

Clarifying misunderstandings regarding vegetation self-organisation and  
spatial patterns of fairy circles in Namibia: a response to recent

*Original*

Clarifying misunderstandings regarding vegetation self-organisation and  
spatial patterns of fairy circles in Namibia: a response to recent  
termite hypotheses / Getzin, Stephan; Wiegand, Kerstin; Wiegand, Thorsten; Yizhaq, Hezi; von Hardenberg, Jost;  
Meron, Ehud. - In: ECOLOGICAL ENTOMOLOGY. - ISSN 0307-6946. - 40:6(2015), pp. 669-675. [10.1111/een.12267]

*Availability:*

This version is available at: 11583/2814858 since: 2020-04-29T13:40:07Z

*Publisher:*

WILEY

*Published*

DOI:10.1111/een.12267

*Terms of use:*

This article is made available under terms and conditions as specified in the corresponding bibliographic description in  
the repository

*Publisher copyright*

(Article begins on next page)

## OPINION

# Clarifying misunderstandings regarding vegetation self-organisation and spatial patterns of fairy circles in Namibia: a response to recent termite hypotheses

STEPHAN GETZIN,<sup>1</sup> KERSTIN WIEGAND,<sup>2</sup> THORSTEN WIEGAND,<sup>1</sup> HEZI YIZHAQ,<sup>3,4</sup> JOST VON HARDENBERG<sup>5</sup> and EHUD MERON<sup>3,6</sup>

<sup>1</sup>Department of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany, <sup>2</sup>Department of Ecosystem Modelling, Faculty of Forest Sciences and Forest Ecology, University of Goettingen, Goettingen, Germany, <sup>3</sup>Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Beer Sheva, Israel, <sup>4</sup>The Dead Sea and Arava Science Center, Tamar Regional Council, Israel, <sup>5</sup>ISAC-CNR, Torino, Italy and <sup>6</sup>Physics Department, Ben-Gurion University of the Negev, Beer Sheva, Israel

## Introduction

Periodic vegetation patterns are a ubiquitous phenomenon in water-limited regions around the world (Deblauwe *et al.*, 2008). For the world's drylands such as Namibia, Goudie and Viles (2015) highlight that patterns like banded vegetation stripes are extensively developed where mean annual rainfall ranges between circa 100 and 600 mm. Observational studies along with mathematical modelling strongly support the notion that regular, nearly periodic vegetation patterns are large-scale self-organisation phenomena that are driven by small-scale ecohydrological feedbacks resulting from plant competition for scarce soil water (Deblauwe *et al.*, 2008, 2011; Rietkerk & van de Koppel, 2008; Meron, 2012). For example, a study by Deblauwe *et al.* (2008) used data on the occurrence of known periodic vegetation patterns together with data on environmental factors to determine the environmental drivers of their worldwide distribution. Their results confirm that periodic patterned vegetation is mainly explained by a combination of climatic variables and physical properties of soil. Their modelled map extends to the dry Namib Desert with < 100 mm mean annual precipitation (MAP) and correctly shows the potential fairy circle area within the accuracy limits of global data.

Studies on self-organisation also account for the morphological changes the patterns may go through along a precipitation gradient, from uniform cover, to periodic gap patterns, through stripe or labyrinthine patterns to spot patterns, and finally to bare soil. Spot patterns exist in the hyper-arid Namib Desert, and other periodic vegetation patterns have been described by Goudie and Viles (2015) for several Namibian regions. They hypothesised that the non-appearance of labyrinthine or striped patterns at areas with complete aeolian sand cover may be

attributed to restricted overland flow of rain water which drives this type of pattern.

The strong dependence of patterned vegetation on rainfall implies, in particular, the existence of gap patterns in a relatively narrow range of climatic conditions. This prediction was confirmed by a 'habitat model' for the occurrence of fairy circles (FCs) on the regional scale of Namibia (Cramer & Barger, 2013), which showed that the occurrence of FCs is indeed strongly driven by climate, i.e. MAP and temperature seasonality. Besides fieldwork evidence for vegetation self-organisation, they also showed that the narrow band of sites with FCs is embedded within the much wider distribution of the component grass species and that FC size is inversely correlated to MAP. The FC phenomenon appears, therefore, as a particular example of gap patterns, a phenomenon that has been observed in other regions such as Sudan (Fig. 1) or eastern Africa with different plant species (Barbier *et al.*, 2006; Deblauwe *et al.*, 2008, 2011). By conducting for the first time a detailed spatial point pattern analysis of the FCs using the pair and mark correlation functions, Getzin *et al.* (2015) showed that FCs are extremely ordered and regularly distributed at small scales, while their distribution is highly homogeneous over large areas up to at least 25 ha (we show this here up to 100 ha and beyond). They also showed that patterns with exactly the same characteristics emerge from predictions of a mathematical model of self-organisation and used this model as additional support for their hypothesis. As we further clarify in the following, FCs contain the necessary ingredients for the existence of ecohydrological feedbacks that can cause this pattern via vegetation self-organisation.

## Clarifying misunderstandings

### Typical characteristics of the FC patterns

Getzin *et al.* (2015) have shown that FCs exhibit characteristic spatial patterns that are remarkably similar across different areas

Correspondence: Stephan Getzin, Department of Ecological Modelling, Helmholtz Centre for Environmental Research - UFZ, Permoserstr. 15, 04318 Leipzig, Germany. E-mail: stephan.getzin@ufz.de



**Fig. 1.** Gap patterns as a consequence of vegetation self-organisation are rare but may occur in arid environments where vegetation is unstable. The figure shows a gap pattern in Sudan (details given in Deblauwe *et al.*, 2011).

of northern Namibia, although the density of FCs in their study sites varied by a factor of 2. In a new analysis provided here, the Giribes G2-plot (Getzin *et al.*, 2015) has been extended to  $1000 \times 1000 \text{ m}^2$  (Fig. 2; Figure S1). We present the enlarged plot in this paper as an exemplary data set that confirms the very characteristic spatial pattern that is so typical for the FCs.

As a fundamental summary statistic of spatial pattern analysis we used the pair correlation function  $g(r)$  (Wiegand & Moloney, 2014), which describes the neighbourhood density of FCs at distance  $r$  away from the 'typical' FC, relative to the overall density of FCs in the study area (Getzin *et al.*, 2015). The FC characteristics as quantified by the pair correlation function  $g(r)$  include the following particular features:

- (i) At the first few metres,  $r < r_{\min}$ , we find the value of  $g(r) = 0$  (Fig. 2a). Thus, the centres of neighbouring FCs are always at least a distance of  $r_{\min}$  apart and no circle is detected by  $g(r)$  (i.e. strong regularity/overdispersion).
- (ii) The  $g(r)$  shows a first clear peak with high amplitude at a distance  $r \geq 12 \text{ m}$ , which indicates the most frequent distance between nearest-neighbour FCs. This first peak is pronounced and substantially outside the simulation envelopes of the null model of complete spatial randomness (Fig. 2a). This indicates a 'hexagonal' spatial arrangement where each FC has six nearest neighbours located at approximately the same distance from the focal circle. Note that a hexagonal pattern is a special form of a regular pattern with an extraordinary degree of spatial ordering.
- (iii) The  $g(r)$  shows a damped oscillation around the null model (Fig. 2a,b), indicating an extremely high degree of ordering of the pattern that persists well beyond the nearest neighbours. The second minimum of  $g(r)$  reflects the radius with 'empty space' behind the first (nearest) neighbours and the second peak of  $g(r)$  is the next row of neighbours. This fluctuation is also evident in the cumulative  $L$  function, which is basically the integral of  $g(r)$ , between  $r = 15 \text{ m}$  and  $r = 30 \text{ m}$  (Fig. 2c).
- (iv) The pattern is characterised by large-scale homogeneity, where  $g(r)$  and  $L(r)$  remain within the envelope of the null model of complete spatial randomness for all investigated

large scales up to  $r = 500 \text{ m}$  (Fig. 2b,c). This means that the smaller-scale ( $r < 50 \text{ m}$ ) properties (i–iii) of the hexagonal pattern are exactly preserved across a large area (hundreds of metres).

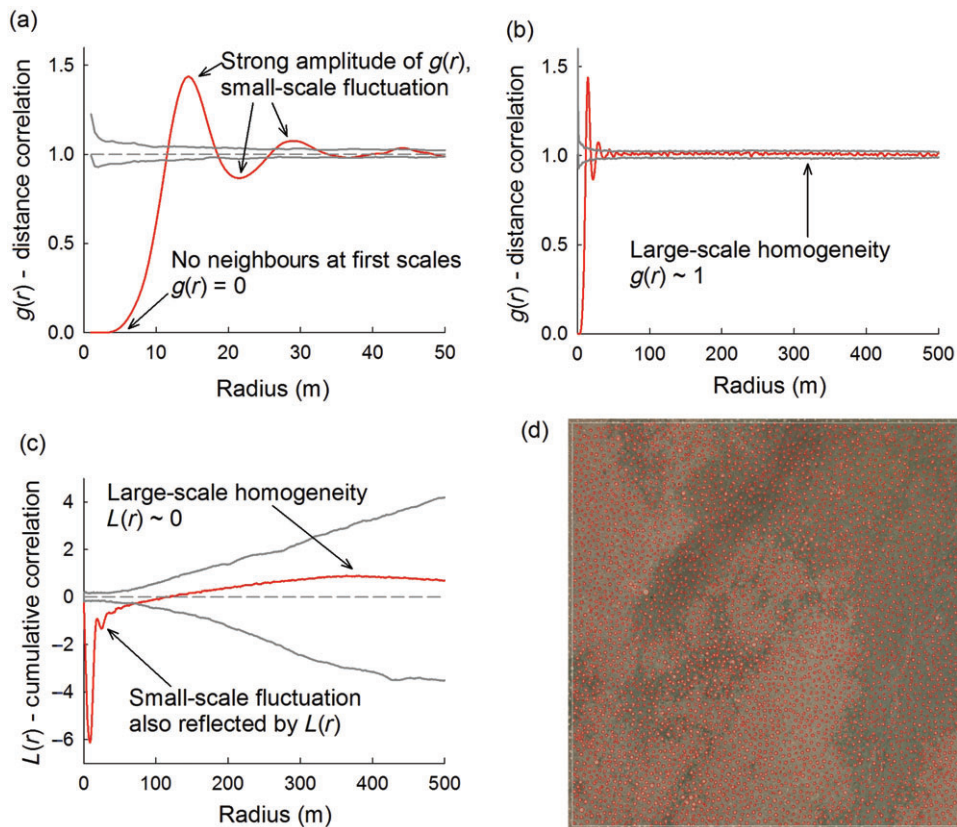
Furthermore, an additional Fourier analysis of four  $2 \times 2 \text{ km}^2$  plots of the Giribes plains demonstrates that all four plots have the same spectral peak at  $14 \text{ m}$  (Fig. S2). Hence, the FCs are equally strongly ordered at the large landscape scale. In summary, FCs not only exhibit a regular pattern (which is also known from insect nest patterns), but they additionally exhibit an exceptionally strong order that prevails equally over the landscape. Any mechanism for explaining the origin of FCs must account for all characteristics of the spatial structure (i–iv) captured by the pair correlation function.

#### *Insect nest patterns do not match fairy circle patterns*

The FC patterns described in the previous section agree in all aspects with patterns generated by ecohydrological feedbacks (Meron, 2012). However, they do not agree with the only two insect examples provided by Juergens *et al.* (2015), because neither the pair correlation function  $g(r)$  of *Macrotermes* (their Fig. 4c) nor that of *Pogonomyrmex* (their Fig. 4d) shows a first clear peak with high amplitude which is pronounced and substantially outside the simulation envelopes of the null model. So there is no strong deviation of the pair correlation function from the upper simulation envelopes of the random null model and therefore less strong ordering, as compared with the FC pattern. There is also no damped oscillation around the null model as described by us and shown in our Fig. 2a, but their  $g(r)$  fluctuates only within the simulation envelopes of the null model, i.e. no significant deviation. Thus, the two insect examples show regularity but they do not show the extreme ordering of the FC patterns. Additionally, the  $g(r)$  does not remain within the envelope of the null model for larger scales,  $r > 60 \text{ m}$ , indicating large-scale heterogeneity, as also reported for the *Pogonomyrmex* pattern by Wiernasz and Cole (1995).

We propose that, in particular, the non-mound building, subterranean termites and disc-clearing ants with hypogeal (below-ground) nests, such as *Pogonomyrmex*, are not able to create such extremely ordered, and at the same time large-scale, homogeneous patterns over hundreds and thousands of metres. This is shown by the low  $R$ -value of Clark and Evans (1954), which is, for *Pogonomyrmex*, just above one (e.g. 1.17; Picker *et al.*, 2012) as compared with  $\sim 1.6$  for FCs (see later). In light of this, the described migration behaviour of *Psammotermes* between ephemeral nests (Vlieghe *et al.*, 2015) seems unlikely to cause the extremely ordered pattern of FCs (see also McGlynn, 2012).

Nest distributions of insects are generally less ordered because young nests are typically aggregated (Adams & Tschinkel, 1995; Wiernasz & Cole, 1995; Korb & Linsenmair, 2001; Grohmann *et al.*, 2010) and small- and large-scale variabilities in colony or nest spacing are due to variability in colony age and size. Additionally, neighbouring colonies may have interdigitated foraging areas, interspecific competition may cause heterogeneity, founding queens can experience reduced survivorship near



**Fig. 2.** Spatial pattern analysis with the pair correlation function  $g(r)$  and its cumulative counterpart, the  $L$  function. The pair correlation function (red line) detects no fairy circles (zero values) for very small neighbourhood radii around focal circles and fluctuates strongly around the random null model (grey simulation envelopes). The dashed line of  $g(r) = 1$  indicates the mean expectation of the random null model. Panel (a) shows the spatial pattern analysis of the 1000 × 1000 m<sup>2</sup> Giribes plot (d) only up to  $r = 50$  m to emphasise the small-scale features of the pattern. Panel (b) shows the same function up to  $r = 500$  m. The large-scale homogeneity of the pattern is evident from the red line staying within the grey simulation envelopes of the homogeneous null model. Panel (c) shows analysis of the plot with the  $L$  function, where the large-scale homogeneity of the pattern is also evident from the red line being inside the envelopes.

existing colonies, or the number of dispersing queens may vary spatially (Crist & Wiens, 1996; McGlynn, 2012). These latter processes typically cause large-scale heterogeneity in nest patterns (Wiernasz & Cole, 1995; Schooley & Wiens, 2003; Davies *et al.*, 2014). Importantly, due to the inherent biotic population dynamics of insects, this large-scale heterogeneity can be completely independent of abiotic factors, such as altitude or soil type (Blanco-Moreno *et al.*, 2014).

The proposed sand termite hypothesis on the origin and maintenance of FCs takes the mima-like mounds (heuweltjies) of South Africa as an example of termite activity (Juergens, 2015; Vlieghe *et al.*, 2015; Juergens *et al.*, 2015). However, the only comprehensive tests of several competing hypotheses on the causation of heuweltjies, including the termite hypothesis, have been done by Cramer and Barger (2014) and Cramer and Midgley (2015), based on 11 and 10 mound characteristics, respectively, including spatial pattern analysis. Scientific progress rests always upon the latest evidence, so we concur with these newest studies and consider heuweltjies as being patterns primarily caused by vegetation interaction in combination with abiotic aeolian or erosion effects.

Owing to the water-limited environment, the uniform grasslands of the pro-Namib are unstable vegetation systems that are highly susceptible to disturbances which may initiate a vegetation gap. It has been shown that it is the strong competitive interaction between the grasses that forms the circular shape as a localised structure (Fernandez-Oto *et al.*, 2014). Grasses are probably forming a ring-like structure because a circle has the smallest circumference-to-area ratio. This optimises their water usage inside the gap and keeps the competing grasses from the matrix effectively outside. Since most self-organised vegetation patterns are created by just one or a few plant species (Barbier *et al.*, 2006; Deblauwe *et al.*, 2008), this mechanism will work at all FC areas alike, irrespective of whether the grassland community is composed of one or two species.

In light of this, we do not question that multiple disturbing agents, such as the irregularly spaced and poisonous remains of *Euphorbia* species (Meyer *et al.*, 2015), harvester termites (Becker & Getzin, 2000), ants (Picker *et al.*, 2012), or sand termites (Juergens, 2013), may potentially disrupt the grass matrix and cause vegetation-free patches at one point or another. However, none of these causal agents has, to the current stage



of knowledge, the ability to cause the observed highly ordered, and at the same time large-scale, homogeneous spacing that is so typical of the FCs. There are indeed some aggregated FCs that may have arisen due to insect activity, but these are locally confined disturbances that are not typical for the overall large-scale hexagonal spacing. In those untypical cases where mature FCs are close together and even overlapping each other, this is, rather, evidence against the termite hypothesis because an extremely ordered pattern such as the FCs requires very strong ordering forces.

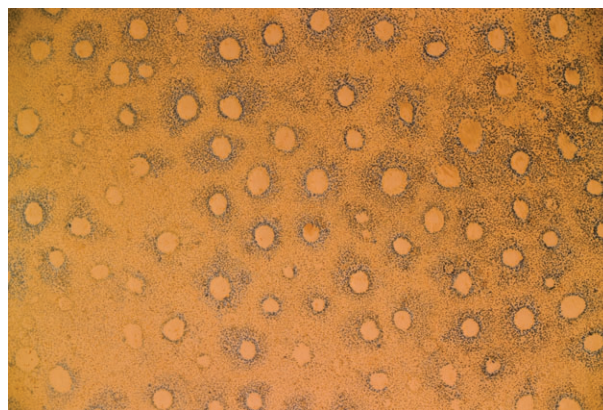
### *The mechanisms underlying self-organisation*

One common misperception in understanding vegetation self-organisation is the idea that the characteristic scales of the process causing a pattern should be identical to the characteristic scales of the pattern. However, by definition, self-organisation is a phenomenon in which a landscape pattern such as FCs emerges from local processes, such as root competition via positive feedback. In the context of FCs, Getzin *et al.* (2015) could identify two processes that are jointly capable of producing vegetation gap patterns with the characteristics (i–iv). These processes are: (i) local vegetation growth, which enhances water uptake by the plant's roots and forms soil-water gradients; and (ii) soil-water diffusion towards the vegetation growth locations. As demonstrated by Kinast *et al.* (2014), soil-water diffusion can accelerate the local vegetation growth but inhibit the growth in the neighbourhood at further distances because soil-water diffusion draws water from this neighbourhood. As water is limited in these unstable grasslands, this process may initiate plant death and subsequently a new FC emerges where the biomass and soil-water distributions are in so-called 'antiphase'. We refer the reader to Kinast *et al.* (2014; their Fig. 1b) and Figure S3, which show that the uptake-diffusion feedback can indeed generate the water reservoirs in the centre of the FCs, because once the vegetation dies off, precipitation of the next rainy season can percolate deeply into the soil. Note that this mechanism is also fully in agreement with the botanical observation of 20–30 cm lateral root length of *Stipagrostis* associated with FCs (Juergens, 2013).

Figure 3 shows that the matrix contains gradients of green biomass where the least, or even no, vegetation is found at large distances away from the gaps but biomass increases towards the water reservoirs of FCs. These biomass differences are equal to moisture differences in arid grasslands and it is likely that such subtle gradients are best revealed with special field techniques. For example, preliminary investigations based on stable isotope analysis have shown that, within days, there is water movement over more than 4 m between the inside of FCs and the matrix (M. Cramer, unpublished). The reasons why FCs are not re-colonised by plants have still to be solved. It is likely that the uppermost soil layer is too dry or too hot in the absence of plant shading and thus the bare soil state is stable, no matter whether gap diameters are 3 or 30 m.

### *Fairy circle dynamics*

Another misunderstanding is related to the timescales of FC dynamics. According to Tschinkel (2012), the final size of FCs

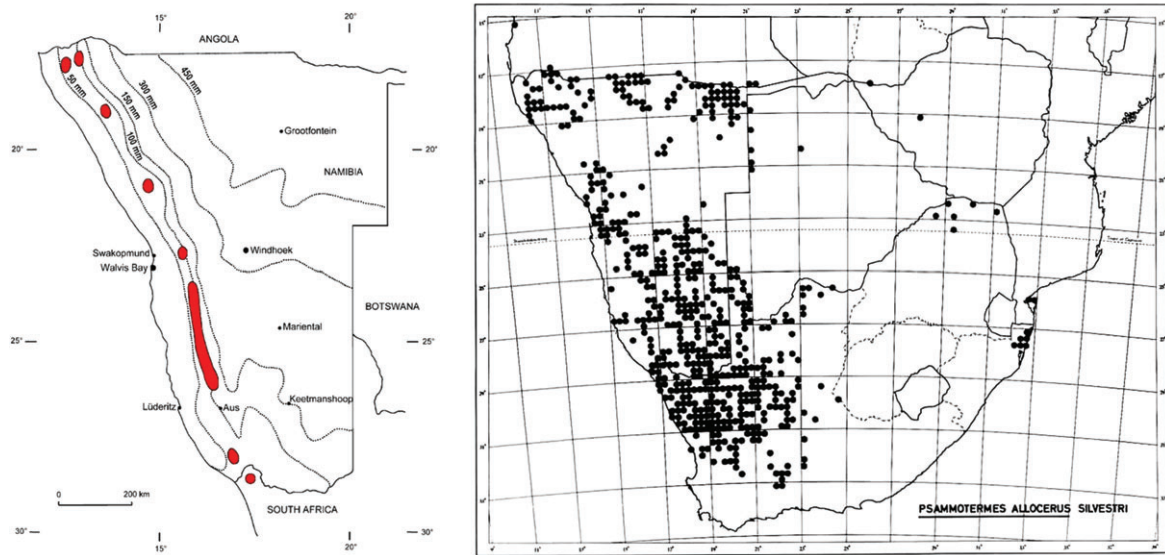


**Fig. 3.** Aerial image showing gradients of green biomass accumulation around the water reservoirs of fairy circles. According to vegetation self-organisation and the uptake-diffusion feedback, plants with higher biomass and transpiration will cause larger soil-moisture 'vacuums' around their root systems and thus have the ability to draw more water than plant neighbours with lower biomass. This positive, short-range ecohydrological feedback mechanism induces spatial gradients in water availability, leading to long-range moisture depletion and the death of grasses at distances further away from the fairy circles, thereby initiating a new gap. (Image: © Michael Fay, National Geographic Creative).

is reached within less than 4 years. This timescale is about 10-fold shorter than estimates of the life span of FCs. This is in agreement with pattern formation theory, which associates the appearance of gap patterns from a uniform state with the growth of spatially structured modes. This growth is determined by linear processes (i.e. can be described with linear equations), which are much faster than the non-linear processes that drive pattern changes. Although FCs do not appear instantly in their final size, it is relative to their life span that FCs seem to appear already in their final size.

Detailed investigations of the spatiotemporal pattern of FCs are needed to further advance our understanding of their generation. The anecdotic sequence of photographs showing the appearance of atypical small and aggregated FCs during wetter years and their sudden disappearance during drier years (Juergens *et al.*, 2015; their Fig. 1) strongly contradicts the results shown in Cramer and Barger (2013; their Fig. 5b,c), which demonstrate that the percentage of area covered by FCs and their individual area decreases with precipitation. It is also in strong contradiction with recent findings showing that FC disappearance relies on sequential years of good rainfall because grass cover has a positive relationship with rainfall in arid areas (Vlieghe *et al.*, 2015). Indeed, detailed statistical analyses of rain data from 1990 to 2012 and satellite images of four different areas of NamibRand Nature Reserve showed that new FCs appeared to a greater extent after accumulated below-average rainfall measured over at least 5 years and more FCs disappeared after accumulated above-average rainfall years (Zelnik *et al.*, 2015).

Most FC research has so far been undertaken at Wolwedans in the NamibRand Nature Reserve, which has an exceptionally high proportion of FC area ha<sup>-1</sup> (see Juergens, 2013). Zhang and Sinclair (2015) adopted the same Voronoi-tessellation approach

Distribution of fairy circles (left) and *Psammotermes* (right)

**Fig. 4.** There is no regional-scale correlation between the distributions of fairy circles and *Psammotermes allocerus*. But there is strong regional-scale correlation between fairy circles and the 70–120 mm rainfall isohyets. Unlike termites, self-organised processes related to plant competition for soil moisture can also explain the disappearance of fairy circles towards the east, where the mean annual precipitation exceeds 150 mm. The left map is after van Rooyen *et al.* (2004), and the right map is after Coaton and Sheasby (1973).

that we have previously used for FCs in north-west Namibia and they found that, also at Wolwedans, the proportion of six-cornered Voronoi tiles makes up  $\sim 45\%$ . Hence, a hexagonal spacing dominates the FCs in central Namibia, too, similar to the 43–46% found for Giribes and Marienfluss in north-west Namibia (Getzin *et al.*, 2015). In this regard, it should be emphasised that a ‘perfect’ hexagonal pattern will hardly be attained in nature. For such a pattern under the condition of maximum spacing, the theoretically expected  $R$ -value of Clark and Evans (1954) will be 2.1491. However, the  $R$ -values for Wolwedans lie in the range 1.59–1.63 (Zhang & Sinclair, 2015) and for the three plots at Giribes and Marienfluss in the range 1.60–1.61. Only our theoretical and more deterministic model of vegetation self-organisation attained a higher  $R$ -value of 1.85 and hexagons dominated the pattern with 57%. This demonstrates that stochasticity and associated ‘noise’ is partly affecting the spacing of observed FCs in nature, but nonetheless the dominance of hexagons indicates their extreme ordering. We emphasise here that it is not only the degree of pattern matching between FCs and a ‘clean’ theoretical model that supports the self-organisation hypothesis, but it is also the known low variability in the wavelengths of self-organised vegetation patterns (Meron, 2012; Figure S2), the decrease of FC cover with precipitation, and the dependency of the gap pattern on a very narrow rainfall range (Fig. 4) that leave self-organisation as the most reasonable working hypothesis.

### Scepticism towards the sand termite hypothesis

Not only are the FC spatial patterns unlikely to be caused by subterranean insects, but Vlieghe *et al.*’s (2015) proposed

mechanism of destructive feeding on live grasses appears doubtful. Sand termites of the genus *Psammotermes* are abundant in many regions of Africa, including the Sahel zone or Egypt, and the species *Psammotermes allocerus* is not confined to Namibia only but lives in neighbouring countries, too. If the sand termite were the ecosystem engineer claimed by Juergens (2013), we could expect that *P. allocerus* would eat holes in the grass throughout its entire range in southern Africa, and the other *Psammotermes* species should do that elsewhere in Africa too. But apparently it seems to be only able to eat holes in the grassland in a very narrow rainfall range from around 70 to 120 mm, which is the same narrow rainfall range that is necessary for vegetation self-organisation to generate gap patterns. Why does it not eat holes into the grassland at 160 or 180 mm rainfall? This is surprising because the sand termite is a wood and litter feeder and a ‘true habitat generalist’ (Zeidler, 1997), which occurs over the entire rainfall gradient from 30 mm to more than 600 mm. In areas with average rainfall below 420 mm, *Psammotermes* occurs with a probability of 50–90% (Zeidler, 1997). Moreover, there is not even a correlation between the regional-scale distribution of *P. allocerus* and FCs (Fig. 4). Clearly, FCs just coincidentally overlap with *Psammotermes*.

The supporters of the termite hypothesis often make a direct analogy between *Psammotermes* and the disc-clearing behaviour of the harvester ant *Pogonomyrmex* (Juergens *et al.*, 2015), but this analogy is weak. Several species of *Pogonomyrmex* (e.g. *P. occidentalis*, *P. barbatus* and *P. rugosus*) create bare areas (holes) over the wide 200–600 mm precipitation range of the arid to semi-arid grasslands of North America. Importantly, the different species all create the vegetation-free discs over this large range of ecosystems with

different MAP (Crist & Wiens, 1996; Schooley & Wiens, 2003; Nicolai *et al.*, 2010).

The sand termite hypothesis also cannot explain why FCs are strongly ordered at 120 mm MAP, and then become randomly distributed as rainfall increases, occupying only 1–2% of the land surface, and then suddenly disappear at the transition to 150 mm (Cramer & Barger, 2013). The argument of the sand termite hypothesis is that a rainfall-driven higher standing biomass would lead to greater faunal productivity and an expansion of social insect colonies (Juergens *et al.*, 2015). Why do we then find fewer FCs in more productive systems towards the east, if they are the primary result of termite activity? However, plant competition for water can explain the disappearance of FCs at the transition to 150 mm MAP, because these are the areas sufficiently moist for uniform, stable vegetation cover. Vegetation self-organisation can thus also explain the absence of FCs in the slightly moister Kalahari grasslands in the east of Namibia.

To support the termite hypothesis, it would be necessary to show that new FCs, caused by surviving new nests, appear at hexagonal spacing in-between older circles and not in an aggregated manner, as is typical for social insects. Additionally, it would be necessary to show that it was not plant necrosis following competition for water that initiated a fairy circle but that termites actually caused, not merely colonised, the new gap with dead plants. So far, only correlation between FCs and *Psammotermes* has been shown, not causation – a correlation that is also evident for other termite and ant species (Picker *et al.*, 2012; Juergens, 2013, suppl. data).

The hypothesised dependency of *P. allocerus* on the water reservoir deep inside FCs is also not as certain as suggested by Juergens (2013). For example, the water balance of *P. allocerus* has been studied in detail by Grube and Rudolph (1995) in the sparsely vegetated central Namib with annual rainfall < 28 mm, where, for example, ‘early morning dew during the winter months ... moistens the soil surface and seeps away into the sand’. The important facts that early morning dew does occur at all FC areas and that ‘fog is still frequent up to 80 km inland’ (van Rooyen *et al.*, 2004) have been overseen by Juergens *et al.* (2015). Both provide essential sources of water at the soil surface. In this context, Grube and Rudolph (1995) emphasise that ‘the only reliable source of water supply for *P. allocerus* is the water confined in the soil capillary system; to get access to this water the hypopharyngeal surface is firmly pressed to the soil surface’. This independence of deep-reaching water reservoirs could explain why Vlieghe *et al.* (2015) found similar high termite numbers inside and outside of FCs when comparing mature and senescent circles with the matrix vegetation. If the survival of *Psammotermes* does not rely on the water reservoir of the FCs, as suggested by the study of Grube and Rudolph (1995), the proposed causal link between sand termites and the typical hexagonal spacing pattern of FCs is weakened.

## Conclusion

Science works in a way that new knowledge builds upon old knowledge. In our paper (Getzin *et al.*, 2015) we provided new

observations on the spatial patterns of FCs, and all subsequent studies aiming to explain the formation of FCs must account for these observations and, specifically, the four particular characteristics of these patterns defined here. In our view, subterranean sand termites can explain neither the extremely ordered patterns that extend homogeneously over dozens of square kilometres in the landscape nor the confined regional-scale distribution of FCs or their sudden disappearance at moister areas around 150 mm MAP.

In contrast, based on many observations from the world’s drylands and on ‘aggregated knowledge’ provided in aerial images, we argue that vegetation self-organisation is very well-known to ultimately cause such patterns and the distribution within a narrow precipitation range. Resolving the FC mystery requires future research, and in particular, more data are needed that document the dynamics of emerging and vanishing FCs in this fascinating ecosystem.

## Acknowledgements

We thank the editor and two anonymous referees for their time and effort in helping to improve this manuscript. S.G. and T.W. were supported by the ERC advanced grant no. 233066 to T.W.

## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12267

**Figure S1.** For this study we analysed the spatial pattern of the Giribes G2-plot used in Getzin *et al.* (2015) but extended its size from the previously used 25 ha (lower interior square) to 100 ha. With this 1000 × 1000 m<sup>2</sup> plot we were able to analyse the spatial patterns up to neighbourhood radii of  $r = 500$  m. The upper 25 ha square is the G1-plot which was also analysed in Getzin *et al.* (2015).

**Figure S2.** Four 2 × 2 km<sup>2</sup> plots of the Giribes plains (a) were examined with a Fourier analysis (b). These are additionally analysed plots to enlarge the examined landscape extent. The power spectra of the four plots show the same peak at 14-m distance in-between fairy circles, which indicates that their hexagonal ordering is based on the same wavelength in the entire landscape. This implies that the exceptional strength of the ordering forces is related to a homogeneously limiting resource factor which is most likely soil water in this arid grassland–desert transition.

**Figure S3.** The left image shows the most relevant feedback mechanism for fairy circles, which is the uptake-diffusion feedback. Stronger plants transpire more water than weaker plants, thereby they draw more water from their neighbourhoods, enabling them to grow even more vigorously (positive feedback loop). The image on the right is after Kinast *et al.* (2014, their Fig. 1b) and shows the ‘antiphase’ behaviour of biomass and soil-water distributions.



## References

- Adams, E.S. & Tschinkel, W.R. (1995) Spatial dynamics of colony interactions in young populations of the fire ant *Solenopsis invicta*. *Oecologia*, **102**, 156–163.
- Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V. & Lejeune, O. (2006) Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. *Journal of Ecology*, **94**, 537–547.
- Becker, T. & Getzin, S. (2000) The fairy circles of Kaokoland (north-west Namibia) – origin, distribution, and characteristics. *Basic and Applied Ecology*, **1**, 149–159.
- Blanco-Moreno, J.M., Westermann, P.R., Atanackovic, V. & Torra, J. (2014) The spatial distribution of nests of the harvester ant *Messor barbarus* in dryland cereals. *Insectes Sociaux*, **61**, 145–152.
- Clark, P.J. & Evans, F.C. (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, **35**, 445–453.
- Coaton, W.G.H. & Sheasby, J.L. (1973) National survey of the isoptera of southern Africa. 3. The genus *Psammotermes* Desneux (Rhinoitermitidae). *Cimbebasia*, **3**, 19–28.
- Cramer, M.D. & Barger, N.N. (2013) Are Namibian ‘fairy circles’ the consequence of self-organizing spatial vegetation patterning? *PLoS ONE*, **8**, e70876.
- Cramer, M.D. & Barger, N.N. (2014) Are mima-like mounds the consequence of long-term stability of vegetation spatial patterning? *Palaeogeography, Palaeoclimatology, Palaeoecology*, **409**, 72–83.
- Cramer, M.D. & Midgley, J.J. (2015) The distribution and spatial patterning of mima-like mounds in South Africa suggests genesis through vegetation induced aeolian sediment deposition. *Journal of Arid Environments*, **119**, 16–26.
- Crist, T.O. & Wiens, J.A. (1996) The distribution of ant colonies in a semiarid landscape: implications for community and ecosystem processes. *Oikos*, **76**, 301–311.
- Davies, A.B., Levick, S.R., Asner, G.P., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2014) Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography*, **37**, 852–862.
- Deblauwe, V., Barbier, N., Couteron, P., Lejeune, O. & Bogaert, J. (2008) The global biogeography of semiarid periodic vegetation patterns. *Global Ecology and Biogeography*, **17**, 715–723.
- Deblauwe, V., Couteron, P., Lejeune, O., Bogaert, J. & Barbier, N. (2011) Environmental modulation of self-organized periodic vegetation patterns in Sudan. *Ecography*, **34**, 990–1001.
- Fernandez-Oto, C., Tlidi, M., Escaff, D. & Clerc, M.G. (2014) Strong interaction between plants induces circular barren patches: fairy circles. *Philosophical Transactions of the Royal Society A*, **372**, 20140009.
- Getzin, S., Wiegand, K., Wiegand, T., Yizhaq, H., von Hardenberg, J. & Meron, E. (2015) Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia. *Ecography*, **38**, 1–11.
- Goudie, A.S. & Viles, H.A. (2015) *Landscapes and Landforms of Namibia*. Springer, Dordrecht, Netherlands.
- Grohmann, C., Oldeland, J., Stoyan, D. & Linsenmair, K.E. (2010) Multi-scale pattern analysis of a mound-building termite species. *Insectes Sociaux*, **57**, 477–486.
- Grube, S. & Rudolph, D. (1995) Termites in arid environments: the waterbalance of *Psammotermes allocerus* Silvestri. *Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie*, **10**, 665–668.
- Juergens, N. (2013) The biological underpinnings of Namib Desert fairy circles. *Science*, **39**, 1618–1621.
- Juergens, N. (2015) Exploring common ground for different hypotheses on Namib fairy circles. *Ecography*, **38**, 12–14.
- Juergens, N., Vlieghe, K., Bohn, C., Erni, B., Gunter, F., Oldeland, J. *et al.* (2015) Weaknesses in the plant competition hypothesis for fairy circle formation and evidence supporting the sand termite hypothesis. *Ecological Entomology*, **40**, 661–668. DOI: 10.1111/een.12266.
- Kinast, S., Zelnik, Y.R., Bel, G. & Meron, E. (2014) Interplay between Turing mechanisms can increase pattern diversity. *Physical Review Letters*, **112**, 078701.
- Korb, J. & Linsenmair, K.E. (2001) The causes of spatial patterning of mounds of a fungus-cultivating termite: results from nearest-neighbour analysis and ecological studies. *Oecologia*, **127**, 324–333.
- McGlynn, T.P. (2012) The ecology of nest movement in social insects. *Annual Review of Entomology*, **57**, 291–308.
- Meron, E. (2012) Pattern-formation approach to modelling spatially extended ecosystems. *Ecological Modelling*, **234**, 70–82.
- Meyer, J.J.M., Senejoux, F., Heyman, H.M., Meyer, N.L. & Meyer, M.A. (2015) The occurrence of triterpenoids from *Euphorbia gum-mifera* inside the fairy circles of Garub in the southern Namibian pro-desert. *South African Journal of Botany*, **98**, 10–15.
- Nicolai, N., Feagin, R.A. & Smeins, F.E. (2010) Spatial patterns of grass seedling recruitment imply predation and facilitation by harvester ants. *Environmental Entomology*, **39**, 127–133.
- Picker, M.D., Ross-Gillespie, V., Vlieghe, K. & Moll, E. (2012) Ants and the enigmatic Namibian fairy circles – cause and effect? *Ecological Entomology*, **37**, 33–42.
- Rietkerk, M. & van de Koppel, J. (2008) Regular pattern formation in real ecosystems. *Trends in Ecology and Evolution*, **23**, 169–175.
- van Rooyen, M.W., Theron, G.K., van Rooyen, N., Jankowitz, W.J. & Matthews, W.S. (2004) Mysterious circles in the Namib Desert: review of hypotheses on their origin. *Journal of Arid Environments*, **57**, 467–485.
- Schooley, R.L. & Wiens, J.A. (2003) Spatial patterns, density dependence, and demography in the harvester ant, *Pogonomyrmex rugosus*, in semi-arid grasslands. *Journal of Arid Environments*, **53**, 183–196.
- Tschinkel, W.R. (2012) The life cycle and life span of Namibian fairy circles. *PLoS ONE*, **7**, e38056.
- Vlieghe, K., Picker, M.D., Ross-Gillespie, V. & Erni, B. (2015) Herbivory by subterranean termite colonies and the development of fairy circles in SW Namibia. *Ecological Entomology*, **40**, 42–49.
- Wiegand, T. & Moloney, K.A. (2014) *A Handbook of Spatial Point Pattern Analysis in Ecology*. Chapman and Hall/CRC Press, Boca Raton, Florida.
- Wiernasz, D.C. & Cole, B.J. (1995) Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality and overdispersion. *Journal of Animal Ecology*, **64**, 519–527.
- Zeidler, J. (1997) *Distribution of termites (isoptera) throughout Namibia – environmental connections*. Thesis, Faculty of Science, University of the Witwatersrand, Johannesburg, South Africa.
- Zelnik, Y.R., Meron, E. & Bel, G. (2015) Gradual regime shifts in fairy circles. *PNAS*. DOI: 10.1073/pnas.1504289112.
- Zhang, H. & Sinclair, R. (2015) Namibian fairy circles and epithelial cells share emergent geometric order. *Ecological Complexity*, **22**, 32–35.

Accepted 3 August 2015

First published online 1 October 2015

Associate Editor: Rebeca Rosengaus