

Ants and the enigmatic Namibian fairy circles – cause and effect?

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Abstract. 1. Parts of the Namibian landscape show extensive surface perturbation in the form of long-lived, yet dynamic ‘fairy circles’. While exerting profound ecological effects on 7.3% of the land surface, the origin and nature of these large bare discs embedded in an arid grassland matrix remains unresolved.

2. We found no evidence to support the current hypothesis of a termite origin for fairy circles but instead observed a strong spatial association between fairy circles and large nests of the ant Black pugnacious ant *Anoplolepis steingroeveri* Forel, with much higher ant abundances on the circles compared with the matrix.

3. Aggression trials showed that different colonies of *A. steingroeveri* were located on different circles, and that the species was polydomous.

4. Fairy circles and *Pogonomyrmex* ant nests both have a bare disc surrounding the nest, are overdispersed (evenly spaced), and are associated with elevated soil moisture. Fairy circle soils exhibited a five-fold increase in soil moisture when compared with the matrix.

5. Senescent *Stipagrostis obtusa* (Delile) Nees seedlings were only observed on the circles and not in the matrix, and were found to have a reduction in both root length and number of roots.

6. *Anoplolepis steingroeveri* excavated the root system of both *S. obtusa* seedlings on the disc and *Stipagrostis ciliata* (Desf.) de Winter grasses on the perimeter of the circles, where they tended honeydew-secreting Meenoplidae bugs that fed on grass roots and culms. The bugs occurred almost exclusively on grasses associated with the circles. This ant–bug interaction is a possible mechanism for the observed reduction in root length and number of senescent grass seedlings on the circles.

Key words. *Anoplolepis*, Ant nests, ecosystem engineers, fairy circles, Namibia, *Pogonomyrmex* discs.

Introduction

‘Fairy circles’ are conspicuous biogenic features of Namibian landscapes, whose origin continues to defy explanation. These large circles (2.2–12.2 m diameter, Moll, 1994) are evenly spaced, and typically devoid of vegetation, although embedded in a well-vegetated grassland matrix (Becker & Getzin, 2000; Van Rooyen *et al.*, 2004; Becker, 2007). As seen in aerial images (Fig. 1a, Figure S1), they resemble the evenly spaced, large epigeal discs of *Pogonomyrmex* ant colonies (Fig. 1b) and ‘heuweltjies’ (mounds) of the Southern harvester termite

Microhodotermes viator Hagen (Picker *et al.*, 2006) (Figure S2). They are best developed in deep sandy deposits (although see Becker, 2007) from southern Namibia to southern Angola (Fig. 2), in areas of low (50–100 mm) annual rainfall (Becker & Getzin, 2000). Covering on average 7.3% of the land surface area, they are evenly spaced (‘overdispersed’ – Clark & Evans, 1954), dynamic features of the landscape (exhibiting a genesis and maturity), with senescent circles gradually developing a covering of vegetation (Albrecht *et al.*, 2001) until they fade into the matrix. Some circles have a longevity of at least 22 years (Van Rooyen *et al.*, 2004), with new circles having been noted to arise over an 11-year period (Becker, 2007).

Although the origin of the circles is unclear, their effect on ecosystem processes is consistent with that of ecosystem

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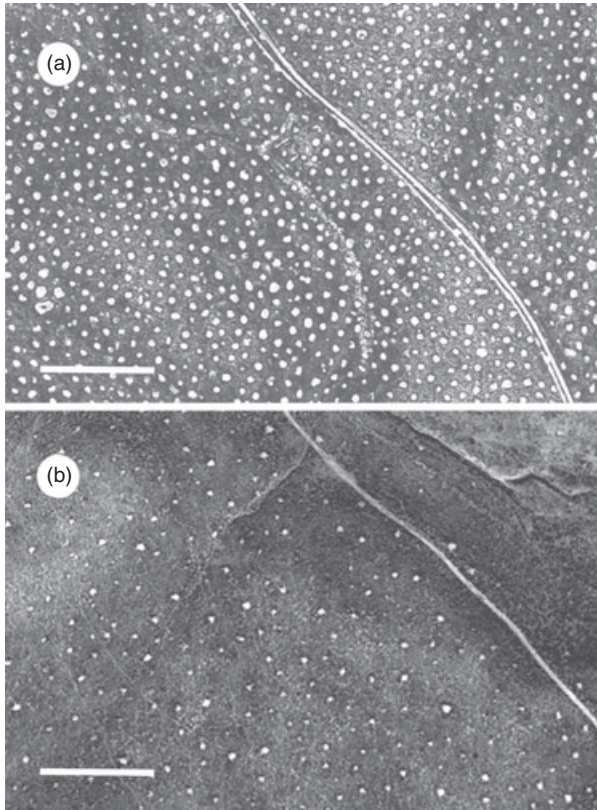


Fig. 1. Aerial images of Namibian fairy circles at Giribes Plain (a) and *Pogonomyrmex* discs at Rodeo, New Mexico (b). Scale bars represent 100 m.

engineers. Termites and ants, classic ecosystem engineers (Elmes, 1991; Dangerfield *et al.*, 1998; Jouquet *et al.*, 2006), produce an extended phenotype, the nest, through their allogenic activities. The most dramatic feature of fairy circles is a bare surface, bounded by a peripheral band of grass tussocks, typically *Stipagrostis giessi* Kers (Theron, 1979; Eicker *et al.*, 1982; Moll, 1994) that is denser and taller than matrix grasses (Becker & Getzin, 2000). Fairy circles thus represent a vegetative discontinuity within the species-poor grassland matrix in which they occur. Although typically bare, they may support a few chlorosed adult or dead seedlings of *Stipagrostis uniplumis* Licht. (ex R & S) (Van Rooyen *et al.*, 2004). These have a reduced number of root hairs lacking vesicular arbuscular mycorrhizae (Joubert, 2008) – fungi that enhance nutrient utilisation and confer drought stress resistance (Bohrer *et al.*, 2003). Germination trials on soils taken from the circles show some growth retardation compared with enhanced growth on perimeter soils (Van Rooyen *et al.*, 2004; Joubert, 2008). Only seedlings grown in soil from outside the circles survived dehydration and re-hydration trials, prompting Albrecht *et al.* (2001) to postulate that soils from inside the circles have a ‘subtle factor’ (generated by termites) that inhibits dehydration resistance.

The initial hypothesis for their origin, namely allelopathic inhibition from the succulent shrub *Euphorbia damarana*

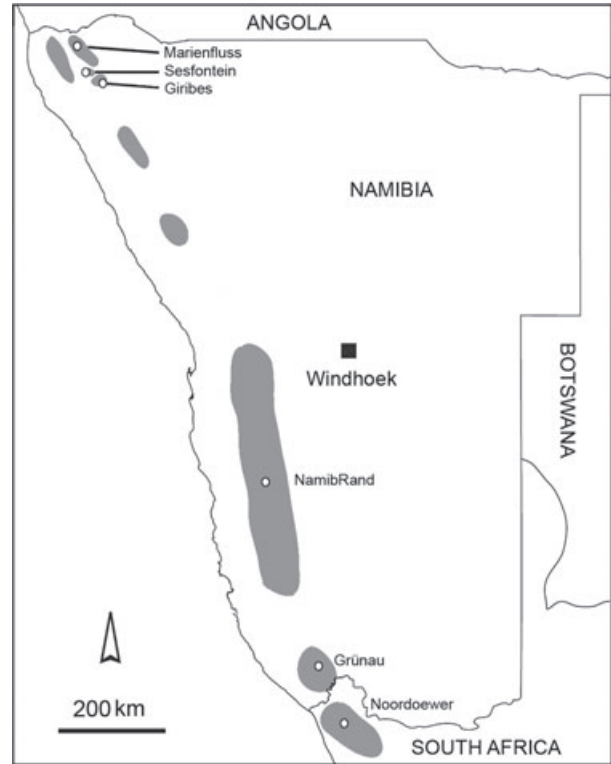


Fig. 2. Study sites (open circles) in Namibia and South Africa, and distribution of fairy circles (grey shading; after Becker & Getzin, 2000; augmented, to include all known records).

Leach (Theron, 1979) is no longer accepted. In its place a termite origin was proposed (Moll, 1994), supported by a theoretical model (Becker & Getzin, 2000) based on behaviour and thermal sensitivity of *Hodotermes mossambicus* Hagen, and the supposition that a semi-volatile chemical that termites produce directly beneath the circles inhibits ‘dehydration-stress resistance’ of the grasses on circles (Albrecht *et al.*, 2001). However, these hypotheses are largely theoretical (Grube, 2002), with no spatial association having ever been demonstrated between circles and termites (Van Rooyen *et al.*, 2004).

The association of fairy circles with social insects was examined to:

- 1 Investigate the spatial association of the termite *H. mossambicus* (the hypothesised progenitor of fairy circles) with Namibian fairy circles for the first time to evaluate the current termite hypothesis for their origin. If this termite species was instrumental in the generation of fairy circles, one would expect high densities of the termite in areas where fairy circles occur, and on a finer scale, a positive association between fairy circles and termite activity patterns, such as foraging ports and soil dumps.
- 2 Assess an alternative hypothesis for an ant origin of fairy circles, as alluded to by Becker (2007). He noted ‘harvesting ants’ collecting seed of the grass *Schmidtia kalahariensis* Stent on bare discs on limestone soils in

Table 1. Description of fairy circle study sites, data collected at each site, and fairy circle dimensions.

| Site | Coordinates | Sampling date | Sampling undertaken | Circle diameter (m) | Circle area (m ²) | Circle eccentricity |
|------------------------|--|--------------------|---|--|---|---|
| NamibRand (sites A, B) | Site A 25°00'40.4"S, 16°00'10.2"E Site B 25°00'05.2"S, 16°01'16.2"E | 12–23 April 2010 | <i>Anoplolepis</i> and <i>H. mossambicus</i> densities (pitfalls) <i>Anoplolepis</i> nest excavation <i>Anoplolepis</i> –bug association Ant communities on fairy circles <i>Anoplolepis</i> colony size estimate <i>Anoplolepis</i> aggression trials | Mean 5.93 SD 1.55 <i>n</i> = 0 | Mean 28.74 SD 14.02 <i>n</i> = 20 | <i>e</i> = 0.60 SD 0.1 <i>n</i> = 20 |
| Marienfluss | 17°22'34.8"S, 12°28'25.3"E | 12–14 October 2008 | Fairy circle and matrix soil moisture <i>H. mossambicus</i> (using soil dumps + foraging ports) and ant densities (nest entrance holes) Association of flowering grasses and fairy circles | Median 5.35 interquartile 1.72 <i>n</i> = 34 | Mean 28.11 SD 13.24 <i>n</i> = 34 | <i>e</i> = 0.53 SD 0.23 <i>n</i> = 34 |
| Giribes Plain | 19°00'58.1"S, 13°19'18.3"E | 16 October 2008 | Observation of ant nest entrance holes on fairy circles | Median 7.28 interquartile 2.1 <i>n</i> = 10 | Mean 47.67 SD 13.71 <i>n</i> = 10 | <i>e</i> = 0.50 SD 0.32 <i>n</i> = 10 |
| Sesfontein | 19°03'29.5"S, 13°31'04.4"E | 15 October 2008 | Association of <i>Messor</i> ant nests with bare discs on stony ground | – | – | – |
| Grünau | 28°03'69.0"S, 18°08'73.9"E | 10, 16 April 2010 | Observation of <i>Anoplolepis</i> and their nest entrance holes on fairy circles | – | – | – |
| Noordoewer | 28°89'00.0"S, 17°73'30.8"E | 9 April 2010 | Observation of <i>Anoplolepis</i> and their nest entrance holes on fairy circles | Mean 6.35 SD 1.16 <i>n</i> = 10 | Mean 39.95 SD 7.26 <i>n</i> = 10 | <i>e</i> = 0.26 SD 0.28 <i>n</i> = 10 |

Namibia, and likened Namibian fairy circles to the bare ellipses formed by the North American harvester ant *Pogonomyrmex occidentalis* Cresson around their nests (Sharp & Barr, 1960). Here we evaluate the hypothesis of an ant origin for fairy circles, and hence, their homology with North American *Pogonomyrmex* discs. If ants were the progenitors of Namibian fairy circles, it should be possible to demonstrate higher concentrations of the dominant and aggressive Black pugnacious ant *Anoplolepis steingroeveri* Forel on fairy circles compared to the matrix over a geographical range (scored by ant and nest entrance hole densities). Further, it should be possible to demonstrate a tight association between *A. steingroeveri* nest entrance holes and fairy circles, compared to the matrix.

- 3 Demonstrate territoriality between *A. steingroeveri* colonies associated with different fairy circles, a basis for the overdispersed spatial distribution of both fairy circles (Albrecht *et al.*, 2001) and *Pogonomyrmex* discs (Alba-Lynn & Detling, 2008).
- 4 Show a uniform size for fairy circles across their geographical range, which would be predicted if they were the product of a single species of social insect.
- 5 Demonstrate higher moisture levels of circles compared to matrix soils, which would be an expected consequence of a large ant nest associated with the circles, as documented for *Pogonomyrmex* ant nests (Wagner *et al.*, 1997).

- 6 Provide a mechanism whereby *A. steingroeveri* could inhibit grass recruitment on fairy circles, hence maintaining the characteristic grass-free disc.

Materials and methods

Study areas

To include spatial patterns of variation, fairy circles were examined at six localities, starting from their southern limit in the northwestern boundary of South Africa (a site 10 km south of Noordoewer, and at Grünau) to their most northerly Namibian distribution at Marienfluss (Fig. 2). Evenly dispersed bare discs resembling fairy circles but occurring on limestone, as opposed to a sandy substrate, were examined approximately 15 km west of Sesfontein. The study sites fall within the Nama Karoo biome, and comprise *Stipagrostis*-dominated grasslands (Van Rooyen *et al.*, 2004). Detailed site information is given in Table 1.

The main study area, NamibRand Nature Reserve, was visited after the summer rains, where work was carried out at sites A and B. This provided a temporal contrast with the northern sites in the arid sandy grasslands of Kaokoveld (Sesfontein, Giribes Plain, Marienfluss) which were visited at the peak of the dry season (6 months after the scant summer rains). At this time of year, all *S. uniplumis* grasses in the matrix were dry, yellow, heavily grazed, and dormant. In contrast, those on the perimeter of all examined circles (*n* = 32), were green and flowering (Fig. 3h).

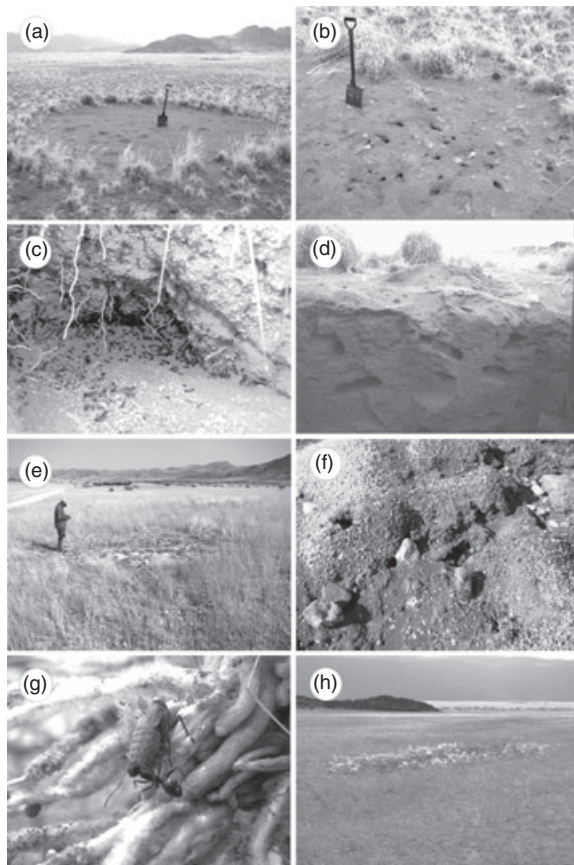


Fig. 3. Features of fairy circles in Namibia. (a) Fairy circle at NamibRand showing well-vegetated perimeter and bare disc, (b) *Anoplolepis steingroeveri* nest openings on the disc of a fairy circle, (c) roots of fairy circle perimeter grasses exposed by ant and small mammal excavation, (d) trenched excavation of *A. steingroeveri* nest on a fairy circle, (e) bare disc resembling a fairy circle on stony ground near Sesfontein, associated with epigeal *Messor denticornis* nest, (f) entrance of *M. denticornis* nest, with white seed husks and plant debris littering the disc surface, (g) Meenoplidae bug feeding on roots of *Stipagrostis obtusa* while attended by worker *A. steingroeveri*, (h) flowering *Stipagrostis uniplumis* on perimeter of fairy circle at Marienfluss.

Association of the termite *Hodotermes mossambicus* with fairy circles

The distribution of the termite *H. mossambicus* was measured on circles and in the matrix at two sites (Table 1) to evaluate the current hypothesis of a *H. mossambicus* origin for fairy circles, for which no quantitative data on termite densities or distribution exists. At Marienfluss, during the dry late summer period of sampling, the foraging activity of the termite was low, thus foraging ports and soil dumps were used to provide a spatial score of their microhabitat utilisation. Surface foraging ports and fresh soil dumps were quantified along 11, 40 m long transects, each starting in the centre of a fairy circle and extending into the matrix. Foraging port density was scored on the surface of 10 further fairy circles, and 10 equal-sized, randomly selected circular areas,

situated 10 m away from circles in the matrix. At NamibRand, *H. mossambicus* was active during the period of investigation, and was sampled using the same pitfall traps as those used to sample ants (see below).

Ant nest associations with fairy circles

Ants were sampled in different ways at the various sites (Table 1). At Marienfluss ant activity was minimal during the period of sampling, possibly as a result of the prolonged dry and hot conditions experienced. Thus ant nest entrance holes were counted on 10 circles, as well as in matched areas of equal dimension to each circle in the adjacent matrix. At Giribes similar conditions restricted the ant census to a count of nest entrance holes on 29 circles and adjacent matrices. At Grünau ($n = 5$) and Noordoewer ($n = 10$) *A. steingroeveri* nests were observed under grasses on circle perimeters.

The association of ants with fairy circles was examined in detail at NamibRand, where ants were active following recent rains. A single sampling unit comprising four pitfall traps was used to sample *A. steingroeveri* on 20 circles, and their adjacent matrices (nine circles at site A, and 11 at site B). Circles were further sub-divided into two areas; a central, bare disc and the well-vegetated perimeter (Fig. 3a). The bare disc, well-vegetated perimeter and the matrix were each sampled using a single sampling unit (i.e. four pitfall traps). Traps in the matrix were placed roughly 7–11 m away from sampled circles, and positioned to be as far away as possible from neighbouring circles. The four evenly spaced pitfall traps comprised 7 cm diameter plastic cups half-filled with soapy water. Pitfall traps were placed in the morning and left for approximately 24 h. For each of the sampled 20 circles and corresponding matrices, the number of ants in the replicate pitfalls was summed. To correct for the increased sampling effort on the circle, those summed values were divided by two, enabling comparisons to be made with the matrix. A Kruskal–Wallis test (performed in STATISTICA 9) was used to compare ant numbers on the disc, perimeter, circle, and matrix. Where a significant difference was found, the Kruskal–Wallis was followed by a multiple comparisons test of the four placements.

A single fairy circle was excavated at NamibRand to examine the nest structure of *A. steingroeveri* and its association with the fairy circles. A 1.5-m long trench was dug across the circle using shovels and a petrol-driven leaf blower. The disc was perforated by numerous conspicuous, wide (ca 5 cm diameter) nest openings (Fig. 3b). Large tunnels leading downward from these holes were followed by inserting a fairly stiff piece of plastic cable into the opening and carefully removing sand from around the tunnel with the leafblower. In addition, the area beneath the peripheral clumps of *Stipagrostis ciliata* (Desf.) de Winter on five circles were excavated using a leafblower, since these were generally utilised by the ants.

In order to estimate the number of *A. steingroeveri* workers in a colony associated with a fairy circle, eight sugar-baited pitfall traps (12.5 cm diameter pots) filled with soapy water were placed near a single active foraging hole on a single circle supporting large numbers of the ant, for a period of 9 days (15–23 April).

Bare discs ($n = 27$) within a grassland on stony limestone near Sesfontein were examined for the presence of the large centralised nest of the ant *Messor denticornis*.

Aggression trials between *Anoplolepis* colonies on adjacent fairy circles

Aggression trials to test for territoriality between colonies of *A. steingroeveri* on different circles were conducted at NamibRand to provide support for the overdispersion of fairy circles within the landscape. Ten foraging worker ants were captured from a circle supporting a colony of *A. steingroeveri*, and stored individually in clean glass vials. Controls were conducted by releasing five of these ants at intervals near to different nest entrance holes, on the same circle from which they had been collected. The responses of the resident ants were noted. This was repeated for five circles. For the aggression experiments, the remaining five ants were released individually onto a neighbouring circle near an *A. steingroeveri* nest entrance hole, and the response noted. If the introduced ant was ignored after initial detection by resident ants, this was scored as a passive response; aggressive responses were characterised by an immediate attack resulting in death. Trials were conducted on 18 neighbouring circles, 16 of which were tested for colony aggression and 2 of which appeared to be inactive. GPS coordinates of circles were plotted using Map Source[®] and Google Earth[®].

Circle dimensions

Circle dimensions and eccentricity scores were taken at NamibRand, Giribes Plain and Marienfluss to compare the size of circles at the different localities. If the circles were constructed by a single species of ant, then circle size and eccentricity should be comparable across sites. As fairy circles were rarely spherical, eccentricity of the ellipse (e) was calculated from the major (transverse or longest) axis (a), and minor axis (b) using the following equation (Berger *et al.*, 1987):

$$e = \sqrt{1 - \left(\frac{b}{a}\right)^2} \quad (1)$$

Values for e range from 0 to -1 , with 0 representing a circle having equal major and minor axes. Areas were calculated using the equation for the area of an ellipse (C), using the approximation of Ramanujan (1914):

$$C \approx \pi \left[3(a + b) - \sqrt{(3a + b)(a + 3b)} \right] \quad (2)$$

Soil moisture

Previous work at NamibRand (Albrecht *et al.*, 2001) indicated that fairy circle soils had higher moisture levels than the matrix. Since this may be attributable to a biological origin, soil moisture content of circle soils was examined in greater detail during the driest time of year (Albrecht *et al.*, 2001 conducted their work after exceptionally heavy rains).

Soil moisture samples were collected in two different ways at Marienfluss (i) from a single point at both the centre and 1 m into the respective matrices, for each of 12 circles to show that the circles have higher soil moisture than the matrix (ii) from two detailed bisecting transects along the shortest and longest axes of a representative circle, extending into the matrix. This was done to map potential gradients of soil moisture extending from a centralised point source on a circle to the perimeter, which would be consistent with soil moisture gradients associated with ant nests (Wagner *et al.*, 1997).

For the first soil moisture sampling method, the 12 circles were selected at 50 m intervals along a single transect. Soil samples were taken either from the depth at which the first visual signs of soil moisture became apparent or in the case where no moisture could be detected (in the matrix), from the depth at which the substrate hardened to rock. Soil samples were immediately stored in sealed 15 ml plastic tubes and refrigerated, before drying for 5 days at 60 °C. The change in mass of reweighed samples provided the % water content.

The second soil moisture assessment examined the spatial distribution of soil moisture of a single fairy circle (1.75 × 2.75 m diameter) and its surrounding matrix. Soil samples were taken at the centre, and then at 0.5 m intervals along each of the two transect lines of the short and long axis, ending approximately 0.5 m beyond the outer perimeter of the ellipse. The transect was truncated 0.5 m into the matrix, as further sampling of soil moisture into the matrix might have been influenced by the proximity of neighbouring circles (mean distance to nearest neighbouring circle for the site was 8.35 m, SD 2.7, $n = 25$; and for the sampled circle 4.7 m, SD 1.22, $n = 4$).

Mechanism for maintenance of grass-free disc of fairy circle

At NamibRand ants were observed tending Meenoplidae bugs on grasses on the circles, and excavating the roots to access the bugs. The exposed roots would likely be subject to thermal and water stress, providing a potential mechanism for limiting grass recruitment on circles occupied by the ants. To evaluate this we examined the spatial association between the bugs and grass roots and the grass root condition on circles and the matrix.

To test for an association between *A. steingroeveri*, the bugs and grass roots, the distribution of bugs on circles was compared with the matrix and was quantified using (i) seedling grasses on the disc, and (ii) perimeter *S. ciliata* grasses. For the seedling grasses, the number of Meenoplidae bugs and *A. steingroeveri* associated with roots and culms was compared on the disc and corresponding matrix of nine circles. For the perimeter *S. ciliata* grasses, the association of ants and bugs on the roots of four carefully uprooted grass clumps were noted on each of 30 circles and their adjacent matrices (ant presence was estimated on a scale of 0–4, with 0 = absence, 4 = ants present under all four clumps). Bug abundance and ant presence on and off circles, were compared using Mann–Whitney tests, and the association of bugs and ants was tested using a contingency table. Bugs were also recovered from the pitfall traps used to sample ants

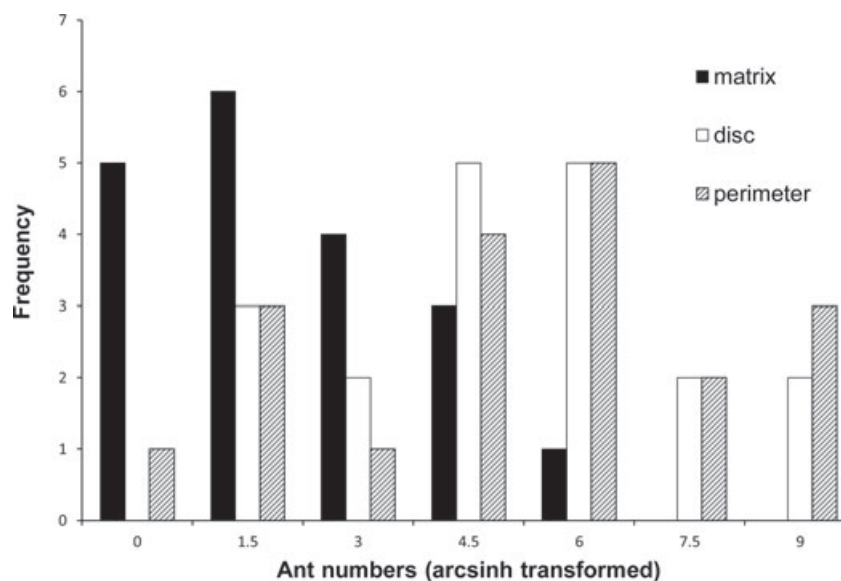


Fig. 4. Frequency distribution of *Anoplolepis steingroeveri* ants showing higher numbers on fairy circles compared with the matrix.

and termites. However, they were poorly sampled using this method (five individuals from circles and one from the matrix), and this data was not used further.

To investigate root and associated grass condition on and off fairy circles, five small replicate *Stipagrostis obtusa* (Delile) Nees seedlings from the three categories; stressed on circle (chlorosed or greying), healthy on circle, and healthy in matrix were sampled from 20 fairy circles and corresponding matrices. For each plant the maximum root length and the total number of roots were recorded. An analysis of variance (ANOVA) was used to compare root length data (square root transformed), and a Kruskal–Wallis test to compare the number of roots for each plant. Tukey HSD and multiple comparisons *post hoc* tests were performed respectively.

Unless otherwise stated, comparison of means was performed using independent sample *t*-tests, Wilcoxon signed-ranks tests, Mann–Whitney *U*-tests, and *z*-tests (STATISTICA 9).

Results

Association of the termite *Hodotermes mossambicus* with fairy circles

At NamibRand the termite *H. mossambicus* was rare in pitfalls at site B (seven individuals collected over the entire 12-day sampling period), and absent at site A. At Marienfluss *H. mossambicus* was more abundant, with termite activity (soil dumps and foraging ports linear m^{-1}) restricted to the matrix, where mean density of termite soil dumps was 0.22 linear m^{-1} (SD 0.15), with none present on the circles. Similarly, there were very few termite foraging holes on fairy circles (mean 0.30, SD 0.95 per circle, $n = 10$) compared with densities nearly 20 times greater (mean 5.3, SD 8.02, $n = 10$) in the matrix ($z = 2.2$, $P = 0.027$). This translates to 0.01 foraging holes m^{-2} on circles, compared with 0.19 m^{-2} in the matrix.

Ant and ant nest associations with fairy circles

Eleven species of ants were recovered from pitfalls at NamibRand, only three of which were more abundant on the circles compared with the matrix. Although *Tetramorium sericeiventre* Emery and *Ocymyrmex barbiger* Emery were more abundant on the circle than in the matrix [$H_{(3,55)} = 9.51$, $P < 0.05$, $H_{(3,59)} = 7.84$, $P < 0.05$, respectively], their abundances on circles were 10 and 20 times less than those of *A. steingroeveri*, respectively. At NamibRand, the large Black pugnacious ant *A. steingroeveri* was the most abundant ant on the circles, showing a diel pattern of early morning and late afternoon activity when it foraged for insect prey. In addition to foraging from nest entrance holes on circles, *A. steingroeveri* also aggregated at the bases of grass tufts around the perimeter of the circles, where the area around the grass roots was often excavated (Fig. 3c). This is reflected in the high numbers of *A. steingroeveri* recorded from pitfall traps placed on circle perimeters (median 65.5, interquartile 194.5), the disc (41.0, 109.0), and circle (57.0, 270.4), compared with the matrix (5.0, 6.3) [$H_{(3,71)} = 12.47$, $P < 0.05$]. Similar numbers of ants were trapped from the centre and perimeter of circles (Fig. 4).

Qualitative observations revealed numerous large *A. steingroeveri* nest entrances were evident only on fairy circles (Fig. 3b), never in the matrix. The subterranean nest appears to have two types of entrances, the eccentric cluster of conspicuous, large (ca 6 cm diameter, up to 20 cm long) nest openings, and those situated beneath the peripheral *S. ciliata* grass clumps. The latter were often enlarged by the digging activities of insectivorous mammals foraging on the ants (Fig. 3c), including Bat-eared fox (*Otocyon megalotis* Desmarest) and Aardwolf [*Proteles cristata* (Sparrman)], both of which are known to feed on ants. Nest openings were oval to lunate in shape, and when traced downwards on a trenched circle, revealed a network of wide tunnels (ca 4 cm diameter) and chambers filled with *A. steingroeveri* ants. The tunnels

extended downwards to a depth of 1.2 m into the bedrock (Fig. 3d), at which point the excavation could not be continued further. Excavation beneath the peripheral *S. ciliata* grasses using a leafblower at NamibRand revealed the presence of ants and associated brood at 16–27 cm depth. Repeated pitfall trapping over a 9-day period from an *A. steingroeveri* nest on one fairy circle yielded approximately 7400 ants (12.58 g wet weight). Large numbers of ants still persisted on this circle after this destructive sampling.

In other parts of the range of fairy circles, ant activity was also concentrated on the circles. At the southern-most distribution of fairy circles (the two sites near Grünau and Noordoewer), *A. steingroeveri* also occurred under the peripheral *S. ciliata* grass of circles. At the northern sites (Marienfluss) there was minimal ant activity in late summer, however the distribution of ant nest entrance holes showed the same pattern of greater densities on the circles (mean 20.3, SD 18.2) compared with the matrix (mean 2.3, SD 3.91; $z = 2.8$, $P = 0.005$), as observed at NamibRand. At Giribes ant nest entrance holes were situated exclusively on the circles.

Smaller, bare ellipsoid discs occurred in grassland to the west of Sesfontein on outcropping limestone bedrock (Fig. 3e), each comprising a large central epigeal colony of the seed-harvesting ant, *Messor denticornis* Forel. The centralised mound on each of the 27 observed circles comprised ant-worked soil, tunnels, and large quantities of white seed husks and *M. denticornis* exoskeletons (Fig. 3f).

Aggression trials between *Anoplolepis* colonies on adjacent fairy circles

There were routine aggressive interactions between foraging trails of different colonies of *A. steingroeveri*. In the experimental trials, controls consistently revealed a lack of aggression by resident ants to an introduced member of the same colony, irrespective of the locality of the nest entrance used on the test circle. The results of between-circle aggression trials showed that a single colony could occupy more than one circle. Colony 1 inhabited six adjacent fairy circles, colony 2 seven circles (which formed two clusters of three and four circles, separated by roughly 50 m), colony 3 occupied two adjacent circles, while ants from colony 4 showed aggressive behaviour to ants from all other circles tested, indicating that this colony occupied a single circle (Fig. 5). Where a colony occupied more than one circle, these were connected by foraging trails of workers.

Circle dimensions

The largest circles occurred at Giribes Plain (median diameter 7.28 m, interquartile 2.1, $n = 11$), with those at Marienfluss (5.35 m, 1.72, $n = 34$) being slightly smaller. However, these differences in diameter were not significant ($P = 0.53$, Mann–Whitney U -test). Circles at NamibRand were of similar diameter to those at the northern sites (mean diameter 5.93 m, SD 1.55, $n = 20$). The mean area of circles at Marienfluss was 28.11 m² (SD 13.24 m², $n = 34$), similar to those at NamibRand (mean area 28.74 m², SD

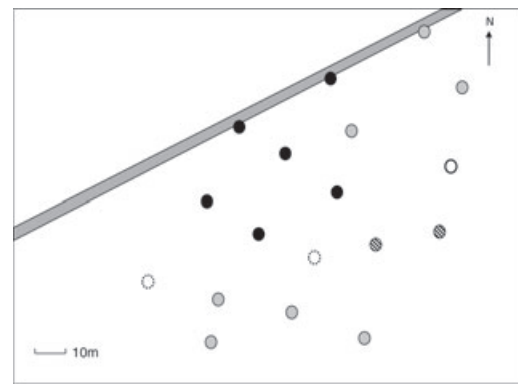


Fig. 5. Polydomy of *Anoplolepis steingroeveri* colonies as revealed by aggression trials between ants of neighbouring fairy circles at NamibRand. Dotted outlines represent circles with very low levels of activity of *A. steingroeveri*, excluded from the aggression trials. Black, grey, bold and hashed circles indicate four separate colonies. The shaded diagonal line represents the adjacent dirt road.

14.02, $n = 20$). Most fairy circles were in fact ellipsoid, and not circular, having similar e values at all measured sites (Marienfluss $e = 0.53$, SD 0.23, $n = 34$; Giribes Plain $e = 0.50$, SD 0.32, $n = 11$; NamibRand $e = 0.6$, SD 0.15, $n = 20$; Noordoewer $e = 0.26$, SD 0.28, $n = 10$).

Soil moisture

Soil samples from the centre of circles had higher soil moisture (median 2.21%, interquartile = 0.67, $n = 12$) than samples taken 1 m outside the circle perimeter (0.45%, 0.14, $n = 12$) ($P = 0.002$, Wilcoxon signed-ranks test). Trenches in the centre of the circle showed the first visual signs of moisture at a mean depth of 0.32 m (SD = 0.21, $n = 10$), while no soil moisture was detected visually in trenches dug 1 m off circles, where the trenching was continued until rock or ferruginised sand was reached, at a mean depth of 0.51 m (SD = 0.05, $n = 10$). Soil moisture gradients showed a clear decline towards the periphery (Fig. 6) where soil moisture was four times lower than at the circle centre, approximating those 1 m off circles.

Mechanism for maintenance of grass-free disc of fairy circle

Examination of grass roots exposed as a result of digging by *A. steingroeveri* revealed the presence of Meenoplidae bugs, attended by ants (Fig. 3g). These bugs commonly occurred both on seedling grasses on the disc as well as on perimeter grasses (typically *S. ciliata*). There were significantly more bugs ($n = 36$) on the surveyed grass roots in the circles [$U_{(9,9)} = 19$, $P < 0.05$] compared with the matrix ($n = 1$). The bugs were always attended by ants.

Many of the perimeter grasses were undermined by large excavations, revealing ants amongst the roots and basal culms of the perennial *S. ciliata* grass. At times these enlarged chambers exposed the roots of the grasses on the periphery (Fig. 3c), revealing the Meenoplidae bugs. These bugs were never found in isolation on circle grasses, but always in

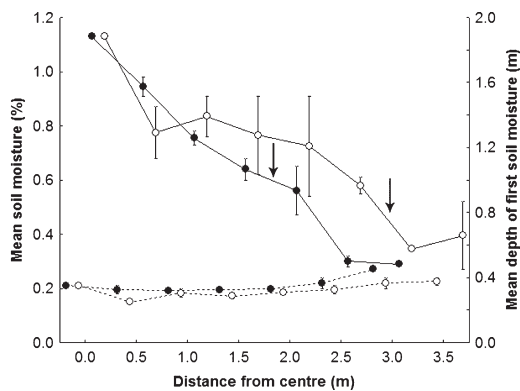


Fig. 6. Soil moisture gradients from the centre to the perimeter of a fairy circle at Marienfluss, Koakoveld. Each value represents a mean of two samples taken along the cardinal axis at the same distance from the centre of the circle. Solid circles, N–S axis; open circles, E–W axis. Arrows indicate perimeter of circle. Dotted lines indicate mean depth of first appearance of soil moisture, solid lines mean soil moisture (and range).

association with ants ($n = 9$ plants), whereas ants also occurred at the base of grasses in the absence of bugs ($n = 10$ plants) [$\chi^2_{(2)} = 9.6$, $P < 0.05$].

Healthy *S. obtusa* seedlings had similar maximum root lengths on the circles (mean = 9.04 mm, SD = 1.85, $n = 100$) and matrices (mean = 10.25 mm, SD = 1.96, $n = 100$) when compared with those of senescing plants found only on the circle (mean = 4.90 mm, SD = 2.12, $n = 100$). Root lengths differed between the three categories [$F_{(2,57)} = 10.68$, $P < 0.001$; ANOVA], and a Tukey *post hoc* comparison revealed that senescing plants on circles had significantly shorter mean root lengths than healthy plants on circles (mean = 2.41, 95% CI [2.24, 2.58], $P < 0.001$) and in the matrix (mean = 2.33, 95% CI [2.18, 2.49], $P < 0.05$).

Additionally, the numbers of roots differed on healthy seedlings on the circles (median = 5.4, interquartile = 2.1, $n = 100$), healthy seedlings on the corresponding matrices (median = 5.2, interquartile = 2.3, $n = 100$), and senescing plants on circles (median = 4, interquartile = 1.25, $n = 100$) [$H_{(2,60)} = 33.85$, $P < 0.001$; Kruskal–Wallis test]. A multiple comparisons *post hoc* test indicated that the senescing seedlings had significantly fewer roots than the healthy plant on circles ($z = 4.33$, $P < 0.001$) and matrices ($z = 5.53$, $P < 0.001$).

Discussion

While previous studies on Namibian fairy circles have focused on local changes in vegetation and soil microbiology, they fail to provide a satisfactory explanation for their origin. The termite hypothesis involving *H. mossambicus* (Moll, 1994; Becker & Getzin, 2000; Albrecht *et al.*, 2001) (currently the most widely accepted theoretical model for fairy circle formation) has been criticised for its lack of supporting data (Grube, 2002). We found a virtual absence of this termite at NamibRand. At the northern sites, *H. mossambicus* activity (assessed by presence of foraging ports) was nearly 20

times lower on the circles compared with the matrix, and soil dumps (evidence of tunnel building) were only present in the matrix. This incongruent spatial association of circles with *H. mossambicus* activity, as well as the very low densities of the termite from areas where fairy circles occur (viz. at NamibRand) does not provide empirical support for the termite central-based foraging model of circle formation (Becker & Getzin, 2000). Additionally, recruitment of annual grasses would soon cover the bare surface of circles in the absence of a permanent association of termites with each circle; however, the majority of ‘active’ circles remain largely grass-free over time (Becker, 2007).

Instead, we found a strong spatial association between fairy circles and nests of the ant *A. steingroeveri*. At NamibRand there were 10 times more ants collected from circles compared with the matrix, suggesting that *A. steingroeveri* colonies were situated on the circles and not in the matrix. This was further supported by the presence of large diameter nest entrance holes of *A. steingroeveri* located eccentrically on each circle, indicating the position of the main portion of the nest. An excavation traced these large diameter nest entrance holes down to a depth of 1.2 m into the bedrock, revealing substantial numbers of ants in the network of tunnels at this depth. A central nest containing brood was not located, possibly because this was situated below the bedrock. However, each circle had aggregations of *A. steingroeveri* and brood beneath the large peripheral *S. ciliata* grass clumps. The *A. steingroeveri* colonies are evidently large, as revealed by the partial trapping out of a single colony on a circle, where 7400 ants (12.58 g wet weight) were trapped over a 9-day period (mature colonies of *Pogonomyrmex barbatus*, Smith) comprise ca 12 000 individuals; Gordon, 1995). The association of *A. steingroeveri* with fairy circles was also apparent at other (southern) sites. At the northernmost sites ant nest entrance holes were concentrated on the circles, and not in the matrix.

This association of large colonies of *A. steingroeveri* with fairy circles might indicate (i) this ant species is preferentially attracted to pre-existing circles (ii) that the circles are engineered by the activities of colonies of this ant. If *A. steingroeveri* only established colonies on pre-existing circles, and not the matrix, there would need to be demonstrable benefits to the ant. More importantly, this still leaves the origin of the circles themselves without an explanation. Alternatively, if *A. steingroeveri* was the progenitor of the circles, this would require various lines of support consistent with the known impact of ants on soils in the immediate vicinity of their nests. The phenomenon of large-diameter bare discs surrounding ant nests is well-documented. *Pogonomyrmex* ant nests have large bare discs of 5.5 m diameter surrounding their nests (MacMahon *et al.*, 2000), of similar dimension to the Namibian fairy circles at our study sites, where fairy circle diameter was found to be similar across their latitudinal range (Giribes – 7.17 m, Marienfluss – 5.55 m, and NamibRand – 5.93 m). In Namibia the seed-harvesting ant *M. denticornis* also produces large bare discs (up to 5 m diameter; Becker, 2007) subtending the conspicuous epigeal nest (Marsh, 1986), thus prompting Becker (2007) to regard the

North American *Pogonomyrmex* discs to be 'an obvious analogy' with both fairy circles and *M. denticornis* discs.

There are a number of similarities between *Pogonomyrmex* discs and Namibian fairy circles:

- 1 Both are regularly spaced, with similar overdispersion values of 1.17 (*Pogonomyrmex* discs; Alba-Lynn & Detling, 2008) and 1.68 (fairy circles; Albrecht *et al.*, 2001). Inter-colonial aggression between nests of social insects remains the most parsimonious explanation for the high overdispersion values associated with fairy circles. We observed high levels of aggression between colonies of *A. steingroeveri*, providing the first evidence that could explain the overdispersion of fairy circles. These aggression trials also revealed *A. steingroeveri* to be polydomous, with only a single colony inhabiting a circle.
- 2 Both fairy circles (Eicker *et al.*, 1982) and *Pogonomyrmex* discs (Whitford & DiMarco, 1995; Wagner *et al.*, 1997; Zaragoza *et al.*, 2007) have elevated moisture compared with matrix soils. We observed elevated fairy circle soil moisture levels 8 months after the last (scant) summer rains, which showed a striking and sudden five-fold drop from the circle centre to matrix soils. This is unlikely to be a result of differential water use and transpiration by matrix grasses (Walter, 1971) which become dormant during the dry season.
- 3 Enhanced growth of perimeter vegetation is a characteristic of both *Pogonomyrmex* discs (MacMahon *et al.*, 2000) and fairy circles (Theron, 1979; Moll, 1994), likely a result of enhanced soil moisture and nutrients (Nicolai & Smeins, 2008; Whitford *et al.*, 2008). This could also explain the observed actively growing and flowering *S. uniplumis* grasses on circle perimeters at the northern sites at the driest time of the year, when the matrix grass was either dead or dormant.
- 4 Both *Pogonomyrmex* colonies (MacMahon *et al.*, 2000) and fairy circles have a cyclical growth pattern, with senescent circles becoming overgrown with grass and disappearing into the matrix (Albrecht *et al.*, 2001; Becker, 2007). This pattern matches the establishment, maturity, and death of ant colonies, with fairy circle longevity (at least 22 years – Van Rooyen *et al.*, 2004) corresponding with that of colonies of seed-harvesting ants [15–20 years for *Pogonomyrmex* – Gordon, 1995; 15 years for *Messor capensis* Mayr, Dean, 2006].
- 5 Ant colonies surrounded by bare discs are able to maintain this vegetation-free disc in various ways. In *Pogonomyrmex*, workers ants employ both fastidious vegetation-removing activities and seed clearing (Alba-Lynn & Detling, 2008; Nicolai & Smeins, 2008). *Anoplolepis steingroeveri* was not observed to clip vegetation. However, it excavated the roots of both seedling grasses on the fairy circle disc, and perennial perimeter *S. ciliata* grasses. Senescent *S. obtusa* seedlings were only observed on circles, and had a reduction in both root number and length compared with healthy seedlings on both the circles and the matrix. This suggests that the compromised root system is related to plant senescence (senescent seedlings were never observed in the matrix).

Since *A. steingroeveri* was observed to excavate seedling roots to access Meenoplidae bugs, this is a potential mechanism for the observed root damage, and subsequent senescence, through exposure of the roots to thermal and water stress. Many seedling grasses on the circle discs were excavated by ants, to the extent that they were typically anchored into the soil by a single or few roots. Meenoplidae bug abundance was far greater on circles compared with the matrix, where they always occurred in association with ants. This association likely provides these primarily carnivorous ants with a major source of carbohydrate in the form of honeydew. The additional excavation by *A. steingroeveri* of the inner side of the perimeter grasses (augmented by that of burrowing mammals) resulted in extensive root exposure, and could account for the observed death of the inner part of the grass clump. This might provide a mechanism for circle expansion, brought about by outward vegetative propagation of the perennial *S. ciliata* (Danin & Orshan, 1995). However, manipulative field experiments utilising ant exclusion would be required to confirm this postulated process. The bare disc of fairy circles would also likely trap fewer of the feathery, wind dispersed seeds of *Stipagrostis* grasses than the matrix, further reducing seedling recruitment on the circles. While the bare discs surrounding the nests of *M. denticornis* resemble fairy circles, the mechanism for their formation may differ to that proposed above for *A. steingroeveri*.

Most recently a geochemical origin has been postulated for fairy circles (Naudé *et al.*, 2011). This was based on elevated levels of microseepage of gases, and the presence of saturated alkenes in the soil on fairy circles, compared with the matrix. This hypothesis does not address the uniform size, or characteristic overdispersion of the circles, which show an even spacing pattern typical of the results of intraspecific competition between sessile organisms. Of greater interest was their detection of higher levels of alkanes and alkenes in the soils of fairy circles, which they attribute to microbial activity. Saturated alkanes (and to a lesser extent, alkenes) are the major component of the Dufour's glands of ants (Katzav-Gozansky *et al.*, 2008), and are used for chemical signalling in a variety of behavioural contexts such as alarm pheromones and laying of foraging trails. Given the association of large colonies of *A. steingroeveri* ants with the fairy circles at NamibRand, it is possible that these ants were the source of the alkanes and alkenes detected by Naudé *et al.* (2011).

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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Figure S1. Fairy circles at NamibRand Nature Reserve, with dirt road intersecting dry river bed (from Google Earth 6.1, 2010 image).

Figure S2. Mounds ('heuweltjies') of the Southern harvester termite *Microhodotermes viator* in Succulent karoo biome, Northern Cape Province, South Africa. (photograph ID: Job number 1026, strip number 9, photo number 3103, year 1997, Spatail Information Services, Survey and Mapping, Rosenbank, South Africa).

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