

**THE ECOLOGY OF NAMIBIAN FAIRY CIRCLES AND THE
POTENTIAL ROLE OF SAND TERMITES (*PSAMMOTERMES
ALLOCERUS SILVESTRI*) IN THEIR ORIGIN**

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DECLARATION

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ABSTRACT

Regularly-dispersed patterning in the landscape occurs globally, both in the form of vegetated patches or gaps of bare earth within a vegetated matrix. Most theories link these periodic patterns to various biotic factors including selective grazing, allelopathy, nests of social insects, and competitive interactions between plants ('self-organisation'). Fairy circles are perhaps the most archetypal of these patterns, taking the form of evenly-spaced, circular to elliptical barren patches 2-12m in diameter. They occur in dense fields within sandy, species-poor grasslands in the Pro-Namib Desert. Fairy circles often display a well-vegetated peripheral ring of grasses and have been shown to retain higher levels of soil moisture compared to the surrounding matrix soils. They can persist in the landscape for decades, and show evidence of birth and senescence, when the bare disc becomes overgrown by grasses and fades back into the matrix. Since the 1970's several hypotheses have been forwarded for their origin including; herbivory by the termite *Hodotermes mossambicus* (or the release of volatile chemicals from their nests), the excavation of grass roots by a widespread and common ant species, an allelopathic chemical released by *Euphorbia damarana* plants, geochemical gas seeps, plant self-organisation, and nest building activities of the Sand termite *Psammotermes allocerus*. A consensus has yet to be reached regarding the origin and nature of fairy circles, and the two theories currently receiving the most attention and debate are the Sand termite hypothesis and plant competition hypothesis. The latter proposes that short-range facilitation of plant growth occurs within the matrix and on the periphery of fairy circles, while long-range competition for resources (primarily water) by *Stipagrostis* roots inhibits plant growth on the bare disc thus generating the regular bare patches. The Sand termite hypothesis states that the termite *P. allocerus* creates and maintains a bare patch around their polycalic nests primarily through central-based foraging on grass roots and culms.

This thesis aims to test the Sand termite hypothesis for fairy circle formation as well as expand on the ecology of fairy circles. Novel features relating to their ecology which are examined include: (1) various potential mechanisms for maintaining the circle's bare appearance (specifically examining seed banks and excavation of seedlings by ants), (2) changes in circle density and size in relation to environmental variables at a local scale (including soil properties and vegetation cover/type), (3) their ontogeny, lifespan and survival, (4) the high degree of spatial ordering seen in fairy circles, (5) soil properties on fairy circles compared to the surrounding matrix (including particle size, temperature, moisture, pH and electrical conductivity) and (6) the influence of fairy circles on nearby plant and insect communities. Fieldwork for the above was carried out in NamibRand Nature Reserve, Southwest Namibia. The specific objectives and experimental approach of this thesis are outlined below:

1. Plant communities on circles were compared to those in the surrounding matrix and the potential processes that maintain the bare surface of circles investigated (Chapter 3). A reduced seed bank on the circle bare disc was hypothesized to have been the cause of a lack of grass seedlings on the circle. To investigate this *Stipagrostis* seed banks were examined from the bare disc, peripheral band and matrix. Another potential mechanism for bare disc maintenance was the excavation of grass roots on the circle by the ant *Anoplolepis steingroeveri* in order to access a mutualistic honeydew producing Meenoplidae bug which fed off *Stipagrostis* roots. Abundances of this ant on and off circles was quantified and its nests excavated on circles in order to determine if *A. steingroeveri* was spatially linked to fairy circles. The presence of *A. steingroeveri* and the meenoplid bugs was compared under grass tussocks on the circle peripheral band and matrix to determine if their mutualistic relationship was most prevalent on circles. The effects on grass seedlings of ant excavations in proximity to their roots was measured by comparing the root and leaf number and length of excavated seedlings on circles with those which had not been excavated on both circles and matrix. Lastly aggression trials were conducted between *A. steingroeveri* nests on neighbouring circles to establish whether each circle contained separate colonies or whether this species was polydomous with many interconnected nests, each on separate circles.
2. The hypothesis that fairy circles represent surface manifestations of the nest system of the subterranean termite species *P. allocerus* was tested, whereby the mode of central-based foraging (enveloping grasses near its nest in sand sheetings and killing the grasses by feeding on their roots and culms) would result in circular grass-free areas surrounding the nest (Chapter 4). The presence of the termite and their sand sheetings was matched with four recognised developmental stages of fairy circles (new, young, mature and senescent circles). In order to confirm the tight spatial relationship of *P. allocerus* with fairy circles, termite abundances were measured in the matrix and on each circle developmental stage. The ability of *P. allocerus* to feed upon and eventually kill living grasses was tested in the laboratory using herbivory trials.
3. The highly overdispersed spatial pattern demonstrated by fairy circles was compared with similar structures made by social insects elsewhere, with intra-colony territoriality between separate colonies considered to be the mechanism for the regular spacing of the colonies (Chapter 5). Google Earth images of *Macrotermes* mounds, South African heuweltjies and American *Pogonomyrmex* ant discs were used to create pair correlation dispersion plots and other measures of dispersion, which were then compared with those of fairy circles as well as with evenly spaced vegetation spots and gaps from Sudan. Further supporting evidence for a termite origin for fairy circles at a local scale would be changes in circle density, area and

dispersion in response to local environmental factors including soil properties (soil particle size, soil depth, pH and electrical conductivity) and vegetation characteristics (vegetation cover, grass height and species composition), that are predicted and consistent with the Sand termite biology. This was investigated along a 4 km transect having 30 sites along its length.

4. Estimates of the lifespan, recruitment and survival probability of fairy circles were generated and compared to similar estimates and observations for known examples of termite nests in the literature (Chapter 5). Historical aerial photography from the 1970's were compared with recent Google Earth images of the same localities in two different regions of Namibia (NamibRand and Giribes) to track circle genesis and death. These were then used to model estimates for circle lifespan, survival, recruitment, and the response of recruitment and survival to variations in annual rainfall.
5. Soil properties of fairy circles (including soil moisture, particle size, pH, conductivity and temperature) were compared to those in the matrix under the hypothesis that any observed differences may be associated with circle occupancy, nest construction and soil excavation by *P. allocerus* (Chapter 6). Soil samples were collected from matrix soils and on replicates of each of the four circle developmental stages to compare soil moisture, particle size, pH and conductivity, while soil temperatures of circles and matrices were compared at two depths. Circle temperature was additionally hypothesized to have a potentially negative influence on grass seedlings if it exceeded temperatures in the matrix, and to complement recordings of soil temperature at both sites *Stipagrostis* seed germination and growth was examined in the lab over a range of soil temperatures. Lastly the potential influence of circle surfaces on selected epigeal insect communities was evaluated.

Circles and matrices were found to have a 52.2 % dissimilarity in plant community, with the matrix overall having higher diversity and more species, and the circles containing two unique plant species. As expected the bare disc did not support as diverse a plant community as the matrix, but it did offer a different environment for some species. The *Stipagrostis* seed bank was significantly lower on the bare disc compared to both the matrix (39 times more seed) and peripheral band (70 times more seed), an observation which may be explained by the lack of deposition of grass seed on the barren patch, as well as removal of the wind-dispersed *Stipagrostis* seed from the bare surface of the circles. Though large colonies of *A. steingroeveri* were often found on circles, this was not always the case, and the presence of their nests did not have a strong spatial link with fairy circles across seasons. *A. steingroeveri* presence at grass tussocks typically predicted the presence of the honey-dew secreting Meenoplidae bugs which inhabited grass roots, and though ant-excavated grass seedlings on the circle

fared worse than unexcavated matrix seedlings with regard to shoot length and colour, seedlings on the circle which had not been excavated were in worse condition than excavated seedlings on the circle. Thus *A. steingroeveri* colonies may play a secondary role in the maintenance of the bare disc through some seedling removal, but are not likely to be causative agents for fairy circle origin.

The termite *P. allocerus* and their sand sheetings covering grasses on which they fed showed a tight spatial relationship with the bare disc and peripheral band, with young circles having the greatest abundances of termites (ca. 2 times that of matrix) and grasses covered in sand sheetings (ca. 1.5 times that of matrix). Herbivory trials in the lab demonstrated that *P. allocerus* focussed its foraging activities on the roots of seedlings, and as a result reduced both leaf and root number and killed 33.3 % of seedlings compared to no deaths in the controls. These results can be linked to observations of chlorosed seedlings on circles in the field which also showed a reduction in root number and length compared to those of seedlings in the matrix. Hence *P. allocerus* had a strong spatial association with circles and their maximal abundances coincided with newly developed circles when their foraging activities on grasses in proximity to their nests was hypothesized to be greatest. Once the circle matured and became a bare patch their foraging activities would move to the peripheral band or nearby in the matrix, possibly leading to the increase in size of the circle.

Fairy circle density and area varied locally in response to changes in vegetation and soil properties. Density increased with soil depth and the proportion of sandy particles, while both area and density correlated with increased numbers of the matrix grass *Stipagrostis obtusa*. Both density and area increased with increased number of *P. allocerus* sand sheetings. The degree of dispersion, given as the ratio value R, increased significantly with both higher circle density and size. These results indicate that fairy circles most likely have a biological origin, and lend support for the Sand termite hypothesis - as the preferred habitat for *P. allocerus* consists of sandy soils, and increased vegetation cover would be able to support larger, denser colonies of the termite. That dispersion changed with density and area suggests that it may be mediated by competitive interactions between circle inhabitants. When looking at the dispersion of fairy circles in detail, they were revealed to have a unique and high degree of spatial ordering which corresponds to a hexagonal pattern (ca. 47 % six-sided polygons). Other examples of spatial dispersion of insect nests shared the same spatial pattern characteristics of fairy circles, as did vegetation patterns from Sudan (although none have as high a degree of ordering as in fairy circles,). The higher degree of dispersion seen in fairy circles may be explained by the unusually homogenous landscape in which they occur, while other examples such as termite nests elsewhere may be influenced more by landscape features such as rivers or slopes.

The soil properties of fairy circles were distinctly different from the surrounding matrix. Overall, circles held higher proportions of finer particles than the matrix, and significantly higher soil moisture levels. Both of these observations are consistent with a termite origin, as termites tend to accumulate finer particles for nest construction and maintain moist conditions within their nests. The higher moisture may be the result of reduced evapotranspiration by plants on the bare disc or potentially the active transport of water into the nest from an outside source. Soil temperature was significantly lower on circles (daily average 37 °C) than the matrix (daily average 39 °C), eliminating temperature as an agent that may have been responsible for inhibiting germination and seedling growth on circles. The germination experiments at different soil temperatures indicated that the two dominant grass species, *S. obtusa* and *Stipagrostis ciliata* both had high heat tolerances (upper limits between 47 °C and 50 °C) as well as high optimum growing temperatures (35 °C to 38 °C), which coincided more closely with soil temperatures on the circle. Hence neither water availability nor temperature appeared to limit the growth of grasses on the bare disc, and as such another factor must be preventing the establishment of seedlings. The contrasting microhabitats of the bare disc and peripheral band had varying effects on ant and scarab beetle communities. Ant species richness was elevated in the peripheral band and abundances depressed on the bare disc, whereas the bare disc was associated with elevated scarab beetle species richness, abundance and diversity. Scarab beetles may seek the bare patch for suitable nesting sites, and the ants may be responding to larger populations of prey insects within the peripheral band.

The last section of the thesis (Chapter 7) critically evaluates the Sand termite and plant competition hypotheses in light of the data generated by this study. It concludes that the Sand termite hypothesis is most consistent with ecological observations of fairy circles and is thus currently the most parsimonious explanation for fairy circle origin.

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PUBLICATIONS DERIVED FROM THIS THESIS AND CO-AUTHOR

CONTRIBUTIONS

Due to the resurgence of interest in fairy circle research during the course of the study, it was necessary to publish much of the work as the thesis progressed. The following papers include work presented in this thesis:

1. The role of *Anoplolepis steingroeveri* in fairy circle formation and maintenance detailed in Chapter 3 is published in **Picker *et al.* (2012)**. The majority of data in this publication are my own except for work conducted by M. Picker, V. Ross-Gillespie and E. Moll in Marienfluss, Sesfontein and Giribes Plain on *Hodotermes mossambicus* and ant abundances, soil moisture levels on fairy circles and circle dimensions. The initial concept and fieldtrip was headed by E. Moll, while M. Picker, V. Ross-Gillespie and I were involved in writing the paper.
2. Data on *A. steingroeveri* abundances on fairy circles taken in 2011 and 2012 (Chapter 3), seed bank comparisons on and off circles (Chapter 3), circle life stage descriptions and association with *Psammotermes allocerus* (Chapter 4 and 6), termite herbivory (Chapter 4), age estimates based on life stages (Chapter 5) and ant and scarab community comparisons (Chapter 6) are included in **Vlieghe *et al.* (2015)**. All data in this publication are my own, with co-authors assisting in data collection (M. Picker and V. Ross-Gillespie), analysis (B. Erini and M. Picker), writing (all authors) and concept (M. Picker).
3. Lastly the comparison of fairy circle spatial characteristics with social insect nests and vegetation patterns in the form of Voronoi tessellations, pair correlation functions and other dispersion values (Chapter 5) is published in **Juergens *et al.* (2015)**. These findings are the only data contributed by me for this publication, with some additional literary input provided for the remainder of the paper by M. Picker, B. Erni and I. All other data for the paper and literary inputs were provided by C. Bohn, F. Gunter, J. Oldeland, B. Rudolph and lastly N. Juergens, who coordinated the publication of the paper.

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1 INTRODUCTION

1.1 Abiotic Environmental Factors and Their Influence on Vegetative Heterogeneity

Plants species and communities have an uneven landscape distribution, with multiple interacting biotic and abiotic processes influencing this distribution at varying temporal and spatial scales (Pickett & White, 1985; Dale, 1999). This can result in a patch mosaic, with different patches in the landscape representing varying stages of vegetation senescence and rejuvenation (Remmert, 1991). Though most of these patch mosaics have an unpredictable and random dispersion, when there is an element of predictability they are said to portray a spatial pattern (Dale, 1999). Describing the spatial and temporal characteristics of these patterns and understanding their underlying causative mechanisms may improve the understanding the dynamics of plant communities (Dale, 1999). In many cases the main driving force of these processes is the affect they have on the distribution of limiting resources such as shelter, nutrients, water and light. Water is often cited as the most important of these, with some of the most striking examples of vegetation patterning occurring in water-scarce areas (Valentin *et al.*, 1999; Deblauwe *et al.*, 2008). Usually the patterns resulting from abiotic processes consist of randomly spaced and uneven plant distributions, which are dependent of the existing orientation of the causative agent itself. Some terrestrial abiotic sources of disturbance resulting in vegetation patterning include aeolian processes, such as the formation of mesquite dunelands in grassland areas through sediment siltation in semi-arid environments (Okin *et al.*, 2006), hydrologic processes, for example the formation of polygons in the soil through frost action and desiccation in Arctic regions, where plants initially colonize the more stable edges of the polygons (Ballantyne & Matthews, 1983; Harris, 1990), fire (Dale, 1999), soil development, soil mass movement and topographical relief. These agents generate, amongst others, pillow lava, rock cracks, glacial moraines, gullies, dunes, beach fronts and ridges (Pickett & White, 1985; Dale, 1999; Turner *et al.*, 2001; Saco *et al.*, 2007). Fire regimes show variation in seasonality, dimension, temporal occurrence and behaviour, which has been referred to by Martin & Sapsis (1991) as 'pyrodiversity', with the resultant heterogeneity potentially progressing, slowing or reverting vegetative succession in areas such as California. Fire also plays a crucial role in maintaining the forest-grassland patch mosaic which exists in the savannahs of sub-tropical Africa (Mourik *et al.*, 2007; Bond & Parr, 2010). These C4 grasslands provide ideal conditions for fire (dry, flammable fuel loads corresponding to the occurrence of thunderstorms, fire-stimulated reproductive traits, persistence through resprouting) which deters the spread of fire intolerant forest vegetation that would otherwise outcompete the grassland biome through shading (Bond & Parr, 2010).

1.2 Evenly Dispersed Vegetation Patterns and the Self-Organisation Hypothesis

In some parts of the world, plant communities exhibit dramatic evenly spaced and extensive spatial patterns with intervening bare ground. These include stripes or bands (Thiéry *et al.*, 1995; Ludwig *et al.*, 1999), labyrinths (von Hardenberg *et al.*, 2001), rings (Danin & Orshan, 1995), spots (Aguiar & Sala, 1999; Couteron & Lejeune, 2001; Rietkerk *et al.*, 2002) and gaps (Deblauwe *et al.*, 2008). Most often these are considered to be a result of biotic processes, with their even spacing being a consequence of competitive interactions between the organisms involved in their formation. These biotically induced patterns are more prominent in largely homogenous landscapes (Couteron & Lejeune, 2001), including vegetated bands forming on slopes in wetlands, isolated spots of woody vegetation within savanna grasslands, striped patterns on alpine tree lines and regularly spaced clumps of sedge in marshlands (Rietkerk & van de Koppel, 2007). The biotic processes involved include intra- and inter-specific competition for resources between plants, localised herbivory by macroherbivores or sessile social insect colonies, and indirect modifications of the soil by subterranean organisms (Jones *et al.*, 1994; Lavelle, 2002).

A process known as vegetative self-organisation (vegetative patterning at a community scale) is hypothesized to be the causative factor for various types of spatial patterning such as bands (Fig. 1.1a), spots (Fig. 1.1b) and gaps (Fig. 1.1c) in resource limited or abiotically stressful semi-arid environments including Eastern and Sahelian Africa, Australia and Mexico through a combination of positive and negative plant interactions (Deblauwe *et al.*, 2008). On a small scale, relatively denser patches of vegetation facilitate growth by increasing nutrient availability, elevating water infiltration and lowering evaporation through shading (HilleRisLambers *et al.*, 2001; Bonanomi *et al.*, 2008; Rietkerk & van de Koppel, 2008). This creates a localised positive feedback loop resulting in “islands of fertility” (Schlesinger *et al.*, 1990). An additional consequence of these larger vegetation patches is the accumulation of a greater seed bank, as seeds are less likely to be removed either by water runoff or wind than in surrounding areas with less cover (Aguiar & Sala, 1999; Valentin *et al.*, 1999). Away from the vegetation patch the benefits related to facilitation break down and competition for resources becomes more pronounced. The longer lateral root systems of vegetation within the patches deplete the surrounding bare areas of water and nutrients, inhibiting the subsequent growth of vegetation between patches (Barbier *et al.*, 2008; Rietkerk & van de Koppel, 2008). This interaction between facilitation and inhibition is referred to as propagation-inhibition (Couteron & Lejeune, 2001) or scale-dependent feedback, and can be also be demonstrated with mussel beds, coral reefs and tidal wetland marsh tussocks (Rietkerk & van de Koppel, 2008). Whether the resultant vegetation pattern is spotted, banded or gapped is dependent on both slope and aridity (Couteron & Lejeune, 2001; von Hardenberg

et al., 2001; Deblauwe *et al.*, 2011). Banded patterns occur on gentle slopes and can result from bare areas producing run-off which collects at the front of pioneering patches of vegetation down-slope, eventually leading to increased growth and creating a positive feedback mechanism (Thiéry *et al.*, 1995; Ludwig *et al.*, 2005). In contrast spotted and gapped patterns form on flat ground. Bare gaps occur in more moist areas and vegetative spots under more arid conditions (Deblauwe *et al.*, 2011). The formation of these self-organised patterns depends to some degree on pre-existing landscape heterogeneity to initiate the feedback between facilitative and inhibitive mechanisms. This heterogeneity can take the form of fire, overgrazing (Lejeune *et al.*, 2004), a dominant woody plant species (Aguiar & Sala, 1999), or termite mounds (Bromley *et al.*, 1997).

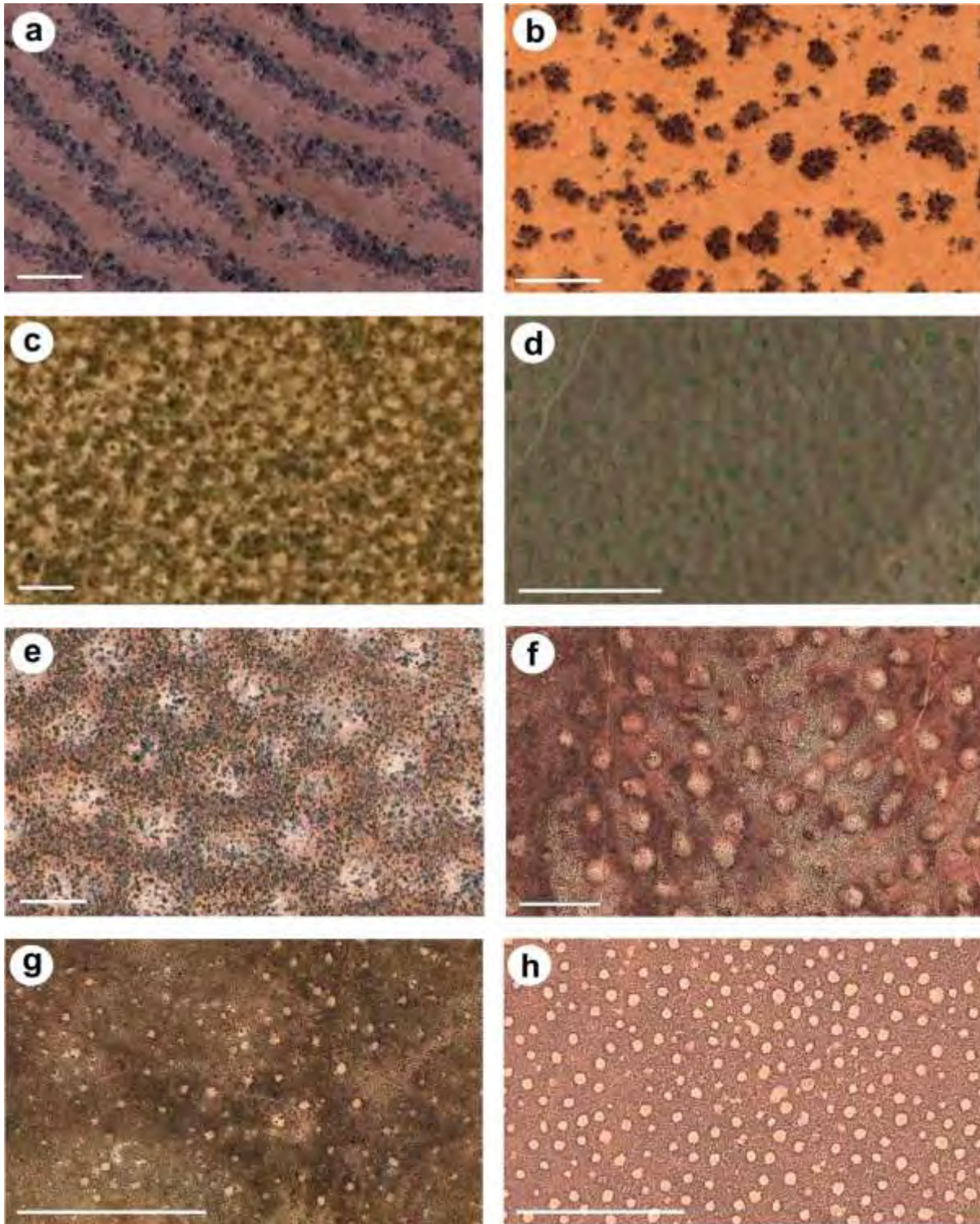


Fig. 1.1. Examples of vegetation patterning in nature (a) banding, (b) spots and (c) gaps in southern Sudan (Deblauwe *et al.*, 2008), (d) mima-mounds in Washington State, USA (Dalquest & Scheffer, 1942), (e) lenticular mounds in Kenya (Darlington, 1985), (f) heuweltjies in the Western Cape, South Africa (Picker *et al.*, 2007), (g) *Pogonomyrmex* discs in Utah, USA (Scott, 1951) and (h) Fairy circles in Giribes, Namibia. Images acquired from Google Earth, imagery date 09/2014. Scale bars represents 100 m.

1.3 Large Mammals and Their Potential Effects on Plant Community Patterns

Various animal species have also been shown to generate both randomly spaced and evenly distributed-vegetation patterns, and can either affect vegetation growth positively (e.g. enhanced growth through the localised accumulation of soil nutrients and physical soil alteration) or negatively (e.g. causing gaps through the active removal, consumption or inhibition of vegetation). Megaherbivores typically generate uneven vegetation patches and gaps and can affect plants through consumption, trampling and the accumulation of nutrients through faeces (Greig-Smith, 1979). The most obvious effect of megaherbivores is a negative one with the selective removal of vegetation in certain patches, creating bare areas. Models have shown that mammalian herbivory can trigger a transition from closed vegetation cover (i.e. no bare patches) to a landscape of vegetative patterning interspersed with bare areas, and eventually to bare soil if plant recruitment is low (HilleRisLambers *et al.*, 2001). However their influences can also be positive. Continued heavy grazing by both hippos and white rhinoceros in the Serengeti and portions of southern Africa on patches of bunch grass eventually produces communities of more stoloniferous grasses known as 'grazing lawns' (Verweji *et al.*, 2006; Waldram *et al.*, 2008). These lawns are maintained as the grazed grass has a higher nutritional value compared to the ungrazed bunch grasses, promoting the return of grazers to particular patches and enrichment via their droppings – these lawns may be maintained for up to 17 years (Skarpe, 1991; Verweji *et al.*, 2006). The lawns may also have a large influence on the fire regime by retarding the spread of larger fires (Waldram *et al.*, 2008). The patchiness of herbivore impacts can be attributed to factors such as their attraction to water, herding behaviour or a preference for previously grazed patches (Adler *et al.*, 2001).

1.4 Examples of Over-Dispersed Vegetation Patterns Linked To Burrowing Organisms

Burrowing organisms, including pocket gophers and soil-dwelling social insects (ants and termites) can produce a variety of striking gapped and spotted vegetation patterns which display uniform spacing. This even spacing is referred to as overdispersion in the biological literature (Clark & Evans, 1954), however the correct statistical term for uniform spacing is underdispersion (for this thesis overdispersion will be used in order to remain consistent with related studies on FCs). Overdispersion is most commonly the result of intra-specific competitive interactions (territoriality) between neighbouring subterranean/epigeal sessile nests or colonies (Cox, 1984; Cushman *et al.*, 1988; Ryti & Case, 1992). This patterning reduces the overlap of foraging area between neighbouring colonies and hence overall competition (Harrison & Gentry, 1981; Pringle *et al.*, 2010). Whether the patterning

is spotted (patches with higher plant productivity than surrounding areas) or gapped (patches lacking vegetation or with lower productivity) will depend on whether the overall influence of the nest and its inhabitants is advantageous (e.g. through the accumulation of nutrients or water) or deleterious (e.g. through herbivory, plant removal or inhibition).

There are several examples of spotted or gapped vegetation patterning believed to be formed by burrowing mammals or insects. In the American Pacific NorthWest, Great Plains, Gulf Coast and California there are large, evenly spaced mounds referred to as mima mounds (Dalquest & Scheffer, 1942; Cox, 1984) (Fig. 1.1d). These mounds can reach 2 m in height and 50 m in diameter, and often support a different plant community to intermound areas (Reichman & Seabloom, 2002). Four primary hypotheses have been postulated to explain their formation, including frost-sorting, erosion, aeolian deposition and fossorial rodents. Newcomb (1940) and Spackman & Munn (1984) postulated that the mounds were fossorial artifacts of cold temperatures triggering the cracking of a frozen silt layer forming large polygons, after which thaw water entered the inter-polygon cracks, froze and expanded. This would result in the long-term accumulation of silt between the frozen polygons to produce mounds, however Washburn (1988) stated that this does not explain mima-mound formation as there is no indication that the climate required to produce this mechanism was present when mounds would have formed. The erosion hypothesis suggested that the mounds are elevated areas left after wind or water had eroded intermound spaces (Cain, 1974). Seifert *et al.* (2009) suggested that mima mounds (which they referred to as 'pimple mounds') in south-central United States were a consequence of aeolian deposition around bush clumps in periods of drought, based on mound structure in relation to the prevailing wind and evidence of drier times in the late Holocene. Cramer & Barger (2014) expanded on this theory of erosion and deposition around vegetation clumps by stating that vegetation self-organisation (similar to that seen for spotted vegetation patterns in other parts of the world (Deblauwe *et al.*, 2008) explains the even patterning of the mima-mounds after the preferential deposition of Aeolian sediment around the vegetation clumps. The most widely accepted explanation for mima mound formation is the burrowing and mound building activities of pocket gophers (Geomysidae) (Dalquest & Scheffer, 1942; Mielke, 1977; Cox, 1984). Supporting evidence for this suggestion includes (i) mima mounds consist entirely of soil material small enough for the gophers to move, (ii) mounds and tunnels conform to the known burrowing habits of gophers and (iii) mima mounds are only found in prairies where gophers are present (Dalquest & Scheffer, 1942). Despite having the ability to reduce large quantities of biomass through herbivory, pocket gophers have an overall positive effect on plant communities inhabiting their mounds (Reichman & Seabloom, 2002). This has been attributed to an increase in the soil's organic matter content, nutrients, aeration and

water holding capacity as well as a decrease in competition for pioneering floral species around the mounds (Mielke, 1977; Huntly & Inouye, 1988; Reichman & Seabloom, 2002).

Large, overdispersed lenticular mounds occur in certain parts of East Africa, and have similarities with the mima mounds of North America, including their large size (10-20 m in diameter and 1.5-2 m in height), densities, uniform dispersion and differing floral communities compared to intermound areas (Cox & Gakahu, 1983; Darlington, 1985) (Fig. 1.1e). Cox & Gakahu (1985) found that the loamier texture of mound soils favoured the growth of palatable grasses on large mounds, and an increase in forbs and shrubs on smaller mounds due to overgrazing of grasses by livestock. The similarities with North American mima-mounds led Cox & Gakahu (1983) to speculate that the East African mounds are a consequence of burrowing rodents, specifically the mole rat *Tachyoryctes splendens* (Rüppell). At study sites in the Kenyan highlands, evidence for the fossorial rodent hypothesis included high mole rat activity on mounds, the presence of a laterite hardpan which creates similar burrowing conditions as the basement layer found in areas where mima mounds exist in North America, and loamier soils than the intermound area which consist of rocks that the mole rats were capable of moving (Cox & Gakahu, 1983; Cox & Gakahu, 1985). Most studies on lenticular mounds however have concluded that they are large termitaria occupied by *Odontotermes* (Glover *et al.*, 1964; Darlington, 1985) or *Macrotermes* (Pomeroy 1977). Glover *et al.* (1964) described 'peacock feather-like' structures on the Loita Plains consisting of a central mounded area inhabited by *Odontotermes*, a ring of taller grass upslope of this which tended to trap run-off, and a down-slope swathe of shorter grasses. Cox & Gakahu (1983; 1985) however argue that lenticular mounds found at elevations above 1 800 m are unlikely to be the nests of fungus-growing termites such as *Macrotermes* as these species are recorded to occur only at lower elevations, and that the vegetation on these mounds is more representative of a burrowing rodent's influence. Darlington (1985) rebutted their argument, finding *Odontotermes* nests in similar mounds at the same study site of the Kenyan highlands. Despite Cox & Gakahu's (1985) claim that termites are unlikely to promote the vegetation cover seen on the lenticular mounds, termites are capable of altering the physical and chemical characteristics of soil, and in this way can increase plant productivity as well as alter plant communities around their nests (Arshad, 1982; Dangerfield *et al.*, 1998; Moe *et al.*, 2009; Sileshi *et al.*, 2010).

In the Western Cape Province of South Africa similar features to lenticular mounds, known as 'heuweltjies' (Lovegrove & Siegfried, 1986) (Fig. 1.1f), have generated substantial controversy and debate regarding their origin and nature. These mounds average 1.5 m in height and 17 m in diameter (Moore & Picker, 1991) and have been estimated to be as long lived as 4 000 to 36 000 years (Moore & Picker, 1991; Midgley *et al.*, 2002; Potts *et al.*, 2009). They generally have a basal calcrete lens, and

show similar-elevated levels of nutrients (including Ca, Mg, P, K and N) to those seen in termitaria (Lovegrove 1991). They also have higher proportions of clay and silt particles compared to the matrix (Lovegrove, 1991; Francis *et al.*, 2012, but see Cramer *et al.*, 2012, who found no significant increase in clay or silt), improved soil aeration and water infiltration compared to intermound soils (Knight *et al.*, 1989; Midgley & Musil, 1990; Potts *et al.*, 2009; Midgley *et al.*, 2012). In an otherwise acidic and oligotrophic landscape, the elevated soil nutrient and water profile of heuweltjies results in them characteristically supporting a different floral community to the surrounding matrix areas (Knight *et al.*, 1989; Midgley & Musil, 1990; Esler & Cowling, 1995). For example, heuweltjies have been shown to support more deciduous and succulent species than off mound soils (Knight *et al.*, 1989; Midgley & Musil, 1990), and have been considered as both areas of rapid adult plant turnover, and of disturbance from which pioneer species can recolonise surrounding areas (Esler & Cowling, 1995). The pioneer vegetation also allows for the succession of long-lived woody plants from matrix to heuweltjie, as the pioneering species either trap seeds or provide seedlings with shelter (Esler & Cowling, 1995). Among the various hypotheses postulated for their origin include geological, vegetative and zoogenic origins. Van der Merwe (1940) proposed that past faulting and folding of the resident Malmesbury shale's limestone horizon produced an uneven landscape which translated as heuweltjies, but this theory has little support. Lovegrove & Siegfried (1986) speculated on a zoogenic origin for heuweltjies based on the distribution and nesting behaviour of both the southern harvester termite *Microhodotermes viator* (Latreille), and the mole-rat *Cryptomys hottentotus* (Roberts). The termite species, which was found on most heuweltjies examined, are proposed to have initially constructed a raised mound which would subsequently be colonised by mole-rats seeking refuge from flooding in the wet season. In the summer months the mole-rats would expand the mound through their outward digging activities and an inward accumulation of soil. Moore & Picker (1991) examined the three-dimensional structure of water-eroded heuweltjies exposed in late summer on the basin of a man-made dam. They were able to identify termite tunnels, storage chambers and a central cavity for the hive, showing for the first time that the internal structure of heuweltjies matched that of typical termite colonies. The low occurrence of mole-rat activity on the earth mounds in this study challenged the claim by Lovegrove & Siegfried (1986) that burrowing rodents played a role in heuweltjie formation. A micromorphological study of particles within a heuweltjie further supported the termite hypothesis, indicating an abundance of organic material that had originated from plant debris carried in by termites, tunnels and galleries with a lining of organic matter, and excrement which matched that of *M. viator* (Francis *et al.*, 2012). Foliage accumulated within the centre of the mounds by the termites and resultant increases in Ca, Mg and organic matter concentrations was suggested to account for a sequence of calcite-sepiolite-silica horizons within the heuweltjie (Francis *et al.*, 2012).

Recently Cramer *et al.* (2012), Cramer & Barger (2014) and Cramer & Midgley (2015) proposed that the earth mounds are the result of differential aeolian deposition around extinct bush clumps which protected the soil around their roots from erosion. This conclusion by Cramer *et al.* (2012) was based on findings of no changes in sand, silt and clay fractions on heuweltjies compare to intermound areas, large stones in both mound and intermound soils, and down-slope slumping caused by erosion. The calcrete hardpans were hypothesized to have formed through increased evapotranspiration underneath the extinct bush clumps which acted as 'island of fertility'. Cramer & Midgley (2015) later compared the presence and absence of heuweltjies with environmental variables in South Africa and concluded that they most often occur in sparse vegetation with high winds speeds, which they took as evidence for aeolian accretion. Cramer *et al.* (2012) considered that the large stones in mound soils could not have been positioned by the actions of termites or rodents, and used this as evidence against the termite hypothesis, However, Moore & Picker (1991) recorded high levels of aardvark excavation on heuweltjies, which may have dug up stones whilst excavating their burrows.

In addition to lenticular mounds and heuweltjies, other species of termite can also produce either gapped or spotted vegetation patterns of varying appearance and spatial scale through the alteration of physical and chemical soil characteristics around their termitaria. The most obvious effect on physical soil properties involves changes in soil particle size and bulk density due to the vertical movement of soil with a smaller particle size from lower soil horizons during termitaria construction (Lee & Wood, 1971). The amount of soil moved can be considerable, as is case for *Macrotermes michaelseni* (Sjöst), which may generate much larger and ecologically important features such as alluvial islands in the Okavango Delta (Dangerfield *et al.*, 1998; McCarthy *et al.*, 1998). These islands are created when rain erodes the large epigeal turret constructed by an established *M. michaelseni* colony to create an outwash pediment (McCarthy *et al.*, 1998). The outwash pediment is expanded by the accumulation of eroded clay from the mound and from soil horizons deep below the ground, and remains in the landscape for a long period of time even after the colony has died. After some time the water retention properties of the pediment, the elevated nutrient enrichment of the termite nest and more importantly the elevation of the large mound above the seasonal flooding level encourages the growth of palatable grasses as well as larger shrubs and trees (Dangerfield *et al.*, 1998; McCarthy *et al.*, 1998), generating bush clumps. The resultant increase in transpiration on the mounds by plants results in the precipitation of calcite from the groundwater, which contributes to the continued growth of the island (McCarthy *et al.*, 1998). A similar example of woody vegetation benefiting from the formation of elevated islands in wetland ecosystems which are possibly formed by termites can be found in Central Brazil, where they are locally referred to as '*murundus*' (Ponce & da Cunha, 1993). In certain termitaria the mound inhibits plant growth as a result of very high soil bulk density, decreasing

water infiltration and increasing soil mechanical impedance (McCarthy *et al.*, 1998; Rogers *et al.*, 1999; Ackerman *et al.*, 2007; Darlington, 2007). This can create circular vegetation-free areas around mounds (Rogers *et al.*, 1999; Ackerman *et al.*, 2007). Darlington (2007) described the evenly spaced, flat, oval patches of bare soil 1-10 m in diameter around the partially subterranean nests of the termite *Odontotermes fulleri* (Emerson) – referred to as ‘arena nests’. The suppressive effect of the compacted mounds is removed when the colony dies (McCarthy *et al.*, 1998; Rogers *et al.*, 1999), and soil porosity, aeration and drainage is restored (Elkins *et al.*, 1986; Konaté *et al.*, 1999). Opposing this suppression of plant growth in the immediate vicinity of the termitarium is a local soil enrichment manifested by enhanced plant growth a few metres away from the mound (Lee & Wood, 1971; Jouquet *et al.*, 2002). Foraged material from a larger area which is brought back to the nest and not consumed, along with other waste such as faeces and corpses, contribute to changes in soil chemistry around the nest and promote vegetation growth (Lee & Wood, 1971; Smith & Yeaton, 1998; Sileshi *et al.*, 2010). Important nutrients for plant growth known to be significantly elevated in termite nests include organic C, N, Ca P, Mg and K (Lee & Wood, 1971; Smith & Yeaton, 1998; Pringle *et al.*, 2010; Sileshi *et al.*, 2010).

In addition to termite-driven changes, circular gapped vegetation patterns can result from some ant species consuming all the vegetation from around their nests, creating a bare disc. The circular appearance of bare areas created by the removal of vegetation by the ants is due to their central-place foraging behaviour, where foraging effort radiates outwards from a localised nest and decreases with distance (Hölldobler & Wilson, 1990; MacMahon *et al.*, 2000). Seed harvesting ants in the genus *Pogonomyrmex* generate evenly spaced gapped vegetation patterns in semi-arid parts of North America (MacMahon *et al.*, 2000) (Fig. 1.1g) which typically take the form of 1-15 m diameter discs devoid of vegetation surrounding a central epigeal nest (Sharp & Barr, 1960; Wight & Nichols, 1966; MacMahon *et al.*, 2000). Vegetation within the disc area is cleared by worker ants (Friese & Allen, 1993). Soil within the disc area is reported to hold higher moisture levels (Wight & Nichols, 1966; Laundré, 1990). This, along with an increase in nutrients around the nest itself (MacMahon *et al.*, 2000; Wagner & Jones, 2006), is thought to be responsible for a peripheral band of enhanced vegetation growth along the edge of the denuded disc (Wight & Nichols, 1966). The peripheral band also has a distinctive plant community when compared to the surrounding matrix, possibly a result of disturbance and seed selectivity by the harvester ants (Soulé & Knapp, 1996; Nowak *et al.*, 1990; Mull, 2003).

Messor ants in semi-arid parts of the world (Arabia - Brown *et al.*, 2012; East Africa - Bequaert, 1922; Darlington, 2007 and southern Africa - Picker *et al.*, 2012) are ecological equivalents of *Pogonomyrmex* and also form bare discs (up to 5 m in diameter) around their nests.

1.5 Namib Desert Fairy Circles – A Controversial Case of Gapped Vegetation Patterns

Fairy circles (FCs) are overdispersed, gapped patterns within arid grasslands, scattered loosely along a narrow band in the Pro-Namib Desert, running from southern Namibia to southern Angola (Fig. 1.1h). They take the form of evenly spaced, roughly circular barren patches within species-poor *Stipagrostis*-dominated grasslands. They are often surrounded by a peripheral band of taller and denser grass (Albrecht *et al.*, 2001; van Rooyen *et al.*, 2004), which may be comprised of the matrix grass or a different *Stipagrostis* species (van Rooyen *et al.*, 2004). FCs typically range in size from 2 m (southern part of range) to 12 m (northern range limit) (Moll, 1994; van Rooyen *et al.*, 2004; Cramer & Barger, 2013; Juergens, 2013). They are generally associated with deep sandy deposits (van Rooyen *et al.*, 2004; Picker *et al.*, 2012; Tschinkel, 2012; Juergens, 2013), but can also be found in lower densities on shallow soils (Becker, 2007) or occasionally on rocky hill slopes. FCs are relatively long-lived features, with an estimated life span of 40-60 years (Tschinkel, 2012). Despite this they are dynamic features, showing evidence of birth, growth and senescence, eventually becoming revegetated and fading back into the matrix (Albrecht *et al.*, 2001; Tschinkel, 2012; Juergens, 2013; Vlieghe *et al.*, 2015).

The origin of FCs is contested by several (mutually exclusive) theories. Theron (1979) initially proposed that dead *Euphorbia damarana* (Leach) plants may release an allelopathic chemical that inhibits the growth of nearby grasses, generating circular patches (halos) after their death. This theory has been rejected on the grounds that the distribution of *E. damarana* and FCs do not overlap and that no allelopathic compound has yet been identified on FCs (Becker & Getzin, 2000; van Rooyen *et al.*, 2004).

Van Rooyen *et al.* (2004) used laboratory bioassays to demonstrate a degree of growth inhibition in soil taken from FCs, and that plants grown in soil taken from under *E. damarana* plants do not demonstrate this inhibition. Joubert (2008) reported on the absence of vesicular arbuscular mycorrhizae on the roots of grasses in the FCs - these mutualistic fungi protect plants from pathogenic infection and facilitate uptake of nutrients and water. Joubert (2008) suggested that the lack of vesicular arbuscular mycorrhizae may lead to decreased drought resistance of plants growing in the FCs, but indicated that this was unlikely to have a large enough effect to be the sole cause of FC formation.

Naudé *et al.* (2011) proposed a geochemical explanation for FC formation through the action of natural gas seeps, based on the detection of elevated levels of gases such as CO as well as saturated alkenes on FCs. This microseepage of gases was postulated to have displaced O₂ from the soil resulting

in anaerobic conditions, as well as altering soil chemical properties such as pH (Naudé *et al.*, 2011), resulting in death of grasses. Higher numbers of anaerobic microbes have been found in FC soils (Eicker *et al.*, 1982) - these were considered as the source of the alkenes (Naudé *et al.*, 2011). However Picker *et al.* (2012) argued that microbial activity is not the only biological source of alkenes, and that alkanes and alkenes are constituents of nest volatiles of some ants, used in chemical signalling (Katzav-Gozensky *et al.*, 2008). Ant nests on FCs have been documented by Becker (2007) and Picker *et al.* (2012). In addition to the above problems with the geochemical hypothesis, it also fails to produce a mechanism that would account for the even spacing of FCs (Picker *et al.*, 2012) or their longevity.

Recently there has been some interest in linking FCs with competitive interactions between plants. The potential link between vegetative self-organisation and FCs was first proposed by van Rooyen *et al.* (2004), who compared FCs with similar gapped vegetation patterns in other parts of the world and to mosaic models generated using the propagation-inhibition and spatial self-organisation model (Couteron & Lejeune, 2001; Rietkerk *et al.*, 2002). They were however unable to provide evidence for such a mechanism with regards to FCs (van Rooyen *et al.*, 2004). Cramer & Barger (2013) revisited this hypothesis and linked FC size, density and landscape occupancy with climate and vegetation characteristics at a regional scale, concluding that they are climate-dependent features formed through the interactions of competition and facilitation of grasses in a resource scarce environment. Tschinkel (2015) conducted four manipulative experiments over six years on FCs to test the hypotheses that a plant inhibiting gas or plant competition maintained the bare disc of FCs. These experiments included laying a rubberised tarp underneath a FC to test for the presence of a toxic subterranean gas, the addition of micronutrients to a FC bare disc, the transfer of soil between a FC and the matrix to detect any inhibiting properties of FC soils, and lastly the creation of artificial FCs in the matrix nearby natural FCs to determine if these would affect neighbouring FCs through plant competition. Although he found no evidence for plant inhibiting substances in the soil, no effect of adding micronutrients and no impacts of artificial FCs on natural ones (hence no evidence for short range vegetation competition feedbacks), he concluded that FCs are formed by long range competitive feedbacks between plants. Using spatial point analysis using satellite imagery, Getzin *et al.* (2014) demonstrated that the spatial patterns of FCs fitted a six-cornered Voronoi cell configuration. They compared this with vegetation patterns generated by the partial-differential-equation model (Gilad *et al.*, 2007). Based on the fit of this model, and by using the spatial structure of FCs and assumptions of existing hypotheses (geochemical seepage, termite herbivory and self-organisation by plants) to generate these patterns, Getzin *et al.* (2014; 2015) concluded that vegetative self-organisation was the best explanation for the observed pattern. However Juergens *et al.* (2015) provide several

arguments against the plant competition hypothesis. These included the paradoxically higher soil moisture on the FC bare disc which would facilitate, not suppress growth), and that the short length of matrix grass roots would not extend to the centre of FC discs. They also argued that a plant competition model would not predict gapped vegetation patterning in the sandy range of FCs due to the low wilting point of sandy soils (Deblauwe *et al.*, 2008), and showed that new FCs were generated in wet (and not dry) years (when plant competition for water would be at its lowest. They finally provided evidence of overdispersed spatial patterns for various social insect nests, and concluded that FCs were also an examples of gapped vegetation resulting from the action of social insects. Most recently Getzin *et al.* (2016) published on the discovery of what they called Australian fairy circles in north-western Australia. These gapped patterns occur within perennial spinifex grasslands, and have the same general appearance and overdispersed patterning of Namibian FCs, yet differ in that they have a significantly higher clay content than the surrounding matrix and lower water infiltration rates (Getzin *et al.*, 2016). They attributed these Australian FCs to vegetative self-organisation through the overland flow of water from the bare patches to the surrounding matrix, inhibiting seedling recruitment and grass growth on the bare patches and at the same time facilitating growth in vegetated areas, and use this as evidence for the similar Namibian FCs having the same causative factor.

FCs resemble North American *Pogonomyrmex* discs and South African *heuweltjies* in that they are all overdispersed, long-lived, circular and hold more moisture than surrounding soils, possibly acting as ecosystem engineers (Becker, 2007; Picker *et al.*, 2012). The first suggestion that FCs were associated with social insects was made by Tinley (1971) who proposed that they were fossilised termitaria. Since then the concept of a termite origin has recurred several times in various guises in the literature. Albrecht *et al.* (2001) proposed that a semi-volatile chemical released by an unspecified termite species may have reduce plant drought resistance and accelerated plant death on FCs. Plants grown experimentally in soils taken along a transect from the centre of a FC into the matrix and subjected to periods of dehydration and re-hydration supported their hypothesis, with plants grown in FC soils unable to survive the dehydration stress when compared to matrix and peripheral band grasses. Linked to this was their finding that grasses on the FCs lacked a sandy root sheath typical of healthy matrix grasses. However the putative semi-volatile substance was never identified. Jankowitz *et al.* (2008) repeated the growth experiment with potted, transplanted grasses buried *in situ* on FCs and found that plants in unsealed pots on FCs performed worse than those grown off the FCs, regardless of whether the soil they were grown in originated from the FC, matrix or peripheral band. However, associating these growth differences with an (unmeasured) environmental variable makes it difficult to support the theory that the compromised growth of plants was related to a gas, and it is possible that there is another explanation for the compromised growth that was not considered by

the authors. Laboratory growth trials conducted by van Rooyen *et al.* (2004) using soil from the FC, peripheral band and matrix also showed some growth inhibition in soils derived from the FC, unrelated to dehydration stress. Van Rooyen *et al.* (2004) could not confirm the lack of root sheaths on *Stipagrostis* grasses reported by Albrecht *et al.* (2001), and could not provide evidence for a growth inhibitory gas.

Moll (1994) suggested that the FCs are a consequence of the foraging activities of termites and concluded that the Northern harvester termite, *Hodotermes mossambicus* (Hagen), was the most likely candidate. This was based on the distribution, nesting and foraging behaviour of this termite and the higher compaction and clay content on FCs which is typical of termite nests (Moll, 1994; Jouquet *et al.*, 2007; Sileshi *et al.*, 2010). However, Moll (1994) did not collect specimens of *H. mossambicus* from the FCs, but did collect the termites *Baucaliotermes hainsei* (Fuller) and *Psammotermes allocerus* (Silvestri). However Moll (1994) did not consider these two species as a potential agents for FC formation due to the restricted distribution of *B. hainsei* (Uys, 2002; Juergens, 2013) and the small nests of *P. allocerus* (Coaton & Sheasby, 1973). Becker & Getzin (2000) developed a hypothetical model of FC formation using the nest structure of *H. mossambicus*, which consists of several subterranean, interconnected hives, over distances of 250 m. Grass harvesting by the termites was hypothesized to result in denuded circular patches surrounding foraging ports. Grube (2002) and van Rooyen *et al.* (2004) argued that the *Hodotermes* foraging model does not reflect the foraging behaviour of *H. mossambicus*, that the termites do not consume entire grass tussocks, and that the model does not account for the inhibition of plant growth on FCs. Becker (2007) subsequently reported on the occurrence of irregular patches denuded by harvester termite activity in other parts of southern Africa, arguing that a specific combination of low rainfall and a species-poor homogenous grassland is necessary for FC formation. He attempted to explain the growth inhibition of plants on FCs through their depletion of organic matter, a major source of nutrients in the sandy nutrient-poor soils where FCs occur (Cramer & Barger, 2013) However Tschinkel (2015) found no significant effect of natural fluctuations of soil nutrients on grass growth. Becker (2007) additionally proposed that 'harvester ants' may be a causal factor in FC formation, and provided images of smaller 'FCs' on rocky ground in Kaokoland which contained seed husks and central ant mounds. These were apparently epigeal nests of the harvester ant *Messor* and are not homologous with FCs (Picker *et al.*, 2012).

Picker *et al.* (2012) examined the spatial association of social insects and FCs and found that *H. mossambicus* presence and activity was unrelated to the FCs, although there were higher numbers of the Black pugnacious ant, *Anoplolepis steingroeveri* (Forel) on FCs. Although this ant does not harvest seeds, the large colonies present on the FCs were found to excavate the roots of grasses

growing on the bare disc as well as along the peripheral band, possibly to access the honeydew resource provided by Meenoplidae bugs that inhabited the grass tufts (Picker *et al.*, 2012). Their extensive excavations at the bases of both seedlings and mature grasses exposed the grass roots and were proposed to lead to the eventual death of the plants. The excavating activities of *A. steingroeveri* were thus suggested to have blocked the recruitment of grass seedlings on FCs, and the constant excavation and death of the peripheral band grasses provided an explanation for FC expansion. The above hypothesis is detailed in Picker *et al.* (2012) is covered in more detail in Chapter 3. Most recently Juergens (2013) provided the first evidence for involvement of the Sand termite, *P. allocerus*, in FC formation through the consumption of grass tussocks around their subterranean nests situated at the base of the grass tussocks. Although the distribution of this termite matches that of FCs, it has been largely overlooked by previous researchers due to the cryptic nature of its small, subterranean nests (Coaton & Sheasby, 1973). Unlike *H. mossambicus*, *P. allocerus* does not forage in the open, and instead encapsulates the roots and stalks of grasses in sand sheetings (Juergens, 2013). He was able to demonstrate large-scale spatial congruence in the distribution of *P. allocerus* and FCs, and locally, in the presence of *P. allocerus* soil dumps and sand sheetings on individual FCs. He additionally found that the number of living grasses on FCs decreased with increased densities of termite soil dumps, concluding that *P. allocerus* was killing grasses on the bare disc by foraging on their roots. Vlieghe *et al.* (2015) also provided evidence for the involvement of *P. allocerus* in FC formation, in the form of an association of termite numbers with FCs at different ages, excavations of *P. allocerus* nests on FCs and laboratory and field observations of the termite's feeding behaviour on grass roots and impacts on the grasses. Juergens *et al.* (2015) provide additional evidence for the Sand termite hypothesis by (1) showing that new FCs appear in wet years (when greater grass productivity would be expected to allow termite colony expansion), (2) showing that the high moisture levels of FCs is isolated to the bare disc and peripheral band and is related to this termites' excavations and 3) by demonstrating parallels between the high degree of overdispersion of FCs and that of other social insect nests. Juergens *et al.* (2015) proposed that the higher levels of alkenes reported on FCs by Naudé *et al.* (2011), along with elevated readings of CO, may be generated by anaerobic bacteria associated with the termite's intestinal tract rather than geochemical gas seeps. The Sand termite hypothesis has received some criticism (Getzin *et al.*, 2015), including that the distribution of *P. allocerus* extends beyond that of FCs, and that termites are not able to produce patterns of such regularity seen in FCs.

Despite their wide distribution and striking appearance in semi-arid parts of Namibia, there is currently a strong dichotomy between the two major hypotheses for FC formation. In this thesis I provide evidence that supports the Sand termite hypothesis for FC formation.

1.6 Thesis Aims and Outline

This study investigates (i) how FCs alter plant communities, and affect grass root structure (ii) whether social insects may be causative agents in FC formation or maintenance, by examining the impact of the Black pugnacious ant *A. steingroeveri* and the Sand termite *P. allocerus* on grass survival, (iii) how habitat heterogeneity at a local scale influences FC area, density and *P. allocerus* abundance (iv) how the high degree of spatial ordering of FCs matches that of other landscape patterns including social insect nests and vegetation patterns, (v) the age, recruitment and survival of FCs and how these are affected by annual rainfall variation, and (vi) how FCs impact soil properties and insect communities on them. Part of the dataset presented in this thesis were published during the period of study, viz. Picker *et al.* (2012), Vlieghe *et al.* (2015) and Juergens *et al.* (2015).

Chapter 3 (the first data chapter) of this thesis examines the effects FCs have on plant diversity, abundance and growth. Plant communities in the matrix and bare disc have yet to be compared quantitatively, though initial observations by previous studies have suggested differences in species prevalence and productivity on the peripheral band (Albrecht *et al.*, 2001; van Rooyen *et al.*, 2004) and the selective use of FCs by some plant species (Juergens, 2013). This chapter also examines the unexplored extent of grass seeds banks on and off FCs. Lastly this chapter investigates the impacts of ant *A. steingroeveri* on grass seedlings on FCs and the spatial association between this ant and FCs. Preliminary studies suggested that *A. steingroeveri* is most abundant on FCs (Picker *et al.*, 2012) and may play a role in either FC formation or maintenance of the bare disc. It is hypothesized that excavating efforts of *A. steingroeveri* to access root inhabiting honeydew producing Meenoplidae bugs may be sufficiently detrimental to cause grass death. The impact of the ant on grass seedlings on FCs was evaluated in terms of damage to roots and shoots (detailed in Picker *et al.*, 2012). Aggression trials were conducted between colonies of the ant on neighbouring FCs to determine if individual FCs were occupied by different ant colonies, which would provide an underlying mechanism for FC spacing

Chapter 4 attempts to provide support for the hypothesis that FCs represent the surface manifestation of the activities of the termite *P. allocerus*. The spatial association of *P. allocerus* with FCs, and its mode of herbivory (described from the field as well as investigated experimentally in the laboratory) are used as a model for FC formation. *P. allocerus* nests, surface sand sheeting structures and abundances on FCs are examined and related to four proposed stages of FC development.

Chapter 5 examines variation in FC area, density and *P. allocerus* abundance in relation to various environmental variables at the landscape scale. Termites occupy landscapes in relation to various species-specific environmental variables, and if FCs are generated by *P. allocerus*, then the

presence, density, size of FCs would fluctuate according to various edaphic and biological parameters. This represents the first study at a landscape scale of how environmental gradients affect FC parameters. Secondly the high overdispersion of FCs is quantified and compared to the spatial ordering of other social insect nests (heuweltjies, *Macrotermes* mounds and *Pogonomyrmex* discs) as well as vegetation patterning (spotted and gapped vegetation in Sudan). Lastly survival and recruitment of FCs are estimated for two sites in response to historic rainfall measurements, under the hypothesis that increased rainfall will have either an inverse or positive effect on FC survival – with an increase providing support for the termite model. Historical aerial images and marked FCs mapped over a period of 3 years are used to provide new estimates for FC ages and compared to other published results.

Chapter 6 examines the effect of FCs on soil properties and insect communities. Changes in soil particle size, soil aeration and higher soil temperatures may create a relatively hostile environment for grasses on the bare discs and maintain the FC's barren surface. Termites are known to aggregate clay and silt particles and increase the soil bulk density, deterring plant growth around their mounds (Rogers *et al.*, 1999; Ackerman *et al.*, 2007). It is hypothesized that this may be the case for FCs, thus creating a surface which deters recruitment of seedlings on the bare disc. Increased temperatures on the exposed bare disc may lead to higher soil temperatures, decreasing the survival of any grasses growing on the FC. The varying microhabitats provided by the bare disc and peripheral band are hypothesised to provide environmental heterogeneity and support different communities of epigeal insects, thus increasing beta diversity.

Chapter 7 integrates the evidence amassed in the thesis to evaluate the current competing hypotheses for FC formation and maintenance, and integrates the features of FCs (from data gathered here and that from published work) with the known biology of termite nest systems.

2 METHODS

2.1 Study Site

Fieldwork was conducted at NamibRand Nature Reserve, south-west Namibia (Fig. 2.1). This reserve falls within the 50 - 100 mm/yr isohyets and consists of both southern Namib sand sea and semi-desert vegetation types (Giess, 1970). Within the reserve high densities of fairy circles (FCs) occur in a flat grassland plain comprised of Namib sand drift interspersed with mountains and inselbergs, as well as in grassy valleys between longitudinal dunes to the west. The grassland is compositionally dominated by *Stipagrostis obtusa* ((Delile) Nees), interspersed with patches of *Stipagrostis ciliata* (Desf.) and *Stipagrostis uniplumis* ((Licht.) De Winter), with *S. ciliata* preferring FC peripheral bands (Cramer & Barger, 2013; Tschinkel, 2015).

Within the reserve three sites were utilised; **A** (25°00'40.4''S, 16°00'10.2''E), **B** (25°00'05.2''S, 16°01'16.2''E) and **C** (25°00'44.8''S, 16°00'17.16''E) (Fig. 2.1). Site B was approximately 2.2 km east of A and separated by a rocky outcrop while site C was approximately 100 m south of A and separated by a sand road. Sites A and C were chosen in order to capture some of the variability present in all four developmental stages of FCs and ensure that they were sampled in sufficient numbers, whilst site B, which was slightly further away, had larger numbers of typical mature FCs used to answer separate sets of hypotheses. Within the area encompassing the three study sites, FCs ranged in size from 2 - 10 m in diameter, with a mean short axis length of 4.54 m (SD 1.01 m, N = 60) and long axis length of 5.59 m (SD 1.45 m, N = 60). Studies were conducted at site B from the 18 February – 5 March 2011 and from the 11 – 20 March 2011, with further studies carried out at all three sites from the 3 – 15 January 2012 and 16 – 24 February 2013. Details of the date and site location of all data collection methods used are given in Table 2.1 The period prior to and during February and March 2011 experienced exceptionally heavy rains (unpublished weather data for the area was provided by NamibRand Nature Reserve), resulting in a dense growth of grasses and annual plants both in the matrix and on the FC peripheral band. In contrast, January 2012 and February 2013 were dry and rains only fell after the study period. At this time the matrix grasses were yellow and dormant with only a trace of greenery visible along the peripheral band. Finally, several FCs were sampled briefly on the 16 January 2012 at a site approximately 40 km south of Grunau, southern Namibia (28°03'69.0''S, 18°08'73.9''E) (Fig. 2.1).

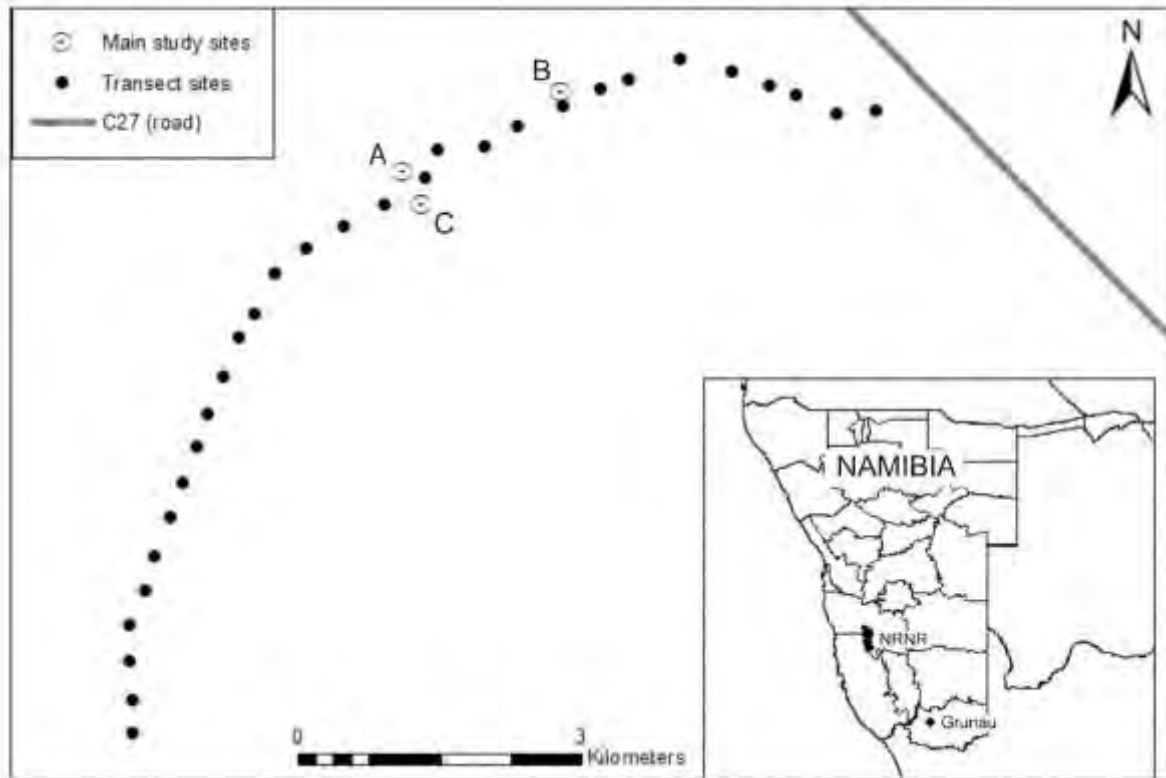


Fig. 2.1. Map showing locality of NamibRand Nature Reserve (NRNR) and study site south of Grunau within Namibia (inset) as well as the three main sites at NamibRand Nature Reserve (A, B and C) and 30 sites used for the environmental transect (black dots) (Section 2.4).

Table 2.1. Details on the sampling date, site and replicate number for each data collection method utilised (chapter section in brackets).

Data Collection Description (Chapter Section)	Sampling Date	Site	Replicate #
Plant community comparison (2.2.1)	Feb. 2011	B	50
<i>Stipagrostis</i> seed banks (2.2.2)	Jan. 2012	B	10
<i>A. steingroeveri</i> abundances (2.2.3)	Feb. - March 2011	B	60
	Jan. 2012	A	25
<i>A. steingroeveri</i> nest excavation (2.2.4)	Feb. 2011	B	3
<i>A. steingroeveri</i> territoriality trails (2.2.5)	March 2011	B	61
<i>A. steingroeveri</i> & Meenoplidae bugs (2.2.6)	Feb. 2011	B	30
Ant excavations of grass seedlings (2.2.7)	Feb 2011	B	15
<i>P. allocerus</i> nest excavation (2.3.1)	Jan. 2012	A	3
FC growth stage descriptions (2.3.2)	Jan. 2012	A & C	10
FC growth stage progression & age estimate (2.3.3)	Feb. 2011, Jan. 2012 & June 2013	B	61
Termite herbivory trails (2.3.4)	Oct. & Nov. 2012	-	10
Grass seedling root comparison (2.3.5)	Feb. 2011	B	20
Landscape factors, FC characteristics & termite abundance (2.4.1 - 2.4.4)	Feb. 2013	NamibRand	30
FC age estimates (2.4.5)	1977 - 2013	NamibRand	ca. 200
	1975 - 2012	Giribes	ca. 200
Growth stage soil moisture and particle size (2.5.1)	Feb. 2013	A & C	10
Soil temperature (2.5.2)	Jan. 2012 & Feb. 2013	B	20
Grass germination temperature pilot 1 (2.5.3)	30 Sept. - 16 Oct. 2011	-	4
Grass germination temperature pilot 2 (2.5.3)	19 Oct. - 3 Nov. 2011	-	1
Long-term <i>S. ciliata</i> germination temperature responses (2.5.3)	26 Nov. - 4 Dec. 2011	-	16
Transplanted <i>S. ciliata</i> temperature responses (2.5.3)	8 - 18 Dec. 2011	-	16
Insect abundances (2.5.4)	Feb. - March 2011	B	60
	Jan. 2012	A	25

2.2 Plant Community Responses to Fairy Circles and Bare Disc Maintenance Mechanisms (Chapter 3)

2.2.1 Plant Community Comparison On and Off Fairy Circles (Section 3.3.1)

Plant communities on FCs and in the surrounding matrix have not been quantified in previous studies, and it was hypothesized that the various factors which may influence plant growth on FCs may additionally affect the structure of plant communities on FCs. To detect changes in plant communities transects were used both on FCs (which included the bare disc and peripheral band) and in the matrix. Transects were marked along the short axis of 50 FCs at Site B from one edge of the bare disc to the other, with a corresponding transect of equal length placed in the matrix equidistant to neighbouring FCs. This means that transect length differed slightly between each FC and matrix pair. FC transects included the peripheral band plant community and ended at the start of the matrix vegetation. The number of each plant species was recorded along 50 cm strips placed perpendicular to the transect at 50 cm intervals. Grasses were identified using Müller (2007) and annual plant species with Mannheimer *et al.* (2008). Identifications were then cross-referenced with the NamibRand Nature Reserve herbarium collection using physical specimens collected in the field (these specimens were not later deposited in a formal herbarium). Multidimensional scaling (MDS) and similarity/distance percentages (SIMPER) analyses were done for the matrix and FC plant communities using a Bray-Curtis similarity resemblance matrix with a $\log(X + 1)$ transformation of data. These analyses, along with Shannon Weiner and Simpson's diversity indices, were calculated in Primer-E (Clarke & Gorley, 2006). Shannon Weiner is potentially a better indice than Simpson's as it takes into account rare species and creates more evenness between species, but both indices are included for comparison.

2.2.2 Stipagrostis Seed Banks On and Off Fairy Circles (Section 3.3.2)

Stipagrostis seed banks were measured on the bare disc, peripheral band and matrix to determine whether a diminished seed bank exists on the bare disc and whether this contributes to its lack of grass seedlings. Surface (plant) debris and the top 2 cm of sand were taken from quadrats of 900 cm² placed on the bare disc, peripheral band and an adjacent area in the matrix of each of 10 FCs. This provided samples of approximately 500 cm³. Samples were stirred into 5L of water, and all plant material was removed from the samples by flotation. The remaining material was dried, weighed and sieved through a 2 mm sieve to remove larger pieces of debris. The sieved material was then weighed and a subsample of 11 cm³ taken and weighed. All *S. ciliata* and *S. obtusa* seeds were collected from

the subsample and number of seeds in the total sieved sample calculated using averaged weights of seeds.

2.2.3 *Anoplolepis steingroeveri* (Formicidae) Abundances On and Off Fairy Circles (Section 3.3.3)

Following the hypothesis of Picker *et al.* (2012) that the ant *A. steingroeveri* excavated nest tunnels under grasses on the FC and compromised their root systems, eventually leading to grass death, abundances of this ant were scored on and off- circles. If this ant's nests were more prevalent on the bare disc than in the matrix, this would provide a mechanism for maintaining a bare surface on the circles. To determine if a spatial relationship existed between the presence of ants and the presence of FCs, abundances of this ant were scored using pitfall traps consisting of plastic cups of 10 cm diameter on FCs and in the matrix. Sixty neighbouring FCs at site B were sampled in February 2011 and 25 FCs and matrices were sampled at site A in January 2012. For each FC the bare disc, peripheral band and an adjacent area in the matrix 7 m away from the FC were sampled with three pitfalls each. Each pitfall was buried flush to the sand surface and filled two thirds with soapy water. Pitfalls were set for two days, emptied and the catch preserved in 96 % alcohol for later sorting and identification. Because *A. steingroeveri* is hypothesised to be associated with the entire FC, including the bare disc and vegetated peripheral band, sampling bias for the total FC was corrected by taking the average between the peripheral band and bare disc totals. An average value for the combined bare disc and peripheral band was used in order to account for the resultant increase in pitfall trap samples which were used in the total circle (eight pitfalls combined) compared to only four in the matrix. This resulted in four locality treatments; matrix, vegetated peripheral band, bare disc and total FC (peripheral band and bare disc). *A. steingroeveri* identification was confirmed using Taylor (2010).

2.2.4 *A. steingroeveri* Nest Excavation and Description (Section 3.3.4)

Nests of *A. steingroeveri* were hypothesised to exist predominantly under FCs. To investigate this, as well as the extent of the nests, three FCs were excavated at site B within the bare disc and under *S. ciliata* tussocks along the peripheral band. A petrol-driven leaf blower (Husquarna Model 356 BTx) was used to remove the upper layer of sand and expose the nest entrances. A fairly stiff piece of plastic cable was inserted into the tunnels leading from these entrances and carefully followed down until bedrock was reached or the tunnels were lost.

2.2.5 *A. steingroeveri* Territoriality and Polydomy (Section 3.3.5)

If *A. steingroeveri* was the agent responsible for FC formation, one would expect evidence of territoriality and aggression between colonies from neighbouring FCs that could then generate the overdispersed pattern of FCs (Ryti & Case, 1986). To test this, aggression trials were used to determine if ants inhabiting different FCs did indeed belong to separate colonies. All *A. steingroeveri* nests on FCs within an area encompassing 61 neighbouring FCs at site B were used to investigate colony territoriality between FCs. Aggressive behaviour between ants from neighbouring FCs would indicate the presence of inter-colony territoriality while a lack of would indicate that this species is polydomic, with a single ant colony inhabiting more than one spatially separated nest (Debout *et al.*, 2007). Five ants were collected in clean polytop vials from a nest entrance and placed one at a time in the proximity of another nest entrance on the same FC to test if each FC housed a single colony. The majority of these nest entrances were found along the periphery of the FCs underneath *S. ciliata* tussocks. The reaction of resident ants to introduced ants was categorized as either aggressive (an immediate attack often resulting in the death of the introduced individual, or with the introduced individual instantly retreating from the resident nest) or passive (no aggression from the resident ants, with the introduced ant not displaying signs of alarm, at times entering the resident nest with no hesitation). Passive responses were interpreted as indicating that nests from which the ants had been drawn belonged to the same colony while aggressive responses indicated the presence of separate colonies. Once it had been established from these control tests that each FC contained a single ant colony, five ants from one FC were collected and introduced in the same way to nest entrances on other FCs. Each FC housing *Anoplolepis* colonies at site B was tested once against all active FCs, regardless of whether they were neighbours or not. The results of these interactions were then mapped on Google Earth as the interpolated extent of each colony.

2.2.6 *Mutualistic Relationship between A. steingroeveri and Grass-Inhabiting Meenoplidae Bugs* (Section 3.3.6)

A. steingroeveri was found to have a strong association with a species of Meenoplidae bug (Order Hemiptera) that inhabited the roots and culms of *S. ciliata*, *S. obtusa* and seedlings of *Schmidtia kalahariensis* (Stent). It was hypothesised that the often vigorous excavations of grass tussocks on the bare disc and peripheral band by *A. steingroeveri* may be related to their attempts to access these Meenoplidae bugs as a honey-dew resource. In order to determine the extent and nature of this association (in relation to FC origin and maintenance), four *S. ciliata* tussocks on each of 30 FC

peripheral bands and corresponding matrices at site B were uprooted and examined for the presence of *A. steingroeveri* and Meenoplidae bugs. The uprooted plants were lowered into 10L plastic buckets and the number of bugs and the presence or absence of *A. steingroeveri* under each grass tussock recorded. The sum of Meenoplidae bugs on each FC and matrix was calculated and the presence of *A. steingroeveri* was given a score of 0-4 (0 indicating no ants found under any of the four grass tussocks on that FC/matrix and 4 representing the presence of ants under all four examined tussocks).

2.2.7 *Effect of A. steingroeveri Excavations on Grass Seedling Condition on Fairy Circles (Section 3.3.6)*

To test whether ant excavation around grass seedlings had a negative enough impact on the grasses to cause grass death, one ant-excavated *S. obtusa* seedling and two healthy seedlings on 15 FCs, as well as two healthy seedlings of *S. obtusa* in 15 localities within the matrix were chosen and marked at site B. Leaf colour (dark green, green, yellow-green or yellow), shoot height, ant presence or absence and number of Meenoplidae bugs on the seedlings were recorded at the beginning of the experiment and then every eight days for 16 days from the 4 - 19 March 2011. At the end of day 16, each grass was carefully excavated and the number of roots as well as maximum root length recorded.

2.3 **Association of *Psammodermes allocerus* with Ontogenetic Development of Fairy Circles (Chapter 4)**

2.3.1 *P. allocerus Nest Excavation and Surface Observations (Results in Section 4.3.1)*

To investigate the hypothesis that FCs are surface features of the subterranean nests of *P. allocerus* formed by their foraging activities around their nests, *P. allocerus* nests were excavated on two FCs as well as one isolated nest in the matrix using the same method described for excavating *A. steingroeveri* nests (Section 2.2.4) at site A. Soil surface signs of subterranean nests were the presence of individual small moundlets resembling those described by Coaton & Sheasby (1973) for *P. allocerus*, and the identity of termites collected from these soil moundlets and excavated nests were confirmed using the key provided by Uys (2002). Visual observations were made on the surface crusting and sand sheetings formed by *P. allocerus* on grass tussocks within the FCs and along the peripheral band.

2.3.2 Fairy Circle Growth Stage Categorisation (Section 4.3.1)

FCs were hypothesised to undergo stages of development linked to the growth of *P. allocerus* colonies. FCs were divided into four broad developmental stages, namely:

- a) New FCs with an even and dense covering of mature but dead grass tussocks which were covered in termite sand sheetings. The dead grass tussocks were still mostly upright but grey, and the FCs lacked well-vegetated peripheral bands (Fig. 2.2a).
- b) Young FCs showing advanced signs of grass herbivory by termites but less obvious than in new FCs, with a more uneven covering of dead grasses compared to new FCs and the tussocks often collapsed and partially dislodged from the soil. The peripheral band usually not well-vegetated (Fig. 2.2b).
- c) Mature FCs with a large bare disc virtually clear of vegetation and possessing an obvious, well-vegetated peripheral band (Fig. 2.2c).
- d) Senescent FCs showing signs of regressing back into the matrix, with at least half the surface occupied by colonising grass seedlings, most commonly along the inner edge of the peripheral band. The well-vegetated peripheral band is usually still evident (Fig. 2.2d).

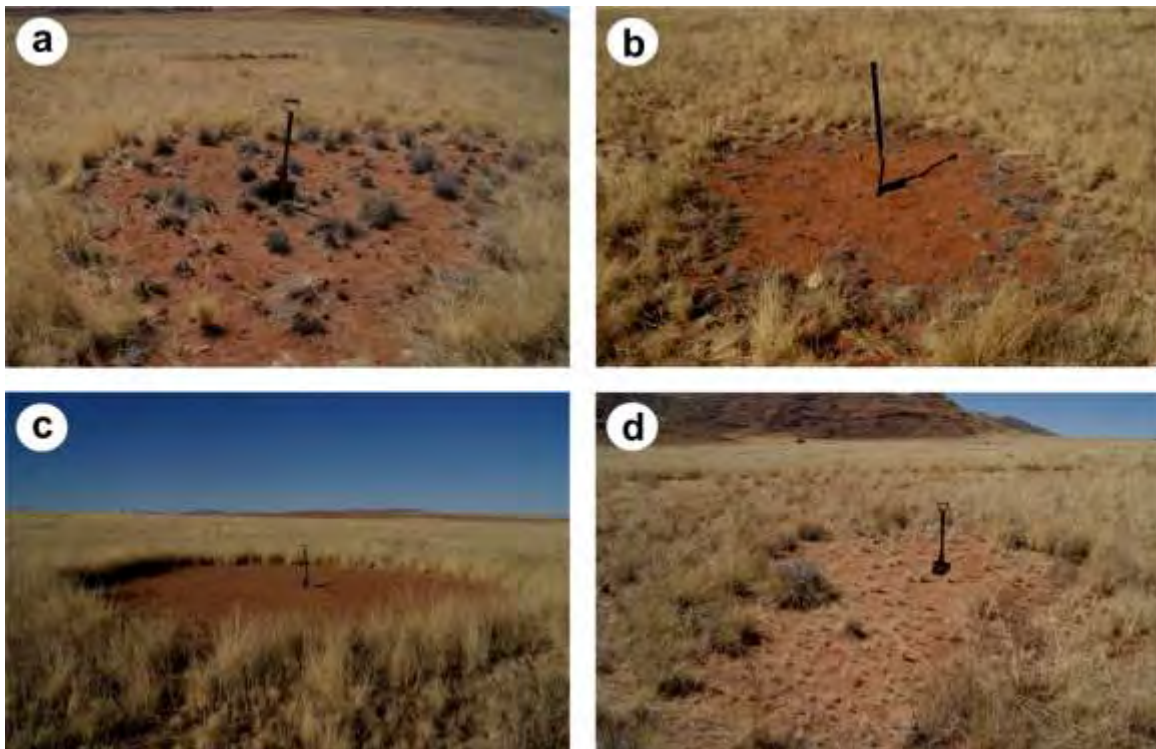


Fig. 2.2. Examples of FC developmental stages (a) new FC consisting of dead, grey matrix grass tussocks covered in termite sand sheetings, (b) young FC with dislodged dead grass tussocks, (c) mature FC with a large bare disc and well vegetated peripheral band and (d) senescent FC covered in recolonising grass seedlings.

2.3.3 *Vegetation, Abundance and Temporal Progression of Fairy Circle Developmental Stages (Sections 4.3.1 and 5.3.5)*

The size, abundance of *P. allocerus*, as well as vegetation cover and condition, were scored for each of the four identified FC developmental stages in order to better describe the defining characteristics of each stage. Ten FCs from each of the four growth stages were randomly selected at both sites A and C, recording the short and long axis length of the bare disc, which were then used to calculate FC area. A transect was marked along the short axis of each bare disc and equal transect lengths marked following the peripheral band as well as 3 m away in the matrix. The number of living grasses (with no sand sheetings) and dead grasses (encrusted with a layer of sand sheeting), as well as grass height of each species, were recorded within a 50 cm wide strip along each of the three transects.

In order to obtain a representation of the relative proportions of the four growth stages in the landscape, four separate transects of approximately 100 m were walked in proximity to sites A and C and each FC encountered on the linear transect scored according to its growth stage.

To test whether FC growth stages differed in their duration, 61 neighbouring FCs from site B were marked in February 2011 (during the rainy season) and revisited in January 2012 (prior to the rains) and in June 2013. For each FC its growth stage categorisation was noted in all three years to track the temporal progression of FC development. Probability matrices were constructed from this transition, and the fundamental matrix $N = (I - T)^{-1}$ (where T is the matrix of transition probabilities and I the identity matrix) was used to estimate age-specific survival (Caswell, 2001).

2.3.4 *P. allocerus Laboratory Herbivory Trials (Section 4.3.2)*

Laboratory feeding trials were conducted to investigate the mode of feeding and potential damage to grass seedlings by *P. allocerus*. Observed root damage was compared with that in the field. The laboratory experiment used 20 active *P. allocerus* nests (each approximately 100 mm in diameter) containing living *P. allocerus*. These were collected from an area 10 km north of Vanrhynsdorp, Western Cape Province, South Africa (31° 29'39.37"S, 018° 42'56.07"E). Each nest was buried in 2 L plastic pots filled with sand which had been collected from the NamibRand Nature Reserve study site. Of the 20 potted nests, 10 were frozen to kill the termites, the remaining 10 contained living termite colonies, and an additional 10 pots were filled with sand alone as a second control. Three week-old *Triticum aestivum* (L.) (wheat) seedlings were planted in each replicate pot after their leaf and root number and length were recorded. Wheat was used in lieu of *S. obtusa* seedlings as the latter were difficult to germinate and grow in the laboratory in sufficient numbers (see also Bahrani & Khartegh,

2006). Non-native plant species have also been used in previous laboratory studies on FCs given the difficulties of germinating *Stipagrostis* seed (e.g. Albrecht *et al.*, 2001 – *Cynodon*; van Rooyen *et al.*, 2004 – *Lolium*; Cramer & Barger, 2013 – *T. aestivum*). Observations of seedlings after 1 week indicated no transplantation impacts, and each replicate was watered approximately every three days for five weeks, after which time seedlings were carefully excavated, re-measured and the number of inflorescences and deaths recorded.

2.3.5 Grass Seedling Root Comparison On and Off Fairy Circles (Section 4.3.2)

To determine whether the condition of roots was linked to the health of grass seedlings on and off FCs and to compare any damage on roots to that observed in the herbivory trials, yellowing and dying *S. obtusa* seedlings on the FCs, healthy seedlings on the FCs and healthy seedlings in the matrix were compared using 20 FCs and their adjacent matrices at site B. Five healthy and yellowing seedlings from each FC and five healthy seedlings from the matrix replicates were carefully excavated. The number of roots, root stumps (thick, short adventitious roots found at the base of the grass) and maximum root length of these seedlings were then recorded.

2.4 Fairy Circle Age Estimates and Influence of Environmental Factors on Fairy Circle Characteristics and *P. allocerus* Abundance at a Landscape Scale (Chapter 5)

2.4.1 Changes in Fairy Circle Density, Area and Frequency of Growth Stage Categories (Results in Sections 5.3.2 and 5.3.3)

The 12 km long landscape-scale transect included 30 sites located at approximately 400 m intervals along a sand road which traverses the large grass plain within the NamibRand Nature Reserve (Fig. 2.1). At each of the transect sites, FC density, area, dispersion index (given as R , Clark & Evans (1954)) and the percentage of the four growth stages were measured and recorded. FC density was measured per 100 km² using Google Earth imagery (2013), and growth stages of the same FCs were then ground-truthed using 20-25 FCs. Area was calculated from 10 FCs selected randomly from each site by mapping polygons in Google Earth and then calculating the area of each polygon using GE-Path software (version 1.4.6.) (Sgrillo, 2012).

2.4.2 *Grass Species Richness and Height, and P. Allocerus Sand Sheeting Abundance (Sections 5.3.1 and 5.3.2)*

To determine the variation in vegetation and abundances of *P. allocerus* between the 30 sites along the transect (Section 2.4.1), three replicate 50 cm² quadrats were placed at random within the matrix at each site. Vegetation cover, mean abundance of each grass species, grass height and number of grasses with *P. allocerus* sand sheetings were calculated for each quadrat.

2.4.3 *Influence of Soil Depth, Particle Size, pH and Electrical Conductivity on Fairy Circle Characteristics (Section 5.3.1)*

Soil depth, particle size, pH and electrical conductivity (EC) were measured at each of the 30 sites along the transect (Section 2.4.1) in order to determine whether soil properties have an effect on FC characteristics at a landscape level. Soil depth was estimated by digging a trench in the matrix until bedrock or a maximum depth of 1 m was reached, and a soil sample of 500 cm³ was taken from each of these trenches at a depth of 50 cm, which was then used to measure soil particle size, pH and EC. Soil samples were weighed and passed through a nest of sieves consisting of 4 mm, 2 mm, 1 mm and 0.85 mm meshes, and the resultant fractions weighed. The fraction that had passed through the 0.85 mm mesh was reduced using a riffle-type sample splitter to obtain two subsamples of ca. 2.5 cm³ each. Particle size from 0.02 – 2000 µm for these subsamples was measured using a Malvern Mastersizer 2000 laser diffraction particle size analyser. Water was used as a dispersant, and samples were measured using a refractive index of 1.55 and absorption value of 0.1. The subsample with the lowest residual weight from each sample was used for subsequent analyses. The Malvern fractions were calculated as percentages of the sample total weight and combined with the coarser sieve fractions. All fractions were then placed into soil particle classes according to the scale proposed by Blott & Pye (2012). This scale classifies particles at equal geometric intervals and has sufficient resolution for an accurate comparison between samples. The soil particle classes in this analysis ranged from medium clay to very coarse gravel.

Soil electrical conductivity and pH were measured using a Crison CM 35 conductivity meter and Crison PH 25 pH-meter respectively on the 500 cm³ samples taken from each of the 30 transect sites. The conductivity meter was calibrated with standards to 147 µS/cm, 1413 µS/cm and 12.88 mS/cm, and the pH meter to 4.01, 7.00 and 9.21. Samples were analysed based on the method described in Smith & Doran (1996) and prepared by combining 28 cm³ of the soil sample with equal parts distilled water and shaking vigorously for 30 seconds. The sample was left to stand for 5 minutes to allow larger

sediment particles to settle. Electrical conductivity was measured first and readings were taken three times for each sample, after which the solution's temperature was recorded and the sample remixed as above and left for a further 5 minutes. pH was measured three times as for electrical conductivity above, after which all containers and instruments were cleaned before subsequent sample measurements using distilled water.

2.4.4 *Statistical Analysis of Fairy Circle Characteristics along Environmental Gradient (Sections 5.3.1, 5.3.2 and 5.3.3)*

Principle component analyses were performed for the soil particle size data and the frequency of FC growth stages for the 30 transect sites using Primer-E. This was done in order to extract relevant summary variables from a large dataset. The first two principle components were then compared with FC density and area, termite sand sheeting abundance, counts of the three most abundant grass species, total vegetation cover and grass height using multiple and generalised linear regressions performed in R (R Core Team, 2015). Additional multiple linear regressions were conducted between FC density and area and the following variables; FC dispersion index (R) (Clark & Evans, 1954), termite sand sheeting abundance, vegetation parameters as well as soil depth, pH and electrical conductivity.

2.4.5 *Overdispersion of Fairy Circles and Comparison of Spatial Patterning with Other Landscape Features (Section 5.3.4)*

The degree of spatial ordering of FCs was compared with that of nests of other species of social insect from various localities around the globe as well as vegetation patterning in the form of both vegetated spots and bare gaps in Sudan. If the social insect nest or vegetation patterns match the spatial ordering of FCs, it would suggest FCs may share a similar origin to these other features. In order to analyse and compare the spatial pattern of each landscape example, a spatial point pattern analysis was used, similar to that done by Getzin *et al.* (2014). Google Earth images were taken of FCs in Giribes (19°02'12.57"S 13°21'01.59"E), heuwetjies near Garies in the Western Cape (30°46'14.58"S 18°00'27.08"E), *Macrotermes* mounds near Outjo in northern Namibia (20°07'22.18"S 16°14'53.33"E), *Pogonomyrmex* discs in Colorado, USA (39°16'07.16"N 109°02'19.07"W) and vegetation spots (11°37'15.57"N 27°57'00.39"E) and gaps (11°03'05.62"N 28°12'38.84"E) in Sudan. Within each image, a square block of a measured size was drawn and all points within the block were given an x-y position. The size of each block differed for each example used as the maximum area in which the landscape was homogeneous (not influenced by rivers, hills etc) as well as the size of the features measured

varied. For FCs the block measured 1500 X 1500 m, heuweltjies 1500 X 1500 m, *Macrotermes* mounds 1000 X 1000 m, *Pogonomyrmex* discs 300 X 300 m, Sudan spots 1000 X 1000 m and for Sudan gaps 500 X 500 m. Voronoi tessellation plots were generated from the x-y coordinates of each point using the spatstat and deldir packages in R. these plots draw polygonal cells around each point at a distance which is closer to the centre of the point than to neighbouring points and allows for a number of dispersion indicators to be calculated. These indicators included the mean number of polygon sides, percentage hexagons, mean and median nearest neighbour distance and R dispersion distance developed by Clark & Evans (1954). A completely regular pattern has all polygons with six sides, therefore the higher the percentage of hexagons, and the more regular a spatial pattern would be. An R dispersion index of 0 indicates a completely aggregated collection of points, 1 indicates a random distribution, and $R = 2.1491$ indicates an even, hexagonal pattern (Clark & Evans, 1954). Lastly pair correlation function (pcf) plots were generated. For these plots, the pair correlation function $g(r)$ was plotted against distance from a random point (r). $g(r)$ is a measure of the average observed number of points at a certain distance (r) from a random point, where a value of $g(r) = 1$ indicates complete spatial randomness (Getzin *et al.*, 2014). Ninety-five percent simulation envelopes of complete spatial randomness were included in the plot, and where the line for $g(r)$ falls outside of the envelope, the pattern can be considered non-random.

2.4.6 Fairy Circle Longevity Estimates Using Historical Aerial Photography (Section 5.3.5)

In order to track the appearance, disappearance and hence estimated lifespan of FCs over extended periods of time, historical aerial and satellite images were obtained for two separate FC localities from the late 1970's until the present. High resolution historical aerial photographs for pre-selected sites in NamibRand Nature Reserve (1977) and Giribes Plain (1975 and 1985) were obtained from the South African National Geo-Spatial Information Agency (Mowbray, Cape Town). Google Earth imagery of the same locations was acquired for consecutive years from 2009 – 2013 for NamibRand and 2010 – 2012 for Giribes. The aerial images were fitted to the Google Earth imagery using known, spatially and temporally fixed landmarks in the images with the aid of GPS TrackMaker software version 13.9 (Ferreira, 2013). All images were then overlaid using CorelDraw Essentials X5 software version 15.2.0.686 (Corel Corporation, 2010) and each FC tracked in time for either appearances (indicating 'births') or disappearances (indicating 'deaths'). The assumption was made that, for image comparisons where there was a temporal gap of a few decades, FCs that were present in the same location on both images had not disappeared and reappeared within the time interval.

FC survival and recruitment were estimated in order to compare values with those of termite nests, and to determine whether rainfall increases survival and recruitment (which would fit the predictions for the Sand termite hypothesis) or lowers these estimates (which would support the plant competition hypothesis). FC survival and recruitment were estimated with Live Recaptures (Cormack-Jolly-Seber) and Pradel Models (for both survival and recruitment) using the MARK program version 8.0 (White, 2014). Time intervals were set based on the year and month in which each image had been taken. The model average value for both survival and recruitment were obtained and the overall weighted geometric mean survival estimate value for each location calculated. This value was used to estimate FC lifespan at NamibRand and Giribes using the equation $L = 1/(-\ln(S))$, where L is the estimated lifespan and S is the survival estimate (Cooch & White, 2014). In order to test whether the probability of recruitment or survival of FCs in NamibRand were influenced by annual rainfall, total rainfall preceding each Google Earth image was used as a covariate within the Pradel Model. Rainfall values used for each year from 2010 – 2013 were 17.4 mm, 12.4 mm, 49 mm and 2 mm respectively.

2.5 Ecosystem Engineering Associated With Fairy Circle (Chapter 6)

2.5.1 Soil Moisture, Particle Size, pH and EC Comparisons between Different Growth Stages of Fairy Circles and the Matrix (Results in Sections 6.3.1 and 6.3.2)

Various soil properties including soil moisture, particle size, pH and EC were measured on 10 representative FCs from each of the four growth stages as well as in the matrix in order to determine whether soil properties on FCs differed from the matrix (and whether these differences may be related to the nesting activities of *P. allocerus*). Representative FCs of each growth stage were chosen from both sites A and C in February 2013 (before the rains). To measure soil moisture a 500 cm³ soil sample was taken at a depth of 50 cm from the centre of each FC's bare disc and an adjacent area in the matrix equidistant from the FC and its nearest neighbours. A 100 g subsample was taken from each sample and dried in an oven at 200 °C for 2 days, with the subsample weighed before and after drying to calculate soil moisture.

Another set of 500 cm³ soil samples were taken at 50 cm depth at each of the 10 FC growth stages and the adjacent matrices. These samples were used to measure soil particle size, pH and EC using the same methods as those described for the transect comparisons (Section 2.4.3). Although the analytic technique used was the same as that done for the transect samples, these samples were used to test different hypotheses. The transect samples were used to detect differences in soil properties between spatially removed points in the matrix to determine if FC density and area differ in response

to environmental changes, while the samples described in this section were used to determine if soil variations exist between FC growth stages and the surrounding matrix which may be related to termite activity.

2.5.2 *Soil Temperature On and Off Fairy Circles (Section 6.3.3)*

The bare surface of FCs was predicted either to show higher soil temperatures than the vegetated matrix due to greater solar radiation or have lower temperatures if evaporative cooling on FCs occurred as a result of their higher soil moisture. To test this soil temperature was measured on 20 FCs and adjacent matrices in site B using Dallas Thermochron DS1921G-F5 temperature data loggers. Measurements were taken over a 2 - 3 day period in January 2012, and again from the same FCs in February 2013, with the temperature being recorded every ten minutes. Measurements were taken in two different years with the aim of recording temperatures both before and during the rainy period. The data loggers were buried in the centre of the FC bare disc and approximately 4m away from the FC in the matrix. Loggers were tied to a length of monofilament nylon cord and sealed in Ziploc bags emptied of air. For each FC and its matrix replicate, one logger was buried in the soil at 15 cm depth and another 1 cm below the surface. The nylon cord was run from the bag to the surface and marked with coloured tape for later retrieval. At the end of each two-three day period, the loggers were removed and the data downloaded digitally using Netgen SoftButton (2010) data logging software. The mean temperature for each 10 minute time interval over the 2 - 3 days was determined for each sample, and mean, diurnal mean, minimum and maximum temperatures for the FC and matrix on the surface and at 15 cm depth calculated.

2.5.3 *Effect of Temperature on Grass Seed Germination and Growth in Laboratory Trials (Section 6.3.3)*

If FCs were found to have higher soil temperatures than the matrix, it was hypothesized that this may play an additional role in limiting grass seedling growth on the FC. In order to investigate the potential adverse effects of high temperatures on *Stipagrostis* germination and seedling growth, and to determine the critical temperature at which mortality occurs, germination and seedling growth trials were done at five different temperatures using *S. ciliata* and *S. obtusa* seeds (seeds for both species were obtained from the Renu-Karoo seed supplies, Prince Albert). Constant soil temperatures were maintained using five water baths, each simulating a different soil temperature. These were situated indoors in a sunlit area for the duration of the experiment. Seeds were grown in 8 cm deep closed

plastic pots using sandy soil and kept moist unless otherwise stated. Two pilot studies were done to determine the optimum experimental temperature range, the correct seed stratification technique, the seed viability of the two grass species, the effect of a short-term exposure to the five temperatures and the effect of keeping the seeds dry or wet during exposure to the temperatures. These were followed by two long-term experiments examining germination success and seedling growth of *S. ciliata* at the five temperatures. For both pilot studies and the long-term germination experiment, the number of germinated seedlings was recorded every day.

Pilot study #1

S. ciliata and *S. obtusa* seeds were exposed to temperatures of 30°C, 35°C, 40°C, 45°C and 50°C for 4-5 hours a day for 17 days after stratification. For the rest of the day, seeds were kept at room temperature. This was done to approximate thermal cycles experienced in nature. Prior to the experiment, all seeds were soaked in water for three hours before half were planted into pots and the rest stratified at 5°C for a further three days in wet conditions. Soaking and stratification aids in breaking the dormancy period of desert grasses (Bahrani & Khartegh, 2006). For both species, four stratified and four non-stratified replicate pots were placed in each of the five water baths at the different temperatures, with 15 seeds planted upright just below the soil surface in each pot.

Pilot study #2

The effect of short-term exposure to 35°C, 37°C, 41°C, 44°C and 47°C on the germination success of both wetted and resting dry seeds (as would be in the dry season) for both species was tested. The minimum and maximum temperature from pilot study 1 (30°C and 50°C) were deemed redundant as both the optimum growth temperature and tolerance threshold occurred within these limits. Half of the seeds from each species were soaked for three days before planting and watered daily, while the remainder received no initial soaking or water for the first three days of temperature exposure. Stratification was not used for this pilot study as results from pilot study 1 indicated that stratification had no significant effect on the success of seed germination. Four pots with 30 seeds were used at each temperature, housing wetted and dry seeds of *S. ciliata* and *S. obtusa*. The seeds were subjected to the experimental temperatures for four hours on the first three days and allowed to rest at optimal growing temperatures for the remainder of the experiment, with the optimal growing temperatures determined from the previous pilot study (viz. 40°C for *S. ciliata* and 35°C for *S. obtusa*). The experiment was run for a total of 16 days, from the 19th of October to the 3rd of November 2011.

Long-term exposure of S. ciliata seeds to high temperatures

Sixteen replicate pots with 25 *S. ciliata* seeds in each were each exposed to 35°C, 37°C, 41°C, 44°C and 47°C for nine days, from the 26th of November to the 4th of December 2011 for six hours each day. The seeds were soaked for three hours before the experiment but not stratified. *S. obtusa* was not used for this experiment due to the low germination success in the pilot studies. The number of germinations was counted every day and at the end of the experiment the seedlings were carefully removed and the number of leaves, leaf length, root length and number of secondary roots was recorded.

Growth of transplanted S. ciliata seedlings under different temperatures

S. ciliata seeds were allowed to grow naturally in a sunlit area for 2 weeks. The seedlings were then carefully removed and transplanted into 16 replicate pots, with one seedling allocated to each replicate pot. The seedlings were allowed to settle for a few days before being grown for 10 days (8th to the 18th December 2011) at soil temperatures of 35°C, 37°C, 41°C, 44°C and 47°C for six hours each day. Leaf number and length, as well as root number and length, were recorded prior to transplantation and at the end of the experiment. A general linear model was used to investigate the effect of temperature on transplanted *S. ciliata* seedling measurements.

2.5.4 *Insect Communities On and Off Fairy Circle (Section 6.3.4)*

If FCs have different soil properties and plant communities (investigated in Chapter 3) when compared to the matrix, this may create different microhabitats for insect communities. To determine whether FCs do in fact support different insect communities, ground dwelling dung beetles (Scarabaeidae) and ants on 61 FCs were sampled using pitfall traps (Section 2.2.3). Ants were identified to genus level using Hölldobler & Wilson (1990) and species level using Taylor (2010) while dung beetles were separated into morpho-species. Subsequently ant species were cross-referenced with those at the Iziko South African Museum of Cape Town to confirm identifications.

2.6 Statistical Analyses

Basic statistical tests employed were ANOVA (Kruskal Wallis), Chi-square (2X2 table) and t-tests (Mann-Whitney U) using STATISTICA[®] version 10 (StatSoft Inc. 2010). For data that was not normally distributed, non-parametric equivalents (bracketed) were used. Results were taken as being

significant when $P < 0.05$. Average and standard deviations were given for results analysed with parametric tests while medians and interquartiles were reported for nonparametric data.

3 FACTORS INFLUENCING PLANT PERFORMANCE ON FAIRY CIRCLES

3.1 Introduction

3.1.1 The Effect of Abiotic Factors on Vegetation Growth

Fairy circles (FCs) stand out prominently in the landscape due to the absence of vegetation on their disc, and enhanced growth of grasses in their peripheral band. This chapter investigates a range of potential causative factors underlying these altered vegetation patterns, from the perspective of both origination and long-term maintenance. Theories attempting to explain the lack of vegetation of discs of Namibian FCs can be divided into three main categories; resource (largely water) limitation due to competitive interactions between plants (Cramer & Barger, 2013; Getzin *et al.*, 2014), the presence of a potentially toxic chemical released either by allelopathic plants (Theron, 1979; Joubert, 2008), geochemical activity (Naudé *et al.*, 2011) or termites (Albrecht *et al.*, 2001), and lastly mechanical damage to plant tissues through direct foraging by ants or termites in proximity to their nests (Moll, 1994; Becker & Getzin, 2000; Becker, 2007; Juergens, 2013).

Various vegetation patterns, including FCs, can be directly or indirectly affected by a number of abiotic (temperature, wind, soil properties, topography and fire) and biotic (herbivory, allelopathy) factors, which may determine the availability of essential resources for plant growth, or influence plant condition in other ways. Typically higher temperatures correlate with increased growth and germination of plants (Bull, 1968; Flores & Briones, 2001), with temperatures above the upper thermal maxima leading to the inactivation of proteins and enzymes, desiccation and increased respiration (Daubenmire, 1974). Low temperatures on the other hand are associated with delayed germination and retarded growth, and temperatures below the critical thermal minima can kill plants by causing precipitation of proteins and the formation of intercellular ice (Gardner *et al.*, 1999). Whether FC soils differ in temperature from matrix soils has yet to be investigated. Here it is hypothesised that increased solar radiation on the bare disc of FCs may raise temperatures above the thermal maxima of the matrix grasses and contribute to grass death (Chapter 6 investigates thermal tolerances of *Stipagrostis*). Wind speed can enhance or reduce plant performance (Wadsworth, 1959), with low wind speeds promoting gaseous exchange through the elimination of the boundary layer of air which develops around the surface of a leaf (Daubenmire, 1974), and high wind speeds resulting in water loss from leaves and desiccation (Whitehead, 1962a; 1962b). In addition wind damage to plants can occur through mechanical breakage, erosion of soil around roots or deposition of new soil which may reduce aeration around the roots (Daubenmire, 1974). In the case of FCs, wind may clear plant detritus and seeds from the surface of the bare disc (Becker, 2007), or dislodge and remove dead grass tussocks

(Vlieghe *et al.*, 2015). Topography, in particular slope orientation and altitude, can affect light intensity and duration, temperature and water availability (Billings, 1952; Daubenmire, 1974; Auslander *et al.*, 2003). Besides the immediate effect of killing plants, fire damage can permanently scar woody plants, damaging bark phloem and leaving them vulnerable to attack by parasitic fungi and insects (Daubenmire, 1974). Fire-adapted species however depend on the heat and smoke produced by fire to stimulate various stages of growth including resprouting, seed release and seed germination (Christensen & Muller, 1975; DeBano *et al.*, 1998). The initial elimination of vegetation after fire also provides benefits to plant growth and germination by allowing more light to reach the soil surface, reducing plant and seed predators, temporarily increasing soil moisture due to lack of competition and returning various nutrients such as N, P, K, Ca, Na and Mg to the soil as ash (Stock & Lewis, 1986; DeBano *et al.*, 1998). However, fire is an infrequent feature of the arid grasslands of Namibia where FC's occur and is not considered to have an important ecological role there (IFFN, 2001) nor is it recorded as having generated periodic vegetation patterns like FCs.

Soil is one of the most important abiotic factors influencing plant performance, as it provides the majority of plants with nutrition, water and anchorage. All soil physical properties which directly influence plant growth (water potential, mechanical resistance, temperature and soil aeration) are themselves affected by the bulk density, texture, aggregation and porosity of the soil (Letey, 1985). Hard, compacted soils create mechanical impedance which prevents the penetration of roots into the soil and therefore reduces their contact with water, oxygen and nutrients (Shierlaw & Alston, 1984; Letey, 1985). Alternatively plants grown in very loose soils with little impedance (such as the grasses in the arid grasslands of Namibia where FC's occur) perform worse than those in soils of an optimum bulk density due to the greater risk of becoming dislodged as well as lowered contact with the soil which impedes resource uptake (Passioura, 2002). Similarly soils containing large 'biopores' created by subterranean organisms can impede plant growth as roots develop in close proximity to one other and reduce the available surface area for absorption (Stirzaker *et al.*, 1996). Soil moisture is important for initiating seed germination and providing a solute for the absorption of certain nutrients, and also affects other soil factors such as mechanical impedance and soil aeration (Daubenmire, 1974; Letey, 1985). In this respect FC's are unusual in having greater soil moisture than surrounding matrix soils, but paradoxically are unable to support vegetation growth (Picker *et al.*, 2012; Juergens, 2013). Organic matter in soil, along with the parent rock composition, affects both the soil chemistry and certain physical properties. Aggregates are more likely to form with organic matter which improves the soil structure, and it often acts in the same way as clay with regards to its high water holding capacity (Daubenmire, 1974; Oades, 1984). The type and origin of organic matter as well as the parent rock determine the availability of plant nutrients and soil pH (Russell, 1973). Both very acidic and

alkaline soils can have negative effects on plant performance, mainly by reducing the plant's ability to take up various ions (Russel, 1973). Soils of the grassy plains in which FCs occur are generally nutrient poor, which led some to suggest that nutrient differences in FC and matrix soils may explain the lack of grasses on the bare discs of FCs (Cramer & Barger, 2013). Although Cramer & Barger found significantly lower values of soil N and organic C on FCs compared to the matrix, these differences have not been reported in other studies (Moll, 1994). Experiments involving the addition of micronutrients to FCs and the transfer of soils between FCs and the matrix by Tschinkel (2015) did not stimulate any increased growth of grasses on FCs, suggesting that nutrient deficiency does not explain their bare appearance.

3.1.2 *Influence of Plant Interactions and Mammalian Herbivory On Vegetation Growth*

The overall impact of herbivory on vegetation is variable, and can be either mostly beneficial (through a compensatory increase in reproductive output, biomass and nutrient supply), harmful (by limiting plant distribution, reducing reproductive success and modifying a plant's ability to compete) or neutral (Maschinski & Whitham, 1989; Skarpe, 1991; HilleRisLambers *et al.*, 2001; Verweji *et al.*, 2006). In cases where herbivory is low or moderate and is followed by an intervening growth period, compensatory mechanisms within the plant including increased photosynthesis and greater availability of resources in remaining tissues can result in overcompensation for losses from herbivory (McNaughton, 1983). This increased growth due to grazing can be seen in 'grazing lawns', where large mammalian herbivores maintain swards of new growth on grasses in response to continued grazing and input of herbivore dung (Georgiadis, 1989; Dale, 1999), leading to a higher leaf to stem ratio and elevated bulk density of the grazed grass (Skarpe, 1991; Verweji *et al.*, 2006). Overgrazing and trampling can however lead to a reduction in plant cover through soil erosion and compaction, lowered water infiltration rates and reduced nutrient availability (Skarpe, 1991; Wilby *et al.*, 2001; Jones *et al.*, 2006). The impacts of antelope herbivory in the arid Namibian grasslands is not known, but typically these mammals occur there in very low densities. Though mammalian herbivory may determine the conditions under which vegetation patterning may occur, or influence existing patterns, it is not reported to be a primary factor resulting in the formation of periodic vegetation patterns elsewhere in the globe (Adler *et al.*, 2001; HilleRisLambers *et al.*, 2001)

Various interrelationships between plants can have both positive and negative consequences on vegetation growth. In resource-limited areas such as deserts, stands of vegetation can facilitate seedling survival through the creation of shaded 'islands of fertility', holding a greater accumulation

of nutrients and water than barer areas, and act as 'nurseries' for seedlings (Escudero *et al.*, 2004; Schade & Hobbie, 2005; Bonanomi *et al.*, 2008). Alternatively plants can be subject to both inter- and intraspecific competition for resources, which may be accentuated by the production in some species of allelopathic chemicals which negatively affect the growth of neighbouring plants (Hierro & Callaway, 2003; Cipollini *et al.*, 2012). The most common classes of chemicals that make up these compounds include phenolic compounds, aldehydes, coumarins, glucosides and terpenes (Daubenmire, 1974; Seigler, 2006). The mode by which these toxins affect other plants can be varied and is not always immediately apparent, but some effects include reduced growth, loss of turgidity, suppression of germination, interference with nutrient uptake and negative effects on the plants symbiotic soil microbes (Daubenmire, 1974; Callaway & Aschehoug, 2000; Cipollini *et al.*, 2012). Bioassays conducted by several researchers suggest that there may be a growth inhibiting compound in FC soils (Albrecht *et al.*, 2001; van Rooyen *et al.*, 2004; Jankowitz *et al.*, 2008; Joubert, 2008). The presence of a compound in the soil capable of affecting grass growth on FCs was first suggested by Theron (1979), who theorised that the succulent *Euphorbia damarana* brought up inhibitory inorganic compounds from deeper soil layers and subsequently released them into the upper soil layers surrounding the plant upon death. This theory has several shortcomings described by van Rooyen *et al.* (2004) and Joubert (2008), however a *Euphorbia* explanation has been recently revisited by Meyer *et al.* (2015). They describe a spatial and size link between *Euphorbia gummifera* and FCs in certain localities within their distribution, and highlight the finding that the compound euphol (a triterpenoid associated with *Euphorbia* species) occurred in 19 out of 20 samples from FCs compared to 3 out of 20 samples taken from the matrix (Meyer *et al.*, 2015). They however did not address a specific mechanism for the formation of barren patches by *E. gummifera*, and only investigated one locality near the southern boundary of the FC range (Meyer *et al.*, 2015). Field observations by Albrecht *et al.* (2001) revealed desiccated and dead recruiting grass seedlings within the FC bare disc which lacked a coating of sand evident on the roots of healthy seedlings growing in the matrix. They related this to an unidentified semi-volatile chemical released by termite nests which inhibited the growth of fine root hairs on grasses growing in FCs and hence reduced their ability to withstand dehydration stress. Naudé *et al.* (2011) proposed that natural gases, including CO, may seep into the soil from geochemical microseeps, and related the presence of stressed or dead vegetation to spikes in CO concentration. High levels of alkenes and alkanes were also detected, and it was hypothesised that aerobic bacteria would view these hydrocarbons as a food source. This increase in microbial activity in FC soils was believed to result in an anaerobic environment which negatively affected plant growth.

Cramer & Barger (2013) proposed a plant self-organisation mechanism for FC formation, and reported lower concentrations of soil organic matter, N and K in FCs soils compared to the matrix.

They then associated this with the reduced growth of wheat grown in FC vs matrix soils. Strongly competing grasses within the matrix, or pre-existing mature FCs, were hypothesized to initiate the creation of a bare patch by reducing the availability of resources to neighbouring grasses (Cramer & Barger, 2013; Getzin *et al.*, 2014). This bare patch would then result in an increase of soil moisture due to reduced plant transpiration, and the decline of nutrients due to the reduced replenishment of soil organic matter (Cramer & Barger, 2013). Eventually the edges of the newly formed FCs facilitate the growth of grasses which take advantage of the reduced competition and elevated soil moisture within the bare disc (Cramer & Barger, 2013).

3.1.3 Impacts of Social Insect Herbivory On Vegetation Patterns and Soil Properties

The amount of living or dead plant material harvested by ants and termites can rival that removed by large mammalian herbivores (Jones, 1990). Fungus cultivating *Macrotermitinae* in East Africa are estimated to consume 1 to 1.5 tonnes of litter $\text{ha}^{-1} \text{y}^{-1}$ which is a similar amount to that consumed by wild and domestic grazers (Jones, 1990). Termites predominantly feed on plant litter or detritus, but certain wood feeding and harvester termites also target living vegetation, and can be serious agricultural pests (Lee & Wood, 1971). The damage caused by harvester termites is accentuated in deteriorated or overgrazed pasture (Annecke & Moran, 1982) and bare areas created by *Anacanthotermes ahngerianus* (Jacobson) can take up 20 % of pasture area in Central Asia (Lee & Wood, 1971). In central Amazonia the leaf-cutting ant *Atta laevigata* (Smith) was shown to delay forest regeneration in cleared plots by selectively foraging on seedlings and reducing their survivability and growth (Vasconcelos & Cherrett, 1997). Seed harvesting *Pogonomyrmex* ants in North America often destructively clip vegetation around their nests to form bare discs (see Chapter 1), with one species potentially clearing 157 – 226 million ha^{-1} of vegetation annually (Clark & Comanor, 1975). Ants can also indirectly reduce plant performance through their mutualistic relationship with sap-feeding bugs (Buckley, 1987; Styrsky & Eubanks, 2007). In many cases the tending and defence of these bugs by ants leads to increased population densities, survival rates and fecundity of the bugs, which in turn disadvantages plants by reducing nutrient and water supply, damaging tissue, and transmitting a range of plant pathogens (Buckley, 1987). However, this ant-bug interaction may in certain instances indirectly benefit plant fitness, as the presence of the often aggressive ants deters other more damaging insect herbivores (Styrsky & Eubanks, 2007).

Both ants and termites increase the amount of organic matter in their nests through the accumulation of food, waste material and faecal matter (Lee & Wood, 1971; Brown *et al.*, 2012), and

certain termites have been shown to modulate the amount of organic matter incorporated in their nest structures through the selective use of their saliva in nest construction (Jouquet *et al.*, 2002; 2007). The increase in soil organic matter within nests, as well as the termite-generated movement of soils from deeper horizons, increases the availability of nutrients to plants. This increase in soil macronutrients such as C, N, P, Ca, K and Mg has been linked to the proliferation of plant growth around social insect nests, leading some to refer to these structures as islands of fertility (Lee & Wood, 1971; Knight *et al.*, 1989; Midgley & Musil, 1990; Wagner *et al.*, 1997; Folgarait, 1998; Levick *et al.*, 2010; Sileshi *et al.*, 2010). This generates a range of ecological responses. Two harvester ant species, *Messor andrei* (Mayr) and *Messor capensis* (Mayr), increase seed production of certain plant species around their nests through the localised increase in nutrient status (Dean & Yeaton, 1993; Brown & Human, 1997). Plant cover and reproductive success are often increased along the margins of cleared discs of *Pogonomyrmex* nests due to increased nutrient availability and reduced competition (Rissing, 1986; MacMahon *et al.*, 2000; Nicolai *et al.*, 2008). Changes in plant species composition and increased productivity in the vicinity of termite nests has been recorded for *Macrotermes*, *Microhodotermes*, *Trinervitermes*, *Odontotermes*, *Nasutitermes*, *Armitermes*, *Anoplotermes* and *Cornitermes*, with mounds often showing increased numbers of forbs and woody plants (Darlington, 1985; Spain & Mclvor, 1988; Moore & Picker, 1991; Ponce & da Cunha, 1993; McCarthy *et al.*, 1998; Smith & Yeaton, 1998; Cadet *et al.*, 2004). Localised increases in soil nutrients at termite nests has been considered to be the cause of the elevated plant productivity on both East African lenticular mounds and South African heuweltjies (Chapter 1). Grass production is increased on Kenyan lenticular mounds and promotes grazing by livestock, while some species of *Acacia* exhibit greater densities and survival in soils directly adjacent to the mounds (Cox & Gakahu, 1985). Vegetation on heuweltjies tends to be more deciduous than intermound areas, with higher nutrient levels on the mounds capable of supporting plants with a higher photosynthetic rate and productivity than the surrounding evergreen vegetation (Knight *et al.*, 1989; Midgley & Musil, 1990). Where heuweltjies occur on cultivated land, crops growing on the mounds appear to be denser than surrounding areas (Lovegrove & Siegfried, 1986; Lovegrove, 1991), and the nutrient status of the plant tissue itself may be increased (Midgley & Musil, 1990).

The mechanical removal of grasses from the surface of FCs by social insects, either through foraging or by other means, has been suggested several times in the literature as a mechanism for generating the bare disc. Moll (1994) was the first to suggest that the removal of grasses from FCs through termite foraging was a potential explanation for FC formation, though he did not provide any direct evidence to support this suggestion. Becker & Getzin (2000) and Becker (2007) drew upon the known feeding habits of the Northern harvester termite *Hodotermes mossambicus* and field

observations on foraging patterns in Kaokoland to explain FC formation. *H. mossambicus* however is not found in large numbers at all FC localities and their nests are not always associated with FCs (Picker *et al.*, 2012). Grube (2002) additionally argued that not enough is known about the polycalic nest system of *H. mossambicus* to substantiate their theory, that the termite's activities would not be influenced by changes in grass species assemblages as Becker & Getzin (2000) claimed, and that the diameter of the FC would not be influenced by either the foraging activities of the termite or their response to temperature. Recently Juergens (2013) and Vlieghe *et al.* (2015) hypothesized the involvement of the Sand termite *Psammotermes allocerus* in FC formation. Juergens (2013) observed that *P. allocerus* forages on grasses on and near FCs under cover of sand sheetings, which were associated with 80 – 100 % of grasses on FC's. Grasses covered in sand sheetings were eventually killed by the termites, leading to a negative correlation between the presence of *P. allocerus* and the number of living grasses on the bare FC disc. Laboratory herbivory trials conducted by Vlieghe *et al.* (2015) showed that *P. allocerus* is capable of killing grass seedlings through targeted foraging on their roots and culms, and that the type of damage observed could be matched to root damage of grass seedlings on FCs (these results are covered in detail in Chapter 4). Foraging by harvester ants has been suggested as a causative mechanism of FC formation by both Becker (2007) and Picker *et al.* (2012), who reported on smaller circular patches in rockier localities of Kaokoland which appeared to be formed by the seed and grass harvesting activities of the harvester ant *Messor denticornis* (Forel). These discs are characterised by the presence of large quantities of seed husks and ant exoskeletons (Becker, 2007; Picker *et al.*, 2012). However these bare discs are not homologous with FCs, and are associated with *Messor* ant nests. Picker *et al.* (2012) suggested that the abundant Black pugnacious ant *Anoplolepis steingroeveri* may initiate grass death on FCs by excavating extensive nests systems at the bases of grasses, exposing the roots to the elements and lowering the fitness of the grasses enough to eventually either dislodge or kill them. Related to the excavated grasses was a honey-dew producing Meenoplidae bug which appeared to have a close relationship with *A. steingroeveri*, and it was hypothesised that the ants actively sought out the bugs below grasses surrounding their nests (Picker *et al.*, 2012). The results presented in Picker *et al.* (2012) are given in more detail in this chapter.

3.1.4 Aims

- This chapter examines the ecology of grasses associated with FCs and describes changes in plant community structure on FCs compared to the matrix.
- It investigates two potential ways in which the bare disc of FCs can be maintained free of vegetation for decades. Firstly seed banks will be examined in FC and matrix soils to determine

if there are limitations on recruitment of grasses on FCs. Secondly the potential role of *A. steingroeveri* (Picker *et al.*, 2012) in reducing plant cover by excavation of both mature grass tussocks and seedlings on the FC will be explored, focussing on the mutualistic association between this ant and a honeydew secreting bug inhabiting grass roots as a possible cause of the root excavating behaviour of the ants.

Manipulative experiments will be carried out to determine if excavation of grass seedling roots by the ants could impact grass survival, in support of the hypothesis that this may underpin the absence of vegetation cover on FC discs.

3.2 Methods

Transects were laid out on 60 FCs and adjacent matrices and abundance of the plant species recorded. Subsamples of soil and plant debris were collected from the bare disc and peripheral band of 10 FCs and 10 matrices to compare the soil seed bank at each locality. Abundances of *A. steingroeveri* on the FC bare disc, peripheral band and matrix were determined using pitfall traps on 60 neighbouring FCs and adjacent matrices. *A. steingroeveri* nests were excavated on three FCs to investigate their structure and extent. In order to test whether individual *A. steingroeveri* colonies were associated with individual FCs, aggression trials were conducted between ants from nests on 61 neighbouring FCs. Lastly the presence or absence of the ant and mutualistic Meenoplidae bugs below grass tussocks on 30 FCs and respective matrices was recorded, and the effect of ant excavations on grass seedlings inhabiting FCs was compared to unexcavated grasses on the FC and in the matrix by measuring root length and number and leaf colour and height over a 16 day period. Detailed methods for this chapter are covered in Chapter 2, Section 2.2.

3.3 Results

3.3.1 Comparison of Plant Communities on Fairy Circles and In the Matrix

Plant communities were compared on FCs and in corresponding matrix plots in order to detect changes in plant species richness, abundance and diversity. MDS ordinations showed that FC and matrix plant communities were fairly distinct (SIMPER analysis: mean dissimilarity = 52.2 %) (Fig. 3.1). Among sample similarity was greater in the matrix than the FC (70.9 % and 49.44 % respectively) with

a tighter clustering of FC communities. The dominant grass species in both the matrix and FC was *S. obtusa* (26.2 % and 25.9 % of all plant species respectively), followed by an *Eragrostis* species (19.6 % and 44.1 % respectively) and *Schmidtia kalahariensis* (13.5 % and 11.6 % respectively). Five species (mostly herbaceous annuals) occurred exclusively in the matrix, while the FC bare disc supported one unique plant species not encountered in the matrix, *Stipagrostis hirtigluma* (Trin. & Rupr.) De Winter, as well as the false ink-cap mushroom *Podaxis pistillaris* (L. ex Pers.).

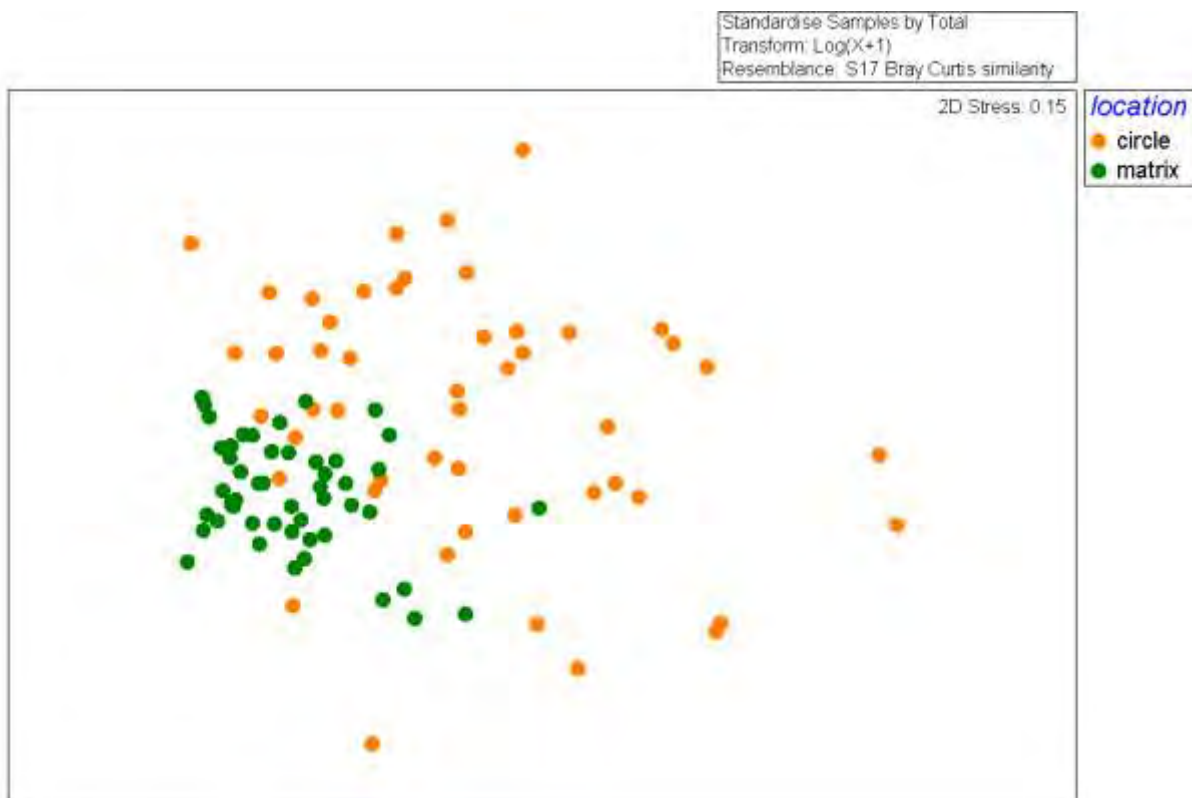


Fig. 3.1. Multi-dimensional scaling (MDS) plot ($\log(X + 1)$ transformed) of FC (orange) and matrix (green) plant communities.

Species richness, overall abundances and overall diversity were greater in the matrix than the bare disc (Table 3.1) (Mann-Whitney U, species number: $U_{50,50} = 41$, $P = 0.0001$; overall abundances: $U_{50,50} = 11.5$, $P = 0.0001$; Shannon Weiner's diversity index: $U_{50,50} = 110.5$, $P = 0.0001$; Simpson's diversity index: $U_{50,50} = 210$, $P = 0.0001$, $n = 50$).

Table 3.1. Median and interquartile (italicised) values for total plant species richness, overall plant abundance/m, Shannon Weiner and Simpson's (1 - λ) diversity indices on the bare disc and matrix (n = 50).

	Total species	Total number	Shannon Weiner	Simpson's (1 - λ)
Circle bare disc	3, 2	3, 3	1.02, <i>0.420</i>	0.59, <i>0.169</i>
Matrix	8, 2	28, 10	1.64, <i>0.291</i>	0.76, <i>0.083</i>

3.3.2 *Stipagrostis* Seed Bank on Fairy Circles

In line with the suggestion that the grass seed bank might not be distributed evenly across all habitats, greater numbers of *S. ciliata* seeds (m⁻²) were found on the FC peripheral band (median, interquartile: 184, 564.30, n = 10) compared to the matrix (0,0, n = 9) and FC bare disc (11, 11.11, n = 9) (Kruskal-Wallis, H_{2,28} = 5.24, P = 0.073). The lowest number of *S. obtusa* seeds were collected on the bare disc (33, 44.44, n = 9), which had considerably fewer seeds than both the matrix (2268, 1910.53, n = 9), and peripheral band (923, 984.37, n = 10) (Kruskal-Wallis, H_{2,28} = 18.48, P = 0.0002 and P = 0.005 respectively).

3.3.3 Abundances of *A. steingroeveri* On and Off Fairy Circles

Picker *et al.* (2012) suggested that *A. steingroeveri* abundances were higher on FCs, and may thus contribute to FC formation. In 2011 *A. steingroeveri* pitfall trap abundances were slightly higher on the FC bare disc (mean \pm S.D.; 119 \pm 198.09) and peripheral band (100.6 \pm 204.11) compared to the matrix (60.96 \pm 186.19) (ANOVA, F_{3,240} = 2.4313, P = 0.066, n = 60). This trend persisted in 2012 with median (interquartile) values of 4 (156), 5 (77), and 1 (3) for the bare disc, peripheral band and matrix respectively (Kruskal-Wallis, H_{3,100} = 6.59, P = 0.086, n = 25).

3.3.4 Structure of *A. steingroeveri* Nests on Fairy Circles

A. steingroeveri nests entrances were most often located along the FC peripheral band at the base of mature *S. ciliata* tussocks, with some entrances further excavated by the foraging activities of insectivorous mammals (Fig. 3.2a). On the three excavated FCs, large tunnels (about 5 cm in diameter) were followed from the surface exits of the ants downwards before eventually being lost at a depth of 59 cm when bedrock was reached (Fig. 3.2b). Brood chambers were found in superficial surface

nests under grass tussocks on all three FCs, and a number of ant repletes were observed within the exposed tunnels on one FC.

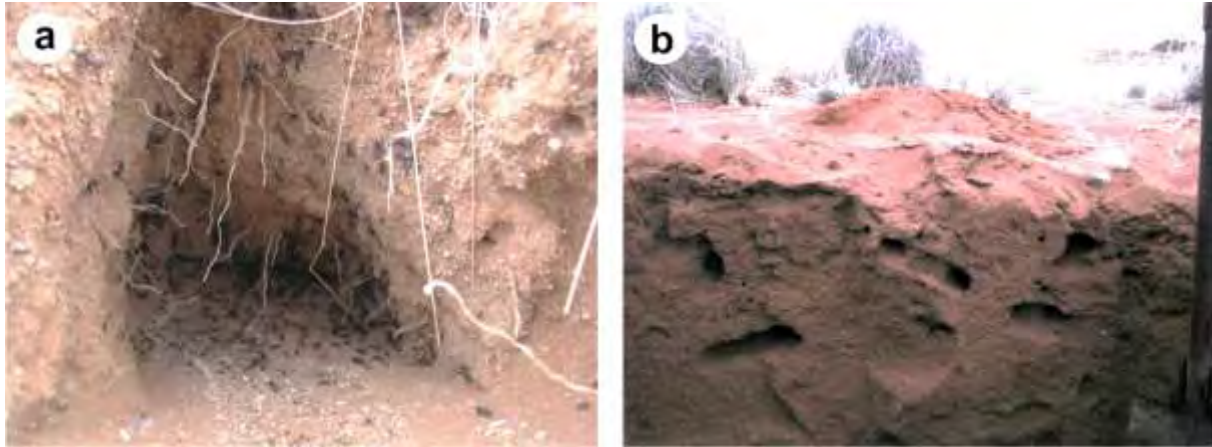


Fig. 3.2. *Anoplolepis* surface holes. (a) Mature grass tussock roots exposed by the excavating activities of *A. steingroeverii* and insectivorous mammals and (b) trench exposing large-diameter subterranean tunnels below a FC disc. Spade in (b) provided for scale. Photographs by V. Ross-Gillespie.

3.3.5 *A. steingroeverii* Colony Aggression and Polydomy

Although *A. steingroeverii* nests were situated on FCs, not all FCs were colonised, and some colonies occupied more than one FC. Of the 61 FCs investigated at site B, 25 were found to have active and permanent *A. steingroeverii* nests suitable for use in aggression trials, while the remaining 36 FCs were unoccupied by ants. All colonies were situated on FCs and none were observed in the matrix. The results of among-FC aggression trials identified seven colonies within the study site of 61 neighbouring FCs, the largest colony (colony 1) utilising 13 FCs, colony 2 inhabiting five FCs, two colonies (3 & 4) inhabiting two adjacent FCs and three colonies (5, 6 & 7) occupying one FC each (Fig. 3.3). Colonies occupying two FCs were situated in close proximity to one other, while the larger colonies (Colonies 1 and 2) were dispersed over the study site with several unrelated colonies or inactive FCs separating the polydomic nests. These colonies occupied FCs that were separated by ca. 150 m.

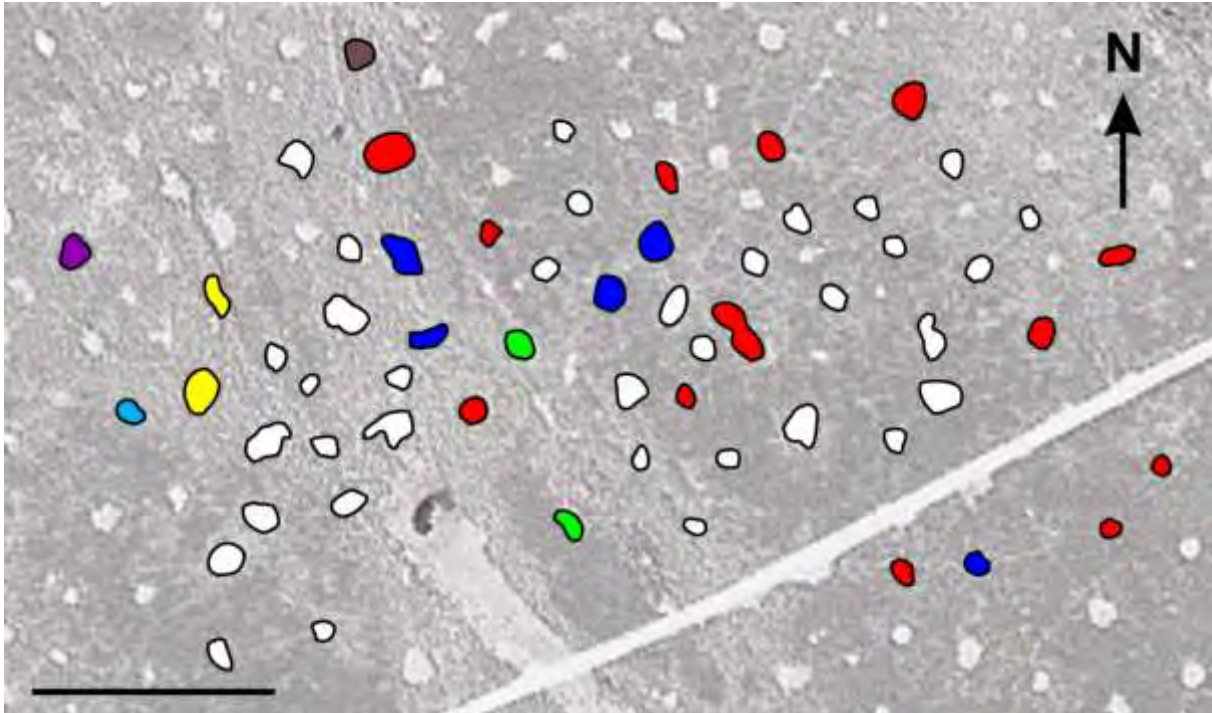


Fig. 3.3. Map of all 61 FCs used for *A. steingroeverii* aggression trials depicting the extent of colony 1 (red), colony 2 (dark blue), colony 3 (green), colony 4 (yellow), colony 5 (light blue), colony 6 (purple) and colony 7 (brown). White FCs represent those with no active *A. steingroeverii* colonies, scale bar = 50 m.

3.3.6 *A. steingroeverii* and Meenoplidae Bug Mutualism and the Excavation of Fairy Circle Grasses

Grass root inhabiting Meenoplidae bugs were found to be closely associated with the presence of *A. steingroeverii*, which could be observed tending the herbivorous bugs (Fig. 3.4). The relationship was likely related to the utilisation of honeydew excretion by the bugs and its use by the ants, but this was not observed. Bugs in association with ants occurred on 70% of FCs surveyed ($\chi^2_2 = 25.45$, $P < 0.0001$), and both were absent in 63.3% of the plots surveyed in the matrix ($\chi^2_2 = 21.67$, $P < 0.0001$). Both bug and ant were better represented on FCs (median, interquartile: ants = 2, 3.75, bugs = 5, 11) than in the matrix (ants = 0, 1, bugs = 0, 2.75) (Mann-Whitney U, *A. steingroeverii*: $U_{(9,9)} = 185$, $P < 0.0001$, Meenoplidae bugs: $U_{(9,9)} = 249$, $P = 0.003$, $n = 10$).



Fig. 3.4. *A. steingroeveri* tending grass feeding Meenoplidae bug. Photograph by V. Ross-Gillespie.

In addition to mature grass tussocks on the FC peripheral band, *A. steingroeveri* nest entrances were also commonly located under grass seedlings on the bare disc. These excavations often exposed the grass roots to the air or partially dislodged the plants, leaving seedlings anchored by only a few roots and were commonly chlorosed or grey (Fig. 3.5).



Fig. 3.5. Examples of chlorosed *Stipagrostis* seedlings on the FC bare disc showing recent root excavation by *A. steingroeveri*. Scale bar represents 2.5 mm.

Over a 16 day period when three separate observations were made of 15 individually marked excavated grass seedlings on the FC, 15 unexcavated seedlings on the FC and 15 unexcavated seedlings in the matrix, *A. steingroeveri* were recorded on 60 % of excavated FC seedlings, 10 % of unexcavated FC seedlings, and 3.3 % of unexcavated matrix seedlings. Thirty three percent of observed seedling deaths on FCs were of excavated seedlings and 67 % were on unexcavated FC seedlings, with no deaths of seedlings in the matrix. Unexcavated grasses on the FC showed the greatest degradation in colour at the end of the 16 days from healthy green to chlorosed yellow, with the change being significant for both this treatment and excavated FC grasses (Table 3.1) (Sign test, unexcavated grasses: number of non-ties = 11, $Z = 3.015113$, $P = 0.003$; excavated grasses: number of non-ties = 7, $Z = 2.268$, $P = 0.023$). Shoot height increased significantly for all three treatments (Table 3.2) (Sign test, excavated grasses: number of non-ties = 15, $Z = 2.582$, $P = 0.01$; unexcavated FC grasses: number of non-ties = 14, $Z = 2.94$, $P = 0.003$, and unexcavated matrix grasses: number of non-ties = 15, $Z = 3.615$, $P = 0.0003$) with the matrix grasses having a much greater shoot height increase than the two FC treatments (ANOVA, $F_{2,41} = 3.74$, $P = 0.032$). The number of roots and root length did not differ between the FC, matrix or excavated grasses (Table 3.2) (Kruskal-Wallis, $H_{2,45} = 0.21$, $P = 0.9$ and $H_{2,45} = 0.197$, $P = 0.906$ respectively).

Table 3.2. Median and interquartile (italicized) values for *S. obtusa* root number, maximum root length (cm) as well as differences in shoot height (cm) and colour rank before and after 16 days of observation for ant-excavated grasses on the FC, unexcavated grasses on the FC and matrix. Values highlighted in bold indicate a significant change from the beginning to the end of the 16 day period.

	Root number	maximum root length (cm)	Change in shoot height (cm)	Change in colour rank
Excavated grass	10, <i>10</i>	14.8, <i>4.8</i>	6, 5	0, 1.5
Circle grass	11.5, <i>5</i>	14.6, <i>2.68</i>	5, 6.5	-1, 1.75
Matrix grass	12.5, <i>3.75</i>	15.05, <i>2</i>	13.5, 12.5	0, <i>0.75</i>

3.4 Discussion

3.4.1 *The Effect of Fairy Circles on Plant Communities*

The FCs not only depressed plant growth, but also had a unique plant community. Matrix and FC samples had 50 % similarity in plant composition, with the matrix communities being more homogenous compared to FCs, which showed greater variation between samples (Fig. 3.1). This may

be due to differences in the developmental stages of FCs (see Chapter 4), and concomitant changes in abiotic factors. The dominant grass species at the NamibRand study site were an *Eragrostis* species, *S. obtusa* and *S. kalahariensis*. *S. obtusa*, *S. uniplumis* and *S. ciliata* have been previously documented as forming the main matrix grasses in this area (Joubert, 2008; Cramer & Barger, 2013; Vlieghe *et al.*, 2015). Both *Eragrostis* and *S. kalahariensis* are not reported as being important matrix grasses in southern Namibian FC plains, and the uncharacteristically high abundances of these annual species observed may be due to the exceptionally high rains preceding the time of sampling in 2011 and the increased proliferation of disturbance and pioneer grasses (Müller, 2007). Only two species, *S. hirtigluma* and *P. pistillaris*, were found only on the FCs, compared to five species which were restricted to the matrix. *Podaxis* species prefer sandy soils with fairly high moisture levels (Morse, 1933), conditions commonly found on FCs (Picker *et al.*, 2012; Juergens, 2013), and the Australian *Podaxis beringamensis* (Priest & M. Lenz) is known to be associated with termite mounds (Lenz & Priest, 1999). Juergens (2013) also noted the preferred use of FCs by *S. hirtigluma*, and Shirtcliffe & Doerr (2009) reported larger numbers of basidiomycetes fruiting bodies on FCs.

Plant diversity was higher in the matrix (1.64 for Shannon Weiner and 0.76 for Simpson's indices) than the FC bare disc (1.02 and 0.59), and this is likely related to a steep decline in species number and overall plant abundance on FCs (Table 3.1). That the lowered abundance (and likely productivity) on the bare disc would coincide with decreased species richness and diversity is expected, and agrees with observations of lowered diversity in less productive microhabitats in deserts such as dunefields (Waide *et al.*, 1999). North American harvester ants build discs that are analogues of FCs, with both having a conspicuous bare disc. As with the FC peripheral band, the area along the edge of the bare disc of *Pogonomyrmex* and *Messor* discs shows elevated plant growth and changes in plant communities, with an increase in annual grasses or woody species (Coffin & Lauenroth, 1990; Brown & Human, 1997; MacMahon *et al.*, 2000). On the bare disc surrounding *Pogonomyrmex* nests, certain plant species (e.g. *Oryzopsis hymenoides* (Roem. & Schult.)) occasionally escape mechanical removal by the ants, (Nowak *et al.*, 1990). In this case the remaining plant species benefit from reduced competition and increased availability of resources (Nowak *et al.*, 1990). However unlike the selective removal or retention of seeds or mature plants by harvester ants, neither *A. steingroeveri* nor *P. allocerus* are known to selectively target particular grass species, and any changes in plant community on or near the FC bare disc is more likely associated with soil modification (viz. high moisture) or reduced plant competition. At a landscape scale, FCs may be expected to have a large effect on overall biodiversity of an area, as their bare discs cover on average 3.4 % of the total land surface (but may cover as much as 20 % in some areas) (Cramer & Barger, 2013). *Pogonomyrmex occidentalis* (Cresson) discs in North American saltsage cover an identical land surface area (3.5 %)

(Sharp & Barr, 1960). Wight & Nichols (1966) investigated the potential loss in productivity caused by *P. occidentalis*-denuded areas in North American rangelands, and concluded that the increase in productivity caused by the presence of a well-vegetated perimeter compensated for any loss by the denuded area. The vegetated peripheral band found around FCs may have a similar balancing effect on production and diversity. The species richness of plants solely within the peripheral band compared to the matrix has yet to be investigated, but this area frequently supports grasses that are rare in the matrix (Theron, 1979; Moll, 1994; Becker & Getzin, 2000; van Rooyen *et al.*, 2004) and provides a source of heterogeneity in an otherwise relatively homogenous grassland. It may therefore have an overall effect of increasing beta-diversity. The high soil moisture of FC soils (Albrecht *et al.*, 2001; Juergens, 2013; Picker *et al.*, 2012; Vlieghe *et al.*, 2015) may support more perennial grass species along the peripheral band compared to the annual grass-dominated matrix. Habitat heterogeneity is known to increase species richness (Ricklefs, 1977), and Juergens (2013) concluded that FCs increase biodiversity by providing a unique habitat for perennial species in an otherwise ephemeral landscape. This in turn may influence faunal community composition (Chapter 6).

3.4.2 *A. steingroeveri* Associations with Fairy Circles and Polydomy

At an early stage of this study, *A. steingroeveri* was considered as a possible causative agent of FC formation, as 2010 data showed a tight spatial association between this ant and FCs (Picker *et al.*, 2012). However, this finding was not replicated in 2011 and 2012. Some FCs did hold large colonies of Pugnacious ants, as evident by excavations of their nests which were found to contain both brood and repletes (an unusual feature of certain desert ants where workers with distended abdomens can store liquid (Marsh, 1986)). The nest structure of *A. steingroeveri* was found to be similar to that described by Marsh (1986); viz. having conspicuous nests with entrances of 5 – 10 mm in diameter with nest openings located under perennial grasses or rock slabs (Fig. 3.2).

If *A. steingroeveri* were the cause of FC formation, it would be necessary for each FC to support an unrelated colony, with among-colony aggression accounting for the observed regular spacing of colonies. However, this was not supported by aggression trials conducted between colonies of neighbouring FCs. Non-aggressive interactions between colonies on certain FCs suggests that each colony can inhabit multiple nests (polydomous colony structure (Debout *et al.*, 2007)). The largest number of FCs inhabited by one colony was 13 (Fig. 3.3), where some FCs were not neighbours and were separated by uninhabited FCs or those with an unrelated colony. It is possible that FCs separating polydomous nests were once inhabited and subsequently abandoned, though this has yet to be

investigated. Prins (1982) stated that *Anoplolepis* species are predominantly unicolonial (i.e. the entire local population interacts frequently and without aggression, (Debout *et al.*, 2007)). However, he did not conduct aggression trials, and *A. steingroeveri* at NamibRand showed very high levels of aggression towards non-nest mates. Ant species often display aggression towards non-nestmate intruders of the same species, and this aggression varies along a gradient including threat displays, grappling of appendages and full blown attacks (Hölldobler & Wilson, 1990). These aggressive responses are similar to those observed in *A. steingroeveri* inter-colony encounters, where individuals instantly engaged in appendage grabbing, stinging and biting, typically leading to the death of an individual. Aggressive intraspecific territoriality can result in the even spacing of colonies and their nests e.g. Both Hölldobler (1976) and Ryti & Case (1986) demonstrated that regular spacing of colonies belonging to *Veromessor* and *Pogonomyrmex* harvester ants was related to intraspecific predation on founder queens near established colonies and competition for foraging space. *Veromessor pergandei* (Mayr) ants tended to forage away from their nearest neighbours (Ryti & Case, 1986), and aggression between *Pogonomyrmex* ants decreased with distance from neighbouring colonies (Hölldobler, 1976). Further evidence for overdispersion of ant colonies resulting from intraspecific territoriality is given by Cushman *et al.* (1988), who demonstrated that colony spacing is density- and size- dependent in the ant *Formica altipetens* (Wheeler), with distance between colonies increasing with colony size and spacing becoming more even with increased density. However the observation that *A. steingroeveri* colonies could inhabit more than one FC at a time, and the lack of consistent correlation between ant abundances and FCs across years, suggests that this species is not responsible for the overdispersed pattern of FCs, and thus is not considered as an agent for FC origination.

3.4.3 Potential Maintenance Mechanisms for a Vegetation-Free Fairy Circle Disc

Where *A. steingroeveri* nest entrances were found to be situated at the base of grass tussocks, excavation there was often extensive, at times exposing large portions of the grass root system (Fig. 3.2a and Fig. 3.5). These would sometimes be further enlarged through excavation by insectivorous mammals. Bat-eared fox, aardwolf and armadillo occur in the reserve and are known to include ants in their diet (Kok & Nel, 1992; Willis *et al.*, 1992; Matsebula *et al.*, 2009). *A. steingroeveri* is primarily a honey-dew feeder and carnivore, and is therefore unlikely to be feeding directly on the grasses, instead they may be concentrated around grass roots (i) to provide a solid structure to protect their nest entrances from the trampling activities of grazing animals (as suggested by Pontin (1963) for *Lasius flavus* (Fabr.)) or collapse of unconsolidated sand and (ii) to reach honeydew providing Meenoplidae bugs which have been observed inhabiting the roots and base of the grass tussocks,

particularly on the FC peripheral band (bugs and ants were associated with 70 % of FC grasses examined as opposed to 36.7 % of matrix grasses). Honeydew is known to make up a large proportion of the diet of *A. steingroeveri* (Steyn, 1954; Marsh, 1986), and this ant was found to have a close spatial association with the Meenoplid bug (Fig. 3.4). This auchenorrhynchan family is generally not considered to be ant-attended (Bourgoin, 1997) though Humphreys (1998) reported an ant association with a cave-dwelling *Phaconeura* species. Significantly higher numbers of both *A. steingroeveri* and the bugs were found under FC peripheral grasses compared to the grasses in the matrix (2X as many ants and 5X as many bugs), possibly a result of the bugs being attracted to the greener and more luxuriant peripheral grasses which benefit from the wetter soils found on FCs (Picker *et al.*, 2012; Cramer & Barger, 2013; Juergens, 2013), especially during the drier months. The vigorous excavations by *A. steingroeveri* exposing the grass roots to the air may in some cases be severe enough to cause the grass to become water stressed and later dislodged from the soil. Air drying of *Pinus taeda* (L.) seedlings was shown to reduce survival and decrease root growth (Feret *et al.*, 1985), and this effect may be more pronounced for grasses with exposed roots in the thermally stressful and moisture deficient environment in which FCs occur.

Despite the observed root excavation of *A. steingroeveri* on mature grass tussocks and grass seedlings on FCs, both excavated and unexcavated seedlings on the bare disc showed similar signs of stress - reduced growth and survival, with retarded shoot growth and ongoing chlorosis. The same stress factors were not evident in matrix seedlings of comparable size, which showed a 2X greater increase in shoot height (root number and length however were the same for all treatments) (Table 3.2). Since not all grass deaths on FCs can be attributed to ant excavations, it seems unlikely that *A. steingroeveri* is the primary causative agent of FC formation, and instead may play a maintenance role by reducing the recruitment of seedlings on the bare disc after the FC has formed. The Pugnacious ants may be preferentially drawn to FCs due to the wetter soils and a greater supply of honeydew producing Meenoplidae bugs under the greener grasses along the peripheral band. The majority of nests were found under the large and more stable mature peripheral grass tussocks, with tunnels extending laterally into the bare disc to excavate grass seedlings inhabited by the bugs. The root systems of the smaller seedlings are more likely to become compromised by ant activity and dislodged through excavation, eventually being blown away. In areas where *A. steingroeveri* does not occur, other ant species such as those belonging to the genus *Tetramorium* may play a role in FC maintenance (Juergens, 2015). However, it should be noted that both excavated and unexcavated grass seedlings on FCs deteriorated in condition, suggestive of another stress factor other than ants.

One potential mechanism for maintaining the FC's bare disc is the greatly reduced *Stipagrostis* seed bank on the bare disc compared to the peripheral band and matrix. A similar reduction in seed bank has been noted for *Pogonomyrmex* bare discs, which have less annual grass seeds than the surrounding vegetation (though more perennial grass seeds than the matrix, possibly related to seed selection by the harvester ants) (Fewell *et al.*, 1991; MacMahon *et al.*, 2000; Coffin & Lauenroth, 1990). A reduction in seed bank on FCs may be related to the reduced production of seeds on the bare disc compared to areas where the grasses are abundant (*S. obtusa* and *S. ciliata* seed banks are 39 and 70X higher in the matrix and on the peripheral band respectively compared to the bare disc). This difference is accentuated further by wind or water dispersal of seed and trapping against existing vegetation. Seeds can concentrate near vegetation patches in spotted or banded patch mosaics (Aguiar & Sala, 1999), with low abundances in areas of bare soil. Even in cases where seeds fall uniformly in the landscape, differences in abundances under vegetation and on bare patches can result from abiotic redistribution or variations in predation (Aguiar & Sala, 1999). This uneven distribution of seed is an important factor in the maintenance of bare patches between tussock and shrub clumps on the Patagonian steppe (Aguiar & Sala, 1999). Lateral removal of seeds was found to be higher on the bare patches and was attributed mainly to wind action (Aguiar & Sala, 1997). Similarly wind is likely to be the major factor in the movement of wind dispersed *Stipagrostis* seeds (van Rheede van Oudtshoorn & van Rooyen, 1999) off the FC disc, and this potential for maintaining the bare disc cleared of plant debris and seeds was noted by Becker (2007) and Cramer & Barger (2013).

Another factor not explored by this study that could be negatively affecting seedlings on the bare disc, and may explain the decline in performance of FC seedlings *not* excavated by *A. steingroeveri* on discs is the presence of volatile growth inhibitors. A semi-volatile chemical hypothesised to be released by termite nests and to stunt growth of grasses on FCs has not been identified (Albrecht *et al.*, 2001; van Rooyen *et al.*, 2004; Jankowitz *et al.*, 2008), however termite nests are known to be sources of volatile and semi-volatile gases such as methane, naphthalene and certain other hydrocarbons (Zimmerman *et al.*, 1982; MacDonald *et al.*, 1998; Šobotník *et al.*, 2010). Termites are a sizable source of global methane (global annual emissions of 1.5×10^{14} g have been estimated by Zimmerman *et al.* (1982)) and this gas has been shown to lead to the impaired growth of seedlings in mangrove habitats (Strangmann *et al.*, 2008). Naphthalene is a potentially toxic polycyclic aromatic hydrocarbon (Fortune *et al.*, 2009) used by some termite species as a chemical repellent incorporated in nest material to deter other invertebrates and detrimental microbes (Wiltz *et al.*, 1998). Naphthalene along with other hydrocarbons is also secreted by the frontal gland as a defence against insects such as ants (Prestwich, 1977). Interestingly, Naudé *et al.* (2011) detected higher levels of hydrocarbons (alkane and alkenes) on FCs compared to the matrix, and attributed this

to a natural gas microseep below FCs viz a geochemical source. However, a wide range of hydrocarbons, including alkanes and alkenes, are produced by both termites and ants for chemical defence or nest-mate recognition (Katzav-Gozansky *et al.*, 2008; Šobotník *et al.*, 2010), and it is possible that the gases detected by Naudé *et al.* (2011) originated from large social insect nests on FCs (Picker *et al.*, 2012). Most recently Juergens (2015) suggested that the chemicals detected by Naudé *et al.* (2011) might be related to the presence of nests of the termite *P. allocerus*, which release significantly higher amounts of both NH₄ and CO than the surrounding soil. The gases are produced by bacteria and protozoa within the termite's intestinal tract, which may also explain the generation of hydrocarbons detected by Naudé *et al.* (2011) (Juergens, 2015).

3.4.4 Conclusions

FCs represent sites that increase plant beta-diversity by increasing turnover in an otherwise homogenous matrix. Although their bare discs represent areas of lowered plant abundance and diversity, the generation of bare ground and an associated well-vegetated periphery provides an increased degree of heterogeneity and is capable of supporting unique species not found in the matrix, through an increased resources such as water and reduced competition. The hypothesis that *A. steingroeveri* might generate FCs through (a) an association of individual colonies on different FCs and (b) create the bare disc through their excavation of grasses was not supported. Data over a few years showed that elevated ant numbers were not consistently associated with FCs, and the polydomous nest system of *A. steingroeveri* does not provide a system whereby among-colony aggression might generate the overdispersed pattern of FCs. Similar reduction in seedling performance on FCs was found for both excavated and unexcavated grasses. Despite this, excavation of seedlings by Pugnacious ants, along with seed removal by wind action, may still play a supplementary role in the maintenance of the FC's barren disc. Another research direction worthy of investigation would be the identification of volatiles from FCs with active *Psammotermes* colonies, and identification of the source of production of these compounds (from the nest itself or from the termites). A last experimental approach investigating the effect of these volatiles on seedling growth would consolidate a role for termite-produced volatiles.

4 LINKING *PSAMMOTERMES ALLOCERUS* WITH FAIRY CIRCLE FORMATION AND DEVELOPMENT

4.1 Introduction

4.1.1 Termite Herbivory

Overdispersion of termite mounds is a result of competitive interactions between neighbouring colonies (Laurie, 2002; Grohmann *et al.*, 2010; Pringle *et al.*, 2010). This even patterning is often accentuated by vegetation responses, either through (i) the proliferation of plant growth and/or changes in plant communities in response to a greater availability of nutrients near the mound, or (ii) the removal of vegetation through termite foraging activities or increases in soil compaction (Chapter 1 and 3). These evenly spaced vegetation patterns can take the form of bush or thicket clumps in *Macrotermes* spp. (Dangerfield *et al.*, 1998; Bloesch, 2008) or earth mounds (heuweltjies) in *Microhodotermes viator* (Moore & Picker, 1991; Picker *et al.*, 2007). However the effect of more cryptic subterranean species of termite (which do not build epigeal mounds) on the vegetation is poorly-studied. This chapter examines the potential role of the Sand termite *Psammotermes allocerus* in the formation of gapped vegetation patterns (fairy circles) through foraging activities on grasses around their subterranean nests.

Although termites are best known as detritivores, certain groups forage on living plant material (both above and below ground) (Lee & Wood, 1971; Wood, 1978). Of these the most prominent are the harvester termites, which include species of Hodotermitidae, certain Amitermitinae and Nasutitermitinae (Lee & Wood, 1971). Harvester termites cut pieces from plant tussocks (often grass) and transport these back to their nests (Lee & Wood, 1971; Ohiagu & Wood, 1976; Duncan & Hewitt, 1989). The volumes of grass harvested by these widespread and abundant species are considerable. *Hodotermes mossambicus* harvests tussocks from the top down until the grass has been trimmed to a height of about 3 cm (Duncan & Hewitt, 1989), occasionally creating uneven denuded patches (Becker & Getzin, 2000). It has been reported to remove from 14.6 to 274 kg ha⁻¹ yr⁻¹ of grass in South African veld (Nel, 1968; Basson, 1972). *Trinervitermes* spp. emerge in foraging parties consisting of several hundred individuals and cut lengths from grass tussocks (Ohiagu & Wood, 1976), removing 81 kg ha⁻¹ yr⁻¹ of grass from Nigerian savannah (Ohiagu, 1979). The consumption of living plant material is not restricted to harvester termites, as some polyphagous species which primarily feed on dead plant material such as wood or humus will also attack living plants (Lee & Wood, 1971). In semi-arid areas of the Sahara, *Psammotermes hybostoma* (Desneux) feeds on virtually all plant species,

including those poisonous to mammals (Harris, 1970). The humus-feeding South American termite *Anoplotermes pacificus* (Müller) additionally feeds on plant roots, particularly the apices of young roots invading their nests (Kaiser, 1953). This herbivory on living plants impacts their condition (see Chapter 3).

Termite herbivory has been proposed several times as a mechanism for FC formation. Initially, it was proposed that *H. mossambicus* cleared irregular patches of grass, generating bare areas (Moll, 1994; Becker & Getzin, 2000). However, no empirical evidence was provided to support this hypothesis, which has been criticised from various perspectives (Grube, 2002; van Rooyen *et al.*, 2004; Picker *et al.*, 2012). Moll (1994) additionally considered *Baucaliotermes hainsei* and *P. allocerus* as candidates for FC origin and noted the high degree of geographical overlap between the distribution of *P. allocerus* and FCs. Nevertheless, he discounted their likely involvement due to their low abundance and small size. *Psammotermes* is an arid-adapted, psammophilous termite genus consisting of four species found in Arabia, Africa, India and Madagascar and are major pests on wooden structures and crops (Lee & Wood, 1971; Sarr *et al.*, 2005). *P. allocerus* occurs across large portions of Namibia and South Africa (Coaton & Sheasby, 1973). Though it thrives in sandy deserts such as the Namib and Kalahari, it occurs along a fairly wide range of vegetation types (from sand desert to coastal tropical forest), rainfall ranges (from less than 100 mm to upward of 800 mm) and altitudes (sea level to over 1600 m), yet has not been recorded in very clay rich soils. It constructs its nests either within wood or as small (30 cm diameter) moundlets buried in the soil, often situated below grass tussocks, and is of great economic importance due to its ability to destroy sound timber and kill plants and crops (Coaton & Sheasby, 1973). Juergens (2013) and Vlieghe *et al.* (2015) independently provided evidence for the involvement of *P. allocerus* in FC formation, based largely on localised foraging by the termites on the roots and culms of grasses from and in close proximity to their subterranean nests (central-place foraging). This was hypothesized to have generated the circular bare disc of FCs. Foraging generates small surface soil dumps and sand sheetings on grasses. A tight spatial association between these and FCs (when compared to the matrix) occurs across their distribution (Juergens, 2013; Vlieghe *et al.*, 2015). Additionally, the distribution of FCs falls within that of the termite, nests of this termite are located on the disc of FCs, and herbivory by the termite in the laboratory was directed towards grass seedling roots, matching the type of root damage seen in the field and ultimately causing death of grass seedlings (Juergens, 2013; Vlieghe *et al.*, 2015). Portions of this chapter have been reported in Vlieghe *et al.* (2015).

4.1.2 Effect of Termite Colony Age on Vegetation Patterns

Although termites are relatively small, their long-lived sessile nests and large colonies result in significant impacts on the surrounding vegetation, through both the consumption of vegetation and the modification of soils around the nest. As colonies grow, there are increases in termite abundance, growth rate and nest/mound size – all impacting the surrounding vegetation in different ways. Colonies initially go through a juvenile period of colony growth (Noirot, 1969). The growth rate during this period seems to differ between lower and higher termite species, with young colonies of lower termites tending to show a slower rate of growth than later stages, and those of higher termites demonstrating rapid growth early on (Lee & Wood, 1971; Collins, 1981; Thorne *et al.*, 1999). The primitive wood-inhabiting *Kaloterme flavicollis* (Fabr.) may produce only 55 individuals over one year (Grassé & Noirot, 1958), and *Neotermes tectonae* (Damm.) (Kalshoven, 1959) produces only 30-70 individuals over 1-2 years. In contrast, the higher termite *Macrotermes bellicosus* (Smeathman) may produce between 6000-7000 individuals after the first two years (Collins, 1981). This ability of higher termites to grow rapidly early in a colony's life may be accredited to greater body reserves in the queen used to produce eggs and nutrition for the first brood (Lee & Wood, 1971). Due to a higher proportion of larvae compared to workers or soldiers, juvenile colonies are characterised by small mounds or nests and a higher death rate due to predation (Collins, 1981; Smith & Yeaton, 1998). The colony reaches maturity when both mound and population growth stabilise to create a physically and microclimatically stable environment, allowing for the production and release of alates (Collins, 1981). Mature colonies are often described as possessing larger mounds and nests (Smith & Yeaton, 1998), with the result that this life stage is generally longer lived than smaller juvenile colonies (Collins, 1981). Mature colonies can persist for much longer than the lifespan of individual reproductive termites through the production of secondary reproductives, which allow a colony to survive for decades (Thorne *et al.*, 1999; Luchetti *et al.*, 2013). At some stage colonies decline and cease producing alates, and the mound is gradually eroded away (Collins, 1981; Smith & Yeaton, 1998).

Termite mounds alter the community structure and productivity of surrounding vegetation (Dangerfield *et al.*, 1998; Arshad, 1982; Moe, 2009), and it is possible to link changes in associated plant communities with the temporal progression of a mound's life stages. Smith & Yeaton (1998) found that plant species composition in South Africa differed on older active mounds of *Trinervitermes trinervoides* (Sjöstedt) in a semi-arid grassland compared to either young or abandoned mounds as they supported the grass *Themeda triandra* (Forssk), and both grass and woody plants grew preferentially on inactive and eroded *Trinervitermes* termite mounds in other African grassland and savannah ecosystems (Steinke & Nel, 1989; Gower *et al.*, 1992). Plant communities in areas alongside

mounds also differ between mound life stages, with some species increasing in abundance while others decrease at varying stages (Smith & Yeaton, 1998). On active termite mounds whose surfaces are bare due to soil compaction and high clay content (e.g. *Coptotermes lacteus* (Froggatt)) vegetation colonises the mound surface at the end of the mound's lifespan when it is no longer maintained (Rogers *et al.*, 1999). Hence the extinction of these mounds is marked by a stage of senescence.

Similarly, vegetation changes are associated with FCs as they age. Aerial views of FCs reveal that FCs at single sites are not uniform in appearance, varying in size, the presence of a peripheral band and the type and amount of vegetation cover (Fig. 4.1). Observations by a number of authors have suggested that these variations can be related to a progression of life stages from birth to senescence (Albrecht *et al.*, 2001; Tschinkel, 2012; Juergens, 2013; Vlieghe *et al.*, 2015), similar to the ontological progression seen in termite mounds. Newly developed FCs are small irregular patches containing mature but dead matrix grass tufts and lack a differentiated peripheral band (Albrecht *et al.*, 2001; Tschinkel, 2012; Vlieghe *et al.*, 2015). The majority of FCs are mature, with a central bare disc and an obvious ring of taller grasses along the periphery. Both Albrecht *et al.* (2001) and Tschinkel (2012) report on an increase in FC concavity with age through wind erosion. Lastly dead/extinct FCs are partially or fully covered with living mature grass tussocks and seedling grasses and eventually form 'ghosts' Tschinkel (2012) (remnants of previous FCs recognised by a concavity and peripheral ring of taller vegetation). Tschinkel (2012) tracked the appearance and disappearance of FCs using Google Earth imagery over several years and also groundtruthed FCs progressing from one stage to another.

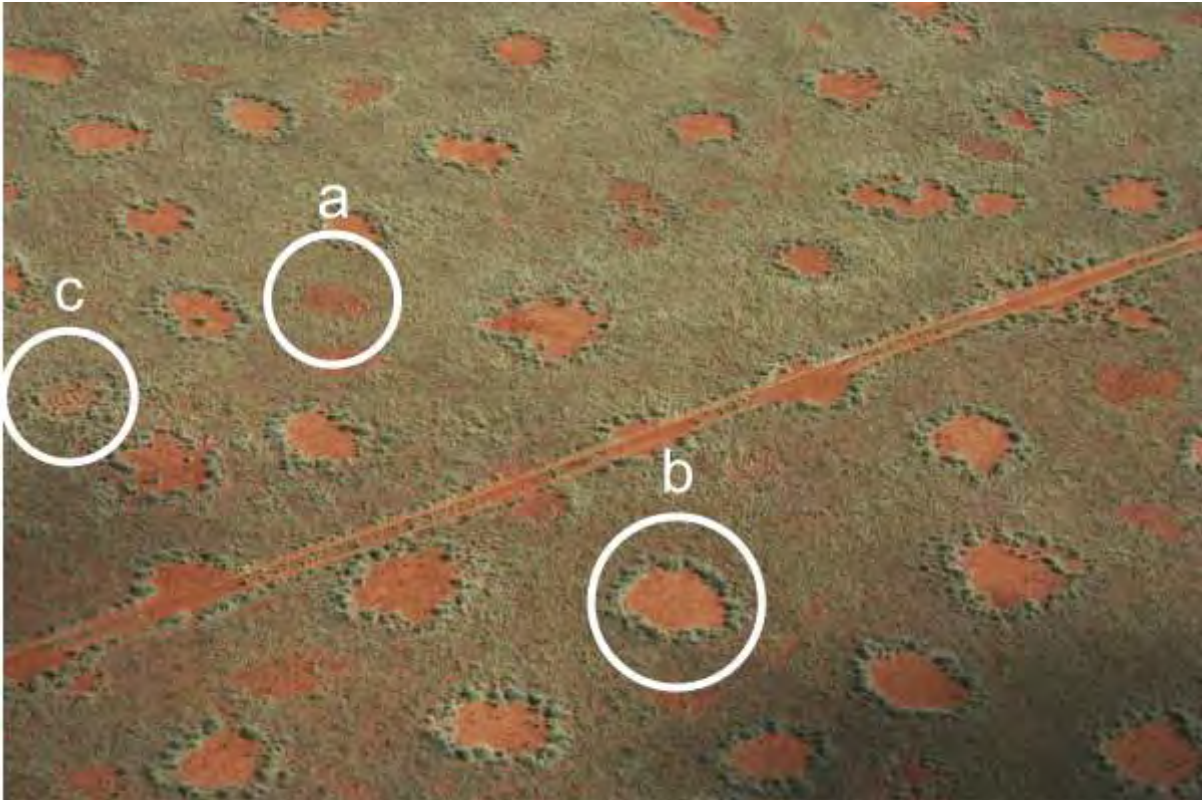


Fig. 4.1. Aerial image of FCs in NamibRand showing (a) smaller FCs with no vegetated peripheral band, (b) mature FCs with a clear bare disc and well-vegetated peripheral band, and (c) senescent FCs overgrown with vegetation. Photograph by M. Picker.

4.1.3 Aims

This chapter aims to test the hypothesis of a Sand termite origin for FC formation, first proposed by Juergens (2013). Specific aims include:

- Investigate the potential for a strong spatial link between the nests of the termite *P. allocerus*, demonstrating that termite numbers increase with FC development and decay with senescence of the FC.
- Proposing life stage categories for FCs (descriptions in Chapter 2, Fig. 2.1) and linking their progression with termite abundances.
- Investigate mechanisms for grass death and subsequently FC formation through *P. allocerus* herbivory in proximity to their subterranean nests, using field observations and laboratory herbivory trials.

4.2 Methods

Four FC growth stages were categorised (Chapter 2, Fig. 2.1), namely new, young, mature and senescent. Transects across the peripheral band and bare disc of 10 FCs and matrices measured vegetation abundance, plant species number and termite and sand sheeting abundance. *P. allocerus* nests were excavated on two FCs in order to describe their subterranean structure and surface features (sand sheetings on grasses). Herbivory trials were conducted in the laboratory using wheat seedlings grown in pots containing either active *P. allocerus* nests, nests with no termites or control pots with no nests or termites. At the end of the experiment root and leaf length and number, inflorescence number and occurrences of seedling deaths were recorded. Lastly root length and number of chlorosed seedlings on the bare disc were compared with healthy seedlings on the bare disc and in the matrix. Detailed methods for this chapter are covered in Chapter 2, Section 2.3.

4.3 Results

4.3.1 *P. allocerus* Abundances and Their Foraging Sheets on Fairy Circle Growth Stages

Four progressive FC growth stages were identified, namely **new** (small, covered in sand sheetings and with no peripheral band), **young** (some sand sheetings and no peripheral band), **mature** (large, clear of dead or living grasses with a well-developed peripheral band) and **senescent** (covered in living grasses, may still have a peripheral band). FCs showed a gradual increase in area from new FCs to mature ones, before decreasing significantly in size with senescence and an overgrowth of grasses (Kruskal-Wallis, $H_{3,40} = 14.91$, $P = 0.002$) (Fig. 4.2a). The number of grasses along the FC peripheral band of all growth stages did not differ from the matrix (Kruskal Wallis, $H_{4,50} = 6.15$, $P = 0.188$), however grass height was significantly greater in mature and senescent FC peripheries when compared to the matrix (Kruskal Wallis, $H_{4,50} = 19.37$, $P = 0.0007$) (Fig. 4.3a,b). On new FCs, grasses covering the central disc were dead and encrusted with sand sheetings constructed by *P. allocerus* (Fig. 4.4a). Consolidated tunnels systems and a honeycomb of galleries connected to these sand turrets ran both horizontally and vertically below the surface of FCs. Similarly, grasses along the peripheral band of FCs were occasionally seen to be either dead or partially dead where sand sheetings were present (Fig. 4.4b). The number of sand sheetings on grasses in the peripheral band was greatest on mature FCs, which was significantly higher than values in the matrix (Kruskal Wallis, $H_{4,50} = 11.87$, $P = 0.0184$) (Fig. 4.3c). The highest numbers of termites and sand sheetings occurred on the bare disc of new FCs, decreasing in number as the FC matured (Kruskal-Wallis, $H_{3,40} = 22.81$, $P = 0.0001$) (Fig. 4.2c,d) and eventually becoming isolated to the FC peripheral band. New and young FC discs contained more sand sheetings

than on their peripheral bands (Kruskal-Wallis, $H_{3,40} = 10.50$, $P = 0.0147$ and $H_{3,40} = 8.20$, $P = 0.0421$ respectively), while mature and senescent FC bare discs had fewer sheetings than the matrix (Kruskal-Wallis, $H_{3,40} = 11.83$, $P = 0.009$ and $H_{3,40} = 15.71$, $P = 0.001$ respectively). As FCs progressed through the growth stages the ratio between sheeted and unsheeted grass tussocks decreased (new = 19, young = 7.63, mature = 0.7, senescent = 0.007 and matrix = 0.18). This reflects the relative absence of living grasses on the bare discs of new, young and mature FCs compared to the matrix and senescent FCs (Kruskal-Wallis, $H_{3,40} = 39.69$, $P = 0.002$) (Fig. 4.2b).

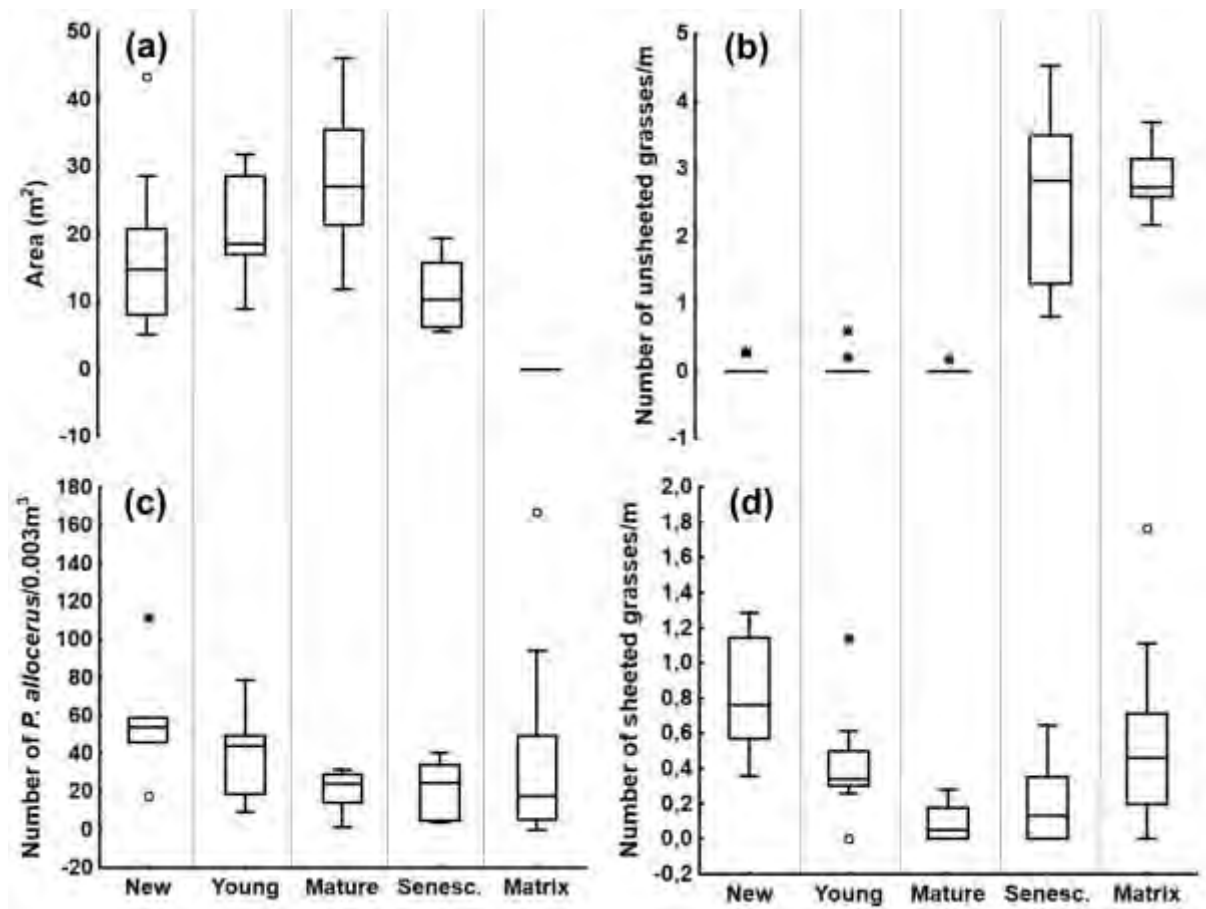


Fig. 4.2. Median and interquartile values (o = outliers, * = extremes) of (a) FC area (m²), (b) number of unsheeted grasses, (c) *P. allocerus* abundance and (d) grasses with termite sand sheetings on the discs of the four FC growth stages and corresponding matrices. Senesc. = senescent. Adapted from Vlieghe *et al.* (2015).

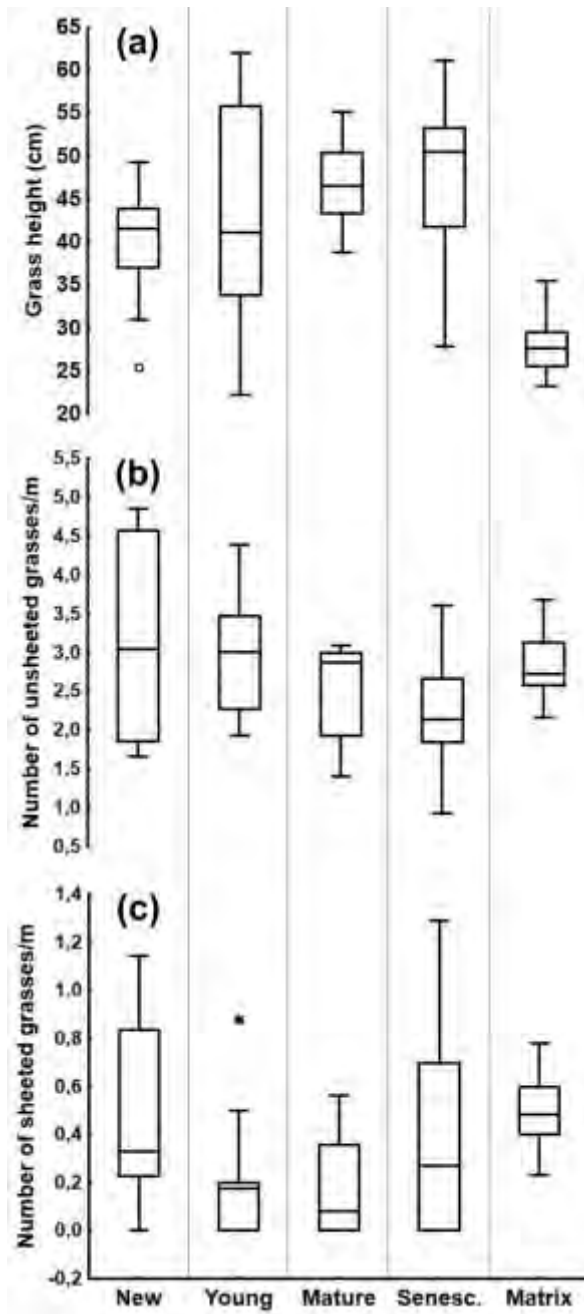


Fig. 4.3. Median and interquartile values (o = outliers, * = extremes) for (a) grass height (cm), (b) number of unsheathed grasses and (c) number of sheathed grasses along the peripheral band of FCs in the four growth stages and the matrix. Senesc. = senescent.

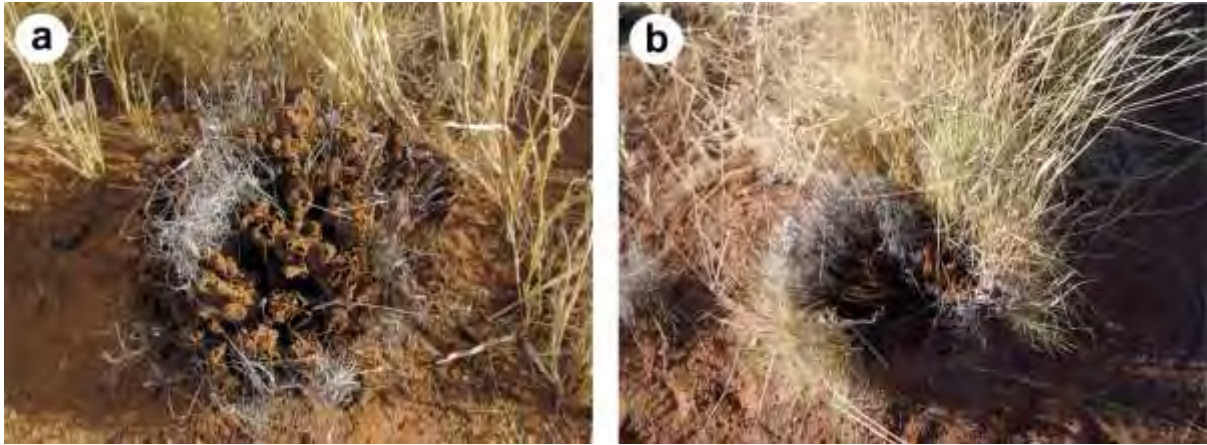


Fig. 4.4. (a) Dead grass tussock on young FC covered in *P. allocerus* sheetings and (b) *S. ciliata* grass tussock partially covered in sand sheetings on the FC peripheral band.

4.3.2 Grass Root Damage Caused by *P. allocerus* Herbivory

Roots of chlorosed seedlings on the FC disc (mean \pm SD length; 4.90 ± 2.12 cm, $n = 20$) were significantly shorter than those of healthy seedlings on the FC (6.54 ± 1.85 cm, $n = 20$) and matrix (10.25 ± 1.96 cm, $n = 20$) (ANOVA, $F_{2,60} = 40.15$, $P = 0.0001$). Additionally root number was reduced in chlorosed seedlings (3.82 ± 1.32 , $n = 20$) compared to healthy FC (5.95 ± 1.78 , $n = 20$) and matrix seedlings (5.55 ± 1.61 , $n = 20$) (ANOVA, $F_{2,60} = 10.22$, $P = 0.0003$ for healthy FC and $P = 0.003$ for healthy matrix seedlings).

Over a period of five weeks in the laboratory experiment of termite herbivory, *P. allocerus* presence reduced both root (Kruskal-Wallis, $H_{2,30} = 9.25$, $P = 0.008$) and leaf number (Kruskal-Wallis, $H_{2,30} = 7.059$, $P = 0.037$) of wheat seedlings when compared to pots without termites or their nests (Fig. 4.5a,c), resulting in 33.3 % seedling mortality compared to 100 % survival in the control ($n = 30$). Seedling root length did not differ between treatments (Kruskal Wallis, $H_{2,30} = 6.974$, $P = 0.306$). Termites were observed creating surface entrances adjacent to and foraging on the culms of seedlings in the termite pots but were not observed feeding on the seedling leaves. Pots containing vacant nests resulted in an increase in leaf length (Kruskal-Wallis, $H_{2,30} = 6.82$, $P = 0.031$) and inflorescence number (Kruskal-Wallis, $H_{2,30} = 9.54$, $P = 0.049$) compared to the other treatments (Fig. 4.5d,e).

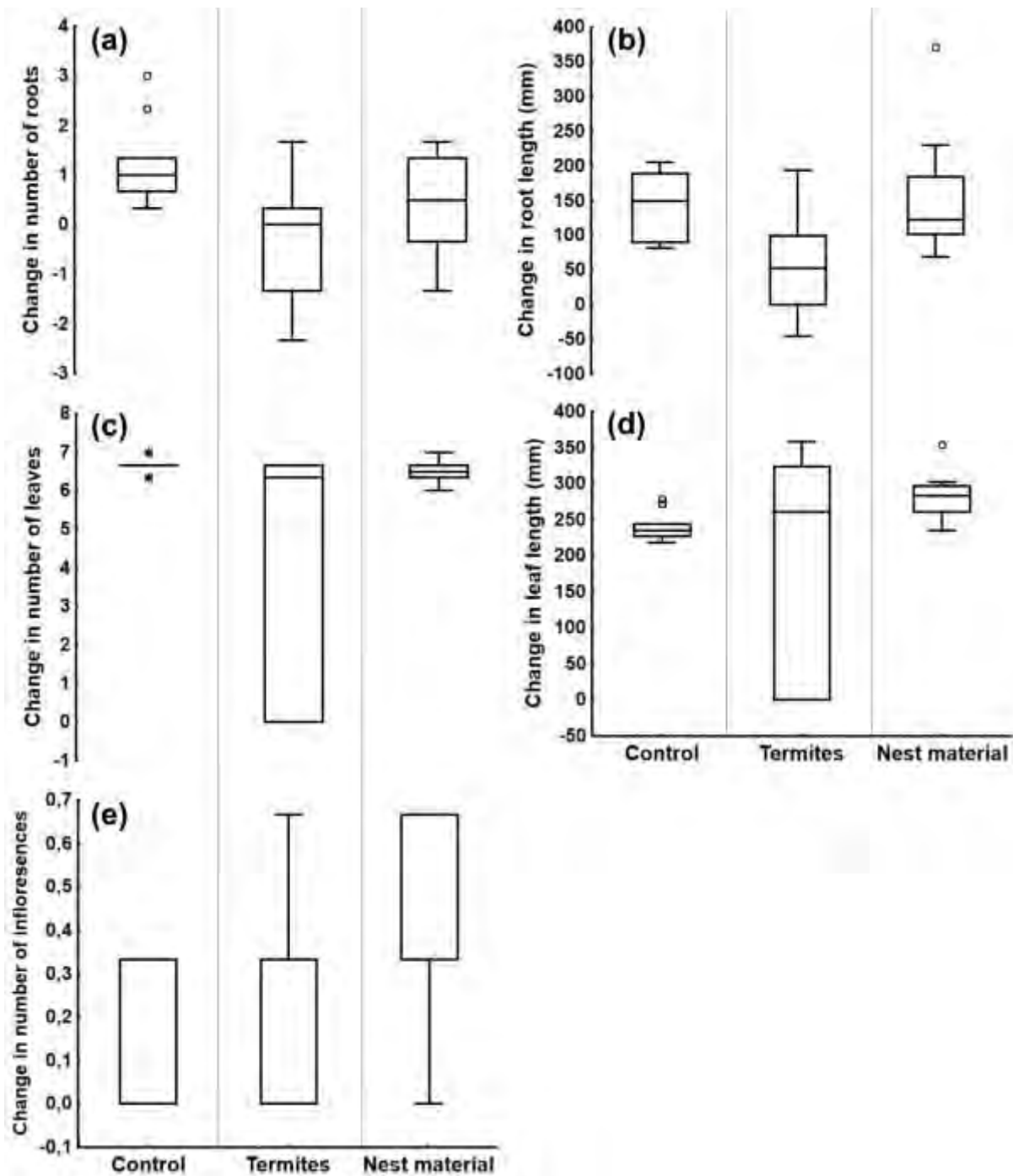


Fig. 4.5. Median and interquartile values (o = outliers, * = extremes) for the change in (a) root number, (b) root length, (c) leaf number, (d) leaf length and (e) inflorescence number of wheat seedlings grown in sand without termite nests, sand with vacant termite nests and sand with living termite nests (n = 10). Adapted from Vlieghe *et al.* (2015).

4.4 Discussion

4.4.1 Could *P. allocerus* Herbivory Drive the Formation of Fairy Circles?

Tschinkel (2012) stated that any theory on the formation of FCs would be strengthened by associating the proposed causative agent not only with mature FCs but also with all FC developmental stages. The highest abundances of termites and their sand sheetings were found on newly formed FCs, which were evenly covered by dead tussocks of mature matrix grasses (Fig. 4.2c,d and Fig. 4.4a). Small subterranean *P. allocerus* nests were located at the base of each of these sheeting-encrusted dead grass tussocks, and were inter-connected by horizontal tunnels, suggesting that the nest system is polycalic (Coaton & Sheasby, 1973; Holt & Easey, 1985). Polycalic nest systems occur when colonies are divided into spatially distinct subunits of nests with separate entrances (Thorne *et al.*, 1999) and are common among primitive groups of subterranean termites including Hodotermitidae and Rhinotermitidae, of which *Psammotermes* is a member (Thorne *et al.*, 1999; Grube, 2002). This suggests that *Psammotermes* herbivory is related to the death of the matrix grasses, in part due to the habit of the termite of feeding on grass roots (observed in laboratory trials). Young FCs still showed evidence of dead matrix grass tussocks, but many had become dislodged, possibly as a result of the weakening of roots after termite herbivory. Laboratory experiments indicated that *P. allocerus* concentrated its foraging activities on the roots and culms of grasses and were capable of significantly reducing grass root number and indirectly affecting leaf number, eventually leading to grass death (Fig. 4.5). Juergens (2013) made similar observations of *P. allocerus* foraging on and killing both grass seedlings and mature grass tussocks. Termites are known to attack the roots of grasses in proximity to their nests (Kaiser, 1953), and Jouquet *et al.* (2004) proposed that *Odontotermes* may prune grass roots that invade their nest chambers and hence reduce plant growth. In a subterranean species such as *P. allocerus*, grass roots would be the first part of a grass encountered, and would be consumed as the termite nest formed around the roots.

The grass tussocks on young FCs fragment and are eventually removed from the bare disc through wind action, creating the characteristic bare appearance of mature FCs. FCs reached a significantly larger size after maturation, almost doubling in area compared to new FCs (Fig. 4.2a). The concept of FCs expanding with age is consistent with the observations of Albrecht *et al.* (2001) as well as observations of haloes of dead peripheral grasses present on some of the bare discs of mature FCs, which may indicate the positions of previous peripheral bands as the FC increases in size (Tschinkel, 2012; Juergens, 2013). The FC peripheral band becomes most prominent once FCs reach maturity and is made up of grasses showing enhanced growth (Fig. 4.3a,b), possibly in response to the elevated moisture content of FCs compared to the matrix (Becker, 2007; Picker *et al.*, 2012; Juergens, 2013).

Mature FCs showed a substantial drop in both termite and sand sheeting abundances on the bare disc, having the lowest number of sheeted grasses of any locality (Fig. 4.2). However this coincided with an increase in sand sheetings along the peripheral band (Fig. 4.3b and Fig. 4.4b). It is proposed that once the majority of grasses on the bare disc have been removed, *P. allocerus* colonies migrate to grass tussocks along the peripheral band and adjacent areas in the matrix, where they either contribute to the expansion of the FC.

The bare disc of mature FCs may be maintained long after the termites have dispersed through a number of factors, including wind action removing seeds from the exposed surface and *Anoplolepis steingroeveri* ants compromising the root systems of recruiting seedlings (Chapter 3). After a number of sequential years of above average rainfall when seedling recruitment is higher (Henschel *et al.*, 2005), FCs begin senescing, usually with seedlings slowly invading from the outer edges of the bare disc closest to the periphery. Senescent FCs had virtually no *P. allocerus*, higher abundances of unsheeted grasses (at levels comparable with that in the matrix) and fewer sheeted grasses (Fig. 4.2e). It should be noted that a characteristic of mature FCs is the presence of chlorosed grass seedlings, not all of which showed current ant or termite activity. While it is possible that prior root herbivory may be responsible for their compromised root system, there may be an additional factor that impacts these seedlings.

4.4.2 Do Overdispersed Vegetation Patterns Have Growth Stages?

The plant competition hypothesis for FC formation (Cramer & Barger, 2013; Getzin *et al.*, 2014) includes FCs with similar evenly-spaced landscape features (vegetation gaps, spots and bands) in other parts of the world. Getzin *et al.* (2014) further indicate that their model predicts the first appearance of gapped vegetation (and FCs) in their final size. Studies on other vegetation patterns indicate that they are relatively stable features over long periods of time which experience little or no change in appearance (von Hardenberg *et al.*, 2001; Deblauwe *et al.*, 2011). However, one of the characteristics of FCs is their growth and differentiation. Banded vegetation may move very gradually up a slope in response to greater run-off collection by the leading edge of the vegetated band (with vegetation in the lower portions of the band eventually dying) (Boaler & Hodge, 1964) but this does not seem to be the case for static features (gaps and spots) on flat ground. Other studies have shown an often abrupt progression of patterns from bare gaps to labyrinths to vegetated spots along a spatial aridity gradient (Deblauwe *et al.*, 2011). This may also be associated with a single locality experiencing a climatic change towards aridity over time, with larger and larger gaps forming between a previously even cover

of vegetation to eventually create a labyrinth pattern of interconnected gaps and finally spots of vegetation surrounded by a bare matrix (Deblauwe *et al.*, 2008). However this kind of abrupt regime shift would not account for the appearance, growth and death of some FCs and the persistence of others within close proximity. If climate was the dominant factor determining the transition of FCs from bare gaps to senescence, one would expect all FCs within an area to show a similar and simultaneous progression. The observation that self-organised vegetation patterning progresses through spots, labyrinths and gaps along a spatial aridity gradient is not shown with Namibian FCs. FCs also disappear abruptly on the periphery of their distribution, with no obvious response in shape to aridity or slope. Though gradual regime shifts are less common in vegetation patterning, Zelnik *et al.* (2015) use models to argue that FC births and deaths are examples of a spatial confined, gradual regime shift whereby individual FCs transition between hybrid states. Using a simplified version of the Gilad *et al.* (2004) model which take water uptake by perennial grasses and soil-water diffusion in sandy soils into account, Zelnik *et al.* (2015) were able to replicate the appearance and disappearance patterns of FCs, however the precise biological mechanism involved remains unclear.

There are however empirically documented similarities in the growth pattern of FCs and that of termite colonies (Noirot, 1969). New and young FCs, with their a dense covering of *P. allocerus* sand sheets, would appear to reflect an early period in colony progression characterised by exponential colony growth (Collins, 1981; Smith & Yeaton, 1998), similar to the increase in disc size from new to mature FCs (Fig. 4.2). Large mature FCs whose dimensions and appearance may be maintained for a long period of time relate to the adult period of termite colony aging, where both mound and population growth stabilise. Finally, FCs undergo a senescent phase comparable to termite colonies, when the population begins to decline and can no longer increase in size (Collins, 1981; Smith & Yeaton, 1998), possibly when the reproductives are no longer present or productive. In termite species with epigeal mounds, age differences between mounds would be reflected in differences in mound appearance within a single population (Collins, 1981; Korb & Linsenmair, 2001; Grohmann *et al.*, 2010).

4.4.3 Criticism of the Sand Termite Hypothesis

In spite of the spatial association of the Sand termite with FCs, similarities between the developmental progression of FCs and that of termite nests, and documentation of Sand termite herbivory that is directed at grass tussocks and has in the laboratory been demonstrated to compromise and even kill grass seedlings, several lines of criticism have been put forward against the Sand termite hypothesis

for FC formation, and there is currently a dichotomy between the two major hypotheses. One of these is that, although FCs fall within the distribution of *P. allocerus* (Moll, 1994), the Sand termite's range is far greater than the narrow Pro-Namib belt in which FCs are restricted. *P. allocerus* occurs over large parts of Namibia, South Africa and to a lesser degree in neighbouring countries, over a range of semi-arid habitats (Coaton & Sheasby, 1973), yet only produce FCs within a very narrow band bordering the Namib Desert. Certain species of termite demonstrate intraspecific variation in mound size and form, depending on local environmental conditions. Pomeroy (1977) found that mound size and shape of two Ugandan *Macrotermes* spp. varied in relation to heat load, soil porosity other soil characteristics. Significantly larger domed mounds were produced in valley bottoms in order to elevate the nests above the water-table level and tall turret-like mounds produced at higher elevations are possibly adapted to increase ventilation in warmer climates (Pomeroy, 1977). There may even be convergence in mound architecture by different species of *Macrotermes* occurring in the same area on several different soil types (Pomeroy, 1977). *Odontotermes fulleri* produces flat, circular patches of bare soil (referred to as "arenas") similar in appearance to FCs in certain parts of the Masai Mara, in contrast to their more typical epigeal mounds (Darlington, 2007). It appears that this restricted range in arena nests is necessitated by very shallow soils over bedrock or are an adaptive feature. Darlington (2007) additionally proposed that the bare surface heats up more than areas shaded by leaves or grass and assists with temperature regulation within the shallow nest. Juergens (2013) proposed that the soft bodied *P. allocerus* may benefit from the water trap found within the bare disc in an otherwise dry habitat, and colonies of the Sand termite may only form FCs within a narrow range of environmental parameters. The bare disc of FC is one of their most prominent features, and its production can be linked to herbivory of matrix grasses. However, where the termite occurs in vegetation types with a higher perennial woody component, less grass and less environmental stress (e.g. less arid localities), termite herbivory is unlikely to entirely devegetate the area surrounding their nests, and as a result no bare disc will form in the vicinity of a colony. Within the homogenous grasslands in which FCs occur, the termite's concentrated herbivory on annual grasses may offer enough prolonged pressure to maintain a bare patch for long periods. A final consideration of the underlying factors related to termite nest variation is genetic variation among populations of what is considered to represent a single species, with local populations showing degrees of variability, through the scale of metapopulation to cryptic species (Pomeroy, 1977). A further complication to the distribution of FCs compared to that of *P. allocerus* is the recent finding of FCs in Australia, a continent away from where the Sand termite occurs (Getzin *et al.*, 2016). Either these Australian FCs are formed by a different mechanism entirely (i.e. vegetative self-organisation), or an unrelated termite species produces convergent gapped patterns around their nests. This has already been shown to be possible with *O.*

fulleri arena nests, and in a response to Getzin *et al.* (2016), Walsh *et al.* (2016) propose that the Australian FCs are pavement termitaria formed by the cryptic termite *Drepanotermes*. These pavements appear as hard, cemented ground with little or no signs of mounds, which themselves are small (2 cm in height) (Walsh *et al.*, 2016). Like arena nests in Kenya, the Australian pavement termitaria inhibit vegetation growth due to their hard surfaces and low water infiltration (Darlington *et al.*, 2007), and their influences can persist after the nest has been abandoned, making them long-lived features (Walsh *et al.*, 2016).

One major line of criticism against the spatial association between *P. allocerus* and FCs (Juergens, 2013; Vlieghe *et al.*, 2015) is that the associations are merely correlative (Tschinkel, 2015), and that the termites might preferentially inhabit the wetter FC soils secondarily after they have formed (Cramer & Barger, 2013; Getzin *et al.*, 2014). However, the highest number of *P. allocerus* and their grass sheetings were found in the early stages of FC formation and are low and virtually absent during the mature and senescent stages respectively (FC moisture levels are still high in mature FCs). Instead, the data suggest that the high numbers of termites in early stages of FC development were associated with intensive herbivory of matrix grasses. It is also argued that the small size of *P. allocerus*, and the fact that termites feed primarily on dead plant material and detritus (Lee & Wood, 1971), suggests that this termite would not be capable of killing living grasses (Getzin *et al.*, 2015). However *P. allocerus* is a pest of serious economic importance and is capable of attacking and killing larger plants such as young date palms, grape vines, maize stems and millet stalks (Coaton & Sheasby, 1973). Additionally the results of the herbivory trials on live grasses (Fig. 4.5) and evidence of living grasses being attacked by the termite in the field (Fig. 4.4b), indicates that they can and do feed on living grass material, and are not simply attracted to a large resource of dead plant material on new FCs. Many other termite species will feed on both live and dead plant matter. Both *H. mossambicus* and *Trinervitermes* spp. feed on a variety of grass species, and have been documented to target living grass tussocks (Sands, 1961; Duncan & Hewitt, 1989).

4.4.4 Conclusion

Including all of the FC growth stages in an analysis of their biological attributes provides greater insight into the processes involved in their genesis. Although the Sand termite hypothesis is the only one for which there is supporting field data, not much is known about the behaviour and ecology of *P. allocerus*. Population genetic studies on *P. allocerus* throughout its range, linked with ecological studies on its nest structure, breeding system and genetic family structure within a colony will shed

light on why its colonies produce the striking surface manifestation of a FC (Thorne *et al.*, 1999; Luchetti *et al.*, 2013).

5 FACTORS DETERMINING FAIRY CIRCLE DISPERSION, SIZE, RECRUITMENT AND SURVIVAL

5.1 Introduction

5.1.1 Factors Influencing Termite Mound Density and Dispersion

One of the most striking features of fairy circles (FCs) is their remarkably even spacing. This chapter examines some of the spatial and temporal characteristics of FCs, including their overdispersion, response to environmental parameters and longevity. Although FC dispersion (Albrecht *et al.*, 2001; Getzin *et al.*, 2014; Zhang & Sinclair, 2015), landscape variability in density and size (Cramer & Barger, 2013; Juergens, 2013), and age (Tschinkel, 2012; Juergens, 2013) have been studied, very little attention has been paid to small-scale variability in these features.

Within a species' geographical range, environmental heterogeneity will result in a mosaic of marginal and optimal habitats, linked to the availability of various biotic and abiotic resources (Morris, 1987). Population density at any given location will be directly influenced by the potential "quality" of a habitat, depending on the specific requirements of each species (Wiens, 1976). The density responses of mobile and sessile individuals to heterogeneous patches differ, with mobile individuals being able to move freely between suitable patches, having a "fine-grained" response to one type of resource (randomly frequenting all suitable patches within a mosaic) and a "coarse grained" response to another (showing preference for specific patches) (Wiens, 1976). For example, an organism may use several habitats non-selectively for feeding, but select a specific habitat patch for nesting purposes. Sessile individuals show a coarse-grained response, having to balance all available resources and constraints to select the most suitable habitat. This strong selection of higher quality patches by sessile organisms can produce stark patterns in the landscape, particularly in more resource limited environments, and can be accentuated by resultant competition and facilitation feedbacks (Wiens, 1976; Gascoigne *et al.*, 2005).

Since the patterns shown by FCs and social insect nests have much in common (Becker, 2007; Picker *et al.*, 2012; Juergens *et al.*, 2015) it is worthwhile comparing the spatial dispersion patterns of both. Although individual social insect workers are mobile, the spatial arrangement of termite and ant nests are effectively those of sessile organisms due to their longevity and central foraging behaviour. Termite mound densities vary in relation to a combination of soil, vegetation and climatic factors (Lee & Wood, 1971). Soil textures which are either too sandy or contain too much clay can exclude termite species from an area, as sandy soils with little to no clay inhibit the construction of mounds while clay-

rich soils may promote waterlogging (Lee & Wood, 1971; Meyer *et al.*, 1999). Contrasting soil textures may favour one colony requirement over another and result in a trade-off between opposing needs (Pequeno *et al.*, 2015). Many species of termite (particularly those which build large mounds) favour soils with a higher clay content for more effective nest construction (Jouquet *et al.*, 2002; Abe *et al.*, 2012), however this is not always the case, as some species may favour the increased tunnelling and foraging efficiency offered by loose, sandy soils (Pequeno *et al.*, 2015). Soil depth and waterlogging potential also play a role in the mound densities of some species, with soil depth particularly influencing large mound building species, which tend to favour deep soils (Lee & Wood, 1971; Schuurman & Dangerfield, 1997). Davies *et al.* (2014) found that at a scale less than 60 m, the density of termite mounds in a catchment area of Kruger National Park (South Africa) varied considerably depending on the presence of hill crests and seep lines. Mounds were denser on raised crests, and in line with findings of other studies (Schuurman & Dangerfield, 1997; Levick *et al.*, 2010), appear to be driven by hydrological factors such as occasional flooding (Davies *et al.*, 2014). FCs are largely restricted to deep, sandy soils (van Rooyen *et al.*, 2004; Tschinkel, 2012; Juergens, 2013), but may also respond to variations in soil texture within that range. When comparing satellite images of FCs in various localities across the length of NamibRand Nature Reserve, Tschinkel (2012) observed increases in FC density and area on sandy plains compared to more gravelly areas (however he did not quantify these differences).

Vegetation determines both the availability of food and microclimate (e.g. the amount and distribution of shade) (Lee & Wood, 1971; Schuurman & Dangerfield, 1997). The density of mounds of the termite *Macrotermes michaelseni* was found to differ between grassland, floodplain woodland and mopane woodland habitats, but also varied considerably within habitats with regards to the microclimate (Schuurman & Dangerfield, 1997). The shaded environment attributed to the floodplain woodland was favoured by this species due to reduced climatic extremes in both summer and winter compared to the other habitats (Schuurman & Dangerfield, 1997). In contrast, the densities of *M. bellicosus* mounds were found to be considerably higher in open shrub savanna compared to closed gallery forest where they were restricted to open stands (Korb & Linsenmair, 1998). This was related to less than optimum mound temperatures induced by the elevated shading in the forest habitat. At a regional scale FC landscape occupancy appears to be strongly influenced by both MAP (mean annual precipitation) and vegetation cover, with larger FCs taking up more overall land surface area in localities with more intermediate rainfall compared to the more arid or mesic portions of their range (Cramer & Barger, 2013), suggesting that they may respond to changes in vegetation or other factors that control vegetation cover.

Larger-scale geographical and altitudinal changes in climate, particularly related to rainfall and temperature, also have an effect on termite densities (Lee & Wood, 1971). *Macrotermes* mound density and termite activity were found to increase in dry savannas compared to wetter habitats (Davies *et al.*, 2014), whereas *Cubitermes* species are more abundant in regions of heavy rainfall (Williams, 1966). Changes in altitude can provide sharp climatic gradients over relatively short distances. Faunal abundances generally decrease with increasing altitude, as was shown by Kemp (1955) for two species of Australian termite which, though common elsewhere, rarely occurred above 900 m and 1200 m respectively. Fire can temporarily decrease termite densities by restricting the availability of food within a portion of habitat (Benzie, 1986). FCs are not recorded to occur over a large altitudinal range, and are mainly restricted to low-lying grassy plains. However they do stretch over a wide latitude range, occurring from southern Namibia to southern Angola (van Rooyen *et al.*, 2004; Cramer & Barger, 2013; Juergens, 2013). Both FC density and area have been shown to change with latitude, with density increasing from north to south and area showing the opposite trend (increasing from south to north) (Juergens, 2013).

Termite mound densities may be influenced by the interaction of a number of environmental factors, making it difficult to define the primary driver of changes in density (Lee & Wood, 1971). For instance, *Amitermes meridionalis* (Froggatt) is most abundant in seasonally waterlogged areas in Australia lacking trees, and less abundant in areas with more trees on well-drained soils, however it is unclear whether seasonal inundation, type of soil, or vegetation is the main driving factor for their distribution (Lee & Wood, 1971). Climate may influence termite distributions directly but also indirectly by affecting vegetation and soils. For example, East African *Cubitermes* species occur in regions of heavy or moderate rainfall and avoid those of light rainfall, but are most likely responding to resultant differences in soil moisture (Williams, 1966). Heuweltjie density increases broadly with rainfall and plant productivity, but the degree to which they do so is influenced by soil fertility and vegetation composition (Picker *et al.*, 2007).

Biological interactions with other species, including predation, parasitism, facilitation and inter-specific competition may affect termite densities both spatially and over time (Lee & Wood, 1971; Lepage, 1984). For example predation from both aardvark and Doryline ants were identified as the cause of a drop in densities of *Macrotermes bellicosus* within a two year period (Lepage, 1984). Density itself can be influenced by intraspecific competition. A higher density of organisms or colonies may offer greater protection from predation as well as an increased likelihood of finding mates, but can also result in elevated competition for resources and exposure to diseases (Haldane, 1956; Cushman *et al.*, 1988; Grohman *et al.*, 2010). The degree to which these density-dependent feedbacks influence

the population may, in turn, depend on the patchiness of the environment, and is predicted to have a greater effect in more uniform habitats (such as the uniform arid grasslands in which FCs occur) than patchier ones (Grant & Morris, 1971). FCs may also demonstrate density-dependent spacing, as their spatial dispersion tends towards evenness with increased FC landscape occupancy (Cramer & Barger, 2013).

Intra-specific interactions, particularly competition for resources, not only affect termite population densities but also the arrangement of colonies in relation to each other. The sessile colonies of subterranean social insects commonly display territoriality with neighbouring colonies as a result of potential competition for resources such as food and nesting sites, leading to an even spacing of colonies in the landscape (Lepage, 1984; Ryti & Case, 1984; Cushman *et al.*, 1988; Bourguignon *et al.*, 2011). Often this spacing is density-dependent and becomes more regular with higher population density as a result of elevated competition and more frequent encounters with neighbours (Cushman *et al.*, 1988). At multiple scales in nature, a hexagonal spatial arrangement has been shown to be the most efficient form of packing, and can also be seen in the regular spacing of many social insect colonies (Laurie, 2002; Dillier & Wehner, 2004; Zhang & Sinclair, 2015). Hexagon is used here to refer to any six-sided polygon, and may not necessarily suggest a shape with symmetrical sides.

Recently this non-random hexagonal arrangement has been clearly demonstrated for FCs (Getzin *et al.*, 2014; Zhang & Sinclair, 2015), and though this is compelling evidence for a biological origin for FCs, there is strong debate regarding the causative agent. The two major competing hypotheses, namely (1) gapped vegetation patterning through plant competition for resources and (2) foraging on grasses by the Sand termite in proximity to their nests, have both been argued to be able to account for the overdispersion of FCs (Getzin *et al.*, 2014, 2015; Juergens *et al.*, 2015). Getzin *et al.* (2014) emphasized the even spacing of FCs as one of their most critical characteristics which must be explained by any proposed mechanism for FC formation, and used comparisons of Voronoi tessellations between FCs and a model based on plant competition as their central piece of evidence for the plant competition hypothesis. Getzin *et al.* (2015) further argued that the same overdispersion seen in FCs had not been demonstrated by any example of social insect nests, and hence the latter could not be considered as candidates for FC formation. Juergens *et al.* (2015) countered this argument by comparing FC spatial patterning with that of various social insect nests, which matched the major spatial characteristics of FC in most cases. This evidence presented by Juergens *et al.* (2015) is included in this chapter, along with responses of FC spatial characteristics (density, area and dispersion) to small-scale landscape gradients in vegetation and soil properties.

The last FC characteristic addressed in this chapter is their longevity. Albrecht *et al.* (2001) first described FCs as dynamic features in the landscape, with some appearing and other fading back into the matrix, while van Rooyen *et al.* (2004) argued that they are stable features which can remain in the landscape for decades. More recent studies suggest that both these observations are correct, with FCs being both long-lived and showing evidence of ontogenic transitions from birth to senescence (Tschinkel, 2012; Juergens, 2013; Vlieghe *et al.*, 2015). Tschinkel (2012) provided a mean age estimate for FCs of 41 years using comparisons of satellite images from consecutive years within NamibRand Nature Reserve, and stated that larger FCs may persist for as long as 75 years. Smaller FCs of less than 30 m² lived on average for 23 years, suggesting that possibly larger FCs lived longer than smaller ones (Tschinkel, 2012). Juergens (2013) suggested that their lifespan may be much longer, perhaps within the range of a few hundred years. Though individual termites do not have lifespans comparable to those of FCs, the generation of a biogenic structure (nest) and a succession of reproductives and presence of totipotent workers (capable of reproduction) means that a colony can survive for a number of decades, and their nests or mounds for longer periods than that (hundreds to thousands of years) (Watson, 1967; Collins, 1981; Moore & Picker, 1991; Midgley *et al.*, 2002).

5.1.2 Aims

- To investigate the relationship between FC density, area, dispersion and life stage with local variability in soil and vegetation characteristics and of *Psammotermes allocerus* abundance. The plant competition hypothesis predicts that FC area and density would decrease in sandier localities due to a lower wilting point in sandy soils (Deblauwe *et al.*, 2008) and increase in areas where vegetation cover is sparser as vegetation patterns transition from gaps to vegetation spots to bare landscapes with increased aridity (Cramer & Barger, 2013). In contrast, the Sand termite hypothesis predicts an increase in FC density and area in sandier areas (due to the psammophilous nature of *P. allocerus*), as well as a positive relationship with greater vegetation cover which would provide an increased food resource for the termite (Coaton & Sheasby, 1973).
- To generate Voronoi tessellations from FCs in Giribes Plain using a block of 1500 X 1500 km to compare the spatial patterning features of FCs with those of various social insect colonies and vegetative self-organisation.
- Use historic aerial photographs and satellite images to estimate FC age, survival probability and recruitment. These estimates are then compared with ages of social insect colonies.

- To model survival and recruitment of FCs over several years in relation to annual rainfall values in order to evaluate the notion outlined by the plant competition hypothesis that FCs would be generated in dry years when competition for soil water is most intense. In contrast the termite hypothesis would predict FC recruitment to be greater following wetter years, which would promote colony expansion and generation of the bare disc.

5.2 Methods

A 12 km long transect was set within NamibRand Nature reserve and 30 sites located at 400 m intervals (Fig. 2.1, Chapter 2). In order to determine the influence of environmental factors on FC density and size, the following environmental and biotic variables were measured at each site: (i) *P. allocerus* sand sheeting abundance; (ii) FC density, area, growth stage percentages and dispersion; (iii) soil particle size, depth, pH and electrical conductivity (EC); (iv) abundances of the dominant matrix grasses, vegetation cover and vegetation height. The spatial patterns of FCs were analysed in detail using a Voronoi tessellation, pair correlation function $g(r)$ and other dispersion indices and compared with those of other social insect nest structures and vegetation patterning from other parts of the world. FC longevity, survival and recruitment were estimated using aerial photography from the 1970s and Google Earth Imagery from 2009 until the present from both NamibRand Nature Reserve and Giribes plain. FC appearances and disappearances between each chronosequence were recorded and used to estimate survival, longevity and recruitment. Finally annual rainfall was included in the survival and recruitment Pradel Model in order to determine the response of FC survival and recruitment to rainfall. Detailed methods can be found in Chapter 2, Section 2.4.

5.3 Results

5.3.1 *Response of Fairy Circle Density, Area and P. allocerus Abundances to Varying Soil and Vegetation Characteristics*

There was considerable variation in soil particle size proportions for each of 30 sites along the transect. Using the sediment textural classification model proposed by Blott & Pye (2012), the dominant soil types were classified as silty sand (53 %), silty sand with a small clay component (10%) and sand with a very slight silt component (13%). A principle component analysis of soil particle size resolved two main principle components which together explained 93 % of the variance between the 30 transect sites analysed (Fig. 5.1). PC1 separates samples which have a proportionally larger medium, coarse

and very coarse sand component from those which have larger percentages of fine to very coarse gravel. PC2 separates along a coarseness gradient from fine to coarse sand particles. Soil EC averaged 93.3 $\mu\text{S}/\text{cm}$ (S.D. 91.78 $\mu\text{S}/\text{cm}$) and soil pH was neutral 7.33 (S.D. 0.41) (Table 5.1).

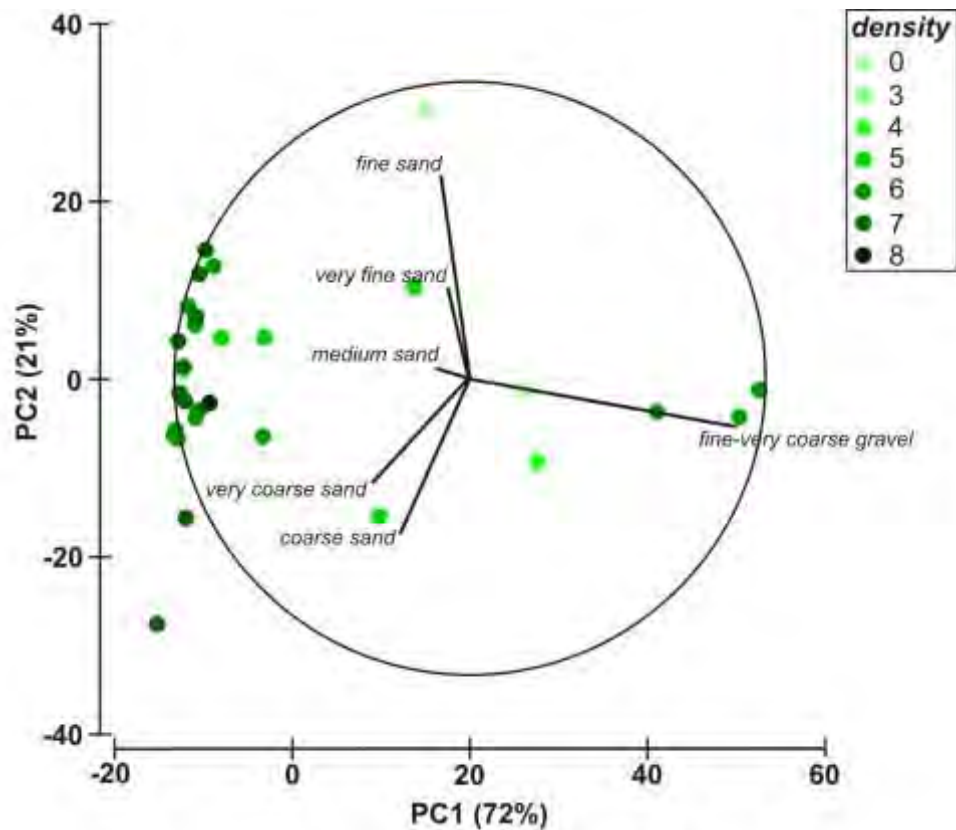


Fig. 5.1. Biplot of PC1 against PC2 obtained from a principle component analysis of soil particle size along 30 transect points. PC1 contributed 72 % to the total variance explained by the principle components and PC2 contributed 21 %. Relative FC density (binned) is indicated for each sample point.

Table 5.1. Descriptive statistics for soil, vegetation and FC properties measured along 30 transect points. Statistics for FC properties exclude two sample points which had no FCs present.

	Mean (S.D.)	Median, interquartile	Min	Max	N
Soil properties					
Depth (m)	59.90 (30.16)	80, 43.75	0	80	30
Electrical conductivity ($\mu\text{S}/\text{cm}$)	93.30 (91.78)	59.35, 51.45	16.4	325	30
pH	7.33 (0.41)	7.415, 7.02	6.5	8	30
Vegetation properties					
Number <i>S. obtusa</i> /50 cm ²	16.13 (14.28)	15.15, 21	0	46.3	30
Number <i>S. ciliata</i> /50 cm ²	2.93 (6.87)	0, 3.5	0	36.3	30
Number <i>S. uniplumis</i> /50 cm ²	3.28 (5.10)	0, 4.2	0	18	30
Total grass number	23.50 (11.45)	19.85, 12.1	5.3	48.3	30
Vegetation cover (%)	40.51 (19.72)	40.8, 32.5	3.7	75	30
Grass height (cm)	30.67 (7.37)	31.45, 10.9	15.6	43.1	30
Number <i>P. allocerus</i> sheetings/50 cm ²	2.93 (3.23)	2, 4.17	0	12	30
Circle properties					
Circle density/100m ²	33 (11.51)	30, 16.25	7	60	28
Circle area (m ²)	28.01 (10.94)	29.87, 13.37	8.9	47	28
Nearest neighbour distance (m)	14.04 (2.02)	12.81, 2.75	10.4	18.2	20
R ratio (dispersion measure)	1.55 (0.22)	1.6, 0.14	0.7	1.7	20
New circles (%)	1.57 (4.66)	0, 0	0	24	28
Young circles (%)	7.71 (7.54)	4, 12	0	24	28
Mature circles (%)	81.47 (14.54)	84, 25	44	100	28
Senescent circles (%)	9.24 (10.86)	4, 18.04	0	33.3	28

FC density showed a negative correlation with soil particle PC1 (linear regression, coefficient estimate (C.E.) = -0.037, S.E. = 0.284, $t_{27} = 3.544$, $P = 0.017$), indicating that density increased significantly with increased proportions of sandy soil compared to gravel soils (Fig. 5.1). Density also correlated positively with soil depth (C.E. = 0.035, S.E. = 0.009, $t_{27} = 3.847$, $P = 0.0007$). FC area and *P. allocerus* abundance (measured as the number of termite sheetings present) did not show a significant relationship with any measured soil properties.

Both FC density and area showed a positive correlation with *S. obtusa* abundance (C.E. = 0.061, S.E. = 0.026, $t_{27} = 2.344$, $P = 0.027$ and C.E. = 0.073, S.E. = 0.024, $t_{27} = 3.001$, $P = 0.006$ respectively). Changes in FC density and area did not however show any relationship with total grass number (all species) and grass height, but *P. allocerus* abundance correlated positively with total grass number (C.E. = 0.037, S.E. = 0.016, $t_{27} = 2.389$, $P = 0.024$).

5.3.2 *The Relationship between Fairy Circle Density, Area and P. allocerus Abundance*

FC density and area showed a near significant positive relationship (C.E. = 0.32, S.E. = 0.17, $t_{28} = 1.884$, $P = 0.071$) with *P. allocerus* abundance. Both FC density and area showed a positive relationship with the number of *P. allocerus* sheetings, but only density was significantly correlated (C.E. = 0.956, S.E. = 0.293, $t_{28} = 3.264$, $P = 0.003$), with area being near significant (C.E. = 0.611, S.E. = 0.318, $t_{28} = 1.926$, $P = 0.064$).

Mature FCs were the only life stage to show a significant relationship with any soil or vegetation properties, and were found to increase in number with higher proportion of sandy soil, and increased soil depth and grass height (soil PC1: C.E. = 0.858, S.E. = 0.357, $t_{28} = 2.404$, $P = 0.0247$; soil depth: C.E. = -1.122, S.E. = 0.467, $t_{28} = -2.401$, $P = 0.0248$ and grass height: C.E. = -0.26, S.E. = 0.124, $t_{28} = -2.091$, $P = 0.0478$ respectively). FC density and termite sheeting abundances in the matrix showed no correlation with percentage of any life stage, but FC area was greater in localities with higher proportions of young and mature FCs (C.E. = 0.108, S.E. = 0.026, $t_{28} = 4.173$, $P = 0.0004$ and C.E. = 0.038, S.E. = 0.016, $t_{28} = 2.337$, $P = 0.0285$ respectively).

5.3.3 *The Influence of Fairy Circle Density, Area and Life Stage on Dispersion Patterns*

The degree of dispersion of FCs, given as the dispersion coefficient R (Clark & Evans, 1954) was positively correlated with FC density (C.E. = 36.41, S.E. = 11.34, $t_{18} = 3.212$, $P = 0.005$) and FC area (C.E. = 24.88, S.E. = 9.505, $t_{18} = 2.618$, $P = 0.0174$). There was no association between FC area and nearest neighbour distance (C.E. = -0.5053, S.E. = 1.23, $t_{18} = -0.411$, $P = 0.686$). New FCs occurred in lower percentages in areas with higher dispersion values (C.E. = -0.035, S.E. = 0.006, $t_{18} = -5.416$, $P < 0.0001$).

5.3.4 *Hexagonal Patterning of Fairy Circles and Other Landscape Features of a Biological Nature*

For all biological spatial patterns analysed using Voronoi tessellation (viz. FCs, various insect nests and vegetation patterning), the majority of points were arranged in a close to hexagonal pattern with each point having six neighbouring FCs (Table 5.2). FCs had both the highest mean number of sides per polygon (5.95) and the highest percentage of hexagons (47 %), followed by heuweltjies (5.92, 43 %) and vegetation spots in Sudan (5.90, 47 %). Vegetation gaps had the lowest mean number of sides per polygon (5.80) and *Pogonomyrmex* discs had the lowest percentage of hexagons (34 %). Nearest neighbour distances differed between the types of structures, with vegetation spots having the

highest distance followed by *Macrotermes* mounds. FCs and *Pogonomyrmex* discs had the shortest distance between neighbouring discs.

For all pair correlation functions $g(r)$ examined (describing the probability of finding a point at distance r from another point) $g(r) = 0$ for low values of r (Fig. 5.2) before increasing at point r_{min} (indicating the first appearance of neighbouring structures). These values differed between the structures analysed, with r_{min} falling approximately 30 m for *Macrotermes* mounds, 25 m for heuweltjies and vegetation spots, 20 m for vegetation gaps, 7 m for FCs in Giribes and 5 m for *Pogonomyrmex* discs. All pair correlation function (PCF) plots demonstrate a high initial $g(r)$ peak value (Table 5.2). This is clearest for FCs, which had the highest $g(r)$ value of 1.7. The only other $g(r)$ peak values which fell outside the simulation envelope were for heuweltjies (1.4), *Macrotermes* mounds (1.3) and vegetation gaps (1.4), but not *Pogonomyrmex* discs (1.3) or vegetation spots (1.2). With the exception of FCs, which had two $g(r)$ peaks after the initial high amplitude peak that reached outside of the simulation envelope, all structures examined showed an immediate decay in peak amplitude which did not reach outside of the simulation envelope (Fig. 5.2). This decay continued into greater r distances, and can be seen for FCs at distances greater than $r \approx 35$ m.

Table 5.2. Summary Voronoi cell tessellation (mean number of sides/polygons, percent hexagons, nearest neighbour distances, R value) and pair correlation function values (PCF highest g-value, the distance at which highest g value occurs) for various biological landscape patterns.

Structures (site, reference)	Coordinates	Proposed origins of structure	Mean sides/polygons	# % hexagons	Mean/Median NN* distance (m)	R dispersion index	PCF highest g-value†	Highest g-value distance (m)
Fairy circles (Giribes)	19°02'12.57"S 13°21'01.59"E	<i>P. allocerus</i> ; vegetative self-organisation	5.95	47	12.66/ 12.72	1.67	1.7	14.91
Fairy circles (Marienfluss, Getzin <i>et al.</i> 2014)	17°35'42.1"S 12°36'01.0"E	<i>P. allocerus</i> ; vegetative self-organisation	5.97	46	16.26 / 16.55	-	1.6	-
Model (Getzin <i>et al.</i> , 2015)	-	Vegetative self-organisation	5.98	57	12.60 / 12.68	-	2.3	-
Heuweltjies (Garies)	30°46'14.58"S 18°00'27.08"E	<i>M. viator</i> ; aeolian deposition/erosion	5.92	43	44.81 / 43.80	1.56	1.4	48.58
Heuweltjies (Cramer & Midgley, 2015)	-	<i>M. viator</i> ; aeolian deposition/erosion	5.8	-	-	1.27 ± 0.03	-	40 ± 1.7
<i>Macrotermes</i> mounds (Outjo)	20°07'22.18"S 16°14'53.33"E	<i>Macrotermes</i> spp.	5.86	39	49.21 / 48.11	1.54	1.3	55.07
<i>Pogonomyrmex</i> discs (Colorado, USA)	39°16'07.16"N 109°02'19.07"W	<i>Pogonomyrmex</i> spp.	5.87	34	10.88 / 10.34	1.37	1.3	17.3
Vegetation gaps (Sudan)	11°03'05.62"N 28°12'38.84"E	Vegetative self-organisation	5.80	40	34.30 / 34.34	1.57	1.4	39.67
Vegetation spots (Sudan)	11°37'15.57"N 27°57'00.39"E	Vegetative self-organisation	5.90	47	57.59 / 56.99	1.52	1.2	67.70

* Nearest neighbour

† Maximum positive peak for $g(r)$ from PCF analysis

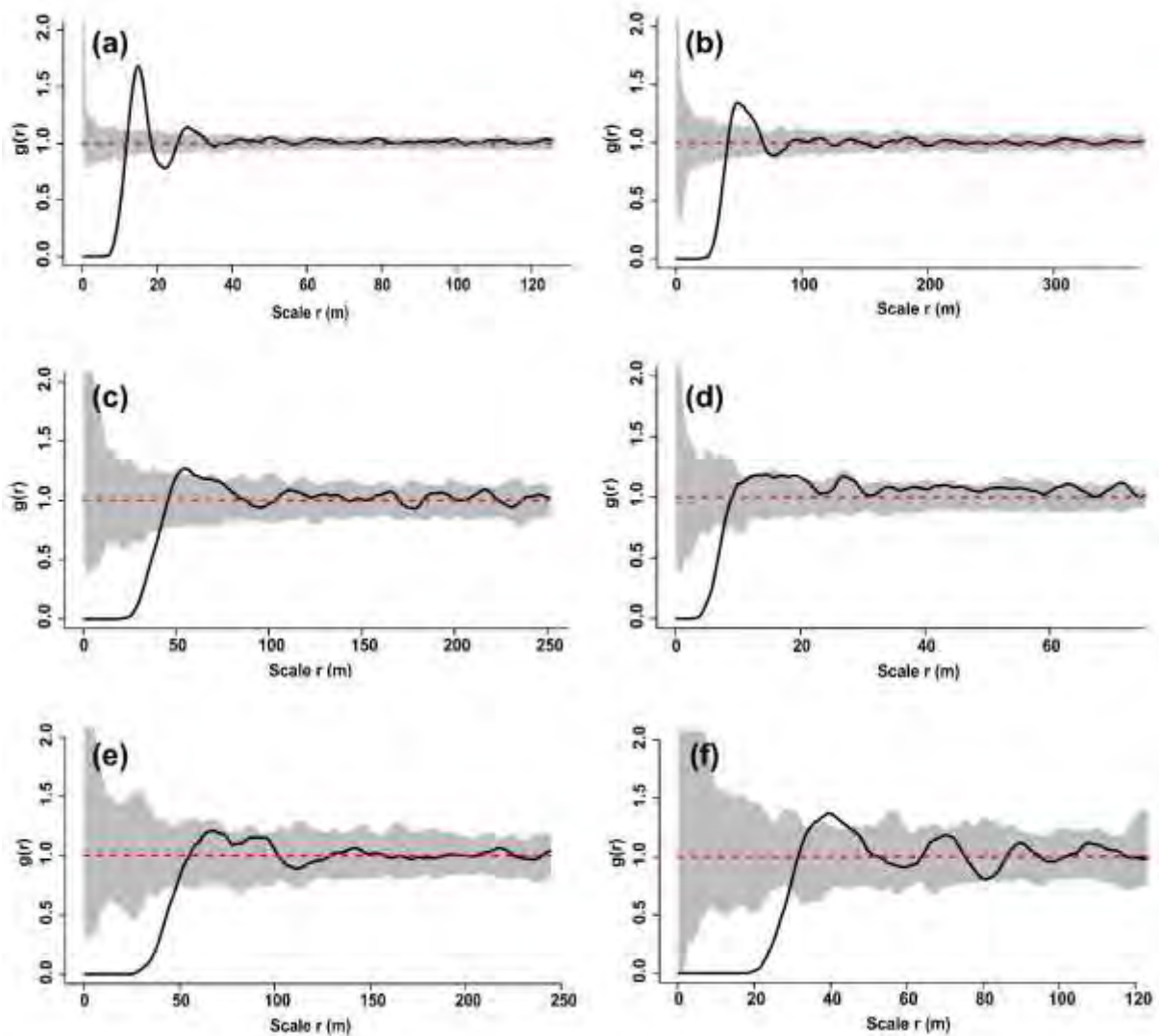


Fig. 5.2. Pair correlation function (PCF) plots for (a) FCs (Giribes), (b) *heuweltjies* (Garies), (c) *Macrotermes* termite mounds (Outjo), (d) *Pogonomyrmex* ant discs (Colorado), (e) vegetation spots (Sudan) and (f) vegetation gaps (Sudan). Grey shaded area = simulation envelope, red line = theoretical value for $g(r)$ under complete spatial randomness and solid black line = observed value for $g(r)$.

5.3.5 Fairy Circle Age, Recruitment and Survival

When comparing aerial photographs and satellite images between the 1970's and recent years it was possible to detect appearances and disappearances of FCs, and estimate lifespan, survival and recruitment using live recapture models. The mean survival probability for FCs per year was estimated as 0.972 ($n = 330$) for NamibRand using data over a period from 1977-2013, and 0.974 for Giribes based on data over a period from 1975 to 2012 (see Appendix 1 for details on the model used and goodness of fit tests). The model calculated FC longevity as 34.7 years for NamibRand and 37.6 years

for Giribes. A second estimate for FC age was obtained when the change and disappearance of FCs at various life stages was ground-truthed at NamibRand from 2011 to 2013. When monitoring 57 neighbouring FCs over three consecutive years, frequencies of the four progressive FC life stages (new, young, mature and senescent) changed from 2 : 12 : 84 : 2 (%) to 0 : 2 : 86 : 12 (%) and finally 0 : 0 : 86 : 14 (%) (n=57) for 2011, 2012 and 2013 respectively. The mean estimated times spent in each stage in years (standard error bracketed) were: new 1 (0), young 1 (0) and mature 13.9 (13.4), with a total time of 15.9 (11.0) years taken to reach the senescent stage. When considering only the 2012-2013 transition, the total time spent in young and mature stages combined was estimated as 50 (47.5) years.

FC recruitment probability per year was estimated to be 0.014 (n = 330) for NamibRand using the period from 2010 - 2013. A comparison of recruitment and survival estimates with total rainfall for the period preceding each Google Earth image is given in Fig. 5.3. Both survival and recruitment showed a sharp decrease after the summers of 2010 and 2011, which followed exceptionally heavy rainfall of the summer of 2010 and 2011. This had been preceded by a few years of decreasing rainfall (2008 to 2010). Following the sharp decline between 2010 and 2011, FC survival probability increased between 2011 and 2013, following a drop in total rainfall. The trend is that survival and rainfall were inversely related. Recruitment increased slightly following lower rainfall of 2011 and 2012, but then dropped between 2012 and 2013. There were therefore contrasting recruitment responses in relation to rainfall. The best fitting model for predicting FC recruitment and survival incorporates a combination of both time and rainfall covariates, while a model which considers rainfall alone has little support (see Appendix 1).

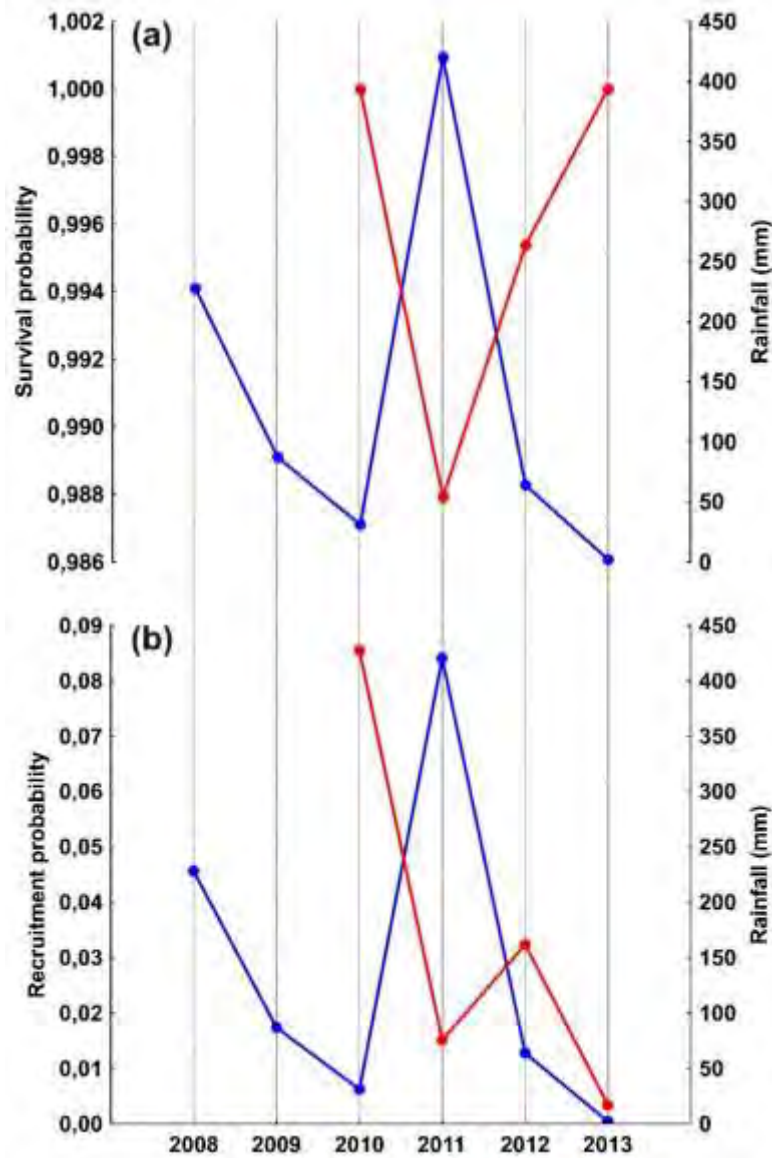


Fig. 5.3. Total rainfall plotted against (a) FC survival and (b) recruitment probability estimates per year in NamibRand. Rainfall = blue line and recruitment/survival estimate = red line. Total rainfall is taken for the period preceding each indicated year.

5.4 Discussion

5.4.1 Environmental Heterogeneity and Its Influence on Fairy Circle Dynamics

At a local scale, FC density and area showed a positive correlation, however this relationship was not significant ($P = 0.07$). Using local and landscape scale analyses, Tschinkel (2012) came to the same conclusion that FC area and density were not necessarily related and varied independently of one another. Juergens (2013) indicated that FC density decreased towards the northern part of their range

while FC area increased. This suggests that both properties may be influenced by different environmental factors, or respond to the same factors in different ways. How these characteristics respond to environmental factors is currently poorly understood, and any explanation would be heavily influenced by the interpretation of the nature and origin of FCs.

FCs are known to be largely restricted to sandy soils at a regional scale (Becker & Getzin, 2000; Picker *et al.*, 2012; Tschinkel, 2012). On a local scale, FC density increased with soil depth and increasing sand fraction in the soil (Fig. 5.1), however area did not respond to any changes in soil properties. Tschinkel (2012) noted variations in FC density and area, providing images of larger FC densities and size on sandy substrates compared to nearby alluvial gravelly deposits. However Cramer & Barger (2013), found no correlation between FC properties and soil texture at five sites within the same reserve. The increase in FC densities on deep sandy soils may be explained by the affinity of *P. allocerus* for sandy habitats (Coaton & Sheasby, 1973).

Despite the observation that many termite species favour clay soils for constructing mounds, sandy soils can be selected for if the need for more efficient foraging takes precedence. For instance, the termite *Neocapritermes braziliensis* (Snyder) which builds its nests out of mostly organic matter exhibits higher nest densities in areas of lower clay content and subsequently higher sand content (Pequeno *et al.*, 2015). *Psammotermes* species are however unusual as they are the most psammophilous group of termites known, and are sandy desert specialists (Coaton & Sheasby, 1973) which may not be as reliant on soil clay content as they do not build large and elaborate mound structures. Instead sandy soils may benefit the construction of their subterranean foraging networks which provide protection from desiccation and predators.

Density and area of FCs increased with increasing abundance of the grass *Stipagrostis obtusa*, which being the dominant matrix grass species would most likely be the major food item for *P. allocerus* in this habitat. Assuming greater FC area is representative of a mature termite colony with a larger population (Korb & Linsenmair, 1999), a more favourable habitat in the form of a greater abundance of the matrix grass would be able to support larger populations of termites and hence larger colonies. Hence grass biomass could be considered to be a primary limiting factor in local abundance of FCs at NamibRand, which is consistent with the termite hypothesis of FC formation. This positive relationship between FC area and matrix grass abundance may apply at a regional scale as well and explain the increase in FC area with decreasing latitude. *Stipagrostis* species turnover with latitude, with *S. obtusa* and *Stipagrostis uniplumis* given way to the larger and more luxuriant species *Stipagrostis giessi* (Kers) further north. However termite colony size is generally not known to increase with decreasing latitude (Porter & Hawkins, 2001) and termite mound size was reported by Davies *et*

al. (2014) to increase in drier savannas compared to wetter savannas in the Kruger National Park. However, these studies were done on termites inhabiting relatively mesic habitats, as few mound-building termites occupy desert habitats.

Higher densities of FCs were found in localities with higher numbers of *P. allocerus* termite sheetings in the matrix, and although FC area was also associated with greater numbers of the termites, the relationship was not as strong as that for density, where there was a strong positive correlation. Greater *P. allocerus* abundance was, in turn, associated with higher grass cover and height, but surprisingly not sandier soils. One would expect higher abundances of the sand-loving *Psammotermes* to respond to changes in sand volume as was demonstrated for FC density. However, abundances used for this analysis were counts of termite sand sheetings from the matrix only. The highest termite abundances (scored by any method) were always on the bare disc or peripheral band FCs and not in the matrix (see Chapter 4).

The regularity of FC spacing was greatest at sites with higher densities and larger FCs. Cramer & Barger (2013) came to the same conclusion when they compared regional FC landscape occupancy (i.e. percentage land surface covered) with dispersion coefficient values (R). According to Cushman *et al.* (1988) intraspecific competition is the likely cause of overdispersed patterns when density correlates positively with a more regular dispersion, and negatively with nearest neighbour distance between structures with a greater diameter (density- and size-dependent spacing). As the density and size of an organism or colonies increase the demand for resources becomes greater, and even spacing provides the most parsimonious allocation of resources. Cushman *et al.* (1988) demonstrate these patterns with the ant *Formica altipetens* in northern Arizona, Ryti & Case (1986) showed that nearest neighbour distance increased with the size of *Veromessor pergandei* and *Pogonomyrmex californicus* (Buckley) colonies, and Cramer & Midgley (2015) reported a similar increase in distance between heuweltjies with increased mound diameters. Age of a structure may be another variable affecting dispersion in the landscape. Korb & Linsenmair (2001) found that smaller, young mounds of *M. bellicosus* tended to have more clumped distributions compared to larger, mature mounds. This suggests that older, long-lived mounds are under a greater influence of competitive spacing than shorter lived founding colonies, which are influenced primarily by environmental factors (Korb & Linsenmair, 2001). Areas containing a higher proportion of smaller, (new) FCs were shown here to have lower R values. Thus the changes in FC dispersion patterns are consistent with intra-specific competition, and match those reported for termite mounds and ant nests.

5.4.2 Comparison of Fairy Circle Spatial Patterns with Other Overdispersed Landscape Features

All social insect nests and vegetation spatial patterns examined showed a highly regular spacing arrangement with each point surrounded by six neighbours (Table 5.2). FCs had the highest degree of hexagonal spacing (5.97 number of sides and 47 % six-sided polygons), followed by Sudan vegetation spots (5.9 and 47 %) and heuweltjies (5.92 and 43 %) while *Pogonomyrmex* discs had the lowest hexagonal spacing (34 % of polygons were six-sided). Related to this tight hexagonal packing, was the high degree of regular spacing shown by most of the examined landscape features (R values ranging from 1.52 to 1.67), with the lowest value being *Pogonomyrmex* discs (R = 1.37) - where the R value is closer to random (R = 1) than perfect uniformity (R = 2.1491) (Clark & Evans, 1954). Once again FCs show the highest degree of regularity (R = 1.67), with the closest comparison being heuweltjies (R = 1.56) and vegetation gaps (R = 1.57).

According to *Getzin et al.* (2015) who used a PCF to describe FC dispersion, four characteristics related to overdispersion can be identified, and any proposed explanation for their origin needs to explain these characteristics. The first of these is that in close proximity to a typical FC, where the distance $r < r_{min}$, the function $g(r)$ is zero, indicating that no neighbouring FCs are found at these low distances. For FCs in Giribes, this was found to be approximately 7 m, which is not surprising as much of this initial distance falls within the area of the FC or within a few meters of it. Similarly, $g(r)$ is zero at low values of r for the other structures examined though the value for r_{min} differed. The second dispersion characteristic highlighted by *Getzin et al.* (2015) was that FCs demonstrate a clear first peak in $g(r)$, which falls outside of the simulation envelope. This indicates that all nearest neighbours fall within a similar distance and, along with the hexagonal spacing of neighbouring FCs, suggests a high degree of spatial ordering. Most structures analysed displayed this prominent peak with the exception of *Pogonomyrmex* discs and vegetation spots, though the highest $g(r)$ value for FCs was considerably higher than the structure with the next highest value (heuweltjies). The r distance at which these peaks occurred differed considerably between the structures analysed (Table 5.2). This difference can be explained by the relative size of the various structures (heuweltjies, *Macrotermes* mounds and vegetation spots are considerably larger than FCs and *Pogonomyrmex* discs) as well as differing ecological and requirements and territorial behaviour of the species involved. This would in a similar way explain the variation in the r_{min} and nearest neighbour distances (Table 5.2). The third characteristic demonstrated by FC spatial patterns is a damped oscillation after the initial high $g(r)$ peak. It can be seen in Fig. 5.2a that FCs experience a low $g(r)$ trough after the highest initial $g(r)$ peak of 14.91, indicating an area with significantly fewer FCs following the initial array of nearest neighbours. This is again followed by another high $g(r)$ peak value which escapes the simulation

envelope, though it is less than the initial peak before the pattern flattens out. This characteristic is not well represented in the other spatial pattern examples, and while heuweltjies, *Macrotermes* mounds and vegetation gaps also display a low and secondary high peak after the initial $g(r)$ peak, these do not go beyond the simulation envelope. Lastly according to Getzin *et al.* (2015) FCs show large-scale homogeneity at higher r distances, which they interpret as small-scale ordering preserved throughout their larger range. This characteristic is shared with all other spatial patterns analysed, with all showing homogeneity within the simulation envelope at larger distances. This trend would be expected for large areas that are fairly homogenous, and indicates no clear trends in density over the examined area.

Therefore social insect nests and plant patterns in various parts of the world share many dispersion similarities with FCs. Based on these similarities, dispersion patterns alone cannot be used to define the agent generating FCs. However FCs do have the highest degree of ordering of all examples. Several factors might account for this, including a larger sample size used for the Giribes FCs. For most analyses of dispersion of FCs, areas with a homogenous landscape were used, and these would then maximize dispersion indices (Getzin *et al.*, 2014). In the small-scale 12 km transect used here, landscape heterogeneity (mountains, changes in soil structure, soil depth) became an important variable influencing dispersion values. In addition to the increased sample size, the large spatially homogenous grassy plains on which FCs can be found lowers the influence of environmental heterogeneity and highlights the intra-specific spacing effects to a much higher degree than in the other features for which dispersion values were calculated.

Getzin *et al.* (2014), using a vegetation self-organisation model originally proposed by Gilad *et al.*, (2007), concluded that the model they generated was a good match with observed FC dispersions and hence provided the most likely explanation for the formation of these features. Their model estimated mean number of sides as 5.98, percentage of six-sided polygons as 57 % and mean nearest neighbour distance as 12.60 m (compared to 5.95 number of sides, 47 % hexagons and 12.66 m nearest neighbour distance for FCs respectively). However Zhang & Sinclair (2015) argue that the number of hexagonal polygons predicted by the Getzin *et al.* (2014) model (57%) is clearly different from the 45% value they observed for FCs and that it is not as good a predictor of FC spatial patterns as Getzin *et al.* (2014) suggested. In addition, demonstrating the similarities of FC spacing with those of other phenomena such as vegetative self-organised patterns in support of an explanation for their formation should be accompanied by other supporting empirical evidence (Juergens *et al.*, 2015). A near hexagonal polygon arrangement can be seen in many unrelated biological features across various scales. For example, the polygon class distributions of FCs are identical to those of epithelial cells

(Zhang & Sinclair, 2015), breeding pits of cichlids and nests of sea birds (Hasegawa & Tanemura, 1976; Zhang & Sinclair, 2015).

Both ants and termites demonstrate intra-specific territorial interactions between neighbouring colonies, generating the high degree of even spacing similar to that observed in FCs. Even mound spacing has been documented for each of the three examples of social insect nests compared here with FCs, namely *Pogonomyrmex* (Holldobler, 1976; Wiernasz & Cole, 1995), *Macrotermes* (Grohmann *et al.*, 2010; Pringle *et al.*, 2010) and heuweltjies (Laurie, 2002; Cramer & Midgely, 2015). *Pogonomyrmex* species maintain spacing between colonies through aggressive encounters with workers from neighbouring colonies and the expulsion of foundress queens (Hölldobler, 1976; Ryti & Case, 1984, 1986), with an increased nearest neighbour distance correlating with increased colony mortality resulting from aggressive interactions (Wiernasz & Cole, 1995). The foraging range of some *Pogonomyrmex* species is clearly influenced by the presence of neighbouring colonies, with chemically marked foraging trails constructed to avoid encounters with other colonies (Harrison & Gentry, 1981; Gordon, 1995). Ryti & Case (1984; 1992) used a computer simulation to demonstrate that intra-specific competition, mostly causing mortality of establishing colonies, can account for evenly spacing between colonies. Jmhasly & Leuhold (1999a) used arena trails to show that both *Macrotermes subhyalinus* and *M. bellicosus* are capable of intra-specific colony recognition and react to foreign individuals with varying levels of aggression. Along with dead soldier head capsules found within passages, Jmhasly & Leuhold, (1999b) reported on passage blocking and segregation of *Macrotermes* tunnels in response to contact with neighbouring colonies. Getzin *et al.* (2015) regarded heuweltjie mounds to be constructs of vegetation self-organisation (as purported by Cramer *et al.*, 2012; Cramer & Midgley, 2015), but here they are considered to be *Microhodotermes viator* colonies (Moore & Picker, 1991; Laurie, 2002; Picker *et al.*, 2007; McAuliffe *et al.*, 2014). *M. viator* is known to be aggressive towards neighbouring colonies (Coaton, 1958), and Laurie (2002) used this observation in support of a model on termite central place optimal foraging to predict the distribution of heuweltjies. He found that this model was able to produce a hexagonal spacing between colonies, similar to the observed spacing of heuweltjies.

P. allocerus does not appear to display overt agonistic behaviour towards non-colony members (pers. obs for laboratory trials). A lack of aggression, however, does not necessarily rule out the potential for territoriality in this species, and they may be demarcating their colonies using more subtle strategies. A few species of both lower and, more rarely, higher termites show a reduction or complete lack of agonism (Su & Haverty, 1991; Bulmer & Traniello, 2002; Fuller *et al.*, 2004). Species of Rhinotermitidae, including *Psammotermes hybostoma*, employ chemical defences released

through the frontal gland (Šobotník *et al.*, 2010; Krasulová *et al.*, 2012). In *P. hybostoma*, the amount of chemicals released from the frontal gland differed with soldier size, with the chemical composition differing between localities, and to a lesser extent, between colonies within the same locality (Krasulová *et al.*, 2012). Terpenoid mixtures found in termite frontal glands have repellent and toxic properties (Šobotník *et al.*, 2010), and are believed to be used both as a repellent or irritant as well as an alarm pheromone in *Psammotermes* (Krasulová *et al.*, 2012). The chemical properties of the frontal gland of *P. allocerus* have yet to be determined, but most likely it shares a similar chemical composition and function to that of *P. hybostoma*. It may, therefore, be used as a tool for nestmate recognition and as a deterrent for non-relatives, providing a potential mechanism for colony spacing without the need for aggressive encounters.

5.4.3 Fairy Circle Longevity and Recruitment

Based on data taken over approximately 27 years, annual FC survival was shown to be high (mean probability between 0.972 and 0.974), with an estimated lifespan ranging from 35 and 50 years. This supports the suggestion that FCs are fairly stable, long-lived features within the landscape once they appear and reach maturity (van Rooyen *et al.*, 2004; Tschinkel, 2012). The observation that FCs progress through their initial developmental stages (i.e. new and young FCs) fairly quickly and within a few years (Tschinkel, 2012) was also demonstrated here through direct observations of changes in life stages of FCs monitored over a three year period. The estimated FC age obtained here is similar to the lifespan estimate given by Tschinkel (2012) using comparisons of satellite images (41 years on average). However, the use of historical images that only go back a number of decades may produce underestimates of FC age, and it is possible that FCs may, in fact, be much longer lived (Juergens, 2013, SM).

Termite colonies are typically reported to live for anything between several years to a number of decades (Lee & Wood, 1971; Collins, 1981). Colonies of certain species are capable of outliving the lifespan of an individual termite reproductive through asexual queen succession (Thorne *et al.*, 1999; Luchetti *et al.*, 2013). For example, in certain species of Rhinotermitidae, a colony is initiated by a primary king and queen, which upon their senescence are replaced by secondary reproductives (neotenics) which develop from nymphs or occasionally workers within the same colony (Thorne *et al.*, 1999). This family structure can in some instances be complicated by the movement of reproductives between what are termed “mixed families”, which result from colony fusion, pleometrosis (several queens founding a colony together) or the incorporation of foreign queens

(Luchetti *et al.*, 2013). Once a colony does become extinct, their nests and mounds can remain in the landscape for considerably longer periods. Evidence exists of extinct termite mounds persisting for approximately 700 years (Watson, 1967), and heuweltjies may remain in the landscape for thousands of years (Moore & Picker, 1991; Midgley *et al.*, 2002), although it is not known if they are occupied continuously. Hence, termite mounds persist for periods well within the longevity of FCs.

The number of recruiting FCs was found to be low (probability = 0.014). At localities where social insect colonies are densely packed and intra-specific competition is high, the presence of many older, established colonies may hinder the establishment of new colonies and reduce the chances of recruitment. In both ants and termites, colony mortality tends to be highest in younger colonies through predation (Noirot, 1969; Bourguignon *et al.*, 2011). Young nests of the tree-dwelling termite *Anoplotermes banksi* were evenly spread between established colonies but clumped in relation to other young colonies, and occurred more frequently in areas with larger numbers of recently dead nests (Bourguignon *et al.*, 2011).

The disappearance (death) of FCs appeared to be affected by rainfall, with FC survival probability decreasing in wetter years (Fig. 5.3a). This may be related to an increased likelihood of seedlings recruiting on FCs following summers of heavy rainfall (and leading to the eventual incorporation of the FC back into the matrix). Maintenance factors (e.g. seed removal by wind, seedling excavation by ants - Chapter 3) may become less effective once a certain proportion of seedlings have established on the bare disc. In contrast there was no clear pattern between preceding rainfall values and the appearance of new FCs (Fig. 5.3b). Assuming that expansion of founding *P. allocerus* colonies is linked to wetter soils and higher vegetation cover, the Sand termite hypothesis would expect an increase in the number of young colonies and hence FC recruitment directly after wetter years, and less appearing in drier years. However low rainfall summers were followed by decreases in recruitment in some years and increases in others. FC recruitment may be a more complicated process than FCs disappearances, and it is possible that an interplay of several factors exists, or that there is a time lag in the response of recruitment to rainfall events. Results from tracking the life stages of a group of the same FCs for three years revealed that new and young FCs are relatively short stages compared to mature FCs, each taking approximately a year before transitioning to the next stage. Therefore it may take two years for a FC to mature and be detectable in satellite imagery. A longer time sequence of recruitment against rainfall may be needed to detect trends. In a preliminary comparison of repeat photographs of FCs, Juergens *et al.* (2015) showed that wetter years favoured the recruitment of FCs and that a series of drought years led to the death of these young FCs. This conclusion is in conflict with the plant competition hypothesis, which would predict that in

drier years when competition for water between plants would be highest, the likelihood of FC recruitment and survival would be higher. For example Zelnik *et al.* (2015) used vegetation patterning models to show that periodic drought years would lead from a stable hybrid state (represented by a smaller number non periodic of FCs) to a near periodic gap pattern through the addition of FCs, while a series of spate years could take a near periodic pattern to uniform vegetation cover through the gradual elimination of FCs.

5.4.4 Conclusions

The spatial patterns demonstrated by FCs were matched with those of selected social insect nests, particularly those of *Macrotermes* mounds and *M. viator* (heuweltjies) (39 % and 43 % hexagons respectively compared to 47 % for FC). A factor influencing these measures is habitat homogeneity, with homogeneous habitats generating the highest values. Many previous studies on FCs have selected sites (esp. from satellite imagery) having the densest populations of FCs – which have then yielded very high measures of dispersion. However, local variation in FC density and size as demonstrated here across a habitat gradient provide insights into explanatory variables underlying this variation in spatial pattern. Sand fraction and depth of soils were found to be positively associated with FC density, and both density and FC size increased at sites with a higher abundance of *S. obtusa*. Similarly *P. allocerus* abundance in the matrix increased with greater vegetation cover, and FC density (and to a lesser extent FC area) were positively associated with abundances of the termite. Both FC and termite density increased with increasing grass cover, thus providing additional support for the spatial association (Chapter 4) of the Sand termite and FCs. In addition to the fluctuations in FC size and density in response to environmental variables on a small scale, FC size and distance between FCs were positively associated. This is suggestive of a competitive biological process, well documented for sessile organisms, and the observed variability on a small scale is not predicted by the plant competition model. There were fewer new FCs in areas with the highest FC dispersion coefficients, suggesting saturation of the landscape. This would be consistent with competitive interactions relating to dense populations of social insect nests. FC density and area were both greatest in habitats which would favour *P. allocerus*, viz. sites with deep, sandy soils and increased plant productivity. In contrast, although Getzin *et al.* (2014) do not question the formation of vegetation gaps in sandy soils, other workers on the plant competition models (Deblauwe *et al.*, 2008) indicate that globally such patterns are unlikely to form on sandy soils (however see Zelnik *et al.* (2015)). FC size was shown here to increase locally with increasing grass cover, not a lack of rainfall, as predicted by Cramer & Barger (2013) and Zelnik *et al.* (2015). Finally the longevity of FCs (estimated here as 35 – 50 years) matches

that of many termite colonies and their mounds. However despite their longevity they are also dynamic features, and with recruitment, senescence and death occurring in the same area. Survival and recruitment appear to be influenced by rainfall, with survival decreasing following periods of higher rainfall. However, there were no consistent recruitment patterns in relation to rainfall and longer term studies might be required to resolve this.

6 FAIRY CIRCLES AND *PSAMMOTERMES ALLOCERUS* AS ECOSYSTEM ENGINEERS

6.1 Introduction

6.1.1 *The Concept of Ecosystem Engineering*

A wide range of organisms can have effects on the environment and other organisms unrelated to direct trophic interactions – through a process known as ecosystem engineering. The term ecosystem engineer was first coined by Jones *et al.* (1994) and refers to any organism that modifies, maintains and produces habitats for other organisms by directly or indirectly altering the availability of resources. Ecosystem engineers can be broadly divided into autogenic and allogenic engineers based on their mode of influence. Autogenic engineers modify the environment through their own physical structures (e.g. higher plants) while allogenic engineers (e.g. beavers) convert living and non-living material from one physical state to another (Jones *et al.*, 1994; 1997). The concept is relevant to the impacts of a very large number of species and spans a range of spatial and temporal scales (Jones *et al.*, 1994; Hastings *et al.*, 2007; Jones *et al.*, 2010). Effects can last for a matter of seconds (such as bubble nets produced by cetaceans) to hundreds of years (shading by forests), with the engineering effects sometimes outlasting the lifespan of the organism itself (Hastings *et al.*, 2007). In the same manner, spatial scales of influence can vary from a few cm² (soil casts formed by earthworms) to a number of km² (intertidal shell beds formed by soft shelled clams). Ecosystem engineers can also modify their environment ‘intentionally’ or ‘accidentally’ (*sensu* Jouquet *et al.*, 2006). Intended engineering effects involve an extended phenotype or biogenic structure, built to maintain an optimal environment and generally invokes a positive feedback on the engineer (Lavelle, 2002; Jouquet *et al.*, 2006). This is exemplified in soil-inhabiting earthworms, ants and termites (Lavelle, 2002). However engineering effects can also be incidental, and these may have positive, negative or no ramifications on the engineer (Jouquet *et al.*, 2006; Jones *et al.*, 1997).

The high density of fairy circles (FCs) in the Pro-Namib grasslands and their striking lack of vegetation cover suggests that they would have various impacts on local ecological processes (Juergens, 2013). The study of these ecological impacts has been overshadowed by the focus on their origins. If FCs are the result of landscape modification by a specific organism or group of organisms, their effect on associated plant and animal communities may represent a striking example of ecosystem engineering (Juergens, 2013). This chapter aims to investigate changes in physical and chemical properties of FC soils, and thermal and insect community contrasts between FCs and their

adjacent matrices. FCs alter plant communities (Chapter 3), and also may increase the overall diversity of an area compared to those lacking FCs (Juergens, 2013).

6.1.2 Soil Modification by Termites

FCs have been shown to have a tight spatial and ecological association with the Sand termite (Chapter 4). If the Sand termite hypothesis for FC formation is correct and they do represent epigeal manifestations of subterranean nests of *P. allocerus*, then FCs might be expected to display soil modifications consistent with those associated with other termite species.

Termites modify the soil within and around their nests and mounds both physically and chemically. As some mounds may reach a maximum diameter of 20-30 m and each colony can live for several decades (Lee & Wood, 1971; Collins, 1981; Lepage, 1984), their effect extends beyond the spatial and temporal scale of the engineer and individual biogenic structures. The evenly spaced *Macrotermes* mounds have significant effects on an area's overall biodiversity, increasing primary productivity and vegetation heterogeneity in proximity to the mounds and hence increasing associated faunal diversity through both trophic and ecosystem engineering feedbacks (Dangerfield *et al.*, 1998; Traoré *et al.*, 2008; Pringle *et al.*, 2010). The two major mechanisms of ecological engineering by termites include the construction of the biogenic structure itself (the tunnels, galleries and associated mound of the nest) and central-place foraging, which concentrates organic matter and nutrients from a relatively large area within a smaller area of soil and makes these available to plants.

The movement of large amounts of finer particle soils in the construction of termite nests and mounds directly influences physical soil properties and indirectly alters chemical properties related to the transport, compaction and aeration of the soil. The amount of soil moved can be substantial. *Odontotermes* species in northern Kenya translocated the equivalent of about 1059 kg of soil ha⁻¹ y⁻¹ (Bagine, 1984). These larger mounds are known to have generated vegetated alluvial islands in the Okavango Delta and thicket clumps in eastern Africa, improving plant performance and providing an escape from fire and flooding (Dangerfield *et al.*, 1998; McCarthy *et al.*, 1998; Bloesch, 2008). Termites preferentially translocate finer soil particles from deeper soil horizons, altering the proportions of particle sizes compared to the surrounding soils (Bagine, 1984; Abe *et al.*, 2012; Jouquet *et al.*, 2011). Finer particle selection is related to physical constraints on the size of particles that can be carried by workers, and the benefit of finer particles, particularly clay, in the cementing of mounds and subterranean tunnels and galleries (Lee & Wood, 1971; Jouquet *et al.*, 2002; Jouquet *et al.*, 2007; Sileshi *et al.*, 2010; Abe *et al.*, 2012). Jouquet *et al.* (2002) found that the particle size and origin of soil

used by the termite *Odontotermes pauperans* (Silvestri) for various nest structures differed, with foraging tunnels consisting of indiscriminate particles from the top-soil and fungus-comb chambers of selectively acquired finer clay particles from deeper soils. The higher percentage of finer clay particles, together with the cementing properties of the saliva and faeces used in the construction of nests, can increase the mechanical resistance of soils in the mounds and the outwash pediment surrounding certain termite nests (Ackerman *et al.*, 2007).

Termites are capable of increasing the soil water holding capacity and water infiltration of soils around their nests (Lee & Wood, 1971; Elkins *et al.*, 1986; Mando *et al.*, 1996). This is often a direct consequence of soil particle size alteration, with the clay soil content produced by many mound-building termites having a high water holding capacity due to its ability to swell and allow water to condense on clay particles (Russell, 1973). In contrast, the creation of air spaces in the form of tunnels and galleries may increase soil porosity and hence increase water infiltration (Lee & Wood, 1971; Elkins *et al.*, 1986; Mando *et al.*, 1996; Mando, 1997). The retention of water within termite nests can be substantial, and can have obvious effects on the surrounding vegetation. For example, the large *Macrotermes* mounds found in northern parts of Namibia invariably have trees associated with them that are able to retain their leaves in dry winter months due to the elevated moisture levels, while other nearby trees lose theirs (Turner, 2006). This increase in soil water storage and infiltration has led several studies to conclude that, particularly in arid or semi-arid environments, termites play a crucial role in soil water maintenance (Elkins *et al.*, 1986; Mando, 1997; Konaté *et al.*, 1999). The best studied aspect of FC soils is their moisture content, which is consistently higher than the matrix, with FC soils remaining fairly moist throughout the dry winter and early summer (Albrecht *et al.*, 2001; Picker *et al.*, 2012; Juergens, 2013). This higher moisture content may be related to their soil structure. Moll (1994) reported higher clay content on FCs compared to the matrix, though this result was not supported by Cramer & Barger (2013). Juergens (2013) hypothesised that large pore sizes within FC soils may aid in the percolation of water deeper into soils below FCs, preventing evaporation and allowing for the high moisture levels documented on FCs.

Along with increased water infiltration, the creation of galleries and increased porosity also promotes soil aeration in termitaria (Lee & Wood, 1971; Korb & Linsenmair, 1998). Increased aeration affects other soil properties related to the soil atmosphere present within the pores - including soil temperature within the mound (Weir, 1973). Dense, compacted soils would be expected to have higher heat capacity and conductivity (hence higher temperatures) compared to well aerated soils with a lower bulk density (Payne & Gregory, 1988; Singer & Munns, 1996). Excessive temperatures may reduce photosynthetic efficiency and affect the movement of water and nutrients within plants,

ultimately resulting in a failure to reproduce and possible senescence (Larkindale *et al.*, 2005). High temperatures have been shown to decrease plant height and cause chlorosis of the leaves of young maize plants (Lal, 1974), and plants are particularly susceptible to high temperatures in the germination stage (Lal, 1974; Núñez & Calvo, 2000; Pérez-Sánchez *et al.*, 2011). Soil temperature on FCs remains unstudied, but may be expected to be higher than the surrounding matrix soils due to a lack of plant shading (as documented on the exposed mounds of *Pogonomyrmex montanus* (MacKay) ants surrounded by a bare disc (MacKay & MacKay, 1985)), or lower if the higher soil moisture of FCs contributes to evaporative cooling.

Besides the movement of soil to create their mounds, termites enrich soils within and around their nests through the collection and storage of plant debris (food matter) and the accumulation of waste (faeces, termite remains etc). The increase in termite nest nutrients and organic content, as well as the translocation of soil from different soil horizons, affects other elements of soil chemistry including pH and electrical conductivity. Termite nests can either increase, decrease or not affect the pH of surrounding soils (Jouquet *et al.*, 2005; Ackerman *et al.*, 2007; Jouquet *et al.*, 2007; Sileshi *et al.*, 2010). Most researchers report an increase in pH (Lee & Wood, 1971) and a meta-analysis of the effect of termites on soils revealed that mound soils are generally 85 % richer in cations than adjoining soils, which may explain an increase in pH in some cases, particularly when clay-rich soils are transported from lower soil horizons (Sileshi *et al.*, 2010). In soils abundant with water-soluble bases, higher water levels and hence increased evaporation on termite mounds can lead to the concentration of bases and consequently a higher pH. Alternatively, pH can be lowered with high concentrations of organic matter in mounds (Lee & Wood, 1971). Soil electrical conductivity (EC) can be used as an indicator of soluble salts and hence is closely related to pH (Russell, 1973). Higher EC values have been reported on termite mounds, and may be related to elevated evaporation rates in a similar way to elevated pH levels (Watson, 1967; Griffieon & O'Connor, 1990).

6.1.3 Effect of Termite Colonies on Other Organisms

On a local scale, termite colonies have positive effects on vegetation and alter plant communities, largely due to increased water and nutrient availability, improved soil drainage and protection from fire (see Chapter 1, 3). As a result of localised soil modification and the associated positive influence on plant growth, termite mounds can create refuge for a variety of mammals, reptiles and invertebrates, as well as a rich food source for a range of vertebrate and invertebrate primary and secondary consumers (Fleming & Loveridge, 2003; de Visser *et al.*, 2008; Pringle *et al.*, 2010; Jouquet

et al., 2011). Complex trophic networks may be attributed to the presence of termites and their mounds, with some termitophagous invertebrates being attracted to termites as a food source which in turn are consumed by higher predators (de Visser *et al.*, 2008). In cases where vegetation on termite mounds is more luxuriant, herbivorous animals may show preferential grazing and browsing in the vicinity of termitaria (McCarthy *et al.*, 1998; Holdo & McDowell, 2004; Levick *et al.*, 2010; Pringle *et al.*, 2010). Elephants, for example, prefer the woody vegetation on termite mounds compared to that in neighbouring woodlands, possibly because levels of foliar nitrogen are greater in plants growing on termitaria (Holdo & McDowell, 2004). FCs may have the same influence of faunal communities (Juergens, 2013), especially given their positive influence on plant growth in the peripheral band.

6.1.4 Aims and Predictions

This chapter contrasts selected physical and chemical properties of FC and matrix soils (soil particle size, pH, EC, soil moisture and temperature), and relates these to the both the plant competition and Sand termite hypotheses for FC formation. In addition, ant and scarab communities were examined on and off FCs to detect any influence that FCs have on surrounding invertebrate communities.

- 1) Since termites tend to increase the proportion of fine particles within their nests and mounds, it is hypothesised that if the Sand termite was the originator of FCs, the soils on the bare disc would contain higher levels of clay and silt than those of the matrix, and that these proportions may change throughout FC life stages.
- 2) Both pH and EC vary considerably on mounds of different species of termite (Watson, 1967; Lee & Wood, 1971; Griffieon & O'Connor, 1990). However, if differences were found when FCs were compared with the matrix, this might provide evidence for the Sand termite hypothesis as the plant competition model does not predict any changes in either pH or EC. Elevated pH is, however, a common (but not universal) feature of termite mounds (Weir, 1973; Francis *et al.*, 2012) as a result of the higher evaporation rates of termitaria-associated soils. In the same way, EC might be expected to increase on FCs due to water soluble salts accumulating in the soil of the bare disc (Gutterman, 1993). Extreme values of pH and EC can directly or indirectly affect the health of plants and potentially lead to plant death. Plant roots can be damaged at low pH values of less than 3 and plants are unable to absorb phosphates above pH 9 (Russell, 1973). Between these ranges pH can secondarily affect the availability of certain ions to plants and, depending on the tolerance of the plant species, may affect its

fitness (Russell, 1973). High salinity as reflected in higher EC values may inhibit desert seed germination if seeds are not salt-tolerant (Gutterman, 1993).

- 3) Most termite species increase the local soil moisture content, and thus availability of water to plants on and around their nests. If FCs are surface manifestations of subterranean termite nests, one might expect elevated soil moisture levels on FCs. Additionally, soil moisture would be expected to increase with increases in colony size of the Sand termite, through the progression of FCs life stages (Chapter 4). Water is a limiting factor for plant growth in the arid grasslands where FCs occur, and not surprisingly plant growth around FCs is known to be more luxuriant, likely through access to higher soil moisture levels (Albrecht *et al.*, 2001; Picker *et al.*, 2012; Juergens, 2013).
- 4) The thermal environment of FCs has not yet been examined, and may play a role in limiting recruitment and growth of plants on the FC disc. Termite mound soils may be warmer than surrounding soils through the contributions of metabolic heat by the termites and greater solar exposure on bare mounds; alternatively mound temperatures may be lowered through ventilation of mounds or high evaporation rate due to increased soil moisture (Lee & Wood, 1971; Weir, 1973; Korb & Linsenmair, 2000; Jones & Oldroyd, 2006). The generation of bare discs above a nest - and subsequent lack of shading - is known to provide a thermoregulatory benefit to subterranean social insects. *Pogonomyrmex* ant colonies which have a bare disc surrounding the epigeal nest benefit from early morning heating, and are thus able to lengthen their activity time (Bucy & Breed, 2006). If soil temperature on the bare disc is markedly higher than in the matrix, it may exceed the thermal tolerance of colonising grass seedlings and thus play a role in the maintenance of the bare disc. Thermal optima and upper thermal limits of *Stipagrostis* seeds and seedlings are examined here and related to environmental temperatures to which the plants are exposed.
- 5) Termite colonies are known to influence the neighbouring plant communities, which in turn influences faunal communities (Dangerfield *et al.*, 1998; Pringle *et al.*, 2010). FCs with their bare discs and well-vegetated peripheral band provide habitat heterogeneity that may be reflected in usage by various faunal groups. Two invertebrate groups (ants and scarab beetles) were examined for changes in abundance and diversity that may be related to FCs.

6.2 Methods

In order to detect changes in soil physical and chemical properties on FCs, soil samples were taken from 10 representatives of each FC growth stage (new, young, mature and senescent) and the matrix and used to measure soil moisture, particle size, pH and EC. Soil temperature on FCs and in the matrix were measured on 20 FCs using Dallas Thermochron DS1921G-F5 temperature data loggers, both on the soil surface and at 15 cm depth. Based on the hypothesis that FCs may increase soil temperatures beyond the thermal maxima of matrix grasses and hence contribute to grass death on FCs, *Stipagrostis ciliata* and *Stipagrostis obtusa* seeds and seedlings were subjected to four separate thermal tolerance experiments (two pilot studies and two longer term experiments). The two pilot studies were used to determine (i) the appropriate temperature range for the trials (ii) whether stratification was needed for germination and (iii) whether seeds need to be wetted prior to germination. The first pilot study used stratified (chilled) vs non-stratified *S. obtusa* and *S. ciliata* seeds with four replicate pots per treatment (15 seeds per replicate) grown at 30°C, 35°C, 40°C, 45°C and 50°C for 17 days. The second pilot study examined *S. obtusa* and *S. ciliata* germination at 35°C, 37°C, 41°C, 44°C and 47°C with presoaked or dry seed, with four pots of 30 seeds used at each temperature. These were followed by a 9 day long germination trial of *S. ciliata* seeds (16 replicate pots with 25 seeds each per temperature treatment) and a 10 day long trial examining growth of 2 week old transplanted *S. ciliata* seedlings (16 replicates with one seedling per pot) at 35°C, 37°C, 41°C, 44°C and 47°C. Lastly, ant and scarab beetle assemblages on the FC bare disc, peripheral band and in the matrix were analysed using pitfall traps on 60 FCs to detect changes in ground invertebrate communities. Detailed methods for this chapter are covered in Chapter 2, Section 2.3.

6.3 Results

6.3.1 Particle Size of Fairy Circle and Matrix Soils

A principal components analysis of soil particle size of the four FC life stages and the matrix revealed two main principal components. PC1 separated samples with a higher proportion of coarse sand particles from those with fine or very fine sand (explaining 59 % of variation), and PC2 separated out samples with very coarse sand from very fine to medium sand (explaining 26 % of variation) (Fig. 6.1). Of the two principal components, only PC2 differed significantly between life stages and matrix (Kruskal Wallis, $H_{4,50} = 25.95$, $P < 0.0001$), with the matrix having more coarse sand particles than new and senescent FCs ($P = 0.002$ and $P < 0.0001$ respectively), and mature FCs having finer sand particles than senescent FCs ($P = 0.027$).

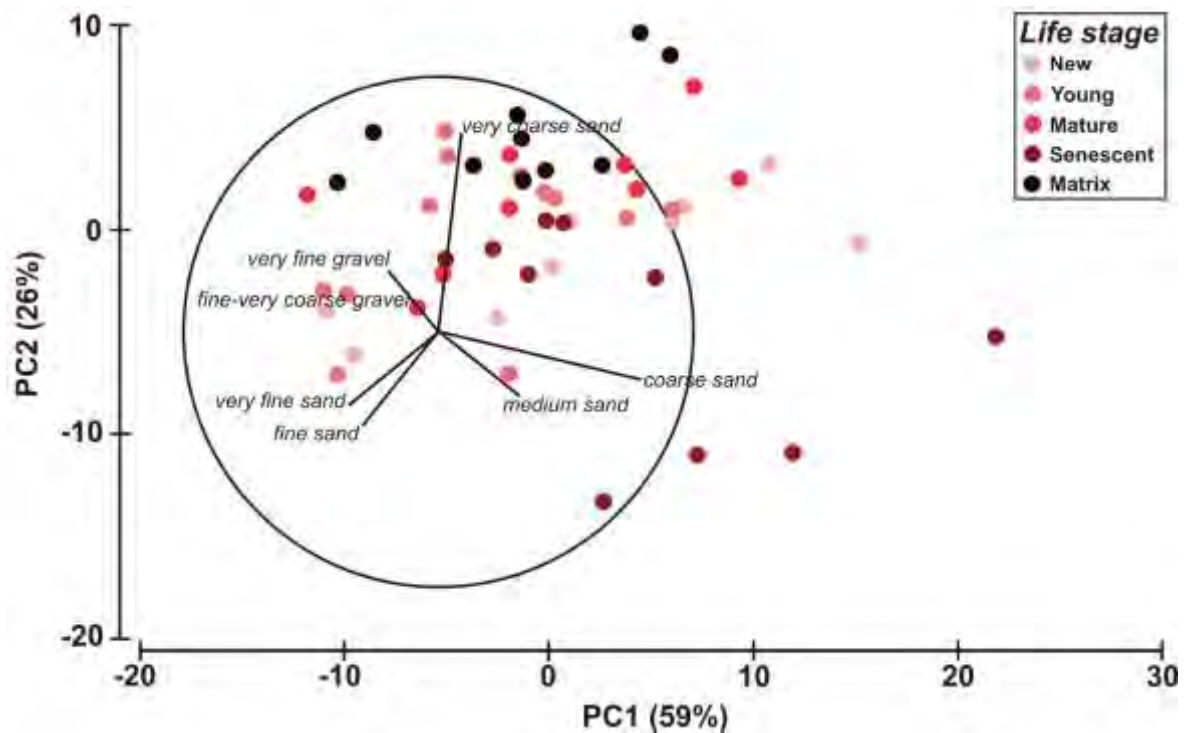


Fig. 6.1. Biplot of PC1 against PC2 for a principal components analysis of soil particle size on four FC life stages and the matrix.

6.3.2 Soil Moisture, EC and pH of Fairy Circle and Matrix Soils

Soil moisture was higher in young and mature FCs compared to both senescent FCs ($H_{4,50} = 29.55$, $P = 0.001$ and $P = 0.013$ respectively) and the matrix ($H_{4,50} = 29.55$, $P = 0.000$ and $P = 0.002$ respectively), and new FCs had higher values than the matrix ($H_{4,50} = 29.55$, $P = 0.05$) (Table 6.1). Soil EC and pH showed no significant difference between any of the four life stage and the matrix ($H_{4,50} = 7.66$, $P = 0.105$ and $H_{4,50} = 3.93$, $P = 0.415$ respectively) (Table 6.1).

Table 6.1. Median (interquartile italicised) values for soil moisture (%), soil EC ($\mu\text{S}/\text{cm}$) and soil pH for all FC life stages and the matrix ($n = 10$ for each of the five categories).

	New	Young	Mature	Senescent	Matrix
Soil Moisture (%)	1.7, <i>0.81</i>	2.6, <i>0.49</i>	2.3, <i>1,18</i>	0.9, <i>0.47</i>	0.7, <i>0.31</i>
Electrical Conductivity ($\mu\text{S}/\text{cm}$)	39.7, <i>15.32</i>	42.5, <i>13.75</i>	34.3, <i>35.64</i>	29.0, <i>20.34</i>	27.1, <i>12.45</i>
pH	7.3, <i>0.64</i>	7.1, <i>0.53</i>	7.1, <i>0.45</i>	7.3, <i>0.58</i>	7.3, <i>0.54</i>

6.3.3 Thermal Environment of Fairy Circles and Thermal Limits of *Stipagrostis* Seed and Seedlings

Matrix soils were found to have higher overall (24 hr) average, diurnal average and maximum *soil surface* temperatures than FCs (Mann-Whitney U, $U_{20,20} = 83.5$, $P = 0.002$ for overall average, $U_{20,20} = 73.0$, $P = 0.001$ for diurnal average and $U_{20,20} = 85.0$, $P = 0.002$ for maximum temperature). However the temperature range did not differ between all of the sites ($U_{20,20} = 170.5$, $P = 0.43$) (Fig. 6.2). This trend was mirrored at *15 cm soil depth* ($U_{20,20} = 15.0$, $P = 0.000$ for overall average, $U_{20,20} = 54.0$, $P = 0.000$ for diurnal average, $U_{20,20} = 71.5$, $P = 0.001$ for maximum and $U_{20,20} = 182.5$, $P = 0.460$ for temperature range) (Fig. 6.2). Average diurnal temperatures, maximum temperatures and temperature range were lower at 15 cm depth compared to the surface for both FCs and the matrix (Kruskal Wallis, $H_{3,80} = 60.65$, $P = 0.000$ for diurnal average, $H_{3,80} = 60.87$, $P = 0.000$ for maximum and $H_{3,80} = 54.08$, $P = 0.000$ for temperature range).

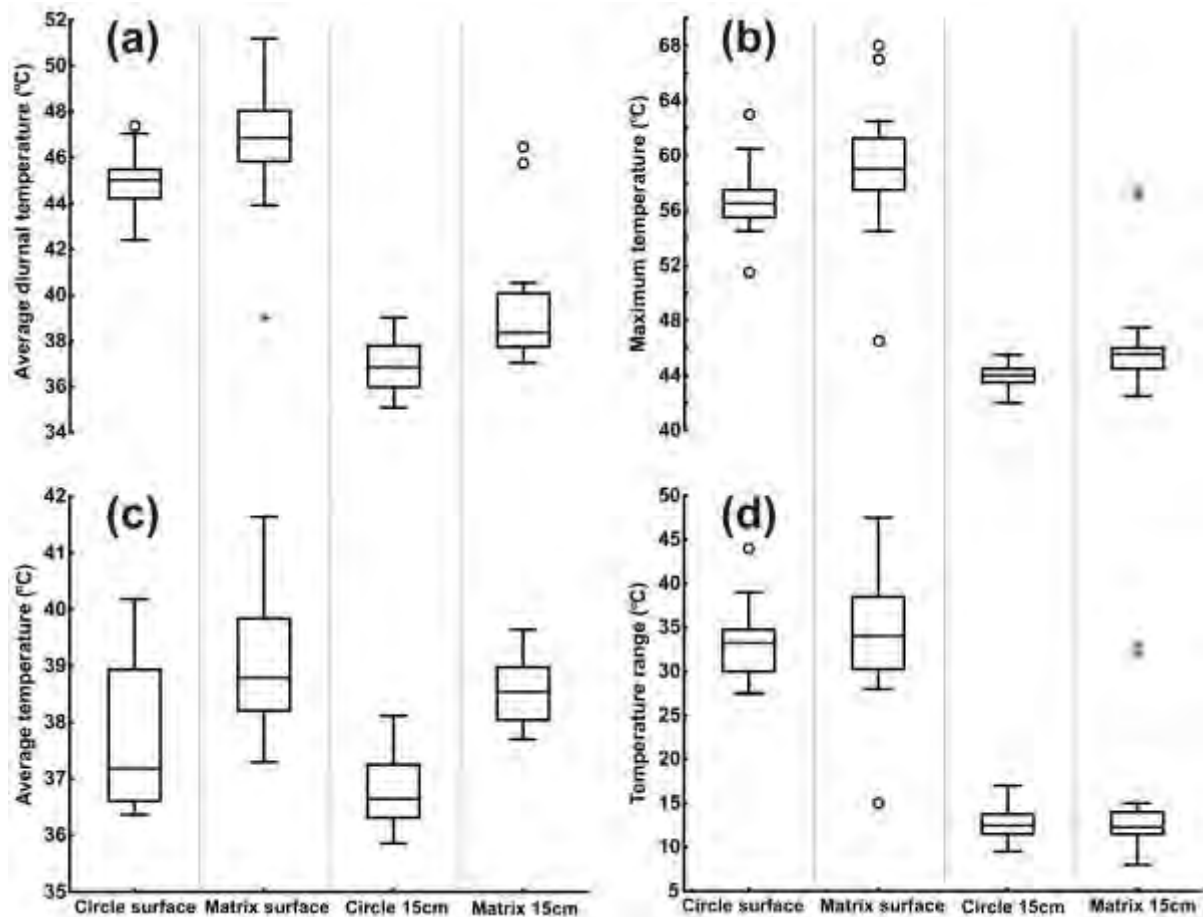


Fig. 6.2. Box and whisker plots of (a) mean diurnal temperature, (b) maximum temperature, (c) average temperature and (d) temperature range of soils on the surface and at 15cm depth on FCs and the matrix (n = 20).

The first pilot experiment on *Stipagrostis* seed germination at 30°C, 35°C, 40°C, 45°C and 50°C revealed that prior stratification of wetted seeds at 5 °C had no effect on germination success ($\chi^2 = 0.03$, $P = 0.869$ for *S. ciliata* and $\chi^2 = 0.43$, $P = 0.511$ for *S. obtusa*) (Table 6.2). For the second pilot study, *S. obtusa* (and to a lesser extent *S. ciliata*) exposed to 35°C, 37°C, 41°C, 44°C and 47°C (temperature range modified based on previous pilot experiment) had greater germination success after being kept moist for three days prior to the experiment compared to those planted dry (Chi-squared, $\chi^2 = 12.28$, $P = 0.001$) (Table 6.3). Overall *S. ciliata* had a significantly higher germination success than *S. obtusa* ($\chi^2 = 17.34$, $P = 0.000$). In the second pilot study germination success dropped at 45 °C, and none occurred at 50 °C for both species. These pilot studies informed the temperature range that was utilised in the two subsequent thermal tolerance trials of *S. ciliata* seed germination and transplanted seedlings.

Table 6.2. Percentage (%) germination of *S. ciliata* and *S. obtusa* stratified and non-stratified seeds at 30 °C, 35 °C, 40 °C, 45 °C and 50 °C.

	30°C	35°C	40°C	45°C	50°C
<i>S. ciliata</i> stratified	16.7	13.3	21.7	6.7	0
<i>S. ciliata</i> non-stratified	10	13.3	26.7	13.3	0
<i>S. obtusa</i> stratified	3.3	8.3	6.7	1.7	0
<i>S. obtusa</i> non-stratified	5	3.3	1.7	1.7	0

Table 6.3. Percentage (%) of germinated wetted and dry *S. ciliata* and *S. obtusa* seeds at 35 °C, 38 °C, 41 °C, 44 °C and 47 °C.

	35 °C	38 °C	41 °C	44 °C	47 °C
<i>S. ciliata</i> wet	33.3	13.3	26.7	20	26.7
<i>S. ciliata</i> dry	0	3.3	0	6.7	10
<i>S. obtusa</i> wet	6.7	0	0	0	3.3
<i>S. obtusa</i> dry	0	0	0	0	0

The two pilot trials were followed by a longer term experiment of nine days whereby *S. ciliata* seeds were germinated at temperatures of 35°C, 37°C, 41°C, 44°C and 47°C. Seed germination number decreased significantly with increasing temperature ($R^2 = 0.947$, $F = 53.80$, $P = 0.005$, $n = 16$), with considerably more germinations occurring at the lowest experimental temperature (35 °C) compared to 47 °C (Kruskal Wallis, $H_{4,80} = 26.78$, $P = 0.000$, $n = 16$) (Fig. 6.3). The number of leaves and roots as well as leaf and root length of the seedlings germinated at the experimental temperatures all decreased significantly with increasing temperature (Permutated MANOVA, $F = 14.16_{4, 80}$, $P = 0.0001$, $n = 16$) (Fig. 6.3).

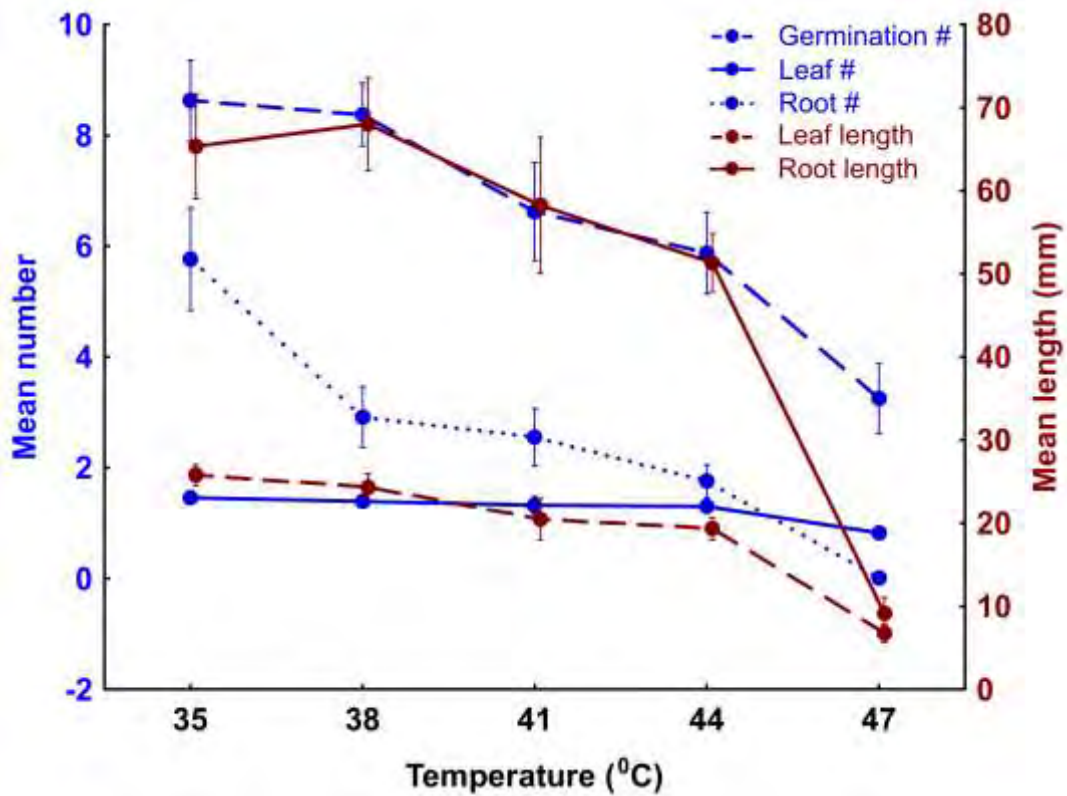


Fig. 6.3. The mean number of *S. ciliata* germinations, seedling leaf number, root number, leaf length and root length at different temperatures after nine days ($n = 16$). Error bars = standard errors.

In the final thermal tolerance trial subjecting two-week old transplanted *S. ciliata* seedlings to 35°C, 37°C, 41°C, 44°C and 47°C for ten days, seedling condition decreased significantly as temperatures increased, with root and leaf length as well as unchlorosed leaf number decreasing with temperature and the number of chlorosed leaves increasing (Permutated MANOVA, $F = 3.075$, $P = 0.006$) (Fig. 6.4). The number of deaths increased marginally with temperature, with one death at 35 °C, two at 38 °C, four at 41 °C, eight at 44 °C and seven at 47 °C ($\chi^2=8.45$, $P = 0.076$).

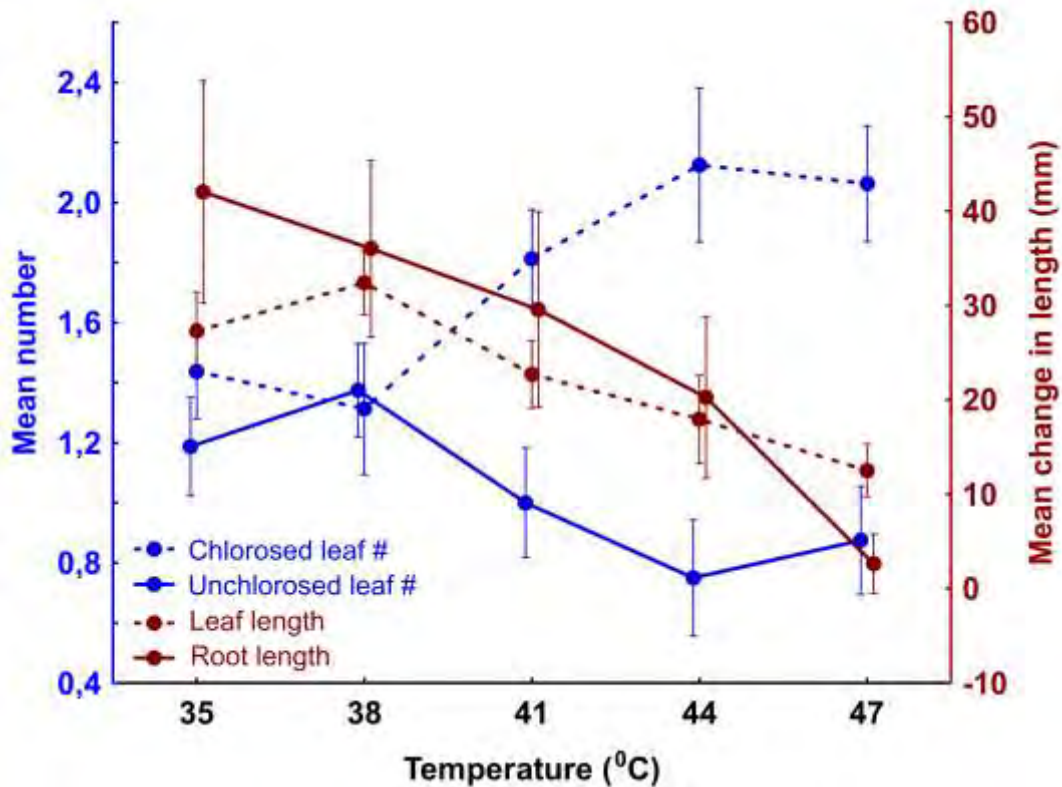


Fig. 6.4. The mean number of unchlorosed leaves, chlorosed leaves and the change in root length and leaf length of transplanted seedlings after ten days exposure to different temperatures. Error bars = standard error, (n = 16).

6.3.4 Ant and Scarab Communities on Fairy Circles

Ant species richness on FCs remained similar in both 2011 and 2012 although abundances increased nearly five-fold in the summer of 2012 after the heavy rains of the previous summer (Table 6.4). Ant species richness was higher on the FC peripheral band compared with the matrix and bare disc in both years, most noticeably in 2011 (ANOVA, $F_{2,75} = 5.92$, $P = 0.007$ and $P = 0.018$ for matrix and bare disc, respectively). Ant abundance was lowest on the bare disc compared with the peripheral band and matrix in 2012 (ANOVA, $F_{2,75} = 8.31$, $P = 0.001$ and $P = 0.011$, respectively). In 2011, the matrix supported one unique *Tetramorium* spp. not found on FCs while another *Tetramorium* spp. was found on the bare disc and peripheral band but not the matrix (Appendix 2).

Scarab-species richness was greater on the disc than on both the peripheral band and matrix (Kruskal–Wallis, $H_{2,180} = 13.74$, $P = 0.032$ and $P = 0.003$, respectively). The same trend was evident for abundances ($H_{2,180} = 19.31$, $P = 0.009$ and $P = 0.001$, respectively), and diversity (Shannon Wiener; $H_{2,180} = 8.81$, $P = 0.012$, Simpson's; $H_{2,180} = 9.18$, $P = 0.01$) (Table 6.4).

Table 6.4. Species richness and diversity of ant and scarab communities on and off FCs (means \pm S.D., medians and interquartiles italicised).

Taxon and microhabitat	S	N	Shannon Weiner	Simpson's (1-λ)
Formicidae (Jan 2012)				
Bare disc	8.0 \pm 1.1	350.0 \pm 267.8	1.136 \pm 0.322	<i>0.587, 0.230</i>
Peripheral band	9.1 \pm 1.1	796.2 \pm 521.5	1.077 \pm 0.440	<i>0.571, 0.364</i>
Matrix	8.1 \pm 1.4	734.9 \pm 633.5	0.965 \pm 0.330	<i>0.534, 0.253</i>
Formicidae (Feb 2011)				
Bare disc	8.0 \pm 1.5	145.7 \pm 240.6	1.359 \pm 0.419	<i>0.665, 0.174</i>
Peripheral band	8.5 \pm 2.0	160.2 \pm 161.6	1.429 \pm 0.399	<i>0.711, 0.155</i>
Matrix	7.9 \pm 1.6	109.9 \pm 76.0	1.442 \pm 0.306	<i>0.715, 0.146</i>
Scarabaeidae (Feb 2011)				
Bare disc	1.4 \pm 1.3	6.0 \pm 10.9	0.268 \pm 0.389	0.161 \pm 0.229
Peripheral band	1.0 \pm 1.3	3.3 \pm 8.4	0.176 \pm 0.384	0.103 \pm 0.221
Matrix	0.8 \pm 1.2	4.1 \pm 17.1	0.111 \pm 0.295	0.067 \pm 0.175

A SIMPER analysis of ant communities in January 2012 on the FC bare disc and matrix showed a 70.50 % similarity between FC samples and 69.63 % similarity between matrix samples. FC and matrix samples were 70.1 % similar. An MDS ordination separated ant communities in 2012 on FCs and matrices into two main groupings with 50 % similarity between them. However, each of the major clusters comprised a mixture of FC and matrix samples (Fig. 6.5a). When an MDS was constructed for 2011 data, the stress factor could not be reduced below 0.23, hence the ordination was not a reliable representation of the relationships between the ant communities in the data set, in spite of efforts to transform the data in various ways and eliminate outliers.

A SIMPER analysis of scarab communities on the FC bare disc and in the matrix revealed a 54.03 % similarity between bare disc samples and 43.53 % similarity between matrix communities. The overall average similarity between FC and matrix samples was 38.14 %. The primary separation of communities at 40% level isolated many of the matrix communities, but there was no clear separation of scarab communities from FC and matrix sites (Fig. 6.5b).

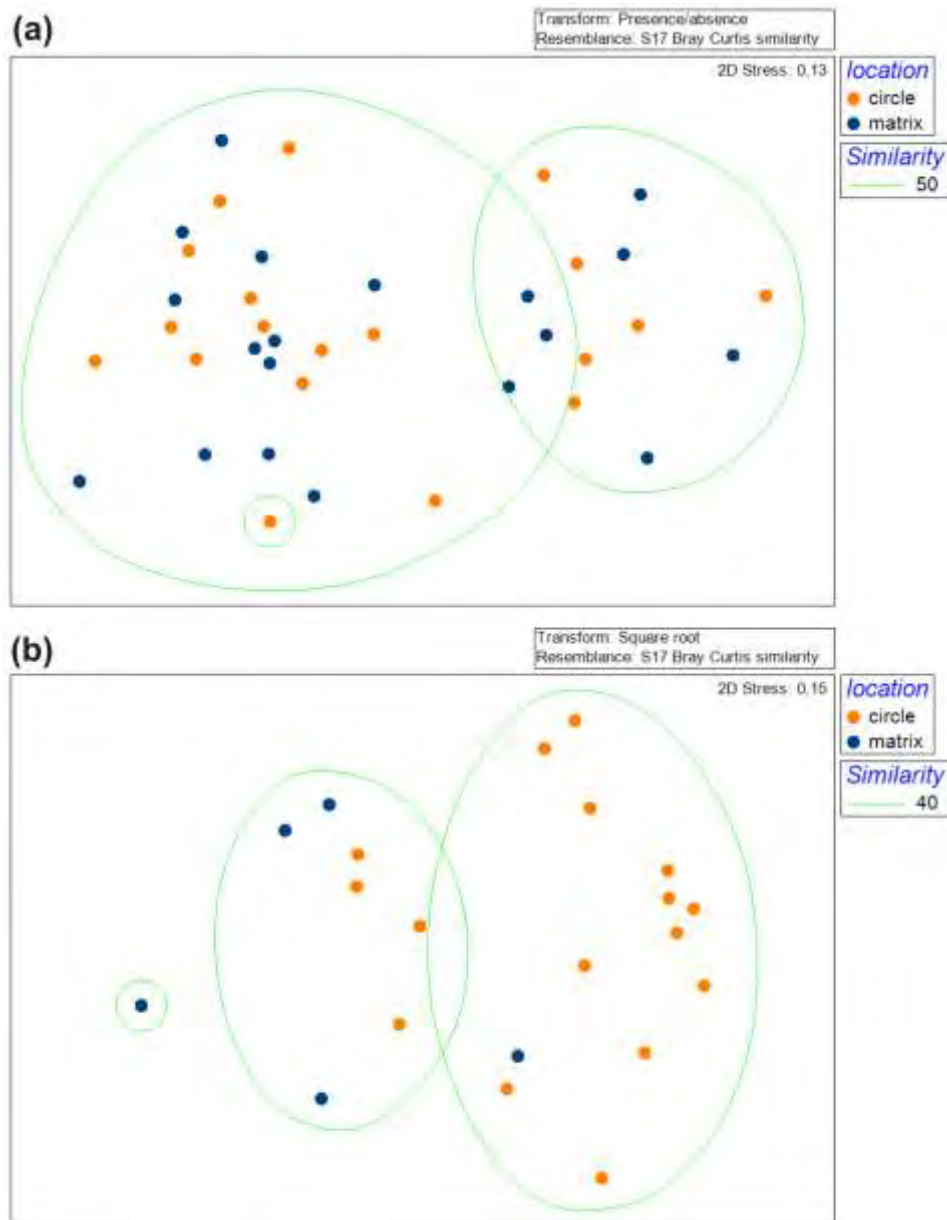


Fig. 6.5. Bray Curtis similarity MDS plots of (a) 2012 ant communities using a presence/absence transformation and (b) scarab communities using a square root transformation of abundances. Green bubbles indicate 50 % and 40 % similarity between clusters respectively.

6.4 Discussion

6.4.1 Do Fairy Circle Soils Differ From Those Of The Matrix?

FC soils generally contained finer sand particles than those of the matrix, with new and senescent FCs having finer particles than the matrix and mature FCs finer particles than senescent ones (Fig. 6.1). This is in agreement with Moll (1994) who found greater percentages of silt and clay and lower

proportions of sand on FCs, however, Cramer & Barger (2013) found no difference in soil texture between FCs and the matrix. Although finer particle selection by termites is most often associated with clay-rich mounds (McCarthy *et al.*, 1998; Sileshi *et al.*, 2010) finer particles may also be used for subterranean structures such as comb walls or foraging galleries (Jouquet *et al.*, 2002). *P. allocerus*, being a sand specialist, may not require the large amounts of clay that mound building species do (which may explain the discrepancy in differences in soil particles between studies) but likely still requires finer sand particles to construct their (stable) subterranean nests and tunnels.

FCs soils did not differ in soil pH or EC at any life stage compared to matrix soils (Table 6.1). This finding is in agreement with previous studies (Moll, 1994; van Rooyen *et al.*, 2004; Cramer & Barger, 2013). Cramer & Barger (2013) additionally found no change in electrical resistance, however, van Rooyen *et al.* (2004) detected a slight increase in resistance on the FCs. No change in EC may be an indication of no changes in soluble ions in FC soils, possibly as a result of the very low rainfall of the areas where they occur. Many termite species having no effect on local soil pH (Arshad, 1982; Jouquet *et al.*, 2005; Jouquet *et al.*, 2007), and the small and subterranean nests of the Sand termite would not be expected to have major effects on pH. Increases in pH are often associated with an increase in CaCO₃ (or release of exchangeable bases from decomposing vegetation matter brought in by termites (Watson, 1974)) while a decrease is related to the higher organic matter in the termite nest soils (Lee & Wood, 1971). Neither of these is reported as having higher levels on FCs (Cramer & Barger, 2013).

The most dramatic changes to FC is that of elevated soil moisture in the period prior to the summer rains; 2 - 3X greater than soil moisture of the surrounding matrix and particularly high for young FCs (Table 6.1). This property of FC soils is widely documented (Becker & Getzin, 2000; Albrecht *et al.*, 2001; Picker *et al.*, 2012; Juergens, 2013), but this is the first documentation of ontogenetic differences in soil moisture levels of FCs, showing that high moisture levels are achieved early in their development. Potential explanations that have been proposed for this increase in moisture content on FCs include reduced evapotranspiration due to decreased plant cover (Becker & Getzin, 2000; Picker *et al.*, 2012) and increased percolation to deeper soil layers due to large soil pore sizes on FCs (Juergens, 2013). Social insects in arid or semi-arid environments need to maintain constant high humidity conditions within their nests to survive (Lee & Wood, 1971; Uys, 2002). This need for a moist environment led Juergens (2013; 2015) to hypothesize that *Psammotermes allocerus* may construct FCs as water traps in a water deficit environment. As well as increasing the water holding capacity and water infiltration of their nest soils, termites may also be capable of either physically transporting moisture into their nests by collecting it from the water table deeper underground, or by contributing metabolic water (Lee & Wood, 1971; Turner, 2006). Metabolic water generated by *Macrotermes*

colonies, which may reach values of 190 litres per year, amounts to 10 % of the colony's annual evaporation budget (Darlington *et al.*, 1997). The subterranean termites *Reticulitermes santonensis* (Feytand) transports water in paired labial gland reservoirs, each capable of taking up 0.25 µl of capillary water (Grube & Rudolph, 1999). *Psammotermes* species in the Sahara have been recorded collecting water from several meters depth and bringing it up to their shallow nests even though there is no continuity between the nest and water table (Grassé & Noirot, 1948). The ability of *P. allocerus* to transport water in this way from lower ground water resources has not been demonstrated, but since related species within the Rhinotermitidae exhibit this behaviour it remains only a possibility and needs to be explored further.

6.4.2 Do Soil Temperatures On Fairy Circles Restrict Recruitment Of Grasses?

Germination and growth experiments on *S. ciliata* seedlings showed negative responses to increasing temperatures, with the range 45-50 °C being close to the upper thermal limit. (Table 6.2 and Fig. 6.3). Prior wetting of seeds for three days increased the germination success of *S. ciliata* and *S. obtusa* by 6 X and 3 X respectively when compared to dry control seed (Table 6.3). This is similar to the wetting and stratification dormancy breaking technique used by Bahrani & Khategh (2006) for *Stipagrostis pennata* (T. De Winter), however in the case of *S. ciliata* and *S. obtusa* preliminary wetting was sufficient to trigger germination without stratification. Overall the number and length of both leaves and roots on germinated and transplanted seedlings declined significantly between an experimental temperature range of 35 °C and 47 °C while the number of chlorosed leaves and deaths increased across this range (Fig. 6.3 and Fig. 6.4). This decrease in germination rate and root and shoot growth are known to occur when plants are thermally stressed (Gardner *et al.*, 1999). Optimal temperatures for previously germinated transplanted *S. ciliata* seedling growth (indicated by the highest number of roots and leaves and longest roots and leaves) appears to be in the range of 35 °C to 38 °C, indicative of relatively high soil temperature preferences in this desert-adapted species. *S. ciliata* seed germination was inhibited when exposed to 50 °C for a number of hours per day, with no germinations occurring.

The negative impacts of soil temperatures above 38 °C on seedling growth and germination might exist in certain thermal microhabitats where FCs occur and thus reduce vegetation cover. Field readings over a typical summer period showed that FC soils were in fact consistently cooler than matrix soils, both at the surface and at 15 cm depth (Fig. 6.2). Over a day seedlings and seeds on the soil surface would be subjected to summer soil temperatures of around 37 °C on the FC and 39 °C in

the matrix, but would for brief periods need to tolerate diurnal temperatures of 45 °C on the FC and 47 °C in the matrix. During certain parts of the day they may even be briefly exposed to temperatures as high as 56 °C on the FC and 59 °C in the matrix. However, temperatures drop rapidly with depth due to the soil acting as a vast thermal sink (Russell, 1973), and at 15 cm depth temperatures were predictably lower and less variable than those at the surface. These temperatures are likely a better representation of what grass seedling roots and germinating seeds would be exposed to. The average temperatures at 15 cm depth on the FC (36 °C to 38 °C) were a good match to the optimum growing temperatures for *S. ciliata* in the experimental trials (35 °C to 37 °C), with the matrix being roughly two degrees warmer on average. This indicates that temperatures on the FC bare disc would not limit grass growth as was hypothesised, and may, in fact, provide more favourable thermal conditions than matrix soils. One would expect bare soils to be warmer than vegetated areas due to solar radiation being unaffected by vegetation shadows (Breshears *et al.*, 1998), but that is not the case here. The soil particle size (and hence bulk density) can affect temperature through the creation of pore spaces filled with either water or air (Gardner *et al.*, 1999; Tan, 2009). Coarser soils, such as those found in the matrix, would be expected to have larger pore sizes which, during drier times of the year, would contain air (Singer & Munns, 1996). Air is not as an efficient heat conductor as soil particles, hence soils with a lower bulk density would not hold heat up as well as finer grained soils with few pore spaces (Singer & Munns, 1996; Xie *et al.*, 2010). This may partially explain higher matrix soil temperatures. The most likely explanation for the significant decrease in soil temperature on FCs is the elevated soil moisture content. Water is a good temperature buffer due to its high heat capacity and role in evaporative cooling, and directly influences the temperature of the soil (Russell, 1973). This putative evaporative cooling of FC soils appears to have the greater influence on temperature contrasts, and the small amount of shade provided by the short grasses on the matrix before rains (when the readings were taken) does not appear to have lowered matrix soil temperatures. The temperature contrast between matrix and FC bare disc soils may be narrowed during the rainy season when the landscape is uniformly wet.

Termites have been shown to change soil temperatures around and within their nests and mounds, in most cases leading to an increase in temperature through metabolic heat (Lee & Wood, 1971). The moist soils within FCs, along with maintaining an optimally humid environment, may incidentally benefit *P. allocerus* colonies by providing a cooler and more stable thermal microclimate in the absence of a large ventilated mound typically employed by other termite species for thermoregulation. Darlington (2007), when describing arena nests built by *Odontotermes fulleri* which closely resemble FCs in appearance, speculated that they served a thermoregulatory function in the absence of large mounds which could not be constructed on the shallow soils where arena nests are

found. Passages were found throughout the soil beneath the arenas which weren't connected to any chambers, and may act to redistribute heat.

6.4.3 *Insect Community Responses to Ecologically Engineered Habitats on Fairy Circles*

The modification of soils by termites and the resultant change in plant communities around their nests also affect associated invertebrate communities. Soil inhabiting macrofaunal communities respond to (i) the generation of microhabitats and refugia provided by the construction of tunnels, galleries and mounds and (ii) food resources created by a proliferation of microbes due to increased nutrient supplies and the termites themselves (Cadet *et al.*, 2004; de Visser *et al.*, 2008; Jouquet *et al.*, 2011). Above-ground changes in the plant communities similarly alters invertebrate communities by providing refugia and trophic opportunities for plant inhabiting prey and predator invertebrates (Pringle *et al.*, 2010).

The community structure of ants and scarabs, the most abundant invertebrates on FCs, did not appear to be influenced by the changed vegetation cover, soil moisture content and thermal properties of FCs. Ordinations of ant and scarab communities on FCs and the matrix did not show clear separation – with primary breaks containing groups of mixed FC and matrix communities. These groupings most likely relate to locality rather than microhabitat, and although samples were taken within a few hundred meters of each other, neighbouring FC and matrix communities appeared to cluster together.

However, species richness, abundance and diversity indices of ants and scarabs were different when FC discs, peripheral bands and the matrix were compared (Table 6.4). Both the matrix and FC (encompassing both the peripheral band and bare disc) displayed one unique *Tetramorium* sp. in 2011 (Appendix 2). Ant species richness and abundance were highest on the peripheral band in both years and abundances lowest on the bare disc in 2012. There were far higher ant abundances overall in 2011 when compared to 2012. This may be accredited to the exceptional rains which occurred during and just prior to sampling in 2011 and a proliferation of vegetation growth both in the matrix and along FC peripheral bands at this time (Chapter 3). The bare disc supported the highest scarab beetle species richness, abundance and diversity when compared to the peripheral band and matrix. This suggests that the contrasting microhabitats provided by FCs in the form of a well-vegetated peripheral band and a bare disc have varying effects on organisms, supporting greater species richness and abundances when compared to the matrix. This potentially influences the overall abundance and diversity of insect communities in areas where FCs occur, where they can contribute to 3.5 % of the landscape (Cramer

& Barger, 2013). Juergens (2013) suggested that on a landscape scale, biodiversity in landscapes with FCs was found to be greatly increased (by one or two orders of magnitude) by species using FCs as nesting sites (certain ants including *Messor denticornis* (Forel) and various bees and wasps), sources of water (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) and Acacia trees), mating sites (springbok) and food sources in the form of *P. allocerus* (utilised by spiders, omnivorous ants, mammals including bat-eared fox, armadillo, golden mole and black-backed jackal).

The unconsolidated fine sand found on heuweltjies support nests of various ant species (including *Crematogaster melanogaster* (Emery), *Camponotus fulvopilosus* (De Geer) and *Messor* sp.) and burrowing anthophorid bees (Moore & Picker, 1991). Pringle *et al.* (2010) found that the abundances of aerial and tree-dwelling invertebrates increased with shorter distances to *Macrotermes* mounds. Other social insect structures, such as the bare discs constructed by *Pogonomyrmex* ants around their mounds in North America prudentially attract tenebrionid beetles when compared to surrounding matrices (McIntyre, 1999). The cleared discs provided warmer soil conditions than vegetated areas due to the increased solar radiation, and may serve as important thermoregulatory sites for the beetles during cooler parts of the day. In contrast, FCs provide cooler soil temperatures, but may also provide a thermoregulatory benefit for scarab beetles and other burrowing arthropods, especially for those having a preference for cleared areas, elevated soil moisture and perennial vegetation in the form of *S. ciliata* in the peripheral band. It is possible that scarabs seek the increased exposure to solar radiation on the surface of FCs during cooler parts of the day for thermoregulatory purposes or for mate attraction, and seek refuge underground in the wetter, cooler soils beneath the surface of the bare discs when temperatures increase towards midday. Scarabs may additionally favour the wetter soils for their brood as was demonstrated by Sowig (1995) for some European *Onthophagus* dung beetle species. Ants were more abundant in the well vegetated peripheral band and less abundant and diverse on the bare disc. It is possible that the peripheral band attracts larger populations of prey insects and hemipteran honeydew resources (see Chapter 3) associated with the evergreen *S. ciliata*. The extensive root system at the base of its large tussocks would provide some stability for the construction of ant nests, tunnels and chambers which might otherwise be less stable. The large entrances to the nests of *Anoplolepis steingroeveri* were often located at the base of *S. ciliata* tussocks on the peripheral band of FCs (Chapter 3; Picker *et al.*, 2012), and the majority of *A. steingroeveri* nests were also located on FCs, possibly as a result of their reliance on *S. ciliata*.

6.4.4 Conclusion

FCs display several soil characteristics which distinguish them from the surrounding matrix, the most relevant being higher moisture levels and lower soil temperatures. The greater availability of water and cooler temperatures within the bare patch would present an obvious opportunity for plant growth in a water-deficit environment. The luxuriant growth in the peripheral band around the bare patch, often the only source of living grass cover in the dry winter months, reveals the benefits plants may obtain from the resources associated with FCs. Given these seemingly optimum growing conditions, one must conclude that some process is actively keeping the FC discs bare. If this process is related to the presence of *P. allocerus* nests, they represent a large-scale example of an ecosystem engineer, equivalent in importance to the island forming *Macrotermes* in the Okavango Delta (Juergens, 2013). The presence of FCs has varied and predominantly positive effects on the diversity of organisms within the Pro-Namib Desert grasslands, the importance of which are only just being recognised. Most studies on FCs concentrate on their origins, but more attention should be placed on their mechanisms and ecological significance. Future productive studies could investigate the contribution of FCs at a landscape level to primary productivity and the supply of fodder for macrofauna – especially in the dry winter months. Specific trophic interactions on FCs may also have scope for further studies, as bird, mammal and invertebrate predators may preferentially utilise FCs as prey resources, especially as many rely on *P. allocerus* as a dietary item.

7 DISCUSSION

7.1 Evaluating Competing Hypotheses In Light of the Biology of Fairy Circles

When this thesis was initiated, there were a number of unresolved and competing theories that had been put forward for fairy circle (FC) origin. However, the last 4 years saw a revitalisation of FC research, with two major competing hypotheses emerging for the origin and nature of FCs. They have few commonalities, and are each supported by different lines of evidence. The plant competition hypothesis (Cramer & Barger, 2013; Getzin *et al.*, 2014; Getzin *et al.*, 2015), largely supported by remote modelling has little field-data support, whereas the Sand termite hypothesis (Juergens, 2013; Juergens *et al.*, 2015; Vlieghe *et al.*, 2015) is largely supported by field-based evidence. While both have broadened the knowledge of FC ecology, this has not resolved the question of their origin. The assumptions of the two hypotheses differ markedly. The plant competition hypothesis invokes grass root competition for resources (mainly water) in a semi-arid environment as the primary factor responsible for generating the highly overdispersed FCs, and utilises competition models to generate dispersion patterns (vegetation gaps) similar to those of FC dispersion. The expectations of such a model would be that the vegetation gaps formed would initially have lower soil moisture than surrounding matrix soils thus eliminating grass cover, but soon thereafter moisture levels would recover and exceed those of the matrix as there would be no grasses utilising water on the FCs. However, the models focus on the dispersion of FCs at varying scales and exclude both ecological predictions and have no support from ecological data.

In contrast, the predictions of the Sand termite model are largely ecological, and are related to (1) spatial associations between this termites and FC's and herbivore pressure by subterranean colonies of the termite on grasses above the nest system (FC origin), and (2) interactions between neighbouring termite colonies on FCs (which would generate the overdispersed spatial patterns). It predicts a progression from FC birth, to maturity and senescence that matches the growth phases of more typical termite colonies located in epigeal mounds. This would include a period of increased growth and environmental modification in line with changes of termite-modified soil characteristics, such as increases in finer soil particle size fractions, higher soil moisture and elevated nutrient levels.

Knowledge of the biology of FCs provides a backdrop against which to evaluate the predictions of these two hypotheses (Table 7.1). While the majority of FC research has focussed purely on their most obvious stage – the mature barren FC – this study has focussed on collecting ecological data for each of the four growth stages in the life of a FC, providing a new perspective in the study of FC biology and origins. Any study that considers mature FC alone ignores fundamental stages not only in the early

development of FCs but also in their senescence. In addition, this study has further distinguished FC generation from maintenance of the bare disc, an important distinction as different processes might be involved in both.

Table 7.1. Summary of main FC characteristics and evaluation of both the Sand termite and plant competition hypotheses

FC Characteristic	Sand termite hypothesis	Plant competition hypothesis
Size (approx 2 - 12 m in diameter)	Consistent assuming polycalic <i>P. allocerus</i> nests	Contrary – short root length of matrix grasses
Circular shape	Consistent	Consistent at a certain aridity, but inconsistent on slopes
Bare area	Consistent for some termite nest examples	Consistent
Well-vegetated peripheral band	Consistent	Inconsistent –higher productivity of peripheral band not explained
Even spacing over large area	Consistent, assuming homogenous landscape	Consistent
Range restricted to 50 - 150 isohyets	Inconsistent with larger range of <i>P. allocerus</i>	Inconsistent - gaps tend to occur within 400 - 500 mm rainfall
Restricted to sandy, species-poor grass plains	Consistent	Partially contradictory with some plant competition models
Density and size change with latitude	Consistent	Consistent
Respond to changes in plant abundance	Consistent	Consistent
Persist for decades (approx. 30-70 years)	Consistent	Consistent
Low recruitment	Consistent	Consistent
Developmental stages	Consistent	Inconsistent - vegetation patterns appear in final form
Higher abundance of <i>P. allocerus</i>	Consistent	Inconsistent unless termites are attracted to FCs secondarily
High proportions of finer soil particles	Consistent	No mechanism
Higher soil moisture on bare disc	Consistent	not initially, possibly at later stage
Cooler temperatures on bare disc	Consistent but dependent on habitat	Contrary - vegetated areas predicted to be cooler
Little change in nutrients (C and N lower)	Inconsistent - nutrients higher on termite mounds	Consistent with lower nutrients
Presence of hydrocarbons such as alkanes	Consistent	Inconsistent
Change in plant and animal communities	Consistent	Uncertain
Increased biodiversity	Consistent	Consistent

7.2 The Restricted Distribution of Fairy Circles

The plant competition and Sand termite hypotheses both have different predictions for the expected range of FCs. The former claims that FCs should fall within a narrow range based on vegetation productivity and rainfall parameters as it requires specific levels of aridity in order to effect plant competition and facilitation for resources (Cramer & Barger, 2013). The distributional range of FCs has been shown to be highly restricted, as they only occur within sandy, species-poor grasslands that closely follow the 100 mm isohyet, and rarely occur outside the 50 – 150 mm isohyet range (van Rooyen *et al.*, 2004; Cramer & Barger, 2013; Juergens, 2013). Any theory involving the activities of a specific organism (such as the Sand termite hypothesis) would require that the species in question be found throughout the FC range. That the sand-loving *Psammotermes allocerus* occurs throughout the sandy habitats in which FCs occur is not surprising (Juergens, 2013) given their wide distribution in south-western parts of southern Africa (Coaton & Sheasby, 1973). However one criticism for their involvement in FC formation is that their range extends well beyond the distribution of FCs, where these features do not exist. Juergens (2013) has suggested that FCs may represent a nest modification by the termites in very arid parts of their range to maximize their water use, and plasticity in mound design has been reported for certain termites in response to different environments (Pomeroy, 1977; Darlington, 2007). Alternatively Sand termite herbivory on woody shrubs in the southern parts of their range where no grasslands occur may not kill the larger and more resistant shrubs, and hence not generate any vegetation gap (Juergens *et al.*, 2015).

In vegetation self-organisation theory, vegetation gaps represent a transitional state between uniform vegetation cover and labyrinthine or banded cover, and they have been predicted by certain models to only occur within more humid areas (Deblauwe *et al.*, 2008). Deblauwe *et al.* (2011) recorded gapped vegetation patterns between the 400 – 500 mm isohyets in Sudan, and even when looking at all types of vegetation patterning combined globally, Deblauwe *et al.* (2008) predicted gaps to fall within the range of 160 – 790 mm, above the annual rainfall values to which FCs are restricted. In fact the model produced by Deblauwe *et al.* (2008) would predict FCs within savanna and woodland far east of the Namib Desert, east of Epupa and Ruacana (Juergens *et al.*, 2015). One parameter which may further restrict predicted vegetation patterning occurring within the FCs zone is soil texture, as plant patterning is less likely to occur in sandy soils such as those in which FCs thrive due to associated low wilting points (Deblauwe *et al.*, 2008).

7.3 Spatial Dispersion Patterns

One of the most striking features of FCs is their high degree of overdispersion. Their spatial ordering is hexagonal and has been described in detail by Getzin *et al.* (2014; 2015), Juergens *et al.* (2015) as well as Chapter 5 of this thesis. Getzin *et al.* (2015) argue that the degree and nature of spatial ordering of FCs cannot be matched by dispersion of social insect nests over large areas. However across homogenous habitats several examples of both social insect nests and vegetation patterning from around the world, are capable of exhibiting the same spatial characteristics as FCs (Juergens *et al.*, 2015). Hence neither termite nests nor vegetation self-organisation can be ruled out as potential mechanisms for FC formation based on spatial ordering alone. What makes FCs unique is their exceptionally high degree of spatial ordering, which more closely resembles that of epithelial cells (Zhang & Sinclair, 2015) rather than that of social insect nests or vegetation patterns. This may be a consequence of the large expanses of homogenous landscape (arid sandy grasslands) in which they occur. The high overdispersion of FCs, and the observation that the degree of dispersion increases with FC size (Cramer & Barger, 2013; Chapter 5), suggests an underlying competitive interaction, either in the form of long-range competitive interactions between plants (Couteron & Lejuene, 2001; Tongway *et al.*, 2001), or territoriality between termite colonies (Laurie, 2002; Pringle *et al.*, 2010; Bourguignon *et al.*, 2011). Though no overt aggressive territorial behaviour has been demonstrated between colonies of *P. allocerus*, the inter-colony interactions of many termites (especially subterranean Rhinotermitidae to which *Psammotermes* belongs), are often subtle and may involve chemical cues as opposed to physical aggression (Šobotník *et al.*, 2010; Krasulová *et al.*, 2012).

7.4 Fairy Circle Dimensions

Neither the plant competition nor Sand termite hypotheses predict a specific dimension for FCs, which typically range in size from approximately 2 - 12 m diameter, well within the range of reported sizes for termite mounds. Termite mounds can vary in diameter from a few cm to large 20 – 30 m diameter mounds of Macrotermitinae in Africa or *Microhodotermes viator* (heuweltjies) in the Western Cape (Lee & Wood, 1971; Moore & Picker, 1991). However one criticism against the Sand termite hypothesis is that *P. allocerus* builds relatively small individual subterranean nests (Moll, 1994) reaching only 36 cm in diameter (Coaton & Sheasby, 1973). Although polycalism has not been confirmed for *P. allocerus*, this condition is common amongst advanced rhinotermitids including the related species *Psammotermes hybostoma* (Krasulová *et al.*, 2012). Hence polycalic termite colonies of several linked

small nests spread over a larger area could cause the death of the grass plants above them (Chapter 4; Vlieghe *et al.*, 2015).

Spots, gaps and bands accredited to vegetation patterning in other parts of the world range in size from tens to hundreds of meters, with bare gaps reported as having diameters of 5 – 20 m, and being associated with perennial tussock grasses, shrubs or trees (Rietkerk *et al.*, 2002; Deblauwe *et al.*, 2008). Though FCs fall within the size range of the latter, Juergens (2015) and Juergens *et al.* (2015) argue that the annual grasses most often associated with FCs lack the root length that would facilitate long-distance competition for water and development of barren patches through negative competition feedback. Matrix grasses are spaced on average 10 cm from one other, suggesting that they can grow in close proximity without competition. In addition, Juergens (2015) questions whether the annual grasses within the Namib Desert with root systems on average 30 cm in length would be able to create a significant influence over an area 300 times that length, and thus compete with grasses many metres away. Moreover, even if they were theoretically able to outcompete neighbouring patches and thus generate gaps, in many areas the matrix grasses are annual plants that reseed yearly, and new patterns would thus need to be generated/reset annually as the competitors that had initiated the gaps would be dead.

While the plant competition model requires that patterns appear for the first time *at a particular site* at their final (stable) size, this contrasts with the predictions of the termite model for a progressive increase in size with age and additionally possible size variation at single locality as a result of habitat heterogeneity. FC size does vary along spatial gradients of vegetation cover and rainfall, both at a regional scale (Cramer & Barger, 2013) and at smaller scales (Cramer & Barger, 2013; Vlieghe *et al.*, 2015). Size responses to environmental variables such as these can also be demonstrated for both termites (Davies *et al.*, 2014) and vegetation patterning (Deblauwe *et al.*, 2011), supporting a biological origin for FCs, as opposed to an abiotic factor such as geochemical gas sweeps or radiation (van Rooyen *et al.*, 2004; Naudé *et al.*, 2011). FCs tend to increase in size from south to north and, although they are found in regions within the same rainfall belt regardless of latitude, they do transition between different vegetation zones and hence different matrix grass species. FCs in the most southern region of Namibia fall within the desert and succulent steppe vegetation type, those in the central portion of their range (including NamibRand) are within a transitional zone between semi-desert and savanna, and the most northern sites are found in mopane savanna (Giess, 1971). The dominant matrix grass differs between northern and southern sites as well, with *Stipagrostis obtusa* and *Stipagrostis ciliata* being found in southern to central portions of Namibia and *S. giessii* central to northern regions (Müller, 2007). At a local scale at

NamibRand, FC area was greater in response to increased abundance of the dominant matrix grass (*S. obtusa*). If FCs represented nest systems of the Sand termite, they would be predictably larger in areas with higher grass cover. The same pattern might be reflected on larger scales; in the north the matrix is dominated by *Stipagrostis giessii*, which is a larger grass species than *S. obtusa* (Müller, 2007), and FC size is greatest there. In contrast, the plant competition model predicts greater FC size with increased aridity (Cramer & Barger, 2013).

FCs tend to increase in size as they mature, with the largest FCs always being mature barren ones, while new FCs covered in dead grasses bearing termite sheetings are invariably smaller (Vlieghe *et al.*, 2015; Chapter 4). That FCs increase in size as they mature can be detected by observing the remnants of a concentric ring(s) of dead peripheral grasses within the bare disc, indicating the expansion of a FC beyond a smaller, original peripheral band (van Rooyen *et al.*, 2004; Juergens, 2013). This is in contrast to predictions for the plant competition model which states that FCs arrive more or less at their final size and do not expand (Tschinkel, 2012; Getzin *et al.*, 2014). A mixture of FCs of different sizes (and at different life stages) is consistent to the normal distribution of termite mound sizes within a landscape (Collins, 1981; Korb & Linsenmair, 1999; Korb & Linsenmair, 2001). Similar variations in both size and age within the same locality have not been documented for vegetation gaps.

The shape of FCs is most commonly near-circular, which is consistent with central-place foraging of termites resulting in circular patterns being generated around termite nests and mounds (Laurie, 2002). Self-organisation of vegetation can create a variety of shapes, including gaps, labyrinths and stripes, which primarily respond to both slope and aridity (Rietkerk *et al.*, 2002; Lejeune *et al.*, 2004; Deblauwe *et al.*, 2011). Although circular shapes are commonly generated and superficially resemble FCs, Namibian FCs do not display the characteristic transitions observed and predicted for vegetation patterning viz. transitions from bare gaps in wetter areas to mosaic or labyrinthine patterns in more arid localities and finally spots of vegetation in a bare matrix in the most arid portion of their range (von Hardenberg *et al.*, 2001). None of these transitional patterns are evident in the range of Namibian FCs regardless of rainfall or vegetative productivity (Juergens *et al.*, 2015). In addition, striped patterns running parallel to contours on gentle slopes (a consequence of surface run-off collection) (Deblauwe *et al.*, 2011) would be expected in areas where vegetation self-organisation is operational, but this is not observed in the areas where FCs occur.

7.5 Fairy Circle Ontogeny and Association with Termites

FCs are not static landscape features, and demonstrate a progression of life stages from birth through to senescence (Tschinkel, 2012; Juergens, 2013; Vlieghe *et al.*, 2015). Any theory on the formation of FCs needs to take all of these life stages into account, as they represent the initiation (new and young FCs), stable state (mature) and senescent period whereby the causal and or maintenance mechanism has disappeared (senescent FCs). For both the Sand termite and plant competition hypotheses, one would predict the causative agent to be most prominent in new FCs, and to be weak/absent in senescing FCs. For the Sand termite model this would require higher *P. allocerus* abundances on newly formed FCs compared to other stages, and for the plant competition model (Getzin *et al.* 2014) the presence of competitively superior perennial grasses (or pre-existing FCs) in order to create water deficit areas. The progression of FC life stages has been shown to correlate with the presence of *P. allocerus* and their sand sheetings, with highest termite activity in new and young FCs, declining abundances in mature FCs on which grass resources are limited, and hardly any activity on senescent FCs. Maximal recorded abundances of *P. allocerus* and their sand sheetings were on newly developed FCs suggesting an involvement in the initiation of these structures through intensive foraging on living grasses above and adjacent to their nests.. Sand termites forage on the roots and culms of living as well as dead grasses (Coaton & Sheasby, 1973; Chapter 4) and inflict the same kind of damage on living seedling roots in the laboratory and in the field. The peripheral band does not appear in new and young FCs at NamibRand (a period of approximately two years) and only becomes prominent in mature FCs. This suggests that the peripheral grasses appear secondarily in response to increased, permanent water reserves on the FC, and are not responsible for the formation of FCs through competition as hypothesized by Getzin *et al.* (2014). Alternatively plant competition would require the presence of pre-existing FCs (Cramer & Barger, 2013; Getzin *et al.*, 2014), an argument which does not explain the initiation of the original FCs within an area. The stability of vegetation patterns (Boaler & Hodge, 1964; Rietkerk & von de Koppel; 1997), under constant climatic conditions, appears inconsistent with the dynamic nature of FCs, where new FCs appear while others senesce constantly within the same area. One would expect vegetation gaps to either appear or disappear simultaneously in response to the same changes in aridity, when they occur.

7.6 Altered Soil Properties of Fairy Circles

Soil dwelling termites characteristically impact soil properties around their nests and mounds, resulting in them being considered archetypal ecosystem engineers (Jones *et al.*, 1994;

Jones *et al.*, 2006; Jouquet *et al.*, 2006). These effects typically include the accumulation of finer soil particles, increased soil porosity, changing pH, elevating nutrient levels (including N, organic C, P, K and Mg) and increasing soil water infiltration and water holding capacity. If the Sand termite hypothesis is correct, one would expect similar alterations to FC soils. In contrast vegetation gaps would not be expected to result in changes in soil particle fractions, and would predict increases in soil moisture and nutrients beneath grasses in the matrix, not within bare patches devoid of vegetation.

Termites typically increase the proportions of fine soils, particularly clay, in and around their nests by selectively bringing up fine textured soils from lower soil horizons. Elevated fine particle fractions on FCs were reported by Moll (1994) and observed here at NamibRand (Chapter 6); however Cramer & Barger, (2013) did not detect this. That higher fine particle proportions are sometimes not detected or are lower than those seen for other species of termites may be attributed to *P. allocerus* being adapted to a subterranean lifestyle specifically in sandy soils, and may not need high levels of fine particles for nest or mound construction. In addition, the relatively small colony sizes may not exert change of the magnitude seen in other termite species with huge, very long-lived colonies. Changes in soil texture have been reported in vegetation patterns, mainly attributed to erosion of soils on bare areas and aeolian deposition in vegetated areas (White, 1971; von Hardenberg *et al.*, 2001). How they differ may depend on the soil horizons of the area, and in the case of banded vegetation on slopes soil texture may differ markedly within a bare area according to a series of erosional and depositional zones (Bromley *et al.*, 1997; Valentin *et al.*, 1999). Distinguishable zones of differential deposition and erosion are not evident on FCs, nor is their orientation (long axis) related to the prevailing wind (M. Picker, pers comm.).

Termite colonies typically elevate soil nutrients (Lee & Wood, 1971; Sileshi *et al.*, 2010), however FCs soils do not differ markedly from matrix soils in terms of nutrient levels (including C, N, P and K; Cramer & Barger, 2013) and therefore do not match soil enrichment typical of termite nests. It is unclear from previous studies on FC soil nutrients whether samples were taken from new, young, mature or senescing FCs, which may have affected the concentrations of nutrients present. The Sand termite hypothesis would predict higher nutrients on new or young FCs, with decreasing amounts once the FC is bare and foraging activities move outwards expanding the peripheral band. Growth trials incorporating vacant *P. allocerus* nests into soils of potted plants increased the growth of grass seedlings in the laboratory (Chapter 4). Hence any nutrients present may be restricted to the nest itself and may not always be detectable in samples of FC soil taken from mature FCs. The absence of vegetation on mature FCs compared to the matrix may also play a role in lowering levels of nutrients

on FCs as less organic matter in the form of detritus would accumulate compared to the matrix (Becker, 2007). The plant competition hypothesis would predict lower nutrient levels on the bare disc compared to the peripheral band or matrix as vegetation clumps can act as 'islands of fertility' and accumulate nutrients when compared to unvegetated areas (Ludwig *et al.*, 1999; Ludwig *et al.*, 2005). Cramer & Barger (2013) predict that grasses growing on the bare disc would die due to increased competition from the peripheral grasses for nutrients and water. However soil transfer experiments resulted in no change in grass growth on FCs which had matrix soil and control FCs, suggesting that the slightly lower levels of nutrients on FCs has no role in grass death (Tschinkel, 2015).

Soil moisture was highest in young and new FCs (Chapter 6), and declined steadily as FCs reached maturity (although the values were still significantly higher than those in the matrix and on senescent FCs). This higher soil moisture is consistent with most cases where termite nests have been examined (Mando *et al.*, 1996; Mando, 1997; Konaté *et al.*, 1999; Jouquet *et al.*, 2002), and may help explain cooler soil temperatures on FCs compared to those of matrix soils. Termites require a constantly moist environment, and are able to engineer their nests to meet their moisture requirements by using absorbent nest materials, generating metabolic water and actively transporting water from outside their nests (Lee & Wood, 1971; Chapter 6). Although there might be transpiration by grasses on FC discs (Becker & Getzin, 2000; Juergens, 2013), it is possible that *Psammodermes* actively maintains the balance of water on FCs by transferring it from other sources (e.g. an underlying water table; Grassé & Noirot, (1948)). The reduced soil temperature of FCs may be explained by higher soil moisture levels and resultant evaporative cooling, which most likely imparts a thermal benefit on *P. allocerus*. In contrast the difference in soil water and temperature between FCs and the surrounding matrix is inconsistent with the plant competition hypothesis. In all examples of vegetative self-organisation, the combination of short range facilitation and long range competition results in an accumulation of soil moisture below vegetated patches, not the bare unvegetated areas (Bromley *et al.*, 1997; Valentin *et al.*, 1999; Barbier *et al.*, 2008; Deblauwe *et al.*, 2008). This is opposite to the trend seen in FCs. Getzin *et al.* (2014; 2015) maintain that the creation of these moist bare patches results in more efficient water storage and utilisation within the arid landscape through extended lateral root systems from the matrix and soil-water diffusion. However, Juergens (2015) and Juergens *et al.* (2015) argue that none but the grasses closest to the bare disc (i.e. the well-vegetated periphery) would be able to access the water resource within FC due to their limited root lengths and the lack of evidence that water can move those distances through capillary action alone. Detailed horizontal soil humidity measurements along a transect from the centre of the bare disc going 24 m distance in the matrix revealed that, whilst soil moisture drops from the centre of the FC to the edge of the peripheral band, moisture levels within the matrix remain fairly constant regardless of the

distance from the FC (Juergens *et al.*, 2015). This indicates that there is no gradual depletion of soil moisture from the FC into the matrix and that grasses within the matrix do not benefit from the water reservoir in the bare patch.

Although not investigated in this thesis, multiple papers have speculated on the presence of a volatile gas within the soil which may affect plant growth. Naudé *et al.* (2011) identified hydrocarbons (specifically alkanes) which they believed were produced by geochemical gas seeps, which displaced soil moisture and produced anaerobic conditions due to increased microbial activity, causing plant death. However Picker *et al.* (2012) indicate that alkenes are components of ant cuticles, and that these may have been detected in the FC soils which commonly support very large colonies of *Anoplolepis steingroeveri*. Juergens (2015) also argued that higher alkene levels may be explained by anaerobic bacteria associated with the termites' intestinal tract. In addition to this, most termites produce CH₄ and CO, and some naphthalene (Zimmerman *et al.*, 1982; MacDonald *et al.*, 1998; Šobotník *et al.*, 2010), all of which are capable of inhibiting germination and seedling growth (Strangmann *et al.*, 2008; Fortune *et al.*, 2009) (Chapter 3). This presence of hydrocarbons, naphthalene, CH₄ or CO produced by termite colonies beneath FCs may explain the transferable negative effect of FC soils on grass growth noted by some (Albrecht *et al.*, 2001; van Rooyen *et al.*, 2004; Jankowitz *et al.*, 2008), however this effect is not always observed (Tschinkel, 2015). Vegetative patterning theory does not necessitate the presence of a plant inhibiting volatile gas below bare areas.

7.7 Ecosystem Engineered Effects on Plants and Animals

For both termite nests and vegetation patterning, plant productivity increases in relation to elevated levels of resources such as water and nutrients. In the case of termite mounds, this is due to the ecosystem engineering impacts of the mounds, while vegetation patterning is a consequence of facilitative feedbacks around more vegetated areas resulting in islands of fertility. Thicket formation (Bloesch, 2008) and unique plant communities on *Microhodotermes* colonies (heuweltjies) (Moore & Picker, 1991) are both examples of vegetation changes related to termite altered soils (Arshad, 1982; Konaté *et al.*, 1999; Moe *et al.*, 2009; Fox-Dobbs *et al.*, 2010). With subterranean species the generation of a bare area around the nest is less common, but does occur. One example are the arena nests of *Odontotermes fulleri* in Kenya, which maintain a bare disc in the similar way to epigeal mounds by creating a compacted soils which impedes the penetration of plant roots (Darlington, 2007). These arena nests also support a ring of luxuriant grass growth along their edge

(Darlington, 2007), analogous to the conspicuous peripheral band present on some FCs (Becker, 2007; Picker *et al.*, 2012).

A plant competition model would favour plant growth away from the bare patch. Vegetation stripes related to vegetative self-organisation found on gentle slopes can show zones of higher or degraded vegetation within the band (Thiéry *et al.*, 1995), however gapped vegetation, which resemble FCs most closely, are not reported to have a peripheral band. Under the key assumption of vegetation self-organisation through long-range competition and short range facilitation, vegetated areas should develop higher levels of resources such as water ('islands of fertility') (Couteron & Lejeune, 2001; Lejeune *et al.*, 2004; Barbier *et al.*, 2008) and hence would not be expected to form a peripheral band on their periphery – in an area where facilitation breaks down and competitive feedbacks become greater. Cramer & Barger (2013) have modified the conventional vegetation self-organisation model in relation to FC formation, where the peripheral band itself outcompetes areas in the matrix, generating new bare patches. The plant competition model also fails to explain why the grasses along the peripheral band (which can consist of either the matrix grass or different grass species) are able to benefit from the water supply on FCs but are still unable to colonise the bare disc despite seemingly ideal growing conditions (including lower soil temperatures). It would appear that some mechanism, other than a lack of resources is actively preventing grass recruitment on the bare disc.

Soil engineering by termites increases plant diversity through the creation of heterogeneous vegetation patches around their nests (Dangerfield *et al.*, 1998; McCarthy *et al.*, 1998), which in turn affects the distributions and diversity of associated fauna (Moore & Picker, 1991; Fleming & Loveridge, 2003). Similar influences appear to be operational for FCs, which can cover between 0.8 % and 55.7 % of the land surface area (Juergens, 2013), and increase the diversity of flora and fauna both within an area as a whole compared to neighbouring areas lacking FCs (Juergens, 2013), and between microhabitats (i.e. the peripheral band, bare disc and surrounding matrix). The overdispersed patterning of FCs over large areas may further promote the overall biodiversity and productivity of the arid semi-desert landscape. Pringle *et al.* (2010) found that areas supporting evenly-spaced mounds of *Macrotermes* in Kenya had greater abundance, biomass and reproductive output of consumers compared to areas supporting randomly spaced mounds. Although not much research has been done on the specific effects of semi-arid vegetation patterns on diversity, it is believed that this form of plant spatial organisation allows the spread of vegetation into more arid areas and increases the resistance of an area to desertification (Ludwig *et al.*, 1999;

Rietkerk *et al.*, 2002). Hence the oases of resources (most critically water), produced by overdispersed FCs may have similar positive effects on diversity.

7.8 Fairy Circle Age and Recruitment

FCs are long-lived features, persisting for at least 30 – 40 years (Tschinkel, 2012; Chapter 5), and potentially even hundreds of years (Juergens, 2013). Similarly termite mounds remain for decades if not hundreds or thousands of years, with the mounds maintaining their structure and influence on the surrounding soils and plant communities long after their termite residents have left (Watson, 1967; Moore & Picker, 1991). Like termite mounds, FCs may represent a form of allogenic legacy (Jones *et al.*, 2010). Even when a mature FC has been cleared of grasses on the bare disc and *P. allocerus* focusses its forging efforts on the peripheral band or matrix, the bare disc of the FC is likely maintained through a number of factors including a reduced seed bank (39 times less than the matrix), seedling excavation by *A. steingroeveri* ants, and some ongoing herbivory by *P. allocerus* on the bare disc. The effectiveness of these maintenance mechanisms may fail in wetter years, as FC survival was found to decrease following heavy rainfall (Chapter 5). This may be related to an increased likelihood of seeds recruiting on FCs due to greater overall plant productivity, or the heavy rains overwhelming existing maintenance mechanisms. In terms of the response of FC recruitment to rainfall, Juergens *et al.* (2015) found that more FCs appeared after wetter years. This finding supports the termite model, where increased rainfall and hence increase plant productivity would be expected to result in expansion of social insect colonies and thus recruit more FCs. If the opposite were true and recruitment increased with a decrease in rainfall, this would provide support for the plant competition hypothesis. However data from this thesis could not provide clear insight into recruitment responses to rainfall as recruitment varied unpredictable in relation to rainfall.

7.9 Conclusion

Both the termite and vegetation self-organisation models for FC formation have strengths that support them, but also weaknesses. In the case of the latter, there is a shortage of empirical and field-based ecological data to support the assumptions of the model, and the overdispersed patterns generated by mathematical modelling cannot alone be used as support, as similar patterns can be demonstrated for a range of biological features, including social insect nests. Ground-truthing mechanisms underlying the competitive interactions of the vegetation models is essential in the

validation of the model, and this would include examining soil water movement in relation to root length, and incorporation of the ontogenetic stages of FC development into ecological and modelling work. The termite model, while providing evidence for a close spatial relationships between *P. allocerus* and FC formation, would be strengthened by long-term observational data on colony development, interactions between termites colonies on different FCs, study of *P. allocerus* in other parts of its range where FCs do not exist, the extent and layout of their subterranean nests, and the mechanism by which high moisture is maintained on FCs even in the long dry winter and early summer. There currently appears to be little common ground between the two models – suggesting that one of the proposed mechanisms for FC formation and maintenance might be subordinate to the other. This is only likely to be resolved after more intensive, long-term ecological investigations. These should not be taken as reasons for rejecting the Sand termite hypothesis, but rather as gaps in our knowledge of this cryptic species and its biology.

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APPENDIX 1

List of models used and goodness of fit indicators for Giribes FC survival, NamibRand Fc recruitment and survival for the period 1977-2013, and NamibRand FC recruitment and survival for the period 2010-2013 (model used to in analysis indicated in red). Higher AICc weight and model likelihood indicate higher model goodness of fit, while higher AICc, Delta AICc and deviance indicate lower goodness of fit.

	AICc	Delta AICc	AICc Weight	Model Likelihood	No. Par	Deviance
Giribes FC survival						
$\varphi(t)p(\cdot)$	509.7106	0	0.95491	1	5	0.0007
$\varphi(t)p(t)$	515.8166	6.106	0.04509	0.0472	8	0.0007
$\varphi(\cdot)p(\cdot)$	585.2552	75.5446	0	0	2	81.6057
$\varphi(\cdot)p(t)$	588.1168	78.4062	0	0	5	78.407
NamibRand FC recruitment & survival						
$\varphi(t)p(\cdot)f(t)$	942.0952	0	0.98107	1	11	7.0872
$\varphi(t)p(t)f(t)$	950.2801	8.1849	0.01638	0.0167	15	7.0872
$\varphi(t)p(\cdot)f(\cdot)$	954.7972	12.702	0.00171	0.0017	7	27.9186
$\varphi(t)p(t)f(\cdot)$	956.2343	14.1391	0.00083	0.0008	12	19.1853
$\varphi(\cdot)p(\cdot)f(t)$	967.7331	25.6379	0	0	7	40.8546
$\varphi(\cdot)p(t)f(t)$	975.8626	33.7674	0	0	11	40.8546
$\varphi(\cdot)p(\cdot)f(\cdot)$	978.5666	36.4714	0	0	3	59.7627
$\varphi(\cdot)p(t)f(\cdot)$	981.5229	39.4277	0	0	8	52.6172
NamibRand FC recruitment & survival with rainfall						
$\varphi(t)p(\cdot)f(t) R^*T$	252.067	0	0.29319	1	6	6.895
$\varphi(t)p(\cdot)f(t) T$ only	258.164	6.097	0.01391	0.0474	9	6.895
$\varphi(t)p(\cdot)f(t) R$ only	267.2501	15.1831	0.00015	0.0005	4	26.1222

φ (Phi) = apparent survival parameter

p = encounter parameter

f = recruitment parameter

(t) = parameter is time dependent

(.) = parameter is constant over time

R = rainfall covariate

T = time covariate

APPENDIX 2

Total abundances of ant species in 2011 and 2012 and scarab species in 2011 on the FC bare disc, peripheral band and in the matrix.

	Bare disc	Peripheral band	Matrix
Formicidae (Jan 2012)			
<i>Anoplolepis steingroeveri</i>	3411	5437.5	6093.5
<i>Camponotus</i> sp. 1	39	30	21
<i>Camponotus</i> sp. 2	58	101	18
Formicinae sp.	114	291	31
<i>Monomorium</i> sp. 1	2377	9315	8302
<i>Monomorium</i> sp. 2	559	1901	2492
<i>Monomorium</i> sp. 3	46	78	137
<i>Monomorium</i> sp. 4	2	37	4
<i>Monomorium</i> sp. 5	21	115	98
<i>Ocymyrmex</i> sp.	160	127	67
<i>Pheidole</i> sp.	73	39	55
<i>Tetramorium</i> sp. 1	1147	1077	632
<i>Tetramorium</i> sp. 2	626	736	305
<i>Tetramorium</i> sp. 3	95	183	111
<i>Tetramorium</i> sp. 8	33	429	1
Formicidae (Feb 2011)			
<i>Anoplolepis steingroeveri</i>	4768	4102	1255
<i>Camponotus</i> sp. 1	9	18	12
<i>Camponotus</i> sp. 2	58	126	61
<i>Camponotus</i> sp. 3	21	20	13
Formicinae sp.	441	293	74
<i>Messor</i> sp.	1	3	8
<i>Monomorium</i> sp. 1	621	840	1142
<i>Monomorium</i> sp. 2	388	879	816
<i>Monomorium</i> sp. 3	267	389	632
<i>Monomorium</i> sp. 4	43	53	94
<i>Ocymyrmex</i> sp.	108	113	70
<i>Pheidole</i> sp.	30	75	27
<i>Tetramorium</i> sp. 1	994	1549	1713
<i>Tetramorium</i> sp. 2	289	319	158
<i>Tetramorium</i> sp. 3	668	796	454
<i>Tetramorium</i> sp. 4	7	2	13
<i>Tetramorium</i> sp. 5	6	6	4
<i>Tetramorium</i> sp. 6	5	8	0
<i>Tetramorium</i> sp. 7	5	8	4
<i>Tetramorium</i> sp. 8	0	0	37

Scarabaeidae (Feb 2011)			
Scarabaeidae sp. 1	222	89	70
Scarabaeidae sp. 2	23	6	9
Scarabaeidae sp. 3	77	63	132
Scarabaeidae sp. 4	13	22	19
Scarabaeidae sp. 5	16	12	13
