

The fairy circles (circular barren patches) of the Namib Desert - What do we know about their cause 50 years after their first description?

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Highlights

- Since the first description of the fairy circles 50 years ago, the cause is still hotly debated.
- The first review paper in nearly 20 years on the fairy circles of the Namib Desert.
- The contrasting main theories on the formation and maintenance of fairy circles are discussed.
- The physical characteristics of fairy circles are described and critically reviewed.

Abstract

Since they were described for the first time 50 years ago, more than 30 peer-reviewed papers have been published on a number of extremely diverse theories as the cause of the formation of hundreds of thousands of nearly circular barren patches (fairy circles) found in southwestern Angola, Namibia and northwestern South Africa. However, scientists interested in finding an explanation for the cause and maintenance of these fairy circles in the driest parts of the world are still without agreement on the true reason(s) behind this intriguing phenomenon. In this review we firstly present the four main theories and explain their hypotheses on the formation and/or maintenance of fairy circles. Secondly, we summarise the previously described physical characteristics of the fairy circles, e.g. soil substrate, moisture content, shape, size, lifespan, dynamics and spatial patterning, and then present the supporting evidence as published by the proponents of the theories on vegetation self-arrangement, insects/ants, gas and *Euphorbia* allelopathy, as the causative drivers of this natural phenomenon. We also present the critical views of scientists on the theories they are not supporting.

Keywords

Fairy circles
Namib desert
Barren circular patches
plant-plant interactions
Plant-soil interactions
Allelopathy

1. Introduction

Fairy circles are probably amongst the most intriguing unexplained natural phenomena of the world. The origin and maintenance of fairy circles are still debated and without consensus amongst role players, making it a controversial topic. Contrasting theories have been put forward by scientists from all over the world over the last 50 years to explain the fairy circle phenomenon since they were mentioned for the first time in scientific literature by Tinley (1971). However, this might not be the actual first account of fairy circles, because unexplained circles were engraved in sandstone rock (as well as animals and other objects, Fig. 1) during the Stone Age by Bergdama cultures (Viereck and Rudner, 1957). These petroglyphs at Twyfelfontein, also called Ui-Ais (Namibia), are located about 200 m from many fairy circles. Even with this interest and more than 30 peer-reviewed papers published on research directly linked to the fairy circles, no theory is generally accepted or proven. Four main theories have been proposed to explain fairy circle formation and maintenance, these are (in no particular order): the social insects (ant/termites) theory, the vegetation self-arrangement theory, the gas theory and the *Euphorbia* species allelopathy theory. An overview of the publications of the most important studies on the cause (and occasionally the maintenance) of fairy circles, are shown in Table 1.

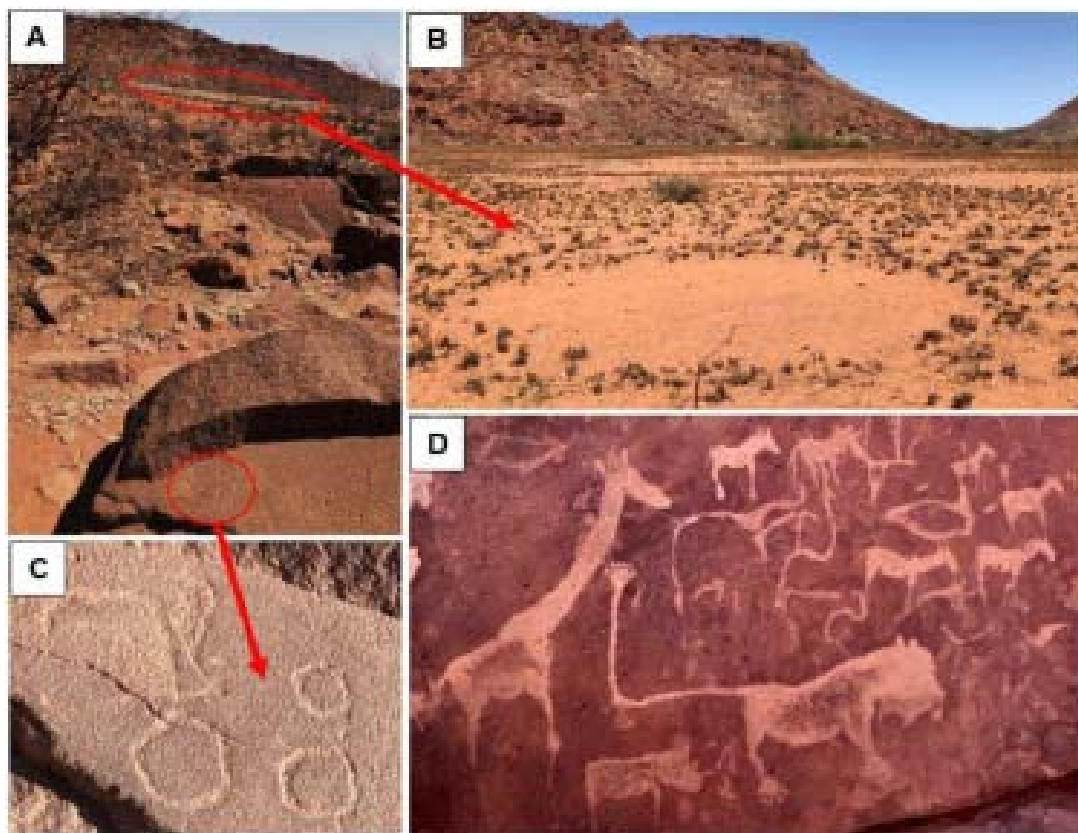


Fig. 1. Unexplained engraved circles in petroglyphs created during the Stone Age by Bergdama cultures at Twyfelfontein, Namibia (Viereck and Rudner, 1957). (A) Engraved circles (bottom red oval) and an area about 200 m away with fairy circles and *Euphorbia damarana* in the background (red oval above). (B) and (C) Enlarged areas of ovals shown in (A). (D) An example of some of the other engravings in rocks.

Table 1. Overview of fairy circle publications of research on the major theories. Not all published papers were incorporated into the table.

Date of publication	Main author (theory)	Social insects	Veg. self-arrangem	Gas	<i>Euphorbia</i> allelopathy
1971	Tinley				
1979	Theron				
1994	Moll				
2000	Becker & Getzin				
2001	Albrecht et al.				
2004	Van Rooyen et al. (review)				
2011	Naudé et al.				
2012	Tschinkel				
2012	Picker et al.				
2013	Juergens				
2013	Cramer & Barger				
2014	Getzin et al.				
2015	Getzin et al.				
2015	Juergens et al.				
2015	Meyer et al.				
2015	Tschinkel				
2015	Vlieghe et al.				
2016	Cramer et al.				
2016	Getzin et al.				
2017	Tarnita et al.				
2017	Ravi et al.				
2019	Getzin & Yizhaq				
2020	Getzin et al.				
2020	Meyer et al.				

Previous research has indicated that the fairy circle phenomenon is confined to a narrow strip, about 50–100 km inland from the Atlantic Ocean (Fig. 2A), which stretches down from southwestern Angola, through Namibia to northwestern South Africa (Van Rooyen et al., 2004; Cramer and Barger, 2013; Juergens, 2013; Cramer et al., 2016, Ravi et al., 2017 and others). Meyer et al. (2020), however, recently reported the occurrence of thousands of fairy circles in southeastern Namibia and the Kalahari Desert, stretching into South Africa, about 400 km east of the coastline. These authors created a GIS model to predict where fairy circles should occur based on rainfall (50–150 mean annual precipitation (MAP)), altitude (500–1200 metre above mean sea level (mamsl)) and a landcover of grassland on sandy soil. In the validation of the model, a number of new fairy circle localities were found (Fig. 2B).

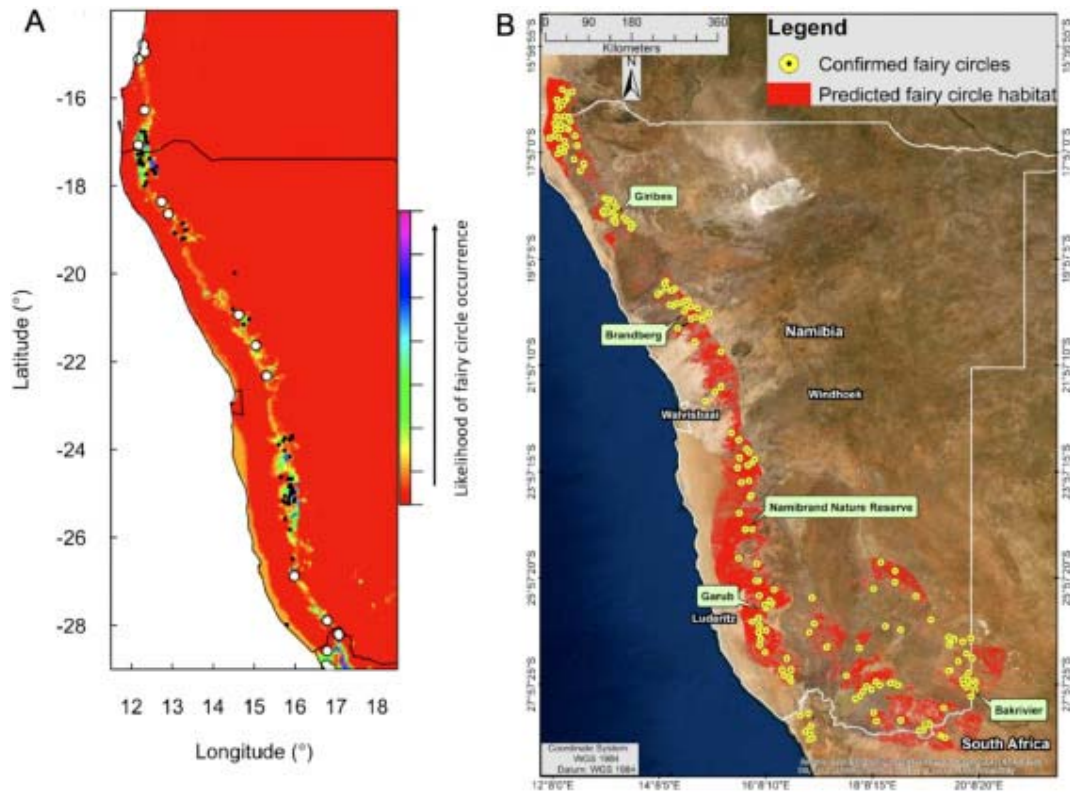


Fig. 2. Maps of confirmed and predicted occurrence of fairy circles. (A) Black dots indicate confirmed sites with fairy circles used in the model development, and open symbols the sites where additional fairy circles were discovered (Cramer and Barger, 2013). (B) Yellow dots indicate confirmed fairy circle locations and red areas are areas predicted to have fairy circles; new locations in southeastern Namibia and the Kalahari Desert are also shown (Meyer et al., 2020).

Cramer and Barger (2013) stated that fairy circle occurrence is not linearly related to MAP and their landscape occupancy can be low in both extremely arid and more mesic areas. They also reported that fairy circle presence/absence is highly predictable by using an empirical model that included narrow ranges of vegetation biomass, precipitation and temperature seasonality as predictor variables, indicating that fairy circles are most likely a climate-dependent emergent phenomenon (Fig. 2A).

Nearly circular barren patches have also been found to occur in western Australia (Getzin et al., 2016; Getzin et al., 2020), but this has not widely been acknowledged as typical fairy circles. Although somewhat similar, the African and Australian fairy circles differ in a number of aspects (Cramer et al., 2016). The Australian ones occur in a much wetter area of 327 mm MAP and on clay-rich soils, whereas the African ones are always found on sandy soils with a MAP of about 100 mm (Becker and Getzin, 2000; Juergens, 2013; Cramer et al., 2016, Meyer et al., 2020).

The only previous review on the properties and theories on the formation of fairy circles was published by Van Rooyen et al. (2004). The current review summarises the existing knowledge regarding the physical properties of fairy circles and also discusses new developments on old and new theories on the origin and maintenance of fairy circles since the Van Rooyen et al. (2004) review. The current review firstly provides a short summary on the

four main theories and then discusses how these rationalise each of the important physical characteristics of the fairy circles.

2. The main theories on the cause and maintenance of fairy circles

2.1. Social insects theory

Tinley (1971) presented a photograph of Marienfluss showing the circular barren patches and described them only in the figure caption, not in the rest of the document. He speculated in the caption that they are probably the weathered remains of fossilised termite nests, without providing any research results. More than 20 years passed without any research reports on ants or termites as the cause of fairy circles, until Moll (1994) published his results on termites as the causative agent behind the formation of fairy circles. Moll was the first author to officially use the term 'fairy ring' which later became known as a 'fairy circle' (Becker and Getzin, 2000). Moll's (1994) hypothesis was formulated on the basis of the physical and chemical cues he observed. This included the foraging behaviour of the termites near their termitaries that he linked to the lack of vegetation from fairy circles. After studying aerial photographs of areas where fairy circles occurred, he noted that not all circles were equally devoid of vegetation.

Moll (1994) concluded that fairy circles were sporadically appearing and disappearing as a result of the lifespan of termite nests which were in turn dependent on seasonal rainfall. Thus, during times of flourishing grass cover termites feed adjacently to their nests leading to circle formation. Also, after comparing termite distribution with the occurrence of fairy circles, he concluded that the termites *Hodotermes mossambicus* and *Psammotermes allocerus* were most likely the causative agents of fairy circles. He also mentioned that fairy circles mainly occur on substrates of a sandy nature.

Van Rooyen et al. (2004), however, reported that fairy circles are limited to a small portion of the distribution range of *H. mossambicus*, with no similar phenomenon found in the rest of the termite's range. Furthermore, according to Coaton et al. (1958) the habitat of *H. mossambicus* does not extend into sand dunes, whereas Van Rooyen et al. (2004) reported that fairy circles do occur on dune slopes and interdune spaces in the central to southern parts of Namibia. These researchers also dug trenches through well-developed fairy circles during 2000 and 2001 and found no evidence of termite tunnels. Although termites were observed aboveground, their activities were not associated with fairy circles. Based on field observations, Grube (2002) concluded that termites did not necessarily forage in circular patterns and that their feeding only resulted in clearly visible barren patches when foraging occurred in areas sparsely covered with grass. Mitchell et al. (1993) did a study on the temperature sensitivity of the *H. mossambicus* termite to determine its critical thermal maximum (CTmax) and critical thermal minimum (CTmin). Their observations indicated that for most worker termites the CTmax was between 43.5 °C to 48.53 °C. Field observations recorded by Grube (2002) supported this, as they found termites foraging during peak summer at temperatures higher than 44°C, which contradicts Becker and Getzin's (2000) observation that *H. mossambicus* has limited surface activity at temperatures at and above 40 °C. Various different factors can possibly affect the termite's temperature sensitivity. Mitchell et al. (1993) concluded that biological factors such as size, age and maturity of termites, as well as thermal history and certain environmental conditions affect termite foraging, thus making any assumptions regarding a link between temperature sensitivity and fairy circle size speculative.

A number of other studies that investigated both termites and ants as causal agents in fairy circle formation were subsequently published by Albrecht et al. (2001), Picker et al. (2012), and Juergens (2013). The mechanisms through which these social insects create fairy circles can be divided into direct and indirect processes. In a direct process, insects harvesting seeds and/or seedlings from inside fairy circles are thought to directly contribute to fairy circle formation (Moll, 1994; Juergens, 2013). In an indirect process active termite nests could produce inhibitory substances that could in turn have detrimental effects on vegetation and contribute to fairy circle formation (Albrecht et al., 2001).

Albrecht et al. (2001) hypothesised that a semi-volatile chemical substance is produced inside termite nests which inhibits the growth of vegetation in fairy circles by decreasing resistance to dehydration. These researchers were the first to use aerial photography to analyse the spatial pattern produced by fairy circles located in the Wolwedans area of the Namibrand Nature Reserve. They found a similar regular spatial distribution pattern for fairy circles and termites and suggested that this pointed towards an association between fairy circles and termites. They were, however, not yet able to demonstrate the presence of the semi-volatile substance in fairy circle soil.

Picker et al. (2012) found no evidence to support the hypothesis of a termite origin for fairy circles. They found a virtual absence of termites at the Namibrand Nature Reserve. The lack of association between fairy circles and *H. mossambicus* activity, as well as the very low densities of this termite in areas where fairy circles occur, they noted as empirical proof that termite foraging was not involved in the formation of fairy circles. Additionally, they stated that the establishment of annual grasses would soon cover the bare surface of fairy circles in the absence of a permanent association of termites with each circle; however, the majority of 'active' circles remain largely grass-free over time.

Picker et al. (2012) then implicated ants as causal agents. They observed 10 times more *Anoplolepis steingroeveri* ants in fairy circles than in the matrix grasses at their study site in the Namibrand Nature Reserve. According to Picker and colleagues (2012), fairy circles and North American *Pogonomyrmex* ant nests are both over-dispersed and associated with elevated soil moisture. They also observed a bare disc surrounding the nests.

Juergens (2013) examined species distribution maps and found only the sand termite, *Psammotermes allocerus* at all fairy circle hotspots (e.g. Giribes Plain and Namibrand Nature Reserve). However, Getzin et al. (2015) noted that fairy circles are limited to a small portion of the range of *P. allocerus*, with no similar phenomenon found in the rest of the termite's distribution, which occurs over the entire rainfall gradient from 30 mm to more than 600 mm MAP. Other species such as *H. mossambicus* is largely restricted to the summer-rainfall climate and *Microhodotermes viator* to the winter-rainfall climate (Juergens, 2013). Another species, *Baicaliitermes hainesi*, also only occurs south of the southern central Namib. Juergens (2013) found three ant species: *Messor denticornis*, *Anoplolepis steingroeveri* and *Tetramorium* species, at several fairy circle locations in his study area, but none of them in all. However, he found high frequencies of the characteristic 'sheetings' (thin layers of cemented sand built over the foraged plant material) of *P. allocerus* at 80 to 100% of his study sites in western Namibia. Moreover, *P. allocerus* nests and underground tunnel-like galleries with a characteristic black organic wall covering (tapetum) were found a few centimetres to decimetres underneath the bare patches, the perennial belt (PB), and the matrix area. The frequency of these observations was halved during the wet season. Although these associations suggest a causal role for *P. allocerus* and fairy circle formation, it is possible that

they may instead merely reflect the colonisation of fairy circles by the termites (Schutte, 2019). Tschinkel (2012) argued that if termites are the cause of fairy circles, then the hypothesis should be able to account for all the important properties of fairy circles – their circularity, their over-dispersion, the proportion of bare surface and their changing diameter in different soils and latitudes.

Getzin et al. (2014) used point pattern analysis to characterise the spatial distribution of fairy circles and developed a mathematical model that could generate the same pattern (discussed below in Section 2.2). A key question of their study was to examine how behavioural processes of social insects such as foraging, nest building, nest movement, and intra-specific competition can generate the intriguing regular spatial patterns characteristic of fairy circles. These researchers identified several characteristics of fairy circle patterns in the Giribes Plain and Namibrand Nature Reserve, including the fact that they are nearly always situated at a distance of 13 m apart in these two areas, and that there is no larger scale aggregation in the pattern. Even though Picker et al. (2012) and Juergens (2013) had convincingly shown strong associations between fairy circles and the presence of ants and/or termites, they did not provide an explanation for the observed lack of any larger-scale clustering at distances less than 60 m (Getzin et al., 2014).

In response, Juergens (2015) used point pattern analysis to highlight the fact that termite colonies of *Macrotermes* spp. and *Pogonomyrmex* spp. can produce regular spatial patterns similar to fairy circles. In a subsequent paper, Getzin et al. (2015) stated that the regularity of fairy circles is not congruent with the only two insect examples provided by Juergens et al. (2015). They also noted that neither the pair correlation function $g(r)$ of *Macrotermes*, nor that of *Pogonomyrmex*, shows a first clear peak with high amplitude which is pronounced and substantially outside the simulation envelopes of the null model. This means that the pattern associated with the two species, although also regular, are less ordered than the pattern of fairy circles. Similar to Juergens (2015), Tarnita et al. (2017) showed that intraspecific competition between termite colonies can generate the large-scale hexagonal patterns found in fairy circles. They also proposed that a combination of the self-organising spatial vegetation (Getzin et al. 2014) and social insects theories explains the fairy circle phenomenon the best (Tarnita et al., 2017).

Moll (1994) previously suggested that the lack of vegetation in fairy circles was the result of termites, specifically the species *H. mossambicus*, having eaten all the grass seeds in the immediate vicinity of their nests. However, Van Rooyen et al. (2004) observed many small seedlings in fairy circles after good rainfall, indicating that the deficiency of seeds could not be the primary cause for fairy circle formation. These researchers also suggested that fairy circles remain bare because seedlings do not survive when the rains have ended. They also stated that termites do not eat plants completely, i.e. they usually eat the leaves, while the tuft or the roots are left behind, but no remnants of any grass parts were to be found in fairy circles. In most cases where plant material was found in the fairy circles, it consisted of the entire dried remains, mostly of seedlings or immature plants (Van Rooyen et al., 2004).

Meyer et al. (2015; 2020) reported the absence of termites and ants associated with fairy circles in studies conducted in Garub, Brandberg, as well as Giribes Plain. Van Rooyen et al. (2004) found no termites inside trenches dug in fairy circles at Giribes Plain, Hartmann's Valley and Marienfluss, and Ravi et al. (2017) reported the absence of sand termites and evidence of root damage from previous termite activity was also not observed in Namibrand Nature Reserve. Theron (1979) also reported that no termite activity was found

inside fairy circles at the Giribes Plain and Marienfluss. Getzin et al. (2016; 2020) reported the absence of termites inside the barren patches of Western Australia.

2.2. Self-organising spatial vegetation patterning theory

Albrecht et al. (2001) were the first authors to determine the distance to nearest neighbour of fairy circles and found that they were arranged in a regular pattern (R-ratio 1.68 in Namibrand Nature Reserve). However, they postulated that the regular pattern was caused by termites and not by vegetation self-arrangement.

Several other researchers have suggested that fairy circles are an example of an emergent vegetation spatial pattern that arises from soil hydraulics and nutritional characteristics which could enable relatively long-range (several metres) resource transport within the soil (Cramer and Barger, 2013; Getzin et al., 2014; Getzin et al., 2020; Tschinkel, 2015; Cramer et al., 2016; Ravi et al., 2017; Getzin and Yizhaq, 2019). This pattern of vegetation self-arrangement is based on the principals of pattern formation and suggests that in an area as arid as the Namib Desert, competition between the root systems of neighbouring grass tufts is so intense that it causes the grass to die back in the observed regular pattern. Getzin et al. (2014) proposed that fairy circles and their pattern are caused by an interaction among plants, while Cramer et al. (2016) showed that the arrangement of fairy circles is linked to characteristics of the soil that enable grasses to competitively interact with each other for water and nutrients over distances exceeding the radius of the root zone (which is typically 1 m). Getzin et al. (2014) provided evidence that the competition is limited to distances of 13 m and shows a 'strongly hexagonal grid-like pattern', close to the ideal pattern of hexagonal honeycombs.

Cramer et al. (2016) hypothesised that the coarse-textured sand on which fairy circles occur creates a hydraulically and nutritionally connected landscape in which neighbouring fairy circles competitively influence each other over several metres. To test if resources could be transported in the soil, Cramer et al. (2016) conducted water and ¹⁵N-nitrogen pulse experiments and showed that edaphic resources were highly mobile, moving up to 7.5 m over a period of 1–3 weeks.

It has been shown that fairy circle size is positively correlated with soil infiltration rates and negatively with precipitation (Cramer et al. 2016), which suggests that higher soil infiltration rates and lower rainfall will result in larger fairy circles. However, as precipitation increases from the west to the east, and fairy circles in the north and south receive a very similar amount of rainfall, why have fairy circles been documented to decrease in size from the north to the south, and not from west to east (Schutte, 2019)?

Getzin et al. (2014) stated that fairy circles are caused by resource depletion, i.e. dehydration. The vegetation self-arrangement theory predicts that new fairy circles develop as a result of competition for water during periods of water shortages. Juergens et al. (2015), however, found no evidence of an increased appearance of fairy circles after years of below average rainfall. They also stated that since the fairy circles are permanent water resources they should be filled with plants and the soil underneath should be a dense network of roots.

Another critique of the vegetation self-arrangement theory relates to the nearest neighbour distances, which results from competition for resources as mentioned above. Juergens (2015) noted that interaction among neighbouring plants can control their size and distance away

from each other. However, Getzin et al. (2014) postulated interaction at a much larger scale; the average distance between two neighbouring grass individuals in the matrix grassland is in the range of 10 cm. When compared to the diameters of fairy circles and interspaces of up to 30 m, this would be equivalent to 300 individual distance units, therefore, it's implicated that the interaction among grass individuals are able to create a bare patch 300 times larger than the distance between neighbouring individuals (Schutte, 2019). Juergens (2015) stated that the matrix is uniformly dry while the maximum amount of water is found in the centre of the bare patch and that it needs to be explained why competition could result in the formation of a fairy circle in exactly that location that stores more water than found anywhere else in a desert habitat.

A recent investigation by Tarnita et al. (2017) integrated the social insect and vegetation self-arrangement theories, stating that the processes behind them are operating together to produce the regular patterns characteristic of fairy circles. These researchers applied mathematical modelling to fairy circle patterning by parameterising the united model and found that it was possible to characterise the vegetation patterns of fairy circles more accurately than the social insects or self-arrangement theories could explain on their own. According to Tarnita et al. (2017) colonies of insects build central nests and forage outwards to acquire resources to fuel colony-population growth and survival. While foraging, the termites harvest the grass surrounding the nests and in doing so they create fairy circles. Mature (established) colonies produce reproductive future queens/kings that disperse randomly throughout their simulated landscapes and attempt to initiate new colonies. Once a new colony is established, the termites create a new fairy circle by harvesting the grass surrounding the nest. Resource availability is constant and uniformly distributed. When the expanding foraging areas (fairy circles) of neighbouring colonies overlap, conflicts ensue via territorial aggression, as is common in many social-insect species. Conflict outcomes depend on relative colony size with larger colonies more likely to eliminate smaller ones, but similar-sized colonies co-exist, whereupon a shared boundary emerges. It is commonly known that two fairy circles can in some instances occur right next to one another, with their boundaries connected. Although this system is intrinsically dynamic owing to continual births and deaths of colonies, the quantities of interest eventually reach a stationarity point (fluctuating around a well-defined constant average).

2.3. The gas theory

Jankowitz et al. (2008) and Naude et al. (2011) found that gas micro-seepage (particularly hydrocarbon micro-seepage) is present inside fairy circles. Naude et al. (2011) measured the carbon monoxide (CO) and oxygen (O₂) concentrations inside five fairy circles and two matrix sites over three days at specific times. The highest O₂ percentage drop was recorded twice in two fairy circles from 20.9 to 20.7%. The highest percentage of CO recorded on one occasion in one of the five circles was 0.007%. Lower percentages were recorded on three occasions in three of the five circles. The O₂ concentration stayed constant at 20.9% in the matrix and no CO was detected. This is postulated by the authors to disturb the soil micro-environment and result in oxygen depletion that impedes plant growth. Naude et al. (2011) also analysed emissions in two circular patches of dead or yellowed vegetation, thought to be newly emerging fairy circles. In these circles with dead vegetation the highest drop in O₂ was recorded on one occasion to be 0.3% and the CO concentration rose once to 0.028%.

Critics of this hypothesis argued that although hydrocarbon micro-seepage is known to result in plant death, this process occurs heterogeneously at the landscape scale and not with the

regular and homogeneous pattern observed for fairy circles (Getzin et al. 2014). Although the gas theory was published in 2011, no results on bioassays have been published to verify that such small changes in O₂ and CO concentrations will result in grass seedling death.

2.4. The *Euphorbia* allelopathy theory

The *Euphorbia* allelopathy theory was the first one published on the cause of fairy circles with data from supporting field and laboratory experiments. The theory was initially proposed by Theron (1979) who found a population of *E. damarana* plants co-occurring with fairy circles at Giribes Plain, about 5 km south of Leopard Rock. *E. damarana* contains a sticky white latex and is commonly known to be highly poisonous (Meyer et al., 2020). Theron (1979) noted that a high percentage of the *E. damarana* plants were dying.

Theron (1979) found a good correlation in diameter of the nearly circular *E. damarana* plants and the fairy circles on the Giribes Plain, and also noted that the fairy circles are elliptical in shape on slopes with the long axes being parallel to the drainage lines. The sizes of these fairy circles were measured and found to be bigger than that of *E. damarana* plants. Theron (1979) showed in preliminary laboratory experiments that this euphorbia contained plant growth-inhibiting compounds and hypothesised that they accumulated an organic or inorganic compound/element from deep below the soil surface and released this in high quantities when the plant died, resulting in an allelopathic effect that inhibited the growth of grass inside the circle area where the plant once occurred. He also reported the emergence of small grass seedlings inside fairy circles after good rainfall and noticed that they died before reaching maturation.

Meyer et al. (2015; 2020) observed that fairy circles and *E. damarana*, *E. gregaria* and *E. gummifera* do not only co-occur in southern parts of the Giribes Plain, but also in several other places near Kolmanskop, Aus, Garub, Namibrand Nature Reserve, several locations near Uis (Brandberg), Twyfelfontein, and in the southwest of Namibia (e.g. near Huns, south of Keetmanshoop) and also in the Kalahari Desert of South Africa. The researchers noted that all these co-occurrences are on sandy soils (Fig. 3) and that large numbers of these plants were in the process of dying, similarly to those on the Giribes Plain that Theron (1979) reported.

Meyer et al. (2015) chemically analysed fairy circle soil at Garub (near Aus) and found evidence that euphol, a characteristic triterpenoid from the *Euphorbia* genus (not previously found in grass species), was present in soil from inside fairy circles and not in the matrix soil. They also found from GC-MS analyses that soil from fairy circles and from under decomposing *E. damarana* plants on Giribes Plain are very similar in phytochemistry (Meyer et al., 2020). They proposed that the adhesive, hydrophobic and toxic latex of *E. damarana*, *E. gummifera*, and possibly other species like *E. gregaria*, cause and maintain the fairy circles. They showed that matrix sand coated with *E. damarana* latex resulted in faster water-infiltration rates, explaining why fairy circles are moister at levels below 30–40 cm of the surface. This they postulated could lead to the death of young seedlings that had emerged after rainfall inside fairy circles, because their roots would still be too short to reach the moisture at those levels.



Fig. 3. Succulent *Euphorbia* species growing on sandy soils with people included for scale. (A) *E. damarana*. (B) *E. gregaria*. (C) *E. gummifera* (Schutte, 2019).

Their GIS analyses showed that perimeter sizes and spatial characteristics (Voronoi tessellations, distance to nearest neighbour ratio, pair correlation function and L-function) of fairy circles are similar to those of fairy circles co-occurring with *E. damarana* in northern Namibia, and with *E. gummifera* in southern Namibia. Historical aerial imagery of 1966 in Garub showed that in a population of 406 *E. gummifera* plants, 134 were replaced by fairy circles over a 50-year period.

Meyer et al. (2020) integrated rainfall, altitude and landcover in a GIS-based site suitability model to predict where fairy circles should occur (Fig. 2B). The model largely agreed with the distribution of three *Euphorbia* species and resulted in the discovery of new locations of fairy circles in the far southeast of Namibia and part of the Kalahari Desert of South Africa.

There have been three main criticisms of the *Euphorbia* allelopathy theory. Firstly, it was mentioned previously that *E. damarana* doesn't grow on deep sandy soil, but mainly in areas consisting of either very coarse rocky material (e.g. Etendeka basalt) or in locations having a very shallow layer of topsoil (Becker and Getzin, 2000; Van Rooyen et al. 2004). However, this is not the type of substrate commonly associated with fairy circles. Secondly, a number of fairy circle locations, e.g. in the Namibrand Nature Reserve, are mainly devoid of the presence of succulent *Euphorbia* species. Becker and Getzin (2000) for example, could not find any *E. damarana* specimens within the Giribes Plain, Marienfluss Valley or in the Hartmann's Valley, despite the presence of fairy circles in these locations. They concluded that the occurrence of *E. damarana* and fairy circles is probably coincidental. Thirdly, Getzin et al. (2015) speculated from observations (not analyses) that *E. damarana* is irregularly distributed, which is in contrast to the uniform pattern of fairy circles. However, Meyer et al. (2020) showed that the spatial distribution of *E. damarana* and *E. gummifera* is

regular, but less regular than that of fairy circles in uniform environments like Giribes Plain, Marienfluss and Namibrand Nature Reserve. Cramer and Barger (2013) found that 42% of fairy circle sites randomly selected in Namibia were clustered. Getzin and Yizhaq (2019) recently acknowledged that *E. gummifera* could be responsible for fairy circle formation in the Garub area, but not elsewhere in Namibia, as *Euphorbia* species do not co-occur with fairy circles everywhere.

3. Physical characteristics of fairy circles

The physical characteristics of fairy circles are important in understanding how they form and disappear, and include aspects like the associated grass species, the substrate on which they occur, their size, shape, spatial pattern, as well as their lifespan. These characteristics are discussed below.

3.1. Associated grass species

The vegetation in which fairy circles occur are comprised of mainly grass species, generally referred to as the matrix grasses, without which, fairy circles are not visible. The grasslands in which fairy circles are found are ephemeral and thus biomass is highly dependent on rainfall and can be completely absent during years of drought (Van Rooyen et al., 2004), and therefore it will appear as though the fairy circles have disappeared. Several grass species have been associated with fairy circles including: *Schmidtia kalahariensis* Stent., *Stipagrostis ciliata* (Desf.) De Winter, *S. giessii* Kers, *S. hochstetteriana* (Beck ex Hack.) De Winter, *S. obtusa* (Delile) Nees and *S. uniplumis* (Licht.) De Winter (Becker and Getzin, 2000, Tschinkel, 2012; Cramer and Barger, 2013, Getzin et al., 2014). The distribution of the grass species in which fairy circles commonly occur extends beyond the rainfall isohyets containing fairy circles (Cramer et al., 2016). In the southern part of Namibia and in the Richtersveld of northwestern South Africa, fairy circles also occur in succulent shrub areas with almost no grass cover. In these areas small shrubs define the outline of the barren patches instead of matrix grasses (Van Rooyen et al., 2004). Similarly, in the Bakrivier (Kalahari Desert) they are occasionally defined by *Arctotis leiocarpa* Harv. (Meyer et al., 2020).

The matrix grass often forms a peripheral belt (PB) surrounding the fairy circles (Theron, 1979; Becker and Getzin, 2000; Juergens, 2013; Meyer et al., 2020, and others) which consists of a thick ring of grass that is much taller than the matrix grass (Fig. 4A). In some instances, the difference in size between the PB and the grass matrix is related to different grass species being present, in others the same species occurs on both the periphery (being taller) and in the matrix (Cramer and Barger, 2013). The PB is apparently essential for this ecosystem functioning as it provides valuable resources to many organisms (Juergens, 2013). In the Kaokoland (northwest Namibia) the most extensive fairy circle locations are found in the Hartmann's Valley, Marienfluss and Giribes Plain. In these areas the vegetation between barren patches is composed mainly of a short-lived grass species, *S. uniplumis*, and the conspicuous fringe (PB) around the edge of the patches consists of either *S. giessii* or *S. hochstetteriana*, which are both perennial species (Becker and Getzin, 2000; Cramer and Barger, 2013). South of the Kuiseb River *S. obtusa* and *S. uniplumis* is found in the matrix and *S. ciliata* forms the PB. In some cases, *S. obtusa* forms both the matrix, as well as the PB (Cramer and Barger, 2013). Tschinkel (2012) stated that the peripheral belt is not a necessary or even unique feature of fairy circles. He compared it to grass along roads which grow taller, perhaps because of reduced competition for water.

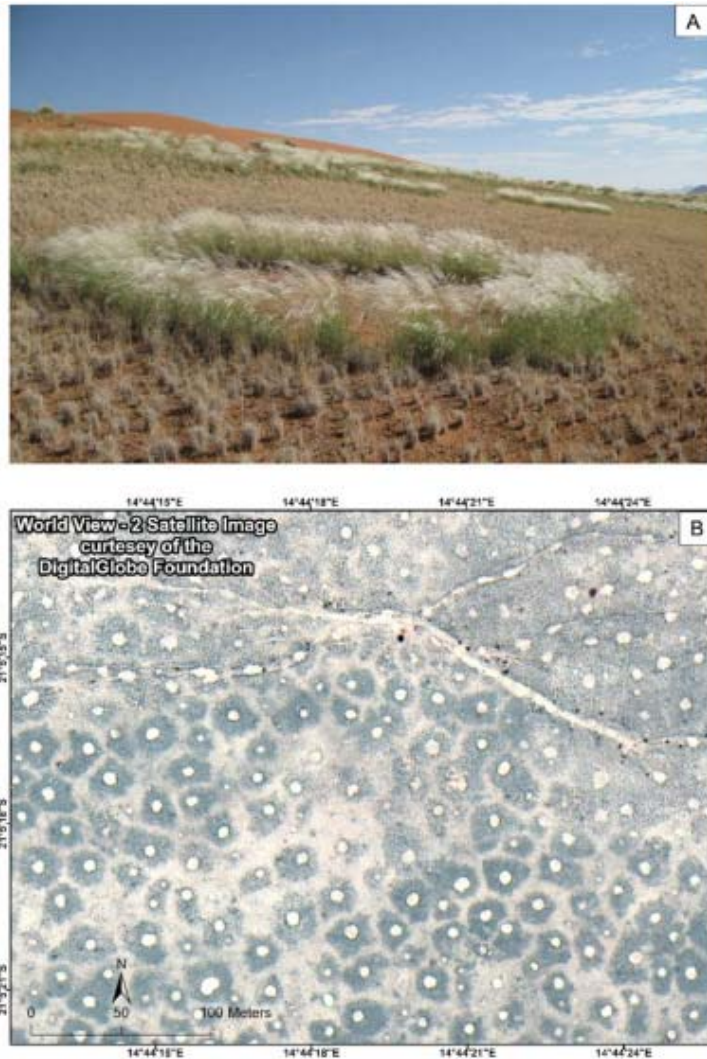


Fig. 4. (A) The perennial belt (PB) with longer grass surrounding fairy circles at Dieprivier, Namibia (Juergens, 2013). (B) Satellite image at Brandberg showing a ‘halo-effect’ instead of a PB surrounding the fairy circles (Schutte, 2019).

A lesser known grass-related feature often documented with fairy circles is that the matrix grass in the immediate vicinity around the circle can form a ‘halo-like’ effect instead of a PB (Fig. 4B). Both these attributes have been linked to the higher soil moisture content inside the fairy circles (Tschinkel, 2012; Juergens, 2013; Meyer et al., 2020).

3.2. *Fairy circle substrate*

It has been suggested that the variable distribution of fairy circles along the Namibian coast is a result of their pronounced restriction to sandy soils (Juergens, 2013). The soil inside fairy circles was classified as 85–90% sand at Giribes Plain (northern Namibia), Brandberg (central to north) and Garub (southern Namibia) by Meyer et al. (2020).

Tschinkel (2012) also stated that fairy circles are primarily found on sandy soils, even when sloped, but are not found on gravelly or alluvial deposits or shifting dunes, in contrast to Van Rooyen et al. (2004) who observed them on dunes. The fairy circles on the gravel plains

near Gobabeb investigated by Van der Walt et al. (2016) also consisted of 91% sand. Cramer et al. (2016) also reported that fairy circles occur on sandy soils, characterized by low fertility and is significantly less suitable for plant growth than soil from the outside (matrix), apart from the higher soil moisture below the surface. They reported that sites containing fairy circles inside Namibrand Nature Reserve had a significant higher percentage of coarse sand ($> 300 \mu\text{m}$) and less smaller particles ($< 30 \mu\text{m}$), and therefore contained less clay and silt than sites without fairy circles. Ravi et al. (2017) confirmed these findings on soil composition and also mentioned in agreement with Cramer et al. (2016), that fairy circles generally occur on soils with exceedingly high infiltration rates and low nutrient-holding capacities. Getzin and Yizhaq (2019) found the soil to be about four times more compacted in the matrix than inside fairy circles and ascribed it to the formation of soil crusts in the matrix.

Getzin et al. (2016; 2020) in contrast, reported that in Australia, the barren gap centres have significantly higher amounts of clay, as well as a clay-rich mechanical crust with resulting lower infiltration rates than the matrix soil. They found the vegetation matrix to consist of sandy soil.

3.3. Soil moisture content

Theron already noticed in 1979 that water infiltrates to about 1.0 m inside fairy circles and only to about 0.3 m in the matrix after good rains (Theron, 1979). Since then, several other studies reported a similar trend. Albrecht et al. (2001) found that the soil moisture content of soil from inside fairy circles is five times higher than that of soil from outside at depths of 32–100 cm for samples collected 12 days after extensive rainfall.

Cramer et al. (2016) reported exceptional high infiltration rates of water in fairy circles locations and a positive correlation between perimeter size and infiltration rate. Infiltration rates were determined using a single ring infiltrometer at 35 sites (Cramer et al., 2016).

Ravi et al. (2017) determined soil water infiltration by employing the use of a mini-disk and a dual-head infiltrometer. More than 200 measurements were taken from the centre of the bare patch, the periphery and from the matrix at three different experimental sites, at nine different locations. Their infiltrometer measurements showed that infiltration rates (and hydraulic conductivities) are significantly higher inside the fairy circles compared to the edges and the interspaces. More water infiltrated on the inside of the circular patches and may therefore provide water to plants along the edges through surface runoff or interflow. The differences in hydraulic conductivity (K_{unsat}) was ascribed to the varying soil texture, with soil present in the fairy circle consisting of smaller mean particle sizes than the matrix and the periphery (Ravi et al., 2017). They also noted that the decreased K_{unsat} of the matrix soil, might be due to the presence of a soil crust.

Picker et al. (2012) studied the soil properties of fairy circles eight months after the last seasonal rainfall and documented a fourfold decrease in soil moisture from the centre of fairy circles towards the surrounding grasses. They noted that the wetness gradient (Fig. 5) could not have been due to evapotranspiration by the matrix grasses, as it was during the dry season and the grasses were dormant. These researchers further noted that the PB consisted of *S. uniplumis*, that was flowering during the dry season, while the matrix grasses were dormant. They attributed this to the higher soil moisture content of fairy circles.

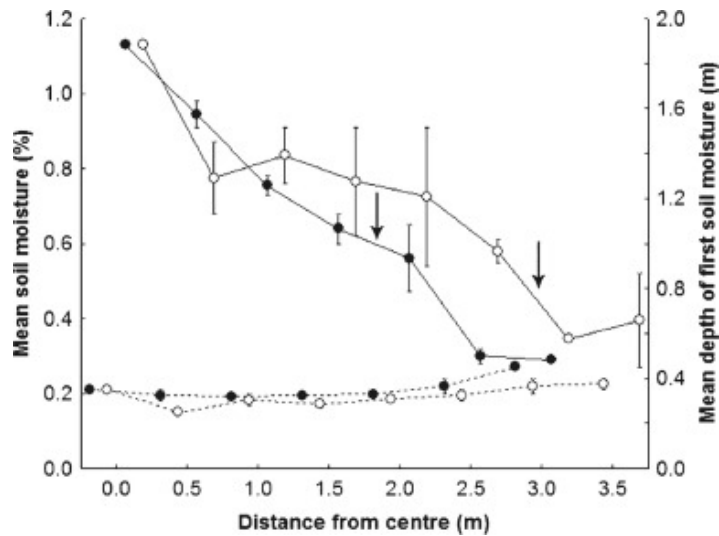


Fig. 5. Soil moisture gradients from the centre to the perimeter of a fairy circle at Marienfluss. Each value represents a mean of two samples taken along the cardinal axis at the same distance from the centre of the circle. Solid circles, N–S axis; open circles, E–W axis. Arrows indicate perimeter of circle. Dotted lines indicate mean depth of first appearance of soil moisture, solid lines mean soil moisture (and range) (Picker et al., 2012).

Juergens (2013) analysed long-term data on the environmental and biogeographical characteristics and dynamics of fairy circles on Giribes Plain. He recorded the volumetric soil water content of fairy circles and the matrix for the period 2006 to 2012 (Fig. 6) and found more than 53 mm of water stored in the upper 100 cm of the soil of fairy circles (including during the driest time of the year). The fact that this area receives on average only 100 mm of rainfall per year makes it even more noteworthy. As a result of the large sand pore sizes, the substrate associated with fairy circles drains rapidly, which allows fairy circles to collect water during rainfall events and to not lose water to evapotranspiration (Juergens, 2013). He also showed that less water infiltrated to deeper levels inside the matrix and attributed it to more evapotranspiration because of grass cover [in contrast to Picker et al. (2012) as described above]. Juergens (2013) also mentioned that rapid percolation of rainwater to deeper soil layers inside fairy circles assists in reducing evaporation loss, and the development of the PB is dependent on the longevity of the water resource beneath fairy circles. He reported that the roots of peripheral grasses (species not mentioned) are about 20–30 cm long and can reach water from inside the fairy circle. Interestingly, the water content at 30 cm soil depth decreases at a significantly faster rate inside fairy circles than in the matrix, and therefore moisture will possibly be out of the reach of grass roots about three months after good rainfall (Fig. 6B). However, Cramer et al. (2016) reported peripheral grass roots (species not mentioned) with lengths of 90 cm.

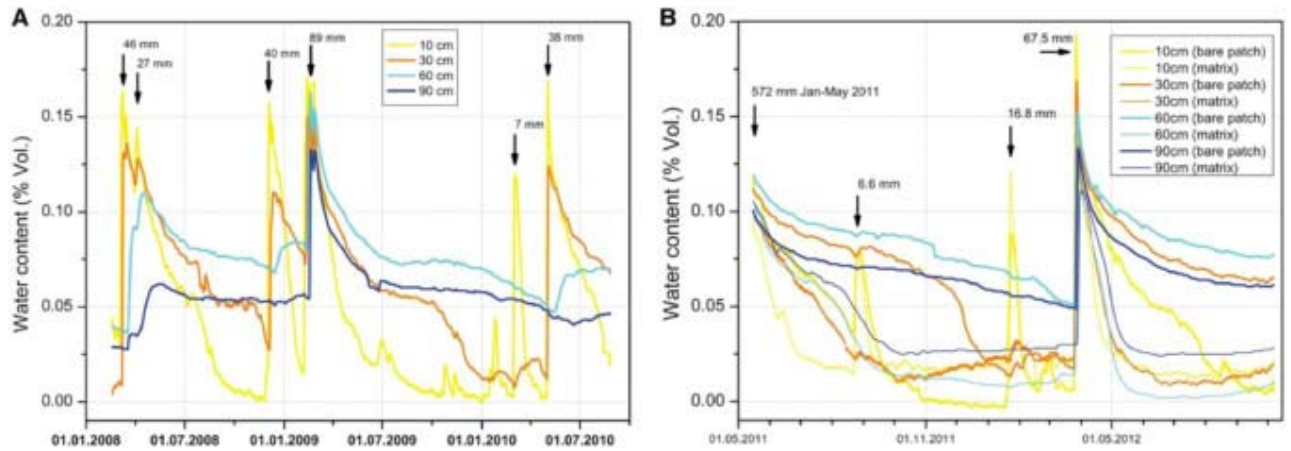


Fig. 6. (A) Rainfall events and volumetric soil water content (volume percent, $\text{m}^3/\text{m}^3 \times 100$) at different depths underneath a fairy circle, measured hourly from early 2008 until mid-2010. (B) Same measurements as in (A) comparing the bare patch (fairy circle, thick lines) and the matrix (MT, thin lines) measured from 15 May 2011 until 6 October 2012 (Juergens, 2013).

Meyer et al. (2020) also recorded higher water infiltration in fairy circle soil than in matrix soil in laboratory conducted infiltration experiments ($p < 0.05$, Fig. 7) and confirmed the experimental field findings above. They also measured soil water infiltration in soil collected from under dead *Euphorbia damarana* plants at Giribes and Brandberg, and from under dead *E. gummifera* in Garub, and recorded much faster infiltration rates in them than in matrix and fairy circle soils. They hypothesised that the latex of *Euphorbia* species causes the higher infiltration rates and found that matrix sand coated with 5% or more *E. damarana* latex increased the infiltration rate to that of soil from under dead *Euphorbia* species.

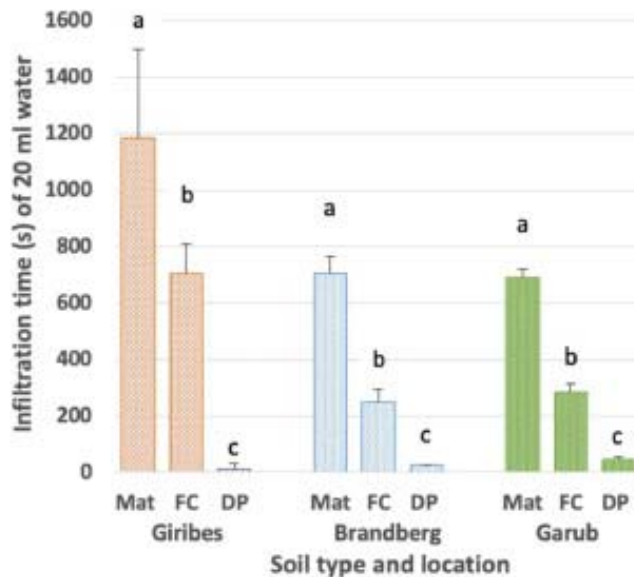


Fig. 7. Infiltration time in soil from the matrix (Mat), fairy circle (FC) and from under dead *Euphorbias* (DP) of Giribes, Brandberg and Garub ($p < 0.05$, soil types compared only inside locations) (Meyer et al., 2020).

In contrast to all of the above findings, Getzin et al. (2020) found the infiltration rate to be the lowest in the Australian bare gaps (also called fairy circles by these authors), and the amount of water after rainfall to be the least when compared to the edge of the gaps and the matrix

(Fig. 8). They explained this was due to the physical clay crust with compacted and sealed surfaces, which hampered rain infiltration and caused runoff water to flow on the surface towards the edge of the bare gap. They also stated that this was in contrast to the Namibian fairy circles, which are found on deep aeolian sand and the induced instability is the ‘uptake-diffusion feedback’. They didn't observe termitaria in their more than 150 excavations in Australia and concluded that it was the high clay content and associated high soil compaction, induced by mechanical weathering, that was causing the absence of vegetation in the Australian bare gaps and similarly in nearby large bare-soil areas, just like in many more Australian drylands.

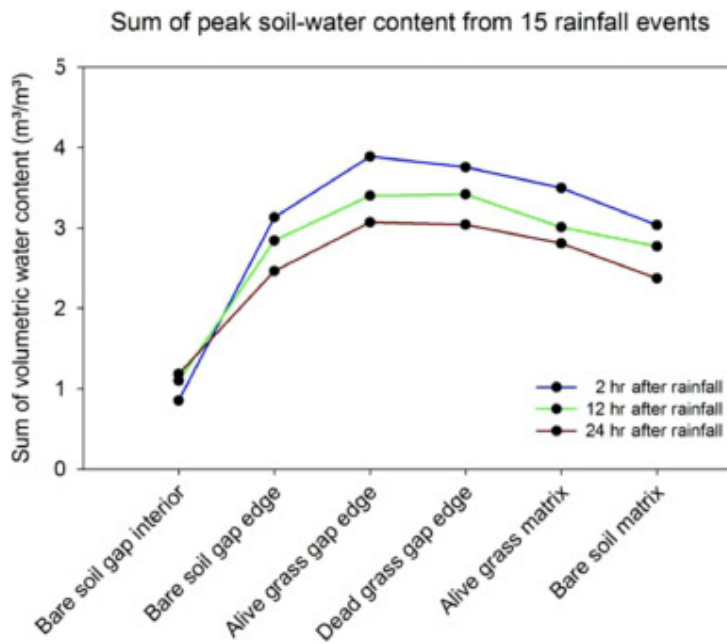


Fig. 8. Sum of the peak soil-water content 2, 12, and 24 hours after rainfall, accumulated over 15 rainfall events in Western Australia (Getzin et al., 2020).

3.4. Shape of fairy circles

The name ‘fairy circle’ implies that fairy circles are circular, however, Cramer et al. (2016) found that fairy circles in the Namibrand Nature Reserve are not actually circular when closely inspected. In their study area the fairy circles were not elongated in any particular direction but rather had convoluted perimeters. They found the shape index to be 1.152 indicating a 15% greater perimeter length than expected for a circular structure.

It has also been observed in various other places in Namibia that fairy circles can have an ellipse shape (Fig. 9) when they are situated along water drainage lines with the fairy circle's longer axis then being parallel to the drainage line (Theron, 1979; Meyer et al., 2015; Getzin and Yizhaq, 2019). However, Getzin et al. (2014) stated that fairy circles are circular because grasses form a ring-like structure since a circle has the smallest circumference-to-area ratio; and Getzin and Yizhaq (2019) commented that the mechanism for the formation of elliptical shaped fairy circles needs further investigation. Meyer et al. (2020) hypothesised that these elliptical shapes are formed along drainage lines (e.g. dry riverbeds) when occasional high rainfall occurs, which then moves the hydrophobic *Euphorbia* latex-covered sand downhill. These authors also reported that some fairy circles that are not round

(sometimes kidney-shaped, Fig. 10) are occasionally found, and are also much bigger than others in that particular area. Likewise, they observed euphorbias that occasionally grow next to each other which might give rise to such 'double' fairy circles, according to the *Euphorbia* allelopathy theory (Meyer et al., 2020).

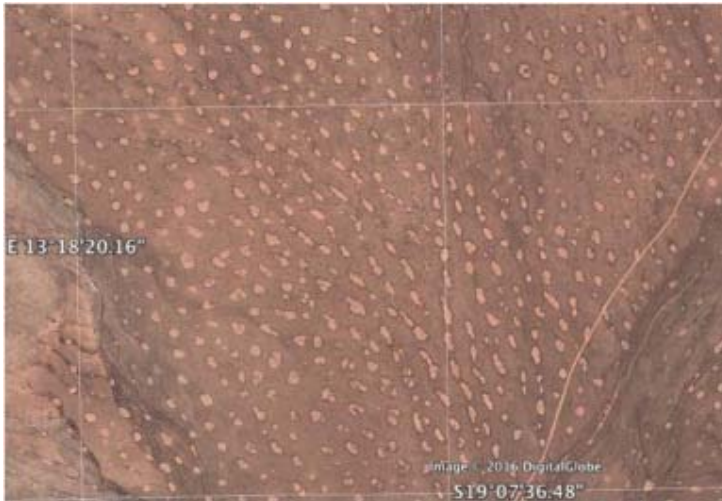


Fig. 9. Google Earth satellite image showing fairy circles with elliptical shapes situated along drainage lines on Giribes Plain.

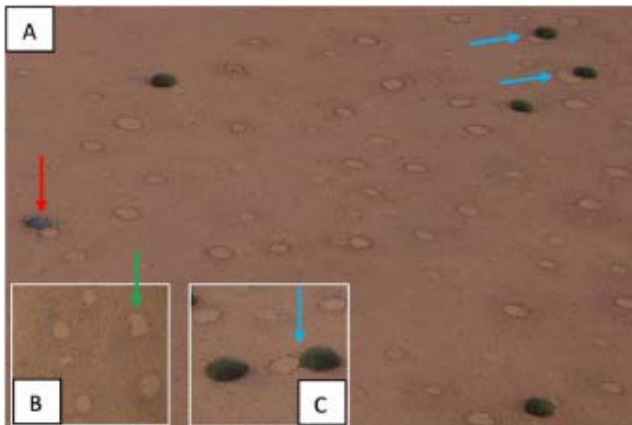


Fig. 10. Formation of kidney-shaped fairy circles by *E. damarana* plants at Brandberg, Namibia. (A) and (C) Dead *E. damarana* next to fairy circle (red arrow), examples of *E. damarana* and fairy circles next to each other (blue arrows). (B) Kidney-shaped fairy circle (green arrow). Adapted from Meyer et al. (2020).

3.5. Size of fairy circles

It has been reported by Van Rooyen et al. (2004) that the sizes of fairy circles in Namibia generally decrease from approximately 10 m in the north to 2 m in diameter in the south. This statement was repeated by many authors and the data presented in Table 2 shows such a trend, but not a clear size-gradient from north to south. Fairy circle sizes in the south are sometimes bigger than in the north, e.g. Picker et al. (2012) reported circles of 6.4 m at Noordoewer, near the Namibia-South Africa border, and several authors reported smaller circles in the north near Brandberg, Dieprivier and Tsondab (Table 2).

Table 2. Fairy circle diameter sizes in Namibia and South Africa arranged from north to south. When more than one publication reported average fairy circle sizes at a location, the average of these were also provided. Some authors only provided the median value, and these are indicated as such.

LOCATION (ARRANGED FROM NORTH TO SOUTH)	FAIRY CIRCLE SIZE (AVG. DIAMETER, M)	REFERENCE
NAMIBIA		
HARTMANN VALLEY	10.0	Van Rooyen et al., 2004
	9.8	Juergens, 2013
	(avg. 9.9)	
MARIENFLUSS	7.5	Van Rooyen et al., 2004
	6.2	Juergens, 2013
	(avg. 6.9)	
	5.4 (median)	Picker et al., 2012
GIRIBES	9.3* and 6.2	Theron, 1979
	6.2	Van Rooyen et al., 2004
	6.8	Juergens, 2013
	6.9 and 4.6	Getzin and Yizhaq, 2019
	(avg. 6.7)	
	7.3 (median)	Picker et al., 2012
BRANDBERG	5.2	Meyer et al., 2020
DIEPRIVIER	3.8	Juergens, 2013
TSONDAB	5.0	Van Rooyen et al., 2004
	4.9	Getzin and Yizhaq, 2019
	(avg. 5.0)	
NAMIBRAND	6.1	Albrecht et al., 2001
	5.9	Picker et al. 2012; Tarnita et al., 2017
	5.0	Cramer and Barger, 2013
	6.5	Juergens, 2013
	6.9	Cramer et al., 2016
	(avg. 6.1)	
	4 to 13	Tschinkel, 2012
GARUB	3.9	Meyer et al., 2015
	3.7	Getzin and Yizhaq, 2019
	3.5	Meyer et al., 2020
	(avg. 3.7)	
ROOIDUIN (ROSH PINAH)	2.0	Van Rooyen et al., 2004
SOUTH AFRICA		
NOORDOEWER	6.4	Picker et al., 2012
NUMEES	4.7	Juergens, 2013
KUBUS	2.0	Van Rooyen et al., 2004
YELLOW DUNE	4.8	Juergens, 2013

Cramer and Barger (2013) reported that fairy circles occur in a narrow range of MAP and enhanced vegetation biomass index (1st principle component) range. There is, however, not a clear difference in MAP from north to south as the fairy circles are mostly found in a narrow band in the same isohyet. Cramer et al. (2016) found that fairy circle size is directly related to the water infiltration rate.

Cramer and Barger (2013), Escaff et al. (2015), as well as Zelnik et al. (2015), stated that fairy circle size is inversely related to MAP inside Namibrand Nature Reserve. Getzin et al. (2014) showed that fairy circle size and nearest neighbour distance were directly associated.

According to Meyer et al. (2020) fairy circle size is determined by the type of *Euphorbia* species which is responsible for its formation. Since *E. damarana* found in the north is

relatively bigger than *E. gummifera* and *E. gregaria*, which both occur in the south, the circles are generally bigger in the north than the south. They hypothesised that other smaller succulent *Euphorbia* species might also cause the formation of fairy circles upon their death.

Becker and Getzin (2000) stated that fairy circle size is related to the temperature sensitivity of the particular termite responsible for the circle's formation and that a species such as *Hodotermes mossambicus* (and other species) can easily fall into distress when temperatures are high and will then be more vulnerable to predators.

There is disagreement amongst authors on fairy circle dynamics. Tschinkel (2012) and Getzin et al. (2014) showed that new fairy circles appeared already in their final sizes, rather than as initial small circles that gradually grew to their final size. In contrast, Juergens (2013) and Vlieghe et al. (2015) provided data to show that they grow bigger over time. Juergens (2013) reported fairy circle sizes of 35 m in Angola but these have not yet been confirmed by other authors.

3.6. Lifespan of fairy circles

Theron (1979) marked the location of 10 fairy circles on the Giribes Plain in 1978. These sites have been inspected on several occasions (Van Rooyen et al., 2004; Meyer et al., 2015; Meyer et al., 2020) and all have been found to be intact in 2019. Consequently, showing that the same marked fairy circles did not disappear after several consecutive years of extreme drought or high rainfall for at least 40 years. However, Getzin et al. (2014) stated that fairy circles disappeared after wet spells and appeared after dry spells, not necessarily on the same spot, whereas in contrast, Juergens et al. (2015) argued that new fairy circles appeared after wet spells and disappeared after dry periods. During a time-series analysis of fairy circles (Juergens et al. 2015, Fig. 11) on the Giribes Plain (for the period 2007 to 2015) they showed a change in fairy circle population, triggered by a series of good rainfall years (from 2008 to 2011) and by three dry years (2012 to 2014). They suggested that the series of photographs show the formation of eight new fairy circles that increased in size from 2009 to 2013, while in 2014 all these new fairy circles disappeared after three consecutive years of drought. They stated that the same trend was observed in the annual monitoring of 160 fairy circles within Giribes Plain (data not shown by authors). According to Juergens et al. (2015) wet years resulted in higher biomass and greater termite reproduction that could expand termite colonies. In the series of photographs (Fig. 11) the biomass of the matrix grasses was also observed to fluctuate during the same period. In their most recent photograph of 2015 (Fig. 11C), the matrix grasses surrounding the fairy circles were nearly entirely absent in some areas and therefore possibly not visualising fairy circles. It would be interesting to see if these fairy circles are visible again after good rains.

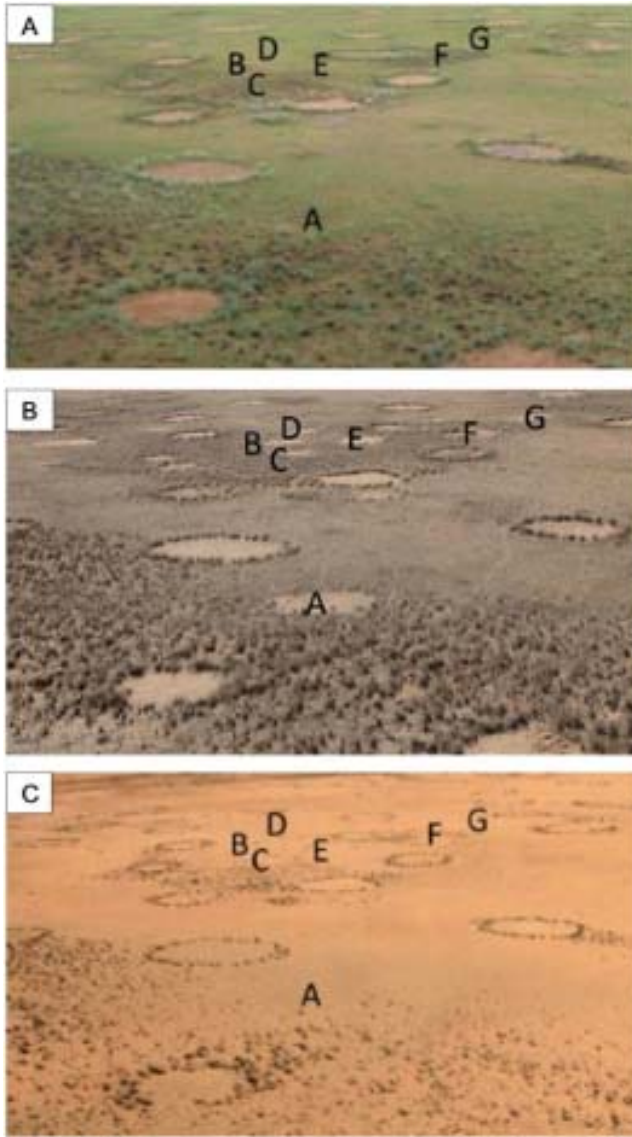


Fig. 11. Fairy circles on the Giribes Plain after: (A) above average rainfall during 2008, (B) normal rainfall during 2012, and (C) after low rainfall during 2015 (adapted from Juergens et al., 2015). The letters in the photographs correspond to the location of newly formed fairy circles visible in 2012 (B).

Getzin et al. (2015) commented that Juergens et al. (2015)'s photographs (Fig. 11) are an ‘anecdotic sequence of photographs showing the appearance of atypical small and aggregated fairy circles during wetter years and their sudden disappearance during drier years’, and strongly contradicts the results shown by Cramer and Barger (2013; their Fig. 5B, C), which demonstrated that the percentage of area covered by fairy circles, as well as their individual area, decreases with precipitation. The findings of Juergens et al. (2015) also seem to contradict those of Vlieghe et al. (2015) and Zelnik et al. (2015).

Photographic evidence of fairy circle appearance and disappearance should be cautiously interpreted as the ephemeral grassland is highly dependent on local rainfall and therefore precipitation data must be assessed in conjunction with the time of the year in which satellite imagery was created (Meyer et al., 2020). Furthermore, to complicate matters, grass seedlings

do commonly establish within fairy circles following good rains, but then rarely survive the following dry period (Theron, 1979; Van Rooyen et al., 2004; Cramer et al., 2016).

Tschinkel (2012) examined two satellite images taken four years apart to determine the age of fairy circles and concluded that they had a lifespan of between 40 and 60 years, and that they are in a constant flux of 'birth' and 'death' (overgrown by grasses). Tarnita et al. (2017) modelled fairy circle population dynamics by including the matrix grasses, as individual grass tufts and suggested that there could be great variation in the age of fairy circles that range between 5 and 165 years. On the other hand, Theron (1979) and Meyer et al. (2015; 2020), stated that fairy circles could only be formed where *E. damarana*, *E. gummifera*, *E. gregaria* and possibly other succulent *Euphorbia* species had once grown on sandy soils, and that they would persist until the allelopathic effect had weakened to a particular point.

3.7. Spatial patterning of fairy circles

As mentioned above, Albrecht et al. (2001) were the first authors to investigate the spatial statistics of fairy circles. They determined the distance to nearest neighbour ratio (R) of fairy circles at the Namibrand Nature Reserve and found it to be 1.68, indicating that they display an over-dispersed (regular) spatial pattern (the average nearest neighbour distance was determined to be 14.4 m). Cramer and Barger (2013) investigated the spatial pattern of fairy circles from southern Namibia to southern Angola by searching for fairy circles on Google Earth imagery, and then generating a random point cloud in a 50 km radius in locations where fairy circles were found. Their results showed that only 58% of the 80 fairy circle locations investigated had over-dispersed regular spatial patterns (Fig. 12). The spatial pattern of fairy circles in these sites varied from clumped ($R = 0.58$) to being regular ($R = 1.67$). Fairy circles were not over-dispersed when landscape occupancy was low in nearly half of the locations.

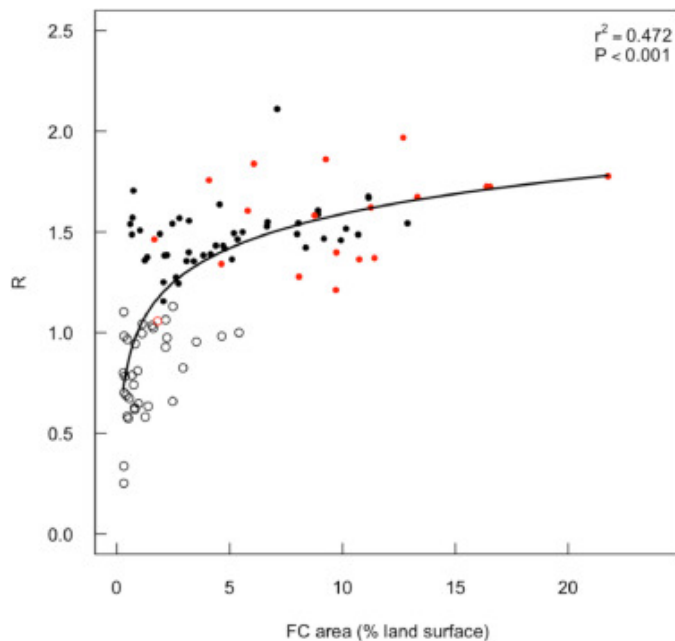


Fig. 12. Variation in fairy circle dispersion (R -ratio) with landscape occupancy based on satellite imagery analysis (black points) and ground survey (red points). Closed symbols indicate significantly over-dispersed R -values (Z-test, $P < 0.05$; Cramer and Barger (2013)).

Several other authors (Getzin et al., 2014; Escaff et al., 2015; Getzin et al., 2015; Juergens et al., 2015; Zelnik et al., 2015; Tarnita et al., 2017; Meyer et al., 2020) investigated the spatial pattern of fairy circles in undisturbed, uniform areas of Marienfluss, Giribes Plain, Brandberg and/or Namibrand Nature Reserve. They all reported that the fairy circles were over-dispersed in these uniform, undisturbed areas. Juergens et al. (2015) stated that an important factor to the regularity of fairy circle spatial patterning, is their occurrence within a homogeneous environment with similar edaphic conditions. Getzin and Yizhaq (2019) recently acknowledged this statement of Juergens et al. (2015) and mentioned that Namibian fairy circles also occur on atypical, non-homogeneous habitat conditions where topographical heterogeneity or extreme aridity are forcing the circles to change their shapes (e.g. mega elliptical fairy circles on drainage lines) and have irregular spatial patterns that are not grid-like hexagonal as in homogeneous terrains like Giribes Plain and Marienfluss. They also mentioned that more studies are needed to explain the formation of these shapes and patterns.

Voronoi tessellations have often been used to characterise the spatial patterning of fairy circles. The number of corners of each tile describes the regularity of the pattern, i.e. the larger the number (percentage) of tiles with 6 corners, the more regular the pattern (Illian et al., 2008). Getzin et al. (2014) was the first to create Voronoi tessellations for fairy circles (at Marienfluss and Giribes Plain) and showed that 43–46% of the tiles consisted of six corners (Fig. 13) and therefore have an over-dispersed (regular) distribution. Zhang and Sinclair (2015) found that 45% of the fairy circles in Wolwedans (Namibrand Nature Reserve) were six-cornered Voronoi tiles. Juergens et al. (2015) showed that 39% and 34% of the Voronoi tiles of termite nests of *Macrotermes* spp. in Outjo (Namibia) and *Pogonomyrmex* spp. in Colorado (USA) had six corners, respectively. They stated that the most regularly spaced nests of social insects will be of those species having stable, long-lived, sessile colonies. Occupancy in an optimal, undisturbed, homogeneous environment will also maximise the degree of regularity.

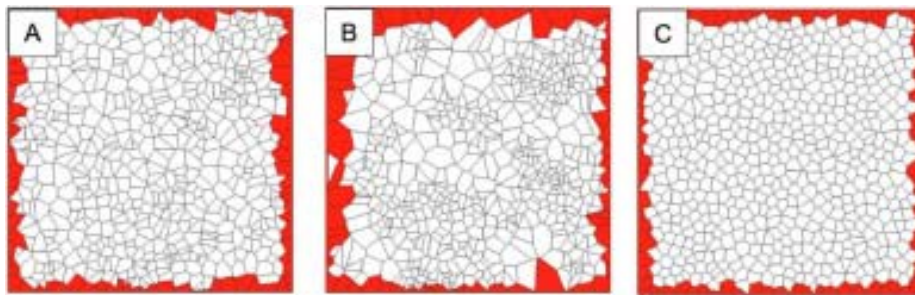


Fig. 13. Getzin et al. (2014) created Voronoi tessellations of artificially created random (A) and clustered point patterns (B) with 630 points, which equals the amount of fairy circles of their Marienfluss plot showing an over-dispersed pattern (C). (The edge tiles in red were removed before the analysis.)

Zhang and Sinclair (2015) showed that the distribution of Voronoi tiles for fairy circles are virtually indistinguishable from metazoan epithelial cells, showing that various processes, operating over vastly different scales, can lead to the same type of Voronoi tile distribution. Meyer et al. (2020) created Voronoi tessellations for fairy circles and two *Euphorbia* species in Brandberg and Garub, and also found the highest percentage of them had six corners. The average percentage of tiles with six corners in Brandberg and Garub were 37.2 for fairy circles, 30.9 for *E. damarana* and *E. gummiifera*, and were in between these values at 33.0% at locations where fairy circles co-occur with the *Euphorbia* species in the same site. They

argued that the co-occurring sites are transition areas between healthy plant populations and fairy circle-only sites.

Getzin et al. (2014) used a number of other spatial statistics to characterise the spatial distribution of fairy circles at Marienfluss and Giribes Plain. The pair-correlation function analysis showed that fairy circles in these undisturbed, uniform locations have a wave-like curve with recurrent appearances of regularity and a pronounced first peak, $g(r)$ at between 11 to 16 m (Fig. 14), which is the most frequent distance to the nearest neighbour. A well-visible second peak is shown pointing to long-lasting order in the over-dispersed pattern and a 'hexagonal' spatial arrangement where each fairy circle has six neighbours located at approximately the same distance from them (Getzin et al., 2015). The graph oscillates around the null model, indicating an extremely high degree of ordering of the pattern that persists well beyond the nearest neighbours. This oscillation was also reflected in the L-function. The spatial pattern of fairy circles at Giribes Plain and Marienfluss was thus characterised by large scale homogeneity that is reflected in both the pair correlation function and the L-function. It was also revealed that fairy circles that are closer to each other have smaller sizes.

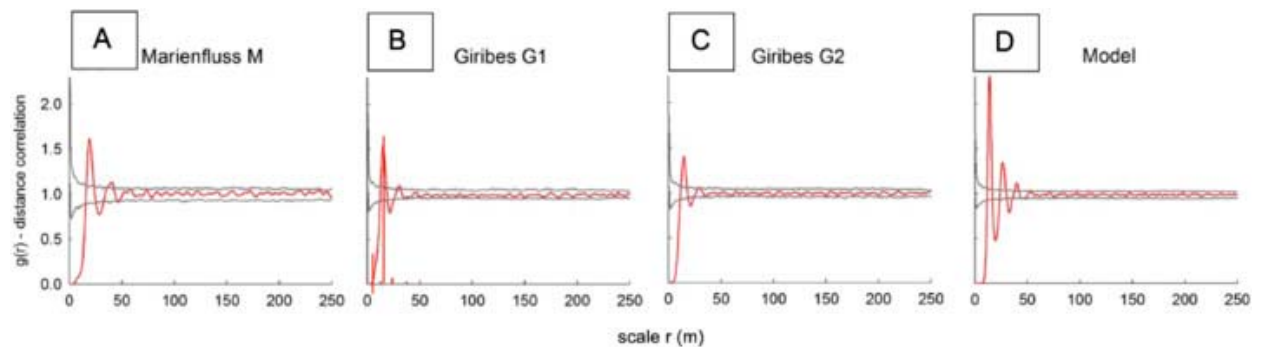


Fig. 14. The pair-correlation function spatial analysis of fairy circles at Marienfluss (A) and Giribes Plain (B and C) observed in aerial images of 500×500 m plots contrasted to random null models, similarly to the theoretical model (D) of numerically created circle patterns using the Gilad et al. (2007) model (adapted from Getzin et al., 2014).

Spatial point pattern analysis by Meyer et al. (2020) revealed that fairy circle sites and co-occurring fairy circle-*Euphorbia* sites were overdispersed. *Euphorbia*-only sites were also overdispersed, but to a lesser extent. They showed that the nearest neighbour R-values of fairy circles and co-occurring *Euphorbia*-FCs sites were similar and to a lesser extent similar to the nearest neighbour ratios of *Euphorbia*-only sites. The co-occurring sites were hypothesised to be in an intermediate state, progressing from a high density of plants and low density of fairy circles, towards a lower density of plants and higher density of fairy circles. This theory was supported by the spatial analysis results which showed that the co-occurring sites shared physical characteristics with both fairy circles and euphorbias. The pair-correlation function for fairy circles and the co-occurring sites were similar in that both sites displayed a significant peak, however the distance at which the peak was formed was greater for fairy circles than co-occurring sites.

Juergens et al. (2015) found regularity in the pair-correlation analyses of *Macrotermes* termite mounds and *Pogonomyrmex* ant nests, but Getzin et al. (2015), however, stated that these do show regularity, but not to the extreme ordering of the fairy circle patterns at Marienfluss and Giribes Plain. They also mentioned that neither the pair-correlation function $g(r)$ of *Macrotermes*, nor that of *Pogonomyrmex*, showed a first clear peak with high

amplitude which was pronounced and substantially outside the simulation envelopes of the null model. Additionally, the $g(r)$ of the insects did not remain within the envelope of the null model for larger scales, $r > 60$ m, indicating large-scale heterogeneity.

Tarnita et al. (2017) showed that interactions among social-insect colonies and vegetation can explain a diverse global suite of regular spatial patterns, but also emphasised the potential for co-occurrence and complementarity among distinct patterning mechanisms in generating multi-scale regularity. They validated their model using data from the same over-dispersed fairy circle plots of Getzin et al. (2015) on Giribes Plain, Marienfluss and from Namibrand Nature Reserve. Data from insect nests were obtained from Kenya (Macrotermitinae: *Odontotermes montanus*), Mozambique (Macrotermitinae: *Macrotermes* spp.), Brazil (Termitidae: *Syntermes dirus*), Australia (Termitidae: *Amitermes meridionalis*) and harvester ant nests in the southwestern USA (Formicidae: *Pogonomyrmex* spp.). Their results demonstrated that intraspecific competition between territorial animals can generate the large-scale hexagonal regularity of these patterns.

In a recent paper by (Lee et al., 2021), they stated that variation in spatial pattern is not only between taxa, but even varies between different plots of the same taxon in the same region. Systems operate on different timescales, e.g. fairy circles have estimated lifetimes of around half of a century compared to days or weeks for nascent ant nests and centuries for trees in unperturbed forests. Overall, fast and slow dynamics of sessile organisms are characterised by a range of spatial distributions, from the random to the regular, that reflect underlying forces of growth, death and competition. (Lee et al., 2021) proposed a minimal quantitative framework to unify this variety by accounting for how quickly sessile organisms grow and die, mediated by competition for fluctuating resources. It is remarkable then that even groups of trees seem to obey this pervasive fractal law, such that the trees of a particular size ‘branched off’ into trees of a smaller size and so on, in such a way that it could be considered, over some range, that the set of large trees was a scaled set of the smaller trees. This self-similar structure, reflected in power law scaling, emerged from consideration of energetic constraints translated into the requirement that trees filled the available canopy space. They proposed a minimal model of sessile organism growth incorporating aspects of allometric scaling theory and area-based competition. From these basic principles, they obtained a general framework for competitive forces driven by metabolic requirements and fluctuating resources. When interaction with the environment dampened resource fluctuations (e.g. niche construction) or changed competitive interactions (e.g. symbiosis), these perturbations would be reflected in the spatial distribution of organisms. Besides indicating limitations of metabolic scaling theory, namely that it might be more accurate in forests with weaker local competition and smaller environmental fluctuations, probing the theory suggested limitations of spatial correlation-based measures of regularity when varying organism size introduced disorder in spacing. Even amongst forests, some were less regular, but others such as the pinyon-juniper ecosystem of the southwest USA were more spatially regular (Lee et al., 2021).

4. Conclusion

These interesting nearly circular barren patches, found mainly in the Namib Desert, have led to several contrasting theories being put forward by scientists. Four of the current main theories on the cause and maintenance of the fairy circles were discussed and the most significant publications on fairy circles were reviewed. Each of the important physical characteristics of fairy circles were described in detail. The fairy circles occur in sandy areas

Table 3. The key characteristics that define fairy circles and how these are explained by the proponents of the four most important theories.

KEY CHARACTERISTICS OF FCS	MECHANISM/EXPLANATION PROVIDED BY DIFFERENT THEORIES			
	Social insects	Self-organising patterning	Gas	<i>Euphorbia</i> allelopathy
PERIPHERAL BELT	Yes, not foraged by termites. Roots on edge utilise FC water.	Yes, roots utilise FC water, different bigger grass species found on edge than in matrix.	Yes, hydrocarbons act like fertiliser to plants, stimulating plant growth at the edge, inhibiting it at peak seepage inside FC.	Yes, water run-off to edge because of hydrophobicity.
HALO-EFFECT	No, mentioned but not explained.	No.	Yes, geochemical signature.	Yes, <i>Euphorbia</i> nutrients utilised by other plants.
SUBSTRATE (FCS ALWAYS ON SANDY SOIL)	No, even though <i>Psammotermes allocerus</i> is distributed widely in southern Africa.	Yes, hexagonal spaced structures could be the result of the homogeneous nutrient-poor sandy soils.	No.	Yes, hydrophobic effect more pronounced in sandy soils.
HIGH-INFILTRATION RATE INSIDE FCS	No, mentioned but not explained.	No, mentioned but not explained.	No.	Yes, hydrophobicity causes high infiltration along drainage channels of explants.
HIGH SOIL MOISTURE CONTENT	Yes, insects removed plants, thus no evapotranspiration.	Yes, plant self-organisation removed plants and thus no evapotranspiration.	Yes, long-term gas and oil seepage bring groundwater to the surface.	Yes, hydrophobicity cause faster infiltration to deeper levels with cool temperatures and thus less evaporation.
CIRCULAR SHAPE	Yes, insect feeding behaviour in a near-perfect circle.	Yes, biomass-water feedback plays a dominant role in FCs circular shape because a circle has the smallest circumference-to-area ratio.	Yes, an apical anomaly, e.g. hydrocarbons are greatest above the source and form a circular pattern around the apical anomaly.	Yes, <i>Euphorbia</i> species are circular in shape.
ELLIPSE SHAPE ON SLOPES	No.	No, mentioned but not explained.	No.	Yes, along drainage lines water will move the latex-covered sand downhill and form elliptical FCs.

KIDNEY-SHAPED FCS (TWO TOUCHING FCS)	Yes, budding or splitting of subterranean termite colonies that are well established.	No, mega-FCS described but not explained.	No, mentioned but not explained.	Yes, two <i>Euphorbia</i> plants growing next to each other.
SIZE VARIATION	No, mentioned FC size is positively correlated with aridity and negatively correlated with latitude, not explained in relation to insect theory.	Yes, positively correlated with soil infiltration rate and negatively with precipitation.	No.	Yes, <i>Euphorbia</i> species have different sizes, resulting in different FC sizes.
AGE AND APPEARANCE/DISAPPEARANCE	Yes, wet years result in higher standing biomass and greater faunal productivity, and would probably promote the expansion of social insect colonies and thus FCs.	Yes, FC disappearance relies on sequential years of good rainfall because grass cover has a positive relationship with rainfall in arid areas, and vice versa.	Yes, depends on release of carbon monoxide and other gases.	Yes, depends on duration of hydrophobicity. It is hypothesised that FCs can last for decades or even centuries. Photographic evidence of appearance/disappearance is not always conclusive. Image quality and previous rainfall records play a crucial role.
SPATIAL PATTERN	Yes, degree of regular spatial patterning of termite mounds varies in relation to environmental heterogeneity, with a single species of termite capable of showing patterns of regular and clustered patterns across short-scale environmental gradients, similarly as FCs.	Yes, FCs are extremely ordered and regularly distributed at small scales, while their distribution is highly homogeneous over large areas up to 100 ha and beyond. The characteristic spatial signature of FCs demonstrates scale-dependent neighbourhood-density functions of unique spatial signatures in regular patterns.	No.	Yes, depends on spatial arrangement of <i>Euphorbia</i> plants which varies from irregular to regular depending on the homogeneity of the location.

with high water infiltration rates and mostly in grasslands, but sometimes small shrubs or herbs define their outline. They may have a peripheral belt of taller grasses in some areas. The soil moisture is higher in the fairy circles and the water infiltrates to deeper levels than in the matrix. The barren patches are mostly circular but may also be elliptic or kidney-shaped. The diameter of fairy circles varies but can be 10 m in the north and 2 m or less in the south, but larger ones can also be present in the south. There is no consensus on the lifespan of fairy circles, and some researchers predict that they are only visible for a few years while others reckon that they are there for many decades. The visibility of the fairy circles is dependent on rainfall and surrounding grass cover. Fairy circles occur in a relatively over-dispersed (regular) spatial pattern in homogeneous terrain, but the spatial pattern may become clumped when the terrain is non-homogeneous.

A theory can only be accepted if it can explain the origin and maintenance, as well as all of the key characteristics of fairy circles as discussed above. In Table 3 we summarised how the proponents of the main theories explain how each of the key characteristics of the fairy circles fits their theory. It can be seen from the table that most of the theories have not yet been tested on some of the key characteristics that define fairy circles. The diverse explanations for some of the key characteristics are remarkable. A valid and important question that can be asked is, can more than one of these diverse theories give rise to this unique phenomenon of the arid areas in southern Africa? This is highly unlikely in our opinion. The barren patches discovered in Australia (Getzin et al., 2016) don't have several of these key characteristics and are therefore not classified as fairy circles in this paper.

Despite the vast distribution of fairy circles over the landscape of the southwestern coast of Africa, and regular observations by locals, tourists, pilots and researchers, their origin and maintenance still needs more research and debate.

Declaration of Competing Interest

None.

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