idea.

In terms of local-scale variation in ant species density, and abundance, firmer conclusions can be reached. In the former case, much of the variation between sites was explained by spatially structured environmental variation, which was perhaps not surprising given the strong spatial gradient in the environmental variables (Fig. 4). In other words, strong spatial variation in a variable such as temperature is probably responsible for strong spatial variation in the dependent variable. Thus, variation in species density explained by the non-spatially structured environmental component only tends to be low. Such an outcome is typical of studies undertaken



**Figure 6** RDA ordination (biplot, sample scaling) of (a) the ant assemblages occurring in the different vegetation types within Mountain Fynbos in relation to the environmental variables and (b) the ant assemblages and species with more than 30% of their variability explained by the ordination subspace. *Cful* = *C. fulvopilosus*, *Cmys* = *C. mystaceus*, *Cang* = *C. angusticeps*, *Mon2* = *Monomorium* sp. 2, *Mfri* = *M. fridae*, *Phe2* = *Pheidole* sp. 2, *Phe6* = *Pheidole* sp. 6, *Ocy1* = *Ocymyrmex* sp. 1, *Tet7* = *Tetramorium* sp. 7, *Tqua* = *T. quadrispinosum*.

over strong environmental gradients, although it is generally more characteristic of regional scale investigations (Borcard *et al.*, 1992; Smith, 1994; Lobo *et al.*, 2002; van Rensburg *et al.*, 2002; McGeoch & Price, 2004). It has been suggested that if the residuals from a model including environmental variables only show no spatial structure, then the analysis can proceed without the inclusion of the spatial variables (Diniz-Filho *et al.*, 2003). However, this still leaves the problem of incorrect degrees of freedom in the model, which might lead to biased conclusions (see Lennon, 2000, for discussion). Therefore, we did not adopt the approach of residual inspection here. Rather we recognize that strong spatial variation in area, mean monthly temperature range and mean monthly temperature are strong correlates with species density, with density tending to increase with area and with mean monthly temperature. These findings are in keeping with species energy theory (see Wylie & Currie, 1993; Rosenzweig, 1995; Hawkins *et al.*, 2003;

Evans *et al.*, 2004), and with results from investigations of ants, other insects and ectotherms more generally (Turner *et al.*, 1987; Kerr & Packer, 1999; Allen *et al.*, 2002; Kaspari *et al.*, 2004). However, variation in precipitation, which is apparently considerable across the transect (Cowling & Holmes, 1992 provide a qualitative estimate of rainfall variation for a nearby transect, but no quantitative data are available), may also have a substantial influence on variation in species density, thus accounting for the generally low total variance explained in our models. Indeed, Hawkins & Porter (2003) found that actual evapotranspiration was the primary explanatory variable for variation in butterfly species richness. Moreover, in water-limited systems such as those of the southwestern Cape (Deacon *et al.*, 1992), water availability is much more likely to be a strong correlate of richness than is absolute energy availability (O'Brien *et al.*, 2000; Hawkins *et al.*, 2003). Linder (1991) found this to be the case for plant species richness in the southwestern Cape, for which rainfall was the best predictor of species richness of several plant taxa typical of the Cape flora.

Variation in total abundance also had a pronounced spatially structured environmental component, for the same reasons as those discussed above. Increases in total abundance were strongly related to an increase in mean monthly temperature range and a decline in absolute maximum temperature, and in the Fynbos only were also positively related to increasing litter and declining vegetation complexity. Ant abundance and richness have been shown to vary considerably with temperature in several other studies (see Andersen, 1995; Parr *et al.*, 2005). In general, abundance and richness increase with an improvement in habitat quality, which is often associated with increasing temperature (e.g. Andersen, 1995; Cerdá *et al.*, 1998; Bestelmeyer, 2000) and then decline as habitats become more stressful (but see also Parr *et al.*, 2005). Several other studies have also found relationships between ant abundance and litter availability and vegetation complexity. For example, Bestelmeyer & Wiens (1996) found that species richness was dramatically greater in areas with higher litter load, but only in the dry season. They argued that the increased leaf litter development might buffer the ant assemblages against a decline in the habitat suitability (e.g. dryer conditions). Furthermore, Robertson (1999) found that reduced litter cover (as a result of fire) might result in a loss of cryptic species (but see also Lassau & Hochuli, 2004).

An important difference between the models for species density and those for abundance was the considerably greater proportion of the variation in the latter explained by the full model (64–70%) in comparison with the former (36–38%). Why this should be the case is not entirely clear. However, the relationship between ant abundance (and especially the dominant ants) and species richness is typically unimodal (Andersen, 1992; Parr *et al.*, 2005). Thus, species richness (or density) can be low at both low and high abundances. If the pattern is driven even partly by a combination of environmental stress and competition, which might well be the case (Parr *et al.*, 2005), then the environment will appear to have a

larger linear influence on abundance than on richness, so resulting in a greater proportion of the variance being explained in linear models of the former, than of the latter. This is precisely what we find.

Time since the most recent fire was never included as a significant variable in the models for variation in species density and abundance. It was likewise unimportant in explaining differences between ant assemblages across the sites. Although these results are in keeping with a well-replicated experimental investigation of ant assemblage responses to fire in a southern African savanna system (Parr *et al.*, 2004), they contrast strongly with several other studies (Andersen & Yen, 1985; Andersen, 1991; Parr *et al.*, 2002; Hoffman & Andersen, 2003), including one on Fynbos ant assemblages (Donnelly & Giliomee, 1985). These differences may well be a consequence of the methods used, and certainly this study did not attempt to investigate post-fire age in a well-replicated explicit fashion (see Parr & Chown, 2003, for discussion). Rather, time since fire was included as a variable in the initial models and was never found to be significant. An explicit focus on time since fire, whilst holding other variables more constant in an appropriate experimental design, might well reveal the effects of post-fire vegetation age on ant assemblages. Alternatively, it may turn out that like the ant assemblages in the fire-prone system studied by Parr *et al.* (2004), those studied here may also be responsive only to whether the vegetation has burnt or not, rather than the subtleties of the burning regime, owing to considerable resilience and resistance born of a long-term exposure to a fire climax system (see Cowling, 1992, for a discussion of fire in Fynbos systems). Carefully replicated work will be required to distinguish these alternatives.

By contrast, temperature, area and several vegetation variables contributed significantly to the separation of the assemblages in the major vegetation types and biomes. These results are not surprising given that temperature and vegetation structure (including proportion of bare ground) have been found to be strong correlates of variation in ant assemblages in a variety of other studies. For example, Andersen (1986) found that ant assemblages were more diverse in Australian woodland, which represents greater structural complexity in terms of vegetation and litter (i.e. less bare ground), compared with the less structurally diverse heath. Furthermore, Perfecto & Vandermeer (1996) indicated that there is significant diversity loss in ground-foraging ant assemblages when the vegetation is altered in such a way as to reduce shade and litter. However, they argued that this loss in diversity is rather a consequence of indirect (alterations in species interactions) than direct effects of habitat modifications (Perfecto & Vandermeer, 1996). Gotelli & Ellison (2002) showed that ant density in New England bogs and forests was related to vegetation complexity (and light availability), with higher density (and subsequently higher species richness) in the more complex forests, while Parr *et al.* (2004) showed that bare ground and litter cover best explained overall patterns in ant diversity in an *Acacia* savanna in the Kruger National Park.

In addition, Lassau & Hochuli (2004) found that ant assemblages in open habitats (which are generally hotter and drier) support a larger suite of opportunists, generalists and hot climate specialists than those in more complex habitats.

Perhaps of most significance is the fact that these strong relationships between temperature and vegetation variables, and ant assemblage structure, suggest that climate change in this region will affect ant assemblages in two ways. First, alterations in climate such as the increase in temperature and increase in variability of temperature predicted for the region (Tyson, 1999; Giorgi *et al.*, 2001; Midgley *et al.*, 2002, 2003) will almost certainly push assemblages from left to right on Fig. 5 if these correlates have a causal basis: that is, higher altitude assemblages such as those typical of Alpine and Ericaceous Fynbos will slowly give way to those more characteristics of Proteoid and Restioid Fynbos, and ultimately Succulent Karoo. In other words, high-altitude assemblages are likely to disappear, and along with them their characteristic species (*Camponotus* sp. 1, *Meranoplus* sp. 1: see Table 6). Secondly, changes in vegetation associated with alterations in temperature and water availability, an important driver of vegetation characteristics in the region (see Linder, 1991; Cowling & Holmes, 1992), are likely to exacerbate these changes owing to direct responses of ants to changes in vegetation cover and soil carbon. It has been shown that organic soil carbon and nitrogen decrease rapidly with an increase in temperature and decreasing precipitation in semi-arid soils (see Smith *et al.*, 2002; Link *et al.*, 2003). Such a reduction in organic matter can affect chemical, physical and biological properties of soil, which in turn contribute to ecosystem function and stability (Link *et al.*, 2003). Moreover, such changes, especially in organic carbon, will ultimately affect plant distributions, which in turn will affect the ant assemblages.

The predicted changes are very much in keeping with those for other insect assemblages in montane regions, where the higher elevation assemblages are at most risk (Haslett, 1997; Fleishman *et al.*, 1998, 2000; Hill *et al.*, 2002). They are also in keeping with predictions of vegetation change for the region, which suggest that only the higher elevations will support Fynbos, whilst the others will become more karroid, as was perhaps the case for other areas in the region that have altered from Fynbos to karroid vegetation as the region has dried out (Deacon *et al.*, 1992). Of course, the changes are likely to be influenced by sharp discontinuities in geology and soil type, as is clearly the case on the eastern edge of the study site where a sharp boundary exists between Fynbos and Succulent Karoo associated with a transition from Table Mountain Sandstone changing to shale (see Cowling & Holmes, 1992; Cowling *et al.*, 1997; Milton *et al.*, 1997; Lechmere-Oertel & Cowling, 2001) and on the western edge where dune sand and Table Mountain Sandstone abut, but the vegetation (Strandveld and Fynbos) and ant assemblages differ considerably.

Because of the functional importance of ants in Fynbos ecosystems as myrmecochores (Westoby *et al.*, 1982; Bond & Slingsby, 1983; Slingsby & Bond, 1985; Breytenbach, 1988;

Hanzawa *et al.*, 1988; Handel & Beattie, 1990; Johnson, 1992; Le Maitre & Midgley, 1992; Midgley & Bond, 1995), there is unlikely to be a unidirectional influence of changing climate on vegetation and then on ants. Rather, the changing climate will directly affect ant assemblages, and will indirectly affect them via plant responses to climate. In turn, changes in the ant assemblages are also likely to affect the ways in which seeds are dispersed owing to differential responses of myrmecochorous species. For example, the abundance of *Camponotus niveosetosus* was negatively related to mean monthly temperature, absolute maximum temperature and vegetation structural complexity, reflecting its numerical dominance at sites from 1300 to 1700 m. By contrast, the abundance of *Tetramorium quadrispinosum* covaried positively with mean monthly temperature and absolute maximum temperature reflecting its predominance at lower altitude (200–1300 m) sites. Increases in temperature in the region are thus likely to mean replacement of the former with the latter species.

Likewise, *Anoplolepis* sp. (cf. *steinergroeveri*), which was collected only at low-altitude sites (200–900 m), was positively related to litter and negatively to clay, reflected by its absence from Succulent Karoo. By contrast, *Anoplolepis* sp. (cf. *custodiens*) was collected at higher altitudes (900–1700 m) and had a negative relationship with bare ground. The altitudinal distribution of the two species only overlapped at 900 m on the western slopes. Both of these *Anoplolepis* species have previously been collected in the same areas, with *Anoplolepis* sp. (cf. *steinergroeveri*) being numerically much less dominant (Linsey & Skinner, 2001), as is the case here. However, *Anoplolepis* sp. (cf. *custodiens*) is present throughout Africa (Prins, 1963) even though it has been hailed as one of the most dominant myrmecochores in the southwestern Cape (e.g. Midgley & Bond, 1995), and it is thus unlikely that this generalist species will be severely affected by climate change.

What these predicted changes are likely to mean for myrmecochory is difficult to determine in the absence of more thorough experimental work. Several studies have indicated that although myrmecochorous plants are clearly adapted to ant dispersal, ants have not evolved any particular trait (either morphological or behavioural) in response (Johnson, 1992; Midgley & Bond, 1995). Furthermore, seeds of myrmecochorous plants have very few physical structures that restrict their dispersal to specific ant species (Johnson, 1992; Midgley & Bond, 1995; see also Wheelright & Orians, 1982). Perhaps it is therefore unlikely that the displacement of one myrmecochorous species by another would affect seed dispersal. However, it has also been postulated that seed size plays a role in restricting the dispersal of large seeds by small ant species (Pudlo *et al.*, 1980; Drake, 1981; Bond & Slingsby, 1983; Auld, 1986; Johnson, 1992; Witt & Giliomee, 2004). In addition, germination of seeds may be a function of burial depth (Brits, 1987; Bond *et al.*, 1990). If different ant species have different seed gallery depths then the success of germination might be related to the ant species involved in dispersal of the seeds. Therefore, despite an apparent lack of

specialization amongst myrmecochores for some seed traits, their changing relative abundances and differences in behaviour and seed-size preference could influence ecosystem functioning. Such a transformation in functioning would mean that conservation plans that seek to incorporate long-term change in the region (e.g. Cowling & Pressey, 2003; Driver *et al.*, 2003; Younge & Fowkes, 2003) might have underestimated the extent and nature of this change, and therefore may fail to capture the biodiversity they seek to maintain over the longer term.

In conclusion, this study has demonstrated that there are likely to be substantial and complex changes to ant assemblages as climates change in the northern Cape Floristic Region. The importance of ants for ecosystem functioning in both Fynbos and Succulent Karoo systems (e.g. Johnson, 1992; Le Maitre & Midgley, 1992; Milton *et al.*, 1992) suggests that these responses are likely not to be a consequence solely of vegetation changes, but are likely also to precipitate such transformation. The dynamic aspects of the response of southern African ecosystems to climate change have enjoyed little attention (contrast the investigations of Rutherford *et al.*, 1999; Erasmus *et al.*, 2002, and Midgley *et al.*, 2002, 2003, with those of the Aspen FACE project – Karnosky *et al.*, 2003), although clearly such consideration is required. The changes that are predicted to take place in the next 50 years in Fynbos and Succulent Karoo ecosystems (Rutherford *et al.*, 1999; Midgley *et al.*, 2002, 2003) could be substantially exacerbated by synergistic effects of the kind outlined here, and only experimental work will determine whether this is likely to be the case. In the meantime, ongoing monitoring of this transect will reveal the nature and pace of the change as it unfolds.

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## REFERENCES

- Adis, J. (1979) Problems with interpreting arthropod sampling with pitfall traps. *Zoologischer Anzeiger*, **202**, 117–184.
- Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545–1548.
- Andersen, A.N. (1986) Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in south-eastern Australia. *Australian Journal of Zoology*, **34**, 53–64.
- Andersen, A.N. (1991) Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Australian Journal of Ecology*, **16**, 273–279.
- Andersen, A.N. (1992) Regulation of ‘momentary’ diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. *American Naturalist*, **140**, 401–420.
- Andersen, A.N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, **22**, 15–29.
- Andersen, A.N. & Yen, A.L. (1985) Immediate effects of fire on ants in the semi-arid mallee region of north-western Victoria. *Australian Journal of Ecology*, **10**, 25–30.
- Anonymous (2004) *Greater Cederberg biodiversity corridor*. Western Cape Nature Conservation, Cape Town, South Africa.
- Auld, T.D. (1986) Population dynamics of the shrub *Acacia sauveolens* (Sm.) Wild.: dispersal and the dynamics of the soil seed-bank. *Australian Journal of Ecology*, **11**, 235–254.
- Berg, R.Y. (1975) Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Ecology*, **23**, 475–508.
- Bestelmeyer, B.T. (2000) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *Journal of Animal Ecology*, **69**, 998–1009.
- Bestelmeyer, B.T. & Wiens, J.A. (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. *Ecological Applications*, **6**, 1225–1240.
- Bond, W.J. & Goldblatt, P. (1984) Plants of the Cape Flora: a descriptive catalogue. *Journal of South African Botany*, **13**, 1–455.
- Bond, W.J. & Slingsby, P. (1983) Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. *South African Journal of Science*, **79**, 231–233.
- Bond, W.J. & Slingsby, P. (1984) Collapse of an ant–plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology*, **65**, 1031–1037.
- Bond, W.J., Le Roux, D. & Erntzen, R. (1990) Fire intensity and regeneration of myrmecochorous Proteaceae. *South African Journal of Botany*, **56**, 326–330.
- Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.
- ter Braak, C.J.F. (1994) Canonical community ordination. Part 1: Basic theory and linear methods. *Ecoscience*, **1**, 127–140.
- ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination (version 4.5)*. Microcomputer Power, Ithaca, NY.

- Bray, R.H. & Kurtz, L.T. (1945) Determination of total, organic and available forms of phosphorus in soils. *Soil Science*, **59**, 39–45.
- Breytenbach, G.J. (1988) Why are myrmecochorous plants limited to Fynbos (Macchia) vegetation types? *South African Journal of Forestry*, **144**, 3–5.
- Brits, G.J. (1987) Germination depth vs. temperature requirements in naturally dispersed seeds of *Leucospermum cordifolium* and *L. cuneiforme* (Proteaceae). *South African Journal of Botany*, **53**, 119–124.
- Campbell, B.M. (1985) A classification of the mountain vegetation of the fynbos biome. *Memoirs of the Botanical Survey of South Africa*, **50**, 1–115.
- Cerdá, X., Retana, J. & Manzaneda, A. (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia*, **117**, 404–412.
- Chapman, H.D. (1965) Total exchangeable bases. *Methods of soil analysis. Part 2* (ed. by C.A. Black), pp. 902–904. American Society of Agronomy, Madison, WI.
- Coleman, B.D. (1981) On random placement and species–area relations. *Mathematical Biosciences*, **54**, 191–215.
- Colwell, R.K. (2000) *RangeModel: a Monte Carlo simulation tool for assessing geometric constraints on species richness*. V3. A users guide and application. Published at: <http://vice-roy.eeb.uconn.edu/rangemodel>.
- Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B*, **345**, 101–118.
- Cowling, R.M. (1992) *The ecology of Fynbos: nutrients, fire and diversity*. Oxford University Press, Cape Town, South Africa.
- Cowling, R.M. & Hilton-Taylor, C. (1994) Patterns of plant diversity and endemism in South Africa: an overview. *Biotic diversity in South Africa* (ed. by B.J. Huntley), pp. 31–52. National Botanical Institute, Pretoria, South Africa.
- Cowling, R.M. & Holmes, P.M. (1992) Flora and vegetation. *The ecology of Fynbos: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 223–261. Oxford University Press, Cape Town, South Africa.
- Cowling, R.M. & Pressey, R.L. (2003) Introduction to systematic conservation planning in the Cape Floristic Region. *Biological Conservation*, **112**, 1–13.
- Cowling, R.M. & Richardson, D.M. (1995) *Fynbos: South Africa's unique floral kingdom*. Fernwood Press, Cape Town, South Africa.
- Cowling, R.M., Richardson, D.M. & Muster, P.J. (1997) Fynbos. *The vegetation of southern Africa* (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 99–130. Cambridge University Press, Cambridge.
- Cowling, R.M., Esler, K.J. & Rundel, P.W. (1999) Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*, **142**, 3–21.
- Cowling, R.M., Pressey, R.L., Rouget, M. & Lombard, A.T. (2003) A conservation plan for a global diversity hotspot – the Cape Floristic Region, South Africa. *Biological Conservation*, **112**, 191–216.
- Deacon, H.J., Jury, M.R. & Ellis, F. (1992) Selective regime and time. *The ecology of Fynbos: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 6–22. Oxford University Press, Cape Town, South Africa.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.
- Dobson, A.J. (2002) *An introduction to generalized linear models*, 2nd edn. Chapman & Hall/CRC Texts in Statistical Science, Boca Raton, FL.
- Donnelly, D. & Giliomee, J.H. (1985) Community structure of epigaic ants (Hymenoptera: Formicidae) in fynbos vegetation in the Jonkershoek valley. *Journal of the Entomological Society of Southern Africa*, **48**, 247–257.
- Drake, W.E. (1981) Ant–seed interaction in dry sclerophyll forest on North Stadbroke Island, Queensland. *Australian Journal of Botany*, **29**, 293–309.
- Driver, A., Desmet, P., Rouget, M., Cowling, R.M. & Maze, K. (2003) *Succulent Karoo Ecosystem Plan: biodiversity component technical report*. Report No. CCU 1/03. Cape Conservation Unit, Botanical Society of South Africa, Cape Town.
- Dufrène, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, **67**, 345–366.
- Erasmus, B.F.N., Kshatriya, M., Mansell, M.W., Chown, S.L. & van Jaarsveld, A.S. (2000) A modeling approach to antlion (Neuroptera: Myrmeleontidae) distribution patterns. *African Entomology*, **8**, 157–168.
- Erasmus, B.F.N., van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8**, 679–693.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2004) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **79**, 1–25.
- Fleishman, E., Austin, G.T. & Weiss, A.D. (1998) An empirical test of Rapoport's rule: elevational gradients in montane butterfly communities. *Ecology*, **79**, 2482–2493.
- Fleishman, E., Fay, J.P. & Murphy, D.D. (2000) Upsides and downsides: contrasting topographic gradients in species richness and associated scenarios for climate change. *Journal of Biogeography*, **27**, 1209–1219.
- French, K. & Major, R.E. (2001) Effect of an exotic *Acacia* (Fabaceae) on ant assemblages in South African fynbos. *Austral Ecology*, **26**, 303–310.
- Giorgi, F., Whetton, P.H., Jones, R.G., Christensen, J.H., Mearns, L.O., Hewitson, B., Vonstorch, H., Francisco, R. & Jack, C. (2001) Emerging patterns of simulated regional climatic changes for the 21st century due to anthropogenic forcing. *Geophysical Research Letters*, **28**, 3317–3320.
- Gómez, C. & Espadaler, X. (1998) Myrmecochorous dispersal distances: a world survey. *Journal of Biogeography*, **25**, 573–580.
- Gómez, C. & Oliveras, J. (2003) Can the Argentine ant (*Linepithema humile* Mayr) replace native ants in myrmecochory? *Acta Oecologica*, **24**, 47–53.



- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Gotelli, N.J. & Ellison, A.M. (2002) Biogeography at a regional scale: determinants of ant species density in New England bogs and forests. *Ecology*, **83**, 1604–1609.
- Greenslade, P.J.M. (1973) Sampling ants with pitfall traps: digging in effects. *Insectes Sociaux*, **20**, 343–353.
- Handel, S.N. & Beattie, A.J. (1990) Seed dispersal by ants. *Scientific American*, August, 58–64.
- Hannah, L., Midgley, G., Hughes, G. & Bomhard, B. (2005) The view from the Cape: extinction risk, protected areas, and climate change. *BioScience*, **55**, 231–242.
- Hanzawa, F.M., Beattie, A.J. & Culver, D.C. (1988) Directed dispersal: demographic analysis of an ant–seed mutualism. *American Naturalist*, **131**, 1–13.
- Haslett, J.R. (1997) Insect communities and the spatial complexity of mountain habitats. *Global Ecology and Biogeography*, **6**, 49–56.
- Hawkins, B.A. & Porter, E.E. (2003) Does herbivore diversity depend on plant diversity? The case of California butterflies. *American Naturalist*, **162**, 40–49.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Obeddorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, J. & Huntley, B. (2002) Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London B*, **269**, 2163–2171.
- Hoffman, T. (1996) Strandveld Succulent Karoo. *Vegetation of South Africa, Lesotho and Swaziland* (ed. by B.A. Low and A.G. Rebelo), 59 pp. Department of Environmental Affairs & Tourism, Pretoria, South Africa.
- Hoffman, B.T. & Andersen, A.N. (2003) Responses of ant communities to experimental fire regimes on rangelands in the Victoria River District of the Northern Territory. *Austral Ecology*, **28**, 182–195.
- Johnson, S.D. (1992) Plant–animal relationships. *The ecology of Fynbos: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 175–205. Oxford University Press, Cape Town, South Africa.
- Karnosky, D.F., Zak, D.R., Pregitzer, K.S., Awmack, C.S., Bockheim, J.G., Dickson, R.E., Hendrey, G.R., Host, G.E., King, J.S., Kopper, B.J., Kruger, E.L., Kubiske, M.E., Lindroth, R.L., Mattson, W.J., McDonald, E.P., Noormets, A., Oksanen, E., Parsons, W.F.J., Percy, K.E., Podila, G.K., Riemenschneider, D.E., Sharma, P., Thakur, R., Söber, A., Söber, J., Jones, W.S., Anttonen, S., Vapaavuori, E., Manakovska, B., Heilman, W. & Isebrands, J.G. (2003) Tropospheric O<sub>3</sub> moderates responses of temperate hardwood forests to alleviate CO<sub>2</sub>: a synthesis of molecular to ecosystem results from the ASPEN FACE project. *Functional Ecology*, **17**, 289–304.
- Kaspari, M., Ward, P.S. & Yuan, M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, **140**, 407–413.
- Kerley, G.I.H., Pressey, R.L., Cowling, R.M., Boshoff, A.F. & Sims-Castley, R. (2003) Options for the conservation of large and medium-sized mammals in the Cape Floristic Region hotspot, South Africa. *Biological Conservation*, **112**, 169–190.
- Kerr, J.T. & Packer, L. (1999) The environmental basis of North American species richness patterns among *Epicauta* (Coleoptera: Meloidae). *Biodiversity and Conservation*, **8**, 617–628.
- Koen, J.H. & Breytenbach, W. (1988) Ant species richness of fynbos and forest ecosystems in the southern Cape. *South African Journal of Zoology*, **23**, 184–188.
- Lassau, S.A. & Hochuli, D.F. (2004) Effects of habitat complexity on ant assemblages. *Ecography*, **27**, 157–164.
- Le Maitre, D.C. & Midgley, J.J. (1992) Plant reproductive ecology. *Fynbos ecology: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 135–174. Oxford University Press, Cape Town, South Africa.
- Lechmere-Oertel, R.G. & Cowling, R.M. (2001) Abiotic determinants of the fynbos/succulent karoo boundary, South Africa. *Journal of Vegetation Science*, **12**, 75–80.
- Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659–1673.
- Legendre, P. & Fortin, M.J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–138.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier Science B.V., Amsterdam, The Netherlands.
- Lennon, J.J. (2000) Red-shifts and red herrings in geographical ecology. *Ecography*, **23**, 101–113.
- Lepš, J. & Šmilauer, P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge.
- Linder, H.P. (1991) Environmental correlates of patterns of species richness in the south-western Cape Province of South Africa. *Journal of Biogeography*, **18**, 509–518.
- Link, S.O., Smith, J.L., Halvorson, J.J. & Bolton, H. (2003) A reciprocal transplant experiment within a climatic gradient in a semiarid shrub–steppe ecosystem: effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen. *Global Change Biology*, **9**, 1097–1105.
- Lindsey, P.A. & Skinner, J.D. (2001) Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. *Journal of Arid Environments*, **48**, 551–568.
- Lobo, J.M., Lumaret, J.P. & Jay-Robert, P. (2002) Modelling the species richness distribution of French dung beetles (Coleoptera, Scarabaeidae) and delimiting the predictive capacity of different groups of explanatory variables. *Global Ecology and Biogeography*, **11**, 265–277.
- Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, **83**, 689–702.

- Low, A.B. & Rebelo, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria, South Africa.
- McGeoch, M.A. & Chown, S.L. (1998) Scaling up the value of bioindicators. *Trends in Ecology and Evolution*, **13**, 46–47.
- McGeoch, M.A. & Price, P.W. (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, **73**, 506–516.
- McGeoch, M.A., van Rensburg, B.J. & Botes, A. (2002) The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. *Journal of Applied Ecology*, **39**, 661–672.
- McLean, E.O. (1982) Soil pH and lime requirement. *Methods of soil analysis. Part 2* (ed. by A.L. Page), 199 pp. American Society of Agronomy, Wisconsin.
- Midgley, J.J. & Bond, W.J. (1995) Relative attractiveness of seeds of myrmecochorous Australian and South African plants to ants, and the chemical basis of this attraction. *South African Journal of Science*, **61**, 230–232.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C. & Powrie, L.W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, **11**, 445–451.
- Midgley, G.F., Hannah, L., Millar, D., Thuiller, W. & Booth, A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, **112**, 87–97.
- Milton, S.J., Dean, W.R.J. & Kerley, G.I.H. (1992) Tierberg Karoo Research Centre: history, physical environment, flora and fauna. *Transactions of the Royal Society of Southern Africa*, **48**, 15–46.
- Milton, S.J., Yeaton, R.I., Dean, W.R.J. & Vlok, J.H.J. (1997) Succulent Karoo. *The vegetation of southern Africa* (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 131–166. Cambridge University Press, Cambridge.
- Minter, L.R., Burger, M., Harrison, J.A., Braack, H.H., Bishop, P.J. & Kloepfer, D. (2004) *Atlas and red data book of the frogs of South Africa*. SI/MAB Series #9, Smithsonian Institute, Washington, DC.
- Mittermeier, R.A., Mayers, N., Thomsen, J.B., Da Fonseca, G.A.B. & Olivieri, S. (1998) Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology*, **12**, 516–520.
- Myers, N. (1990) The biodiversity challenge: expected hotspots analysis. *The Environmentalist*, **10**, 243–255.
- Nelson, D.W. & Sommers, L.E. (1982) Total carbon, organic carbon and organic matter. *Methods of soil analysis, Part 2* (ed. by C.A. Black), pp. 570–571. American Society of Agronomy, Madison, WI.
- O'Brien, E.M., Field, R. & Whittaker, R.J. (2000) Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos*, **89**, 588–600.
- Olson, D.M. & Dinerstein, E. (1998) The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. *Conservation Biology*, **12**, 52–515.
- Parr, C.L. & Chown, S.L. (2003) Burning issues for conservation: a critique of faunal fire research in South Africa. *Austral Ecology*, **28**, 384–395.
- Parr, C.L., Bond, W.J. & Robertson, H.G. (2002) A preliminary study of the effect of fire on ants (Formicidae) in a South African savanna. *African Entomology*, **10**, 101–111.
- Parr, C.L., Robertson, H.G., Biggs, H.C. & Chown, S.L. (2004) Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology*, **41**, 630–642.
- Parr, C.L., Sinclair, B.J., Andersen, A.N., Gaston, K.J. & Chown, S.L. (2005) Constraint and competition in assemblages: a cross-continental and modelling approach for ants. *American Naturalist*, **165**, 481–494.
- Perfecto, I. & Vandermeer, J. (1996) Microclimatic changes and the direct loss of ant diversity in a tropical agroecosystem. *Oecologia*, **108**, 577–582.
- Pressey, R.L., Cowling, R.M. & Rouget, M. (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. *Biological Conservation*, **112**, 99–127.
- Prins, A.J. (1963) A list of the ants collected in the Kruger National Park with notes on their distribution. *Koedoe*, **6**, 91–108.
- Pudlo, R.J., Beattie, A.J. & Cluver, D.C. (1980) Population consequences of changes in an ant-seed mutualism in *Saguinaria cadensis*. *Oecologia*, **46**, 32–37.
- Rebelo, A.G. (1996) Fynbos. *Vegetation of South Africa, Lesotho and Swaziland* (ed. by A.B. Low and A.G. Rebelo), pp. 68–71. Department of Environmental Affairs and Tourism, Pretoria, South Africa.
- van Rensburg, B.J., McGeoch, M.A., Chown, S.L. & van Jaarsveld, A.S. (1999) Conservation of heterogeneity among dung beetles in the Maputoland Centre of Endemism, South Africa. *Biological Conservation*, **7**, 945–965.
- van Rensburg, B.J., Chown, S.L. & Gaston, K.J. (2002) Species richness, environmental correlates, and spatial scale: a test using South African birds. *American Naturalist*, **159**, 566–577.
- Robertson, H.G. (1999) Ants (Hymenoptera: Formicidae) of Mkomazi. *Mkomazi: the ecology, biodiversity and conservation of a Tanzanian savanna* (ed. by M.J. Coe, N.C. McWilliams, G.N. Stone and M.J. Parker), pp. 321–336. Royal Geographic Society, London.
- Rodrigues, A.S. L., Gregory, R.D. & Gaston, K.J. (2000) Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London B*, **267**, 49–55.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, New York, NY.
- Rotenberry, J.T. & Wiens, J.A. (1980) Habitat structure, patchiness, and avian communities in North American Steppe vegetation: a multivariate analysis. *Ecology*, **61**, 1228–1250.
- Rouget, M., Richardson, D.M. & Cowling, A. (2003a) The current configuration of protected areas in the Cape Floristic

- Region, South Africa – reservation bias and representation of biodiversity patterns and processes. *Biological Conservation*, **112**, 129–145.
- Rouget, M., Richardson, D.M., Cowling, R.M., Lloyd, J.W. & Lombard, A.T. (2003b) Current pattern of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation*, **112**, 63–85.
- Rutherford, M.C., Powrie, L.W. & Schulze, R.E. (1999) Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity and Distributions*, **5**, 253–262.
- Samways, M.J. (1983) Community structure of ants (Hymenoptera: Formicidae) in a series of habitats associated with citrus. *Journal of Applied Ecology*, **20**, 833–847.
- Samways, M.J. (1990) Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia*, **84**, 482–490.
- Schlettwein, C.H.G. & Giliomee, J.H. (1987) Comparison of insect biomass and community structure between fynbos sites of different ages after fire with particular reference to ants, leafhoppers and grasshoppers. *Annals of the University of Stellenbosch*, **2**, 1–76.
- Slingsby, P. & Bond, W.J. (1985) The influence of ants on the dispersal distance and seedling recruitment of *Leucospermum conocarpodendron* (L.) Buek (Proteaceae). *South African Journal of Botany*, **51**, 30–34.
- Smith, P.A. (1994) Autocorrelation in logistic regression modelling of species' distributions. *Global Ecology and Biogeography Letters*, **4**, 47–61.
- Smith, J.L., Halvorson, J.J. & Bolton, H. (2002) Soil properties and microbial activities across a 500 m elevation gradient in a semi-arid environment. *Soil Biology and Biochemistry*, **34**, 1749–1757.
- Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wedge, D.C. (1998) *Endemic bird areas of the world*. BirdLife Conservation Series 7. BirdLife International, Cambridge.
- Swart, J.M., Richardson, P.R.K. & Furgeson, J.W.H. (1999) Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). *Journal of Zoology*, **247**, 281–292.
- Tan, K.H. (1996) *Soil sampling, preparation and analysis*. Dekker, New York, NY.
- Todd, S.W. & Hoffman, M.T. (1999) A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology*, **142**, 169–178.
- Turner, J.R.G., Gatehouse, C.M. & Corey, C.A. (1987) Does solar energy control organic diversity? Butterflies, moths and the British climate. *Oikos*, **48**, 195–205.
- Tyson, P.D. (1999) Atmospheric circulation changes and palaeoclimates of southern Africa. *South African Journal of Science*, **95**, 194–201.
- United States Salinity Laboratory Staff (1954) *Diagnosis and improvement of saline and alkaline soils*. USDA Handbook No. 60, 91. US Government Printing Office, Washington, DC.
- Wartenberg, D. (1989) *SAAP: a spatial autocorrelation analysis program*. V4.3. Piscataway, New Jersey.
- Westoby, M., Rice, B., Shelley, J.M., Haig, D. & Kohen, J.L. (1982) Plants' use of ants for dispersal at West Head, New South Wales. *Ant-plant interactions in Australia* (ed. by R.C. Buckley), pp. 75–87. Dr W. Junk Publishers, The Hague, The Netherlands.
- Wheelwright, N.T. & Orians, G.H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist*, **119**, 402–413.
- Witt, A.B.R. & Giliomee, J.H. (2004) The impact of an invasive ant, *Linepithema humile* (Mayr), on the dispersal of *Phyllica pubescens* Aiton seeds in South Africa. *African Entomology*, **12**, 179–185.
- WWF (World Wildlife Fund) and IUCN (The World Conservation Union) (1994) *Centres of plant diversity: a guide for their conservation*. IUC, Cambridge.
- Wylie, J. & Currie, D.J. (1993) Species energy theory and patterns of species richness. II. Predicting mammal species richness of isolated nature reserves. *Conservation Biology*, **63**, 145–148.
- Younge, A. & Fowkes, S. (2003) The Cape Action Plan for the environment: overview of an ecoregional planning process. *Biological Conservation*, **112**, 15–28.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>

**Appendix S1** Sampling areas and vegetation types along the altitudinal gradient.

**Appendix S2** Subfamilies and species collected during the two sampling periods.

**Appendix S3** Sample-based species accumulation curves of the ant assemblages.

**Appendix S4** Pearson's product-moment correlations of the environmental variables.

**Appendix S5** Soil characteristics and ground cover of the sampling sites.

## BIOSKETCHES

**Antoinette Botes** has an MSc in Entomology from the University of Pretoria and is currently a PhD student. Her research interests include macroecology and conservation ecology.

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**Appendix S4** Pearson's product-moment correlations of the abiotic and biotic variables. Significant values are indicated in bold. Alt = Altitude, MMT = mean monthly temperature, Max = mean maximum monthly temperature, Min = mean minimum monthly temperature, Range = mean monthly temperature range, Amax = absolute maximum monthly temperature, Amin = absolute minimum monthly temperature, Cond = conductivity, BG = proportion of bare ground, ER = proportion of exposed rock, Veg = proportion of vegetation cover, TOTHITS = vertical complexity of the vegetation, Height = vegetation height.

	Alt	Area	MMT	Max	Min	Range	AMax	AMin
Alt								
Area	<b>-0.87</b>							
MMT	<b>-0.84</b>	<b>0.62</b>						
Max	<b>-0.68</b>	<b>0.45</b>	<b>0.90</b>					
Min	<b>-0.82</b>	<b>0.63</b>	<b>0.97</b>	<b>0.79</b>				
Range	-0.11	-0.03	<b>0.28</b>	<b>0.66</b>	0.06			
AMax	0.06	<b>-0.20</b>	0.02	<b>0.26</b>	-0.08	<b>0.52</b>		
AMin	<b>-0.44</b>	<b>0.38</b>	<b>0.59</b>	<b>0.29</b>	<b>0.71</b>	<b>-0.39</b>	<b>-0.29</b>	
PH	<b>-0.65</b>	<b>0.84</b>	<b>0.35</b>	0.12	<b>0.41</b>	<b>-0.31</b>	<b>-0.47</b>	<b>0.36</b>
H	<b>0.66</b>	<b>-0.70</b>	<b>-0.46</b>	<b>-0.28</b>	<b>-0.49</b>	0.14	0.05	<b>-0.33</b>
Cond	0.05	-0.11	-0.06	<b>0.21</b>	<b>-0.18</b>	<b>0.57</b>	0.16	<b>-0.43</b>
Rock	0.13	<b>0.27</b>	0.10	0.13	<b>0.17</b>	0.01	-0.04	0.07
P	0.08	-0.14	0.09	0.06	0.14	-0.08	-0.12	0.16
K	0.17	<b>-0.17</b>	0.09	0.04	<b>0.21</b>	<b>-0.19</b>	-0.16	<b>0.20</b>
C	<b>0.58</b>	<b>-0.59</b>	<b>-0.40</b>	<b>-0.34</b>	<b>-0.34</b>	-0.13	-0.13	<b>-0.22</b>
NO <sub>3</sub>	<b>0.40</b>	<b>-0.34</b>	<b>-0.35</b>	<b>-0.47</b>	<b>-0.27</b>	<b>-0.44</b>	-0.11	0.03
Na	<b>-0.20</b>	<b>0.36</b>	0.16	-0.04	<b>0.26</b>	<b>-0.38</b>	<b>-0.51</b>	<b>0.35</b>
Ca	<b>-0.46</b>	<b>0.73</b>	<b>0.17</b>	-0.05	<b>0.22</b>	<b>-0.35</b>	<b>-0.58</b>	<b>0.31</b>
Mg	0.07	-0.04	-0.03	<b>-0.19</b>	0.10	<b>-0.44</b>	<b>-0.38</b>	0.15
Clay	<b>0.19</b>	<b>-0.27</b>	0.16	<b>0.24</b>	0.16	<b>0.20</b>	-0.11	0.07
Silt	<b>0.56</b>	<b>-0.57</b>	<b>-0.31</b>	<b>-0.30</b>	<b>-0.25</b>	<b>-0.18</b>	<b>-0.22</b>	-0.07
Sand	<b>-0.49</b>	<b>0.51</b>	<b>0.19</b>	<b>0.18</b>	0.13	0.13	<b>0.25</b>	0.01
BG	<b>-0.31</b>	<b>0.34</b>	<b>0.17</b>	0.09	0.09	0.04	0.09	0.05
Litter	<b>-0.44</b>	<b>0.35</b>	<b>0.43</b>	<b>0.34</b>	<b>0.46</b>	0.00	0.08	<b>0.39</b>
ER	<b>0.40</b>	<b>-0.37</b>	<b>-0.21</b>	-0.02	<b>-0.17</b>	<b>0.18</b>	0.06	<b>-0.18</b>
Veg	<b>0.18</b>	<b>-0.20</b>	<b>-0.22</b>	<b>-0.29</b>	<b>-0.17</b>	<b>-0.27</b>	<b>-0.23</b>	-0.08

TOTHITS	<b>-0.27</b>	0.01	<b>0.19</b>	0.16	<b>0.21</b>	0.00	0.03	0.07
Height	<b>-0.55</b>	<b>0.25</b>	<b>0.49</b>	<b>0.46</b>	<b>0.50</b>	0.14	<b>0.28</b>	<b>0.19</b>

#### Appendix S4 (continued)

	PH	H	Cond	Rock	P	K	C	NO <sub>3</sub>	Na	Ca	Mg
H	<b>-0.70</b>										
Cond	-0.16	0.04									
Rock	-0.05	-0.02	0.11								
P	-0.01	0.11	-0.10	<b>0.38</b>							
K	0.04	0.03	-0.14	<b>0.70</b>	<b>0.40</b>						
C	<b>-0.47</b>	<b>0.80</b>	-0.02	<b>0.22</b>	<b>0.24</b>	<b>0.35</b>					
NO <sub>3</sub>	<b>-0.28</b>	<b>0.33</b>	<b>-0.67</b>	<b>-0.19</b>	0.00	-0.01	<b>0.29</b>				
Na	<b>0.51</b>	<b>-0.18</b>	<b>-0.33</b>	<b>0.19</b>	<b>0.22</b>	<b>0.36</b>	0.03	-0.13			
Ca	<b>0.92</b>	<b>-0.48</b>	-0.14	-0.06	-0.01	0.02	<b>-0.25</b>	<b>-0.20</b>	<b>0.53</b>		
Mg	<b>0.24</b>	-0.08	<b>-0.28</b>	<b>0.36</b>	<b>0.21</b>	<b>0.75</b>	<b>0.26</b>	0.17	<b>0.56</b>	<b>0.26</b>	
Clay	<b>-0.32</b>	<b>0.25</b>	0.04	<b>0.30</b>	0.12	<b>0.43</b>	<b>0.20</b>	0.07	<b>0.17</b>	<b>-0.34</b>	<b>0.33</b>
Silt	<b>-0.35</b>	<b>0.51</b>	-0.13	<b>0.37</b>	<b>0.36</b>	<b>0.62</b>	<b>0.60</b>	<b>0.19</b>	<b>0.25</b>	<b>-0.23</b>	<b>0.47</b>
Sand	<b>0.35</b>	<b>-0.32</b>	0.14	<b>-0.41</b>	<b>-0.25</b>	<b>-0.59</b>	<b>-0.46</b>	<b>-0.26</b>	<b>-0.19</b>	<b>0.27</b>	<b>-0.50</b>
BG	<b>0.22</b>	<b>-0.39</b>	-0.02	<b>-0.38</b>	<b>-0.37</b>	<b>-0.41</b>	<b>-0.55</b>	-0.03	-0.07	0.15	<b>-0.23</b>
Litter	<b>0.23</b>	<b>-0.32</b>	-0.11	0.03	0.07	0.06	<b>-0.28</b>	-0.13	0.02	0.08	-0.04
ER	<b>-0.25</b>	<b>0.29</b>	<b>0.29</b>	<b>0.52</b>	<b>0.31</b>	<b>0.49</b>	<b>0.42</b>	<b>-0.17</b>	-0.02	<b>-0.18</b>	<b>0.21</b>
Veg	0.00	<b>0.28</b>	<b>-0.24</b>	-0.04	0.10	0.02	<b>0.34</b>	<b>0.29</b>	0.00	0.03	0.10
TOTHITS	-0.07	0.13	-0.09	-0.16	0.13	-0.15	0.13	0.01	-0.14	-0.16	-0.09
Height	0.02	<b>-0.18</b>	-0.04	-0.14	0.06	-0.13	<b>-0.17</b>	<b>-0.18</b>	-0.15	<b>-0.17</b>	-0.12

#### Appendix S4 (continued)

	Clay	Silt	Sand	BG	Litter	ER	Veg	TOTHITS
Silt	<b>0.45</b>							
Sand	<b>-0.57</b>	<b>-0.76</b>						
BG	<b>-0.18</b>	<b>-0.38</b>	<b>0.29</b>					
Litter	-0.11	<b>-0.24</b>	<b>0.23</b>	0.03				
ER	<b>0.25</b>	<b>0.40</b>	<b>-0.34</b>	<b>-0.61</b>	<b>-0.19</b>			
Veg	-0.07	<b>0.21</b>	-0.11	<b>-0.42</b>	-0.11	-0.17		
TOTHITS	-0.14	-0.06	0.15	<b>-0.33</b>	<b>0.24</b>	-0.10	<b>0.40</b>	
Height	-0.12	<b>-0.30</b>	<b>0.30</b>	-0.09	<b>0.38</b>	-0.13	0.06	<b>0.77</b>

**Appendix S1** Sampling areas and vegetation types along the altitudinal gradient stretching from Lamberts Bay over the Cederberg down to Wuppertal. CWA = Cederberg Wilderness Area. “Last fire” refers to the date of the last recorded fire at each site. Where two dates are given the sampling grids at a particular site burnt in different years.

Area	GPS	Altitude	Slope (°)	Last fire	Area (km <sup>2</sup> )	Vegetation type	Geology
<b>Western slope:</b>							
Lamberts Bay	32° 10,682'S 18° 18,858'E	5 m	0.820	-	3082.58	Strandveld Succulent Karroo	Dunesand, in areas highly calcareous Quartzitic sandstone with minor shale and conglomerate lenses
Farm “Aan het Berg”	32° 16,598'S 18° 31,799'E	256 m	3.867	-	1531.61	Restioid Mountain Fynbos	
Sawadee (Cederberg)	32° 20,518'S 18° 59,491'E	370 m	7.873	1988	1531.61	Ecotonal, Succulent Karoo and Proteoid Mountain Fynbos	
Niewoudt's Pass CWA)	32° 21,067'S 19° 00,417'E	537 m	13.516	1988	765.43	Proteoid Mountain Fynbos	
Uitkyk Pass (CWA)	32° 24,471'S 19° 05,079'E	766 m	17.674	1959; 1988	447.53	Proteoid Mountain Fynbos	
Driehoek (CWA)	32° 25,445'S 19° 09,970'E	922 m	6.981	1999	370.14	Restioid Mountain Fynbos	
Jeep track between Welbedacht and Sneekop (CWA)	32° 27,581'S 19° 14,459'E	1133 m	7.003	1979	282.66	Ericaceous Mountain Fynbos	
	32° 26,100'S 19° 13,969'E	1337 m	7.870	1979; 1984	206.59	Ericaceous Mountain Fynbos	

Sneeukop (CWA)	32° 21,435'S	1543 m	9.792	1999	106.73	Ericaceous Mountain Fynbos	Quartzitic sandstone with thin shale and conglomerate lenses
	19° 08,753'E						
	32° 21,310'S	1687 m	27.387	1985	21.47	Ericaceous Mountain Fynbos	
	19° 08,938'E						
	32° 21,305'S	1926 m	8.670	1985;	3.40	Alpine Mountain Fynbos	
	19° 09,695'E			2001			
Eastern slope:							
Between Sneeukop hut and Sneeukop (CWA)	32° 21,241'S	1740 m	36.979	1959;	6.76	Ericaceous Mountain Fynbos	Quartzitic sandstone with minor shale and conglomerate lenses
	19° 10,018'E			1985			
Sneeukop hut (CWA)	32° 20,888'S	1543 m	15.230	1985;	39.32	Ericaceous Mountain Fynbos	
	19° 10,213'E			2000			
Sneeukop to	32° 20,340'S	1365 m	8.448	2000	76.94	Ericaceous Mountain Fynbos	
	19° 10,899'E						
Wuppertal	32° 20,140'S	1158 m	2.471	2000	232.54	Ericaceous Mountain Fynbos	
	19° 11,623'E						
(CWA)	32° 19,637'S	965 m	10.397	2000	607.88	Restioid Mountain Fynbos	
	19° 12,086'E						
Wupperthal	32° 16,674'S	520 m	9.207	-	1353.37	Lowland Succulent Karoo	
	19° 13,161'E						



**Appendix S2** Subfamilies and species collected during October 2002 and March 2003 in the different vegetation types. The abundance of the species collected during each sampling period is given. SV = Strandveld Succulent Karoo, SK = Succulent Karoo, RF = Restioid Fynbos, PF = Proteoid Fynbos, EF = Ericaceous Fynbos, AF = Alpine Fynbos. \* denote myrmecochores.

Subfamily and species	Oct 2002	Mar 2003	Vegetation type
<b>Aenictinae</b>			
<i>Aenictus rotundatus</i>	3	2	RF; PF
<b>Cerapachyinae</b>			
<i>Cerapachys wroughtoni</i>	1	0	PF
<i>Cerapachys</i> sp. 2	1	0	EF
<b>Dolichoderinae</b>			
<i>Tapinoma</i> sp. 1	40	20	RF; EF
<i>Technomyrmex</i> sp. 1	40	78	SV; PF; EF; AF
<b>Dorylinae</b>			
<i>Dorylus helvolus</i>	2	0	PF
<b>Formicinae</b>			
<i>Anoplolepis</i> sp. 1	50	143	RF; PF; EF; SK
<i>Anoplolepis</i> sp. (c.f. <i>custodiens</i> )*	1736	2027	RF; EF; AF
<i>Anoplolepis</i> sp. (c.f. <i>steinergroeveri</i> )*	1576	2921	RF; PF
<i>Camponotus angusticeps</i>	51	117	RF; PF; EF
<i>Camponotus emarginatus</i>	15	17	RF; PF; EF
<i>Camponotus fulvopilosus</i>	104	59	RF; PF; EF; SK
<i>Camponotus maculatus</i>	27	68	SV; RF; PF; EF; AF
<i>Camponotus mystaceus</i>	166	149	SV; RF; PF; EF
<i>Camponotus niveosetosus</i> *	22	25	SV; RF; PF; EF; AF
<i>Camponotus vestitus</i>	14	19	PF; EF
<i>Camponotus</i> sp. 1	19	11	EF; AF
<i>Camponotus</i> sp. 2	18	18	RF; EF; AF
<i>Camponotus</i> sp. 3	2	0	EF; AF

<i>Camponotus</i> sp. 4	0	9	EF; AF
<i>Camponotus</i> sp. 5	23	8	PF; EF
<i>Camponotus</i> sp. 6	2	2	EF
<i>Camponotus</i> sp. 7	8	1	PF; EF
<i>Camponotus</i> sp. 8	0	1	RF
<i>Camponotus</i> sp. 9	1	0	AF
<i>Camponotus</i> sp. 10	3	5	EF; RF
<i>Camponotus</i> sp. 11	1	0	EF
<i>Camponotus</i> sp. 12	0	17	SV
<i>Camponotus</i> sp. 14	3	1	EF; AF
<i>Lepisiota</i> sp. 1	281	845	SV; RF; PF; EF; AF
<i>Lepisiota</i> sp. 2	90	0	RF
<i>Lepisiota</i> sp. 3	35	1	PF; EF
<i>Lepisiota</i> sp. 4	1	85	EF
<i>Plagiolepis</i> sp. 2	369	127	RF; PF; AF

### **Myrmicinae**

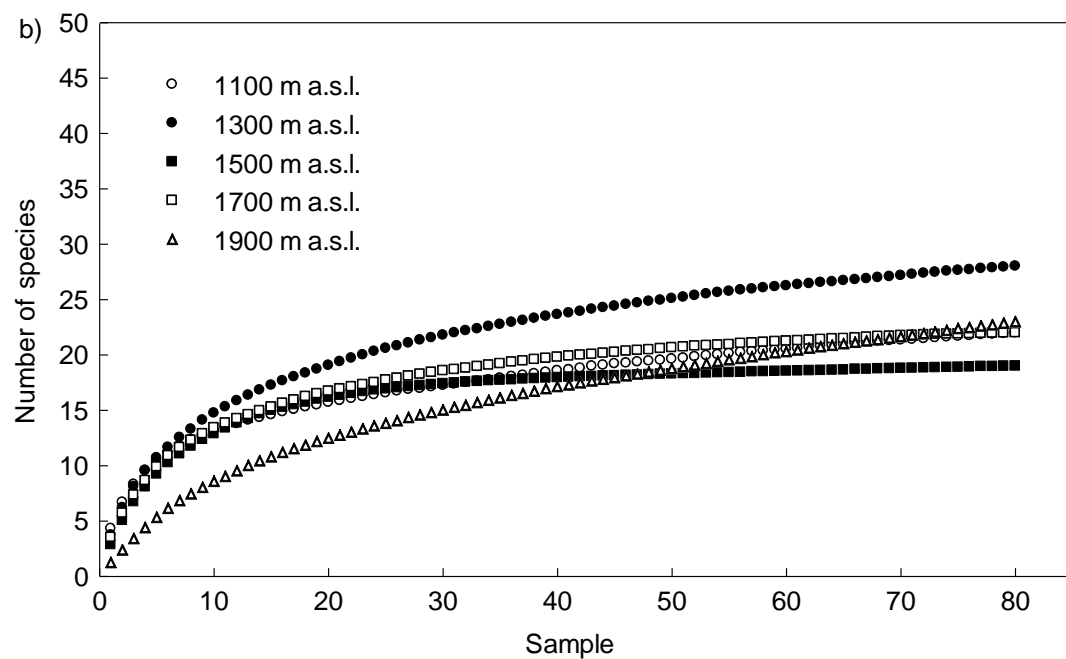
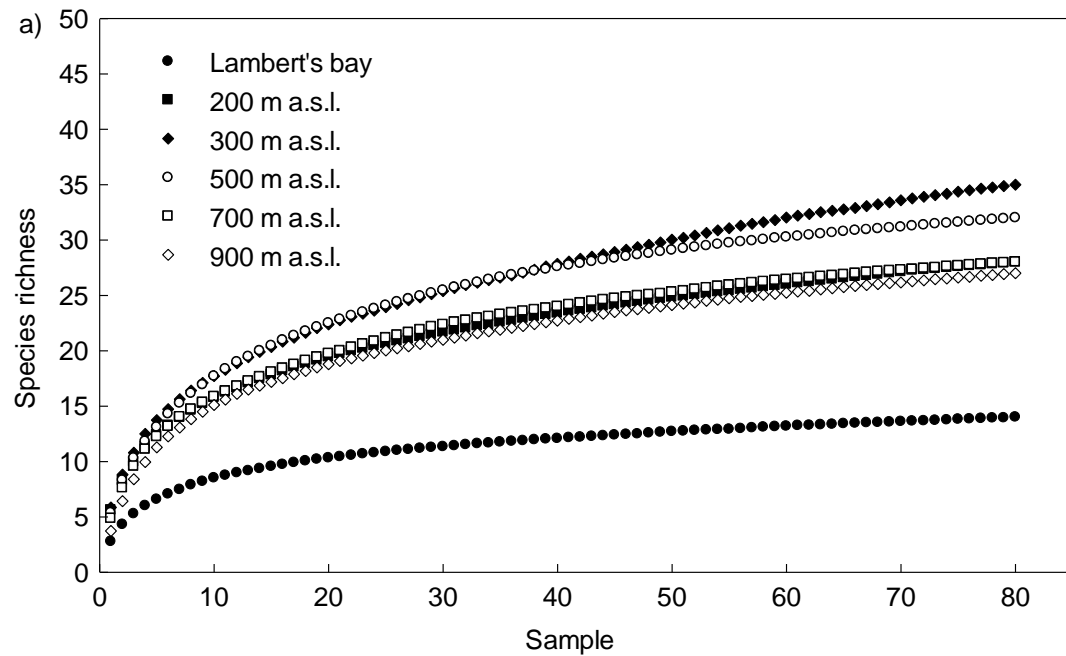
<i>Cardiocondyla</i> sp. 1	88	80	RF; PF; EF
<i>Crematogaster melanogaster</i>	48	20	PF
<i>Crematogaster</i> sp. 1	402	21	SV; RF; PF; EF; AF
<i>Crematogaster</i> sp. 2	10	54	SV; RF
<i>Crematogaster</i> sp. 3	26	1	SV; RF; EF
<i>Crematogaster</i> sp. 5	1	0	EF
<i>Crematogaster</i> sp. 6	0	3	RF; PF
<i>Leptothorax</i> sp. 1	19	0	SV; RF; PF, SK
<i>Leptothorax</i> sp. 2	10	15	PF
<i>Leptothorax</i> sp. 3	5	1	PF
<i>Leptothorax</i> sp. 4	21	39	EF
<i>Meranoplus</i> sp. 1	3	0	EF; AF
<i>Messor</i> sp. 1	12	4	PF; EF; SK
<i>Messor</i> sp. 2	2	3	RF; EF; SK
<i>Monomorium fridae</i>	19987	26012	SV; RF; PF; EF; AF
<i>Monomorium macrops</i>	233	15	RF; PF; EF
<i>Monomorium</i> sp. 1	225	94	PF; EF

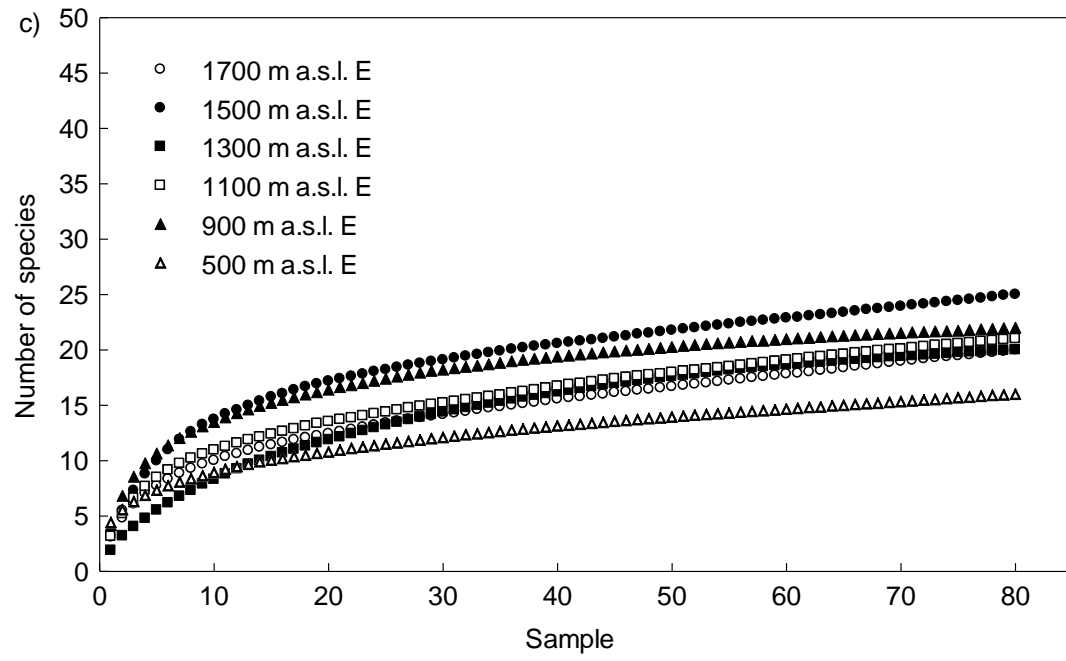
<i>Monomorium</i> sp. 2	390	902	RF; PF; EF; AF; SK
<i>Monomorium</i> sp. 3	4	0	RF; PF
<i>Monomorium</i> sp. 4	21	20	PF; SK
<i>Monomorium</i> sp. 5	13	1	PF; EF; AS; SK
<i>Monomorium</i> sp. 6	74	4	SV; RF; PF
<i>Monomorium</i> sp. 7	307	693	RF; PF; EF; AF; SK
<i>Monomorium</i> sp. 8	1	6	RF; AF
<i>Monomorium</i> sp. 9	7	0	EF
<i>Monomorium</i> sp. 10	164	229	RF; EF; AF
<i>Myrmicaria</i> sp. 1	49	65	SV
<i>Ocymyrmex</i> sp. 1	909	2284	SV; RF; PF; EF; A; SK
<i>Pheidole</i> sp. 1	1040	648	RF; PF; SK
<i>Pheidole</i> sp. 2	1104	1708	RF; PF; EF
<i>Pheidole</i> sp. 3	32	11	PF; EF; AF
<i>Pheidole</i> sp. 4	78	121	RF; EF
<i>Solenopsis punctaticeps</i>	73	15	SV; RF; PF; EF; AF
<i>Strumigenys</i> sp. 1	1	0	EF
<i>Tetramorium quadrispinosum</i> *	739	815	RF; PF; EF; SK
<i>Tetramorium</i> sp. 1	26	5	RF; EF
<i>Tetramorium</i> sp. 2	10	84	RF; PF
<i>Tetramorium</i> sp. 3	196	108	RF; PF; EF; AF
<i>Tetramorium</i> sp. 4	6	0	EF
<i>Tetramorium</i> sp. 5	38	76	RF; PF; EF
<i>Tetramorium</i> sp. 6	49	22	RF; EF; SK
<i>Tetramorium</i> sp. 7	42	54	RF; PF; EF
<i>Tetramorium</i> sp. 8	3	4	RF; PF
<i>Tetramorium</i> sp. 9	4	3	RF; EF
<i>Tetramorium</i> sp. 10	227	8	PF; EF
<i>Tetramorium</i> sp. 11	9	1	EF; AF
<i>Tetramorium</i> sp. 12	33	2	EF
<b>Ponerinae</b>			
<i>Anochetus leviallanti</i>	0	2	PF; SK
<i>Hypoponera</i> sp. 1	0	1	EF

<i>Pachycondyla cavernosa</i>	14	13	RF; PF
<i>Pachycondyla pumicosa</i>	15	10	EF

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**Appendix S3** Sample-based species accumulation curves of ant assemblages of a) sea level to 900 m above sea level on the western slope, b) 1100 – 1900 m above sea level on the western slope and c) 1700 – 500 m above sea level on the eastern slope.





**Appendix S5** Soil characteristics and ground cover of the sampling sites. Soil characteristics were determined once in October 2002, and ground cover was measured during both sampling periods.

Site	Soil composition (%)				Soil variables					Ground cover (%)								
	Rock	Clay	Sand	Silt	P	NO <sub>3</sub>	C	pH	Cond.	BG	Lit	ER	Veg	BG	Lit	ER	Veg	
					(mg/kg)	(mg/kg)	(%)											
											October 2002				March 2003			
0 W	0.00	0.25	98.65	1.10	4.75	2.83	0.24	7.98	2052.50	56.13	13.13	0.00	30.75	59.63	1.75	0.00	38.88	
200 W	0.00	1.10	97.88	1.03	3.50	16.36	0.60	4.10	1595.00	50.63	24.23	0.00	25.75	65.13	8.88	1.25	25.00	
300 W	5.00	2.35	95.38	2.28	2.75	6.46	0.73	4.28	3165.00	44.13	1.38	8.88	45.63	60.63	5.50	5.25	28.63	
500 W	4.00	2.05	95.63	2.33	3.25	9.20	0.90	4.13	2940.00	33.88	7.25	12.00	46.88	43.38	15.00	7.13	34.50	
700 W	6.25	2.20	92.00	5.80	20.00	7.58	1.66	3.73	3165.00	25.38	2.25	29.63	42.75	17.00	16.25	24.13	42.63	
900 W	5.00	1.93	93.33	4.75	9.75	8.20	1.44	3.68	3170.00	40.75	0.75	20.88	37.63	45.88	1.63	18.75	33.25	
1100 W	14.50	1.70	92.40	5.90	24.75	13.91	1.51	4.50	1847.50	40.25	0.50	20.75	38.50	33.63	3.63	16.88	45.88	
1300 W	6.50	4.05	85.28	7.95	4.50	17.48	1.29	4.28	1600.00	47.50	4.00	16.88	31.63	39.25	1.38	16.38	43.00	
1500 W	10.50	3.50	86.90	7.68	13.50	31.21	2.92	3.53	1602.50	28.88	0.25	25.00	45.88	20.25	0.25	12.88	66.63	
1700 W	5.25	3.25	90.13	5.20	8.00	22.10	2.11	3.35	1530.00	26.38	0.00	32.00	41.63	17.50	1.13	41.75	39.63	
1900 S	1.25	1.80	93.38	4.73	7.50	26.47	1.13	2.95	1190.00	52.25	0.00	16.63	31.13	54.75	3.50	12.00	29.75	
1700 E	14.25	2.58	93.08	5.28	10.25	0.23	1.56	3.30	6847.50	22.25	0.75	48.25	28.75	15.25	2.63	51.63	30.50	
1500 E	5.25	1.83	91.20	5.83	9.00	9.89	1.94	3.18	3270.00	42.00	0.00	25.25	32.75	29.25	0.88	27.50	42.38	
1300 E	4.25	2.53	91.68	6.23	6.50	18.40	1.47	3.03	1732.50	48.63	0.00	13.13	38.25	45.63	0.25	8.88	45.25	
1100 E	0.75	3.33	92.13	4.08	5.25	13.37	0.91	3.13	3707.50	66.75	1.00	0.00	32.25	52.63	9.13	0.00	38.25	

900 E	3.25	4.55	91.45	4.00	8.50	5.58	1.54	3.35	5660.00	55.00	0.00	25.13	19.88	49.88	1.00	25.25	23.88
500 E	21.50	5.43	88.25	6.33	21.25	1.68	0.83	4.50	1860.00	39.25	0.75	49.63	10.38	39.88	9.13	44.13	6.875