Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia

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The mysterious 'fairy circles' are vegetation-free discs that cover vast areas along the pro-Namib Desert. Despite 30 yr of research their origin remains unknown. Here we adopt a novel approach that focuses on analysis of the spatial patterns of fairy circles obtained from representative 25-ha aerial images of north-west Namibia. We use spatial point pattern analysis to quantify different features of their spatial structures and then critically inspect existing hypotheses with respect to their ability to generate the observed circle patterns. Our working hypothesis is that fairy circles are a self-organized vegetation pattern. Finally, we test if an existing partial-differential-equation model, that was designed to describe vegetation pattern formation, is able to reproduce the characteristic features of the observed fairy circle patterns. The model is based on key-processes in arid areas such as plant competition for water and local resource-biomass feedbacks.

The fairy circles showed at all three study areas the same regular spatial distribution patterns, characterized by Voronoi cells with mostly six corners, negative correlations in their size up to a distance of 13 m, and remarkable homogeneity over large spatial scales. These results cast doubts on abiotic gas-leakage along geological lines or social insects as causal agents of their origin. However, our mathematical model was able to generate spatial patterns that agreed quantitatively in all of these features with the observed patterns. This supports the hypothesis that fairy circles are self-organized vegetation patterns that emerge from positive biomass-water feedbacks involving water transport by extended root systems and soil-water diffusion. Future research should search for mechanisms that explain how the different hypotheses can generate the patterns observed here and test the ability of self-organization to match the birth- and death dynamics of fairy circles and their regional patterns in the density and size with respect to environmental gradients.

The so-called 'fairy circles' of Namibia are round barren patches devoid of any vegetation. They have varying diameters of a few meters to more than 20 m and occur in millions within the arid grassland matrix of western Namibia, from southern Angola to northern South Africa (van Rooyen et al. 2004, Juergens 2013). Despite their vast distribution over the landscape and regular spotting by local inhabitants, tourists, pilots or researchers, they still remain mysterious. Although evidence indicates that circles regularly appear and disappear (Albrecht et al. 2001) with average life-spans of probably 40–60 yr (Tschinkel 2012) or hundreds of years (Juergens 2013), their actual creation has never been directly witnessed in the field. This lack of direct observation can be attributed to the remoteness of the location of fairy circles – they occur along the 50–150 mm rainfall isohyet of the pro-Namib Desert – and also to the difficulty of monitoring underground processes during fairy circle creation. As a consequence, the mechanisms behind the creation of fairy circles remain unclear (Jankowitz et al. 2008, Tschinkel 2012), but several hypotheses exist.

An early hypothesis by Tinley (1971) related fossil nests of termites to the distribution of circles, and Theron (1979) proposed that the circular patches would be caused by allelopathic chemicals originating from extinct poisonous plants such as *Euphorbia damarana*. These hypotheses, or related speculations on growth-inhibiting radioactive compounds, are nowadays rejected because no support was found during field surveys (van Rooyen et al. 2004). One of the most popular hypotheses on the origin of fairy circles is grass or seed harvesting by social insects such as termites (Moll 1994, Becker and Getzin 2000, Albrecht et al. 2001, Juergens 2013) or ants (Picker et al. 2012). It is believed that the clearing of vegetation results in disc-like structures, similar to those observed for harvester ants in North America (Wiernasz and Cole 1995, Alba-Lynn and Detling 2008), and previous field studies

have demonstrated correlation of fairy circles with ants or termites (Picker et al. 2012, Juergens 2013). Abiotic gas leakage has also been proposed as causal agent. Naude et al. (2011) suggested that fairy circles are the surface expression of geochemical hydrocarbon microseepage. Hydrocarbon microseepage is, for example, composed of methane, ethane, propane, butane and pentane that can alter the physical, chemical, mineralogical, botanical, and microbiological environment (Lammoglia et al. 2008). Near the surface, the gases can displace the soil atmosphere and cause oxygen depletion around roots, resulting in plant stress and even plant death. Finally, our working hypothesis is that competition of grass for water together with positive biomass-water feedbacks involving water transport towards growing vegetation patches results in self-organized vegetation patterns (Tlidi et al. 2008, Meron 2012). A recent field study by Cramer and Barger (2013), based on examining edaphic properties, supported this hypothesis.

Here we propose a different approach to shed light on the phenomenon of fairy circles. We use the rich source of information that is provided by the landscape-scale spatial distribution pattern of fairy circles and conduct detailed analyses of these patterns (McIntire and Fajardo 2009, Wiegand and Moloney 2014). The underlying rationale is that spatial distribution patterns of plants or gaps between plants contain information on processes that have likely caused the current patterns (Stoll and Bergius 2005, Getzin et al. 2008). Thus, such vegetation patterns are 'ecological archives' whose spatial signature can be decoded with spatially explicit statistics. We estimate here several summary statistics of spatial structure to capture different features of the patterns that may hint to the underlying processes (Wiegand et al. 2013). Once we know the detailed characteristics of the spatial patterns we can ask if the mechanisms underlying the different hypotheses would be able to generate patterns with these characteristics (McIntire and Fajardo 2009). This is an approach of 'strong inference' (Platt 1964, Grimm et al. 2005) which is common in most fields of science. However, our study is not limited to description of patterns; we also verify that a mechanistic model, which is an implementation of our working hypothesis on the self-organized origin of the fairly circles, is indeed able to generate spatial patterns that agree with the observed patterns (Wiegand et al. 2003, Grimm et al. 2005).

In this study we provide a novel spatially-explicit perspective to fairy circle research, combining several innovative techniques such as remote sensing, spatial pattern analysis, and vegetation modelling. First, we analyze the spatial patterns of fairy circles found in 25-ha plots obtained from three aerial images of north-west Namibia. Based on this analysis, we then critically inspect the three main hypotheses

on fairy circles (summarized in Table 1) with respect to their ability to generate the observed spatial patterns. Finally, we show that a continuum partial-differential-equations model for vegetation pattern formation is indeed able to reproduce the detailed features of the observed fairy circle patterns. Any hypothesis on the origin of fairy circles must account for the detailed features of their spatial patterns revealed here, and our ultimate goal is to inspire researchers to search for mechanisms that explain how their favoured hypothesis can generate such patterns.

Material and methods

Aerial images

We analyzed aerial images (NIR orthophotos of 1 m/pixel resolution bought from the Ministry of Lands and Resettlement) of north-west Namibia from 2008 and established three sample squares of 500×500 m (Fig. 1). One of these study plots was located in the Marienfluss Valley (17°35.701′S, 12°36.017′E). This plot, thereafter called 'M', had a relatively low density of circles. The other two plots were located approximately 175 km further to the south in the Giribes Plain: the plot 'G1' (19°0.058′S, 13°19.578′E) had a much higher density than the Marienfluss plot and the plot 'G2' (19°0.873′S, 13°19.772′E) had the highest density of circles we could find based on aerial images of north-west Namibia. With this design we have selected three replicate plots that represent a gradient from low to high densities. Due to their spatial separation the plots of the Marienfluss and Giribes Plain are considered as independent sample regions. Plots were placed at homogeneous locations and were thus not affected by heterogeneities such as dry riverbeds, roads or rock outcrops which are not related with our question. The three chosen sample plots belong to the ephemeral *Stipagrostis uniplumis* grasslands with mean annual precipitation of just below 100 mm (Becker and Getzin 2000).

All fairy circles within a plot were manually delineated to create shapefiles (a geospatial vector data format digitized with ArcGIS-9.3 software). Thus for each circle we created one shapefile with geo-referenced information on the circle's x,y-coordinate (centre of mass), area and perimeter. These data were subsequently analyzed with spatial statistics.

Spatial point pattern analysis

The fairy circles are ideal point patterns because they are easily recognizable in aerial images and as nearly round patches, they have clearly defined x,y-positions and diameters. So far fairy circles have not yet been analyzed with advanced

Table 1. The most popular hypotheses on the potential processes causing fairy circles and resulting spatial patterns under expectation. See Discussion section for more explanations.

| Hypothesized process	Expected spatial pattern
1) Abiotic gas leakage, geochemical hydrocarbon microseepage	Clustering on the plot scale and influence of large-scale geological heterogeneity on patterns
2) Grass harvesting by social insects such as termites or ants	Small-scale regularity or randomness, but large-scale clustering due to internal effects of population dynamics
3) Self-organization by plants due to strong competition for water, positive small-scale feedback effects	Hexagonal grid-like spacing of circles, upper limit of density constraints, homogeneous patterns at large scales
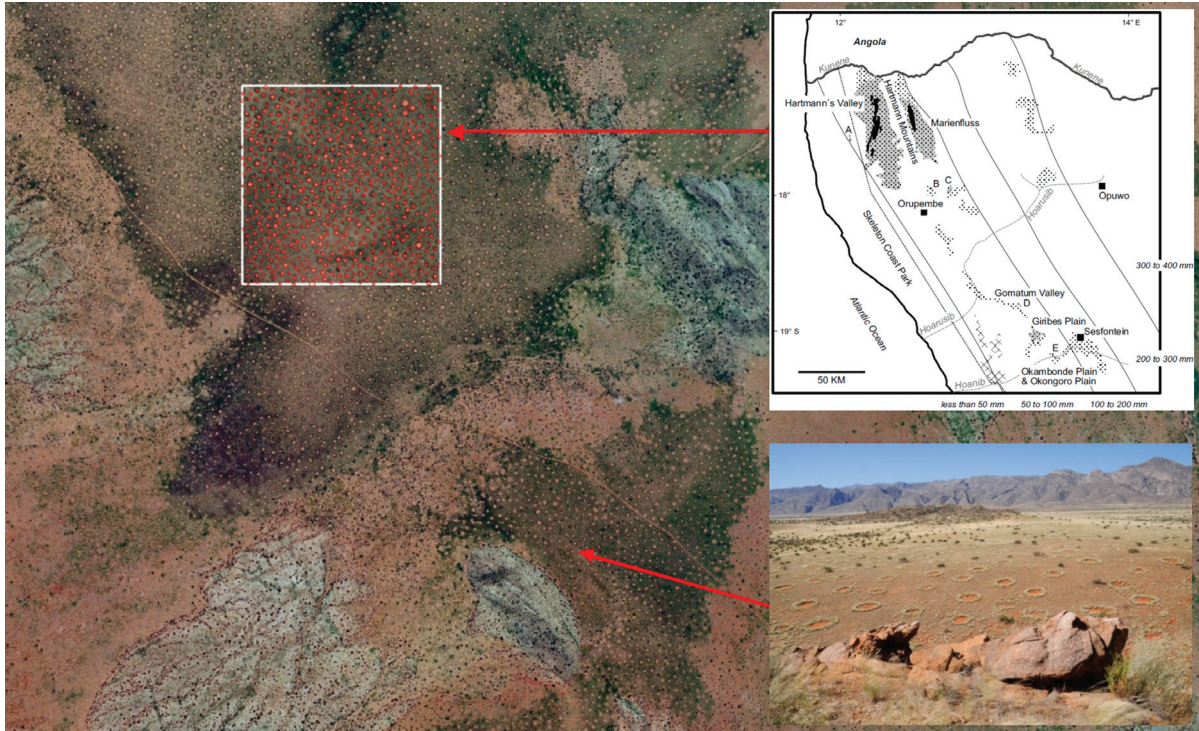
Figure 1. Aerial image of the Marienfluss Valley with digitized fairy circles within a 500×500 m plot (white square). The upper right map illustrates north-west Namibia with the arrow coming from the Marienfluss area, and the Giribes Plain in the south of the map (image adapted from Becker and Getzin 2000). The lower right small photograph shows the fairy circles of the area where the arrow points to. This photograph was taken in May 2009 from the rocky hill (grey in aerial image).

point pattern methods (but see Albrecht et al. 2001 for nearest-neighbour analysis). Unlike nearest-neighbour indices, functional summary statistics such as the pair-correlation or the mark-correlation functions have the advantage that they describe patterns across a wide range of scales that define plant neighbourhoods in continuous space (Wiegand and Moloney 2014). Therefore, critical scales, of for example, competitive interaction due to limiting resources or facilitation due to shared habitat can be assessed and compared for different environmental conditions (Getzin et al. 2008).

In a first analysis we computed Voronoi tessellations for the point patterns (Illian et al. 2008). Voronoi tessellation determines for a given circle centre the surrounding area which is closer to the circle centre than to any other circle centre of the pattern (called Voronoi cell or tile). Two properties of the tile are of special interest. First, the number of corners provides information on the regularity of the pattern (the more tiles have six corners, the more regular is the pattern; Supplementary material Appendix 1, Fig. A1). Note that the tiles of a completely regular pattern (where the distance of all points to their nearest neighbour is exactly the same) all have six corners (i.e. a honeycomb). A second important property is the distribution of the tile areas. For this purpose and for the nearest-neighbour analysis of circles, edge tiles with corners touching the plot borders were removed.

To reveal the degree of smaller-scale order in the pattern of fairy circles we used the pair-correlation function $g(r)$, which is the expected density of points at a given distance r of an arbitrary point, divided by the intensity λ of the pattern. The non-cumulative pair-correlation

function is particularly suitable to reveal critical scales of the pattern (Wiegand and Moloney 2014). Under complete spatial randomness (CSR), $g(r) = 1$. Values of $g(r) < 1$ indicate regularity (or also called overdispersion), while values of $g(r) > 1$ indicate aggregation. In a third analysis, we used a summary statistic based on Ripley's K-function, the cumulative counterpart to $g(r)$, i.e. $K(r) = 2\pi \int_{t=0}^{r} g(t)\,t\,dt$ to assess departures from CSR at larger distances (Getzin et al. 2008). We used the L-function $L(r) = r\left(\sqrt{K(r)/\pi} - 1\right)$ which makes visual interpretation easier; under CSR, $L(r) = 0$ and values of $L(r) < 0$ indicate regularity, while values of $L(r) > 0$ indicate aggregation.

Finally, we were interested if the sizes of two nearby circles showed spatial correlations that depended on their distance r. This was analyzed with the mark-correlation function, $k_{mm}(r)$, for the continuous mark 'area' of the fairy circle. The mark-correlation function $k_{mm}(r)$ is the mean value of the test function $t_1(m_i, m_j) = m_i \, m_j$ of the marks of two points i and j that are separated by distance r, respectively, normalized by the mean value of the test function taken over all $i - j$ pairs regardless of their distance (Illian et al. 2008, Wiegand and Moloney 2014). If the marks show no spatial correlations, we find $k_{mm}(r) = 1$, if $k_{mm}(r) < 1$, there is negative correlation between the marks at scale r (inhibition), and if $k_{mm}(r) > 1$ there is a positive correlation between the marks at scale r (i.e. mutual stimulation).

The summary statistics $g(r)$ and $L(r)$ were assessed against the Poisson null model (CSR) using the 5th-lowest and 5th-highest values of 199 Monte Carlo simulations

to generate approximately 95% simulation envelopes. Similarly, the mark-correlation function was assessed against the independent marking null model by randomly shuffling the mark 'area'. The functions were analyzed up to a maximal radius of 250 m in steps of 0.5 m resolution. All analyses were done using R-software (package Spatstat; <www. R-project.org/>).

The mathematical model

Formation of vegetation patterns in models of self-organization can emerge from small-scale positive feedbacks that lead to large-scale self-organized patchiness. The common denominator of these feedbacks is water transport towards growing vegetation patches, either by overland water flow, soil-water diffusion or water conduction through extended roots. While helping local patch growth (short range activation) these processes inhibit the growth in the surroundings of the patch (long-range inhibition), thereby promoting pattern formation (Meron 2012). In actual landscapes, however, self-organization is unlikely to be the sole driver of vegetation patchiness; environmental heterogeneity (Getzin et al. 2008) and physical templates may interfere with and even enhance the pattern forming feedbacks to create more complex forms of vegetation patchiness (Sheffer et al. 2013).

Fairy circles correspond to a hexagonal array of gaps that can emerge from uniform vegetation under increasing water stress (Tlidi et al. 2008, Meron 2012; Fig. 2). However, an important question is how well the real-world patterns of fairy circles match those predicted by self-organization models? We therefore analyzed patterns generated by the model in the same way as the observed patterns. Only if the modelled processes faithfully reflect the internal organization of the observed system, we will find simultaneous match in several characteristics of the spatial patterns (Wiegand et al. 2003, Grimm et al. 2005).

We used the continuum, partial-differential-equations model introduced by Gilad et al. (2004, 2007), hereinafter also referred to as 'Gilad et al. model'. It consists of a system of nonlinear partial integro-differential equations for a biomass variable $B(x,y,t)$, representing the above-ground biomass per unit ground area, a soil-water variable, $W(x,y,t)$, describing the water content available to the plants per unit ground area, and a surface water variable, $H(x,y,t)$, describing the height of a thin water layer above ground level (i.e. runoff).

The model captures two main pattern-forming feedbacks, increased infiltration of surface water in biomass patches relative to bare soil, and root augmentation in response to biomass growth (Meron 2012). The latter feedback can be implemented for two distinct forms of root architecture, laterally extended and laterally confined root systems. The two feedbacks are positive in the sense that locally growing vegetation draws water from its surrounding, which accelerates its growth and further increases the water transport towards the growing vegetation. They are both capable of forming patterns because the depletion of soil water in the vicinities of growing vegetation patches inhibits vegetation growth there and favours the growth of non-homogeneous perturbations.
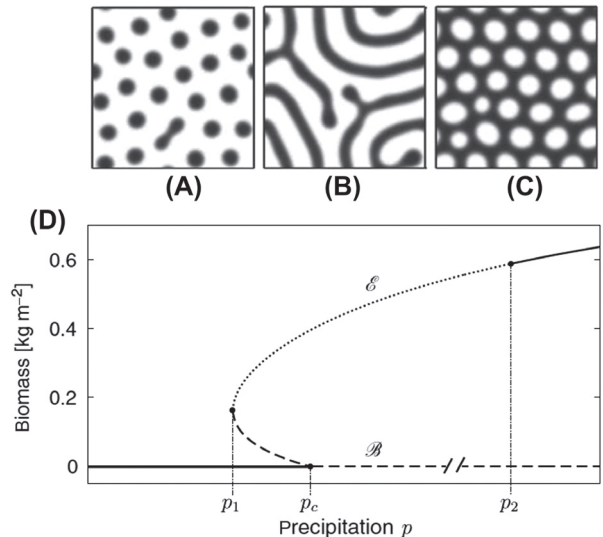

Figure 2. Bifurcation diagram for stationary uniform solutions of the Gilad et al. model (2004, 2007; panel (D)). Solid lines represent linearly stable solutions, dashed lines represent solutions that are unstable to uniform perturbations, and dotted lines represent solutions that are unstable to non-uniform perturbations. Bare soil ($\mathscr{B}$) is stable at low precipitation rates ($p < p_c$) whereas uniform vegetation ($\mathscr{E}$) is stable at high precipitation rates ($p > p_2$), as the solid lines indicate. In between stable pattern states exist, examples of which are shown in panels (A–C). Dark shades of grey represent high biomass. The uniform vegetation state destabilizes at $p = p_2$ to a periodic gap pattern similar to fairy circles, consisting of a hexagonal array of gaps in uniform vegetation (from Gilad et al. 2007).

The water-transport mechanism depends on the particular feedback considered. For the fairy circles that occur in sandy soils, the infiltration feedback appears to be irrelevant because of the high infiltration rate of surface water into sandy soil. The root-augmentation feedback, however, does apply to plant species with laterally extended roots but can also apply to plant species with laterally confined roots, provided soil-water diffusion is fast enough relative to the biomass colonization rate.

Figure 2 shows a bifurcation diagram displaying two uniform solutions of the model equations, describing bare soil and uniform vegetation, along the non-dimensional precipitation axis p, and their stability properties. The uniform vegetation solution loses stability below a threshold precipitation value, $p = p_2$, to non-homogeneous perturbations whose growth leads to a hexagonal gap pattern (Fig. 2C). As the precipitation rate is further decreased a transition to stripe or labyrinthine patterns occurs (Fig. 2B), which is followed by another transition to hexagonal spot patterns (Fig. 2A). Below $p = p_1$ a transition to bare soil takes place. Note that the bare soil solution remains stable above $p = p_1$ and loses stability only at $p = p_c$ (to homogeneous perturbations).

In this study a precipitation value just below $p = p_2$ is chosen where gap patterns (i.e. fairy circles) prevail (Fig. 2). The specific value we choose corresponds to a mean annual precipitation (MAP) of 100 mm which is about the isohyet where the fairy circles of our study sites occur. Because of the sandy soils we assumed that the infiltration rate is con-

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stant (no infiltration contrast between vegetation patches and bare soil, or $f = 1$ in the model equations). We obtained gap patterns for relatively large values for the root-to-shoot ratio, a parameter that controls the strength of the root-augmentation feedback (i.e. $\eta = 1.8$), and high soil-water diffusivity (i.e. $\delta w >> \delta b$). The specific values of the additional non-dimensional parameters were: $\nu = 2$, $\alpha = 6$, $\gamma = 3$, $\rho = 0.6$, $q = 0.05$, $\delta b = 0.042$, $\delta w = 41.7$. For more details about the model, including the definitions of the model parameters, the reader is referred to Gilad et al. (2007).

Results

Point pattern analysis of fairy circles observed in aerial images

We found a total of 630, 1079, and 1217 fairy circles in the 25-ha plots of Marienfluss 'M', Giribes 'G1', and 'G2', respectively (Fig. 3a–c). The diameters of digitized circles ranged from 1.98 to 15.38 m with a mean of almost 6 m (Table 2). The total area of bare circular patches ranged from 7.6 to 12.7 and 14.4%, agreeing approximately with the 7.3 and 13% area coverage found for the Namib Rand Nature Reserve (Albrecht et al. 2001, Tschinkel 2012) and with the 6.3 and 10.1% found for the Marienfluss and Giribes, respectively (Juergens 2013). The M-plot with the lowest cover yielded the largest mean nearest-neighbour distances of around 16 m (M-plot), and the G2-plot with the highest cover yielded the shortest nearest-neighbour distances of around 11 m (Table 2).

We counted 543, 954, and 1095 inner tiles around circles in the M-, G1-, and G2-plots, respectively (Fig. 3e–g). Tile areas appeared visually normally distributed (Fig. 3i–k), but according to the Anderson–Darling test they were not strictly normally distributed (p < 0.001, < 0.001, and < 0.05 for the M-, G1-, and G2-plots, respectively). Due to considerable differences in the densities of circles, the mean of tile areas ranged from 397 m^2 (M) to 205 m^2 (G2). The polygons obtained with Voronoi tessellations resulted in a dominance of hexagonal structures around each fairy circle with a mean number of corners of Voronoi tiles of 5.97 (M, G2) and 5.98 (G1). Tiles with six corners occurred in 43 to 46% of all observed tiles (Table 2; Fig. 3e–g), but, only in 27 and 29% of the random and clustered point patterns, respectively, that had the same point density as the Marienfluss site (Supplementary material Appendix 1, Fig. A1).
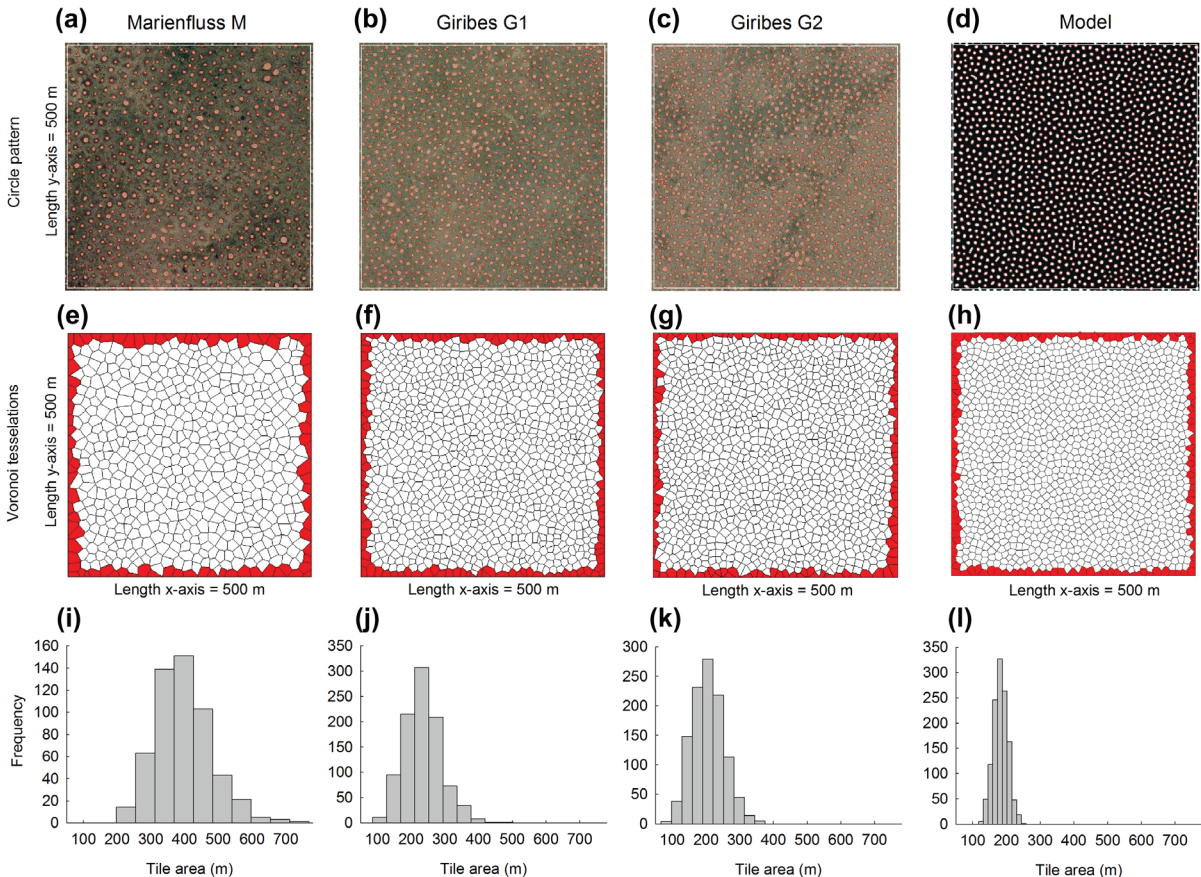

Figure 3. Aerial images of north-west-Namibia were used to digitize fairy circles in 500 × 500 m plots (a–c). Voronoi tessellations, with edge tiles (red) removed for subsequent analyses, reveal a dominance of hexagonal spacing structures around each fairy circle (e–g). A tile for each circle centre is the region of space which is closer to that point than to any other circle centre. Histograms of the tile areas (i–k). Figures on the right of the dashed vertical line (d, h, l) show the same type of data but for a 500 × 500 m plot of numerically created circle patterns using the Gilad et al. model.

Table 2. Main findings of spatial analyses of aerial images and the output pattern produced with the mathematical model. PCF = pair-correlation function, MCF = mark-correlation function.

	Marienfluss M	Giribes G1	Giribes G2	Model
Number of fairy circles	630	1079	1217	1372
Mean/median diameter of circles (m)	5.87/5.64	5.91/5.86	5.97/6.00	5.77/5.88
Range of diameters of circles (m)	2.14–15.38	1.98–11.53	2.26–11.60	2.06–7.47
Total area of bare circular patches (%)	7.6	12.7	14.4	14.6
Mean/median nearest-neighbour distance (m)	16.26/16.55	12.36/12.65	11.53/11.43	12.60/12.68
Mean/median area of Voronoi tiles (m^2)	396.9/388.0	233.9/231.6	205.3/203.7	182.3/182.2
Mean number of corners/% with 6 corners of Voronoi tiles	5.97/46.4	5.98/42.9	5.97/43.1	5.98/56.9
PCF, highest g-value	1.6	1.5	1.4	2.3
PCF, 1st range of negative correlation (m)	15.0	11.5	10.5	11.5
L-function, overall dominance of negative correlation (m)	54.0	66.0	63.0	52.0
MCF, 1st range of negative correlation (m)	13.5	13.0	12.5	10.5

Analysis with the pair-correlation function revealed for all three plots a wave-like curve with recurrent appearances of regularity (overdispersion) and aggregation at various scales. This is a surprising manifestation of regularity which is normally not observed in biological systems. The distances r of the first peaks in $g(r)$ for M, G1, and G2 are 16, 12, and 11 m, respectively, in correspondence with the order of the distance to the first neighbour (Fig. 4a–c, Table 2). Interestingly, the second peak of $g(r)$ is well visible in all three plots and points to long-lasting 'order' in the regular pattern. An additional highly relevant feature of the spatial pattern revealed by the L-function is the apparent absence of any larger scale pattern at distances larger than ca 60 m (Fig. 4e–g). The regular pattern thus extends homogeneously over the 25-ha areas analyzed here, but Fig. 1 and Supplementary material Appendix 1, Fig. A2 indicate that, in areas void of environmental heterogeneities, this regularity extends in fact over much larger areas.
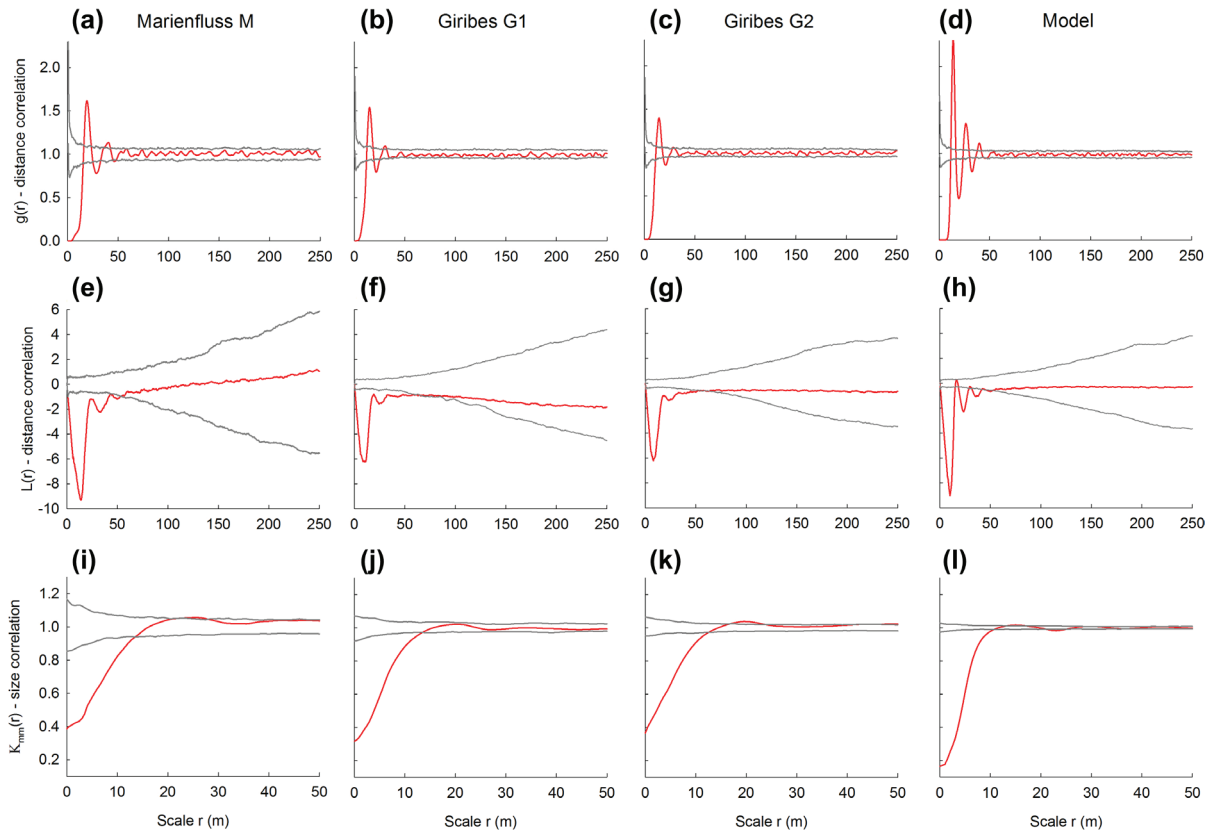

Figure 4. The spatial patterns of fairy circles observed in aerial images of 500 × 500 m plots, contrasted to random null models, using the pair-correlation function (a–c), L-function (e–g), and mark-correlation function (i–k). The pattern is regular and aggregated at circular neighbourhood scales r if the red line of $g(r)$ or $L(r)$ is below the lower and above the upper grey lines of the simulation envelopes, respectively. Similarly, the circle areas are negatively and positively correlated if the red line of $k_{mm}(r)$ is below and above the simulation envelopes, respectively. Approximately 95% simulation envelopes were constructed using the 5th-lowest and 5th-highest value of 199 Monte Carlo simulations of the random null models. For better visual interpretation, results of the mark-correlation function are only shown up to $r = 50$ m. Figures on the right of the dashed vertical line (d, h, l) show the same type of data but for a 500 × 500 m plot of numerically created circle patterns using the Gilad et al. model.

Strikingly, despite the considerable difference in point density (the G2-plot had basically twice as many circles as the M-plot), maximal positive values of $g(r)$ were very similar in the three plots and ranged only from 1.6 to 1.4.

Our analysis with the mark-correlation function revealed that the sizes of two fairy circles that were close together were smaller than the sizes of two fairy circles located farther away. This inhibition (negative correlation) persisted up to distances of 13.5, 13.0, and 12.5 m in the M-, G1-, and G2-plots, respectively. For larger distances onwards, the areas of the fairy circles were uncorrelated (Fig. 4i–k). The main spatial findings are also listed in Table 2.

Point pattern analysis of circles produced with the mathematical model

The model output produced a total of 1372 circles with a total area of bare circular patches of 14.6% which basically agrees with the findings for the G2-plot (Table 2; Fig. 3d). The mean and median diameters of circles, as well as the mean nearest-neighbour distance were very similar to the real fairy circles (Table 2).

Overall we found a strong agreement in the basic characteristics of circles when comparing the patterns produced with the mathematical model with that of the observed real-world patterns. The Voronoi tiles showed, like the G1-plot, on average 5.98 corners (Table 2; Fig. 3h) and 57% of the tiles had six corners. Tile areas were normally distributed (Fig. 3l; $p > 0.05$). The slightly lower proportion of tiles with six corners and departures from normality in the observed patterns are probably caused by stochastic effects that occur in nature but are not considered in the deterministic model. Analysis with the pair-correlation function revealed a grid-like, highly regular pattern of circles that was somewhat more ordered than that of the observed fairy circles; it showed three more clearly visible peaks in the pair-correlation function. The maximal positive value of $g(r)$ was with 2.3 higher than that observed in the field. Again, this is an effect of lack of stochasticity because more nearest neighbours occur at exactly the same distance whereas stochasticity may cause slight displacements that dampen the oscillations in the pair-correlation function. As for the real fairy circles, analysis with the mark-correlation function showed that circle areas of the Gilad et al. model were negatively correlated up to a similar range of 10.5 m (Fig. 4l).

Discussion

In this study we conducted for the first time a detailed spatial pattern analysis of the landscape scale patterns of fairy circles. Our spatially explicit approach revealed spatial structures never discovered before and identified distinct key features of fairy circles. Despite considerable differences in the density of circles among our 25-ha study sites (630 in M-plot vs 1217 in G2-plot) and large distances between study areas (175 km), all plots showed surprisingly similar spatial structures. The circles showed 1) highly regular patterns, 2) homogeneous patterns at large-scale distances, 3) the circle areas were

negatively correlated up to circa 13 m (i.e. nearby circles tended to be smaller than circles farther away), and 4) the circles were arranged on a nearly hexagonal array. As indicated by the mean diameters and nearest-neighbour distances of circles, there was on average always space for at least one fairy circle to fit in between two neighbours. In the following we discuss the likeliness of the three hypotheses presented in Table 1 in the light of these findings.

Hypothesis on abiotic gas leakage and geochemical hydrocarbon microseepage

We found that circles were over the entire 25-ha areas regularly spaced with mean nearest-neighbour distances not dropping below 11 m. We agree with Tschinkel (2012) who commented 'it is hard to picture how such seeps could consist of such evenly distributed subterranean point sources'. Given our findings, proponents of this hypothesis have to explain why gas chimneys are distributed over large areas in a grid-like pattern with a spacing structure of a hexagonal lattice, and why chimneys should always maintain minimum nearest-neighbour distances? Especially at the larger scale and also at scales beyond the size of our 25-ha plots (Fig. 1 and in Supplementary material Appendix 1, Fig. A2), we would expect effects of geological heterogeneity because the localized nature of many anomalies associated with microseeps suggests a migration of gases along surface fractures, joints, fault planes, unconformities, and bedding planes (Harbert et al. 2006). However, the distribution patterns of hydrocarbon microseepage are usually heterogeneously spread at the landscape scale (Almeida-Filho et al. 2002, Harbert et al. 2006, Bowen et al. 2007, Lammoglia et al. 2008, Zhang et al. 2011). In the Marienfluss Valley, however, the distribution of fairy circles occurs homogeneously over approximately 50 km in north-southerly direction.

Hypothesis on grass harvesting by social insects such as termites or ants

Following Crawford (1981), we consider termites and ants together in the social insect hypothesis because several general principles concerning the ecological significance of sociality and the overriding task of maintaining a micro-climatic stability apply to all social insect taxa in desert-like environments. This is because 'compared to habitats of most other desert animals, the nests of termite or ant colonies should be generally much more constant in terms of their temperature and humidity' (Crawford 1981). This justifies why Picker et al. (2012) related directly the fairy circles to the cleared discs of North American harvester ants.

Social insects may build large-scale networks of underground galleries and super colonies may spread over several thousand square meters (Theraulaz et al. 2003). Termites and ants also have the ability to create self-organized patterns in the search of food resources (Sumpter 2006), but detailed spatial pattern analysis using functional summary statistics applied to cleared circles of

harvester ants or nests of social insects in desert-like environments are not available at the scales analyzed here. Overall, it appears that cleared discs that are known to be caused by social insects do not result in the observed strongly hexagonal grid-like patterns because mechanisms other than competition for resources may affect the small-scale and especially the large-scale distribution. For example, Wiernasz and Cole (1995) have shown for ant-created *Pogonomyrmex* discs in Colorado, USA that populations may be random or overdispersed at short distances, the latter possibly as a result of density-dependent mortality, but spatially heterogeneous recruitment results in clumped distributions at large scales with new colonies being concentrated in particular regions of the study area. This is because 'spacing patterns in ant colonies are usually related to establishment of founding queens' which select preferential areas (Nicolai et al. 2010). This leads to large-scale clumping at plot dimensions as used in our study that are substantially different from the uniformly spread fairy circles in Namibia (Wiernasz and Cole 1995). Furthermore, variability in colony spacing is due to variability in colony age and size, neighboring colonies may have interdigitated foraging areas, founding queens can experience reduced survivorship near existing colonies, or the number of dispersing queens may vary spatially (Crist and Wiens 1996). Notably, this large-scale clumping may affect colony spacing independent of abiotic factors (Blanco-Moreno et al. 2014). In other words, clumping will occur even if the soil or spread of resources would be homogeneous over large areas.

Although smaller-scale overdispersion can result from small-scale competition (Alba-Lynn and Detling 2008) evidence for this appears doubtful. According to McGlynn (2012) in most insect systems there is no evidence to suggest that neighbourhood competition triggers nest relocation. In his review, McGlynn (2012) argues: 'colonies might move their nests throughout their life history [but] nest relocation may or may not be related to the local competitive environment [and thus] may or may not affect nearest-neighbour distance'. This rather explains why small-scale patterns of social insects such as ants and termites may be random (Wiernasz and Cole 1995, Bourguignon et al. 2011), which is not a typical characteristic of the observed fairy circle spacing.

A key question for further research related to the social insect hypothesis is therefore how behavioural processes of social insects such as foraging, nest building, nest movement, and intra-specific competition can generate over large areas the intriguing regular spatial patterns without signal of any larger scale aggregation? Even though Picker et al. (2012) and Juergens (2013) have convincingly shown strong correlation between fairy circles and ants or termites, respectively, they do not provide an explanation for the observed lack of any larger-scale clustering at distances > 60 m found here (see also Davies et al. 2014). Based on our new spatial statistical data provided here, we agree with Tschinkel (2013), that 'if this termite is indeed the cause of fairy circles, then it would have to be able to account for all the important properties of fairy circles – their circularity, their overdispersion, the proportion of bare surface, their changing diameter in different soils and latitudes'.

Hypothesis on self-organization by plants

Regular grid-like patterns have been described for self-regulatory vegetation systems where bare circles may emerge at a certain threshold degree of aridity as a result of a non-uniform instability of a uniform vegetation state (Lejeune et al. 1999, von Hardenberg et al. 2001, Deblauwe et al. 2008). The appearance of a periodic hexagonal pattern beyond a non-uniform stationary instability of a uniform state is a general result of pattern formation theory (Cross and Hohenberg 1993). Hence, the appearance of nearly hexagonal arrays of bare circles in water limited systems with pattern-forming feedbacks should not come as a surprise (Tlidi et al. 2008). Indeed, there are indications in earlier observational studies that fairy circles could be a pattern-formation phenomenon driven by a non-uniform instability. Based on high resolution satellite images taken four years apart, Tschinkel (2012) provides evidence that circles appear already in their final sizes, rather than as initial small circles that gradually grow to their final sizes (as e.g. hypothesized by Juergens 2013). Hence, according to Tschinkel's study, their final size is reached within less than four years. This is one of the basic signatures of a non-uniform instability – the growth of a spatially periodic gap pattern with a characteristic length scale (Meron 2012) which in the present context determines the sizes of the circles when they appear. Still, the relative importance of morpho-ecological processes where perennial grass tufts such as *Stipagrostis uniplumis*, *S. ciliata*, or *S. giessii* experience a central dieback of the grass tuft due to self-thinning need to be further investigated. For example, vegetative multiplication at the circular periphery of the genet, leading to ring-like shapes, has been observed for near-monospecific *Stipagrostis ciliata* grasslands of Namibia and also in Israel (Danin and Orshan 1995). In this study, Danin and Orshan (1995) found in Namibia 'that the dead plant remnants forming the circles were rhizomes of perennial plants and not of annuals'.

While the exact spatio-temporal mechanisms of self-organization are so far not fully clear, some basic principles should hold. When fairy circles with their underground water reservoirs are relatively far apart from each other, matrix grasses that are farthest away from the fairy circles will experience the most intense competition for water. This may lead to dieback within the matrix, forming a patch of bare soil at the location where competition for water is most intense. These locations will consequently be at regularly spaced distances away from the surrounding nearest-neighbour circles which lead to the homogenous hexagonal spacing structure over large areas. At this newly formed spot with bare soil, rain water of the next precipitation events can deeply percolate without being transpired by grasses and thus a water reservoir can form which then later can sustain a perennial grass belt. These newly emerging circles with increased water supply are likely attractive to other organisms such as the abundant sand termites (Juergens 2013). While the termites and other animals are likely involved in the maintenance of fairy circles, the reasons for their closure after decades are so far poorly understood. Possibly, years with high rainfall cause a decline in resource limitation and improved chances for colonization by grasses (Cramer and Barger 2013).

Models that capture only the infiltration (Rietkerk et al. 2002) or the fast soil-water diffusion feedbacks (van der Stelt et al. 2013) can generate hexagonal gap patterns below a precipitation threshold but they may not apply to fairy circles because the infiltration feedback is too weak in sandy soils to induce patterns. Soil-water diffusion may play a pattern-formation role in sandy soils, but is more likely to act in conjunction with the root-augmentation feedback. We therefore used the model introduced by Gilad et al. (2004, 2007) and parameterized it for the characteristics of our study sites to yield a biomass-independent form for the infiltration rate (see e.g. also Barbier et al. 2008).

The resulting spatial patterns of self-organized vegetation systems under competition for water match essential signatures of the observed patterns. Simple self-organizing mechanisms leading to hexagonal spacing structures could be well functioning in the regions where fairy circles occur because the homogeneous nutrient-poor sandy soils and limited number of one or two *Stipagrostis* grass species would be a system of low bio-complexity for producing such simple vegetation patterns. This is because involvement of more soil types or grass species and associated niche differentiation would likely have a disrupting effect that would mask the emergence of such grid-like patterns. Interestingly, we found for all three study plots an equal maximal positive g-value of ca 1.5. This indicates the existence of a strong and similarly regulating factor such as a limit in annual precipitation. The slightly higher g-value of the model may be attributed to lack of stochasticity in our model which results in a pattern with a stronger ordering and therefore higher peak in $g(r)$.

Even more supporting for the proposed mechanism of water transport by extended root systems and soil–water diffusion is the result we obtained by analysis with the mark-correlation function. It is remarkable, that all three plots showed strong negative correlation in the circle areas up to the same distance of ca 13 m. Thus, if two circles are located 13 m or closer to each other, their bare areas become significantly smaller than the average circle area found for the entire plot. The strongly reduced bare area at short neighbourhood distances is equivalent to a significant increase of the vegetation coverage. Based on the model studies, we attribute this increase in coverage to the root-augmentation feedback. If the circles of bare soil are far apart, the vegetation in between occupies larger areas and the competition for water is stronger. To survive, the vegetation needs larger circle areas to provide more water through uptake by roots that extend towards the circle. In contrast, if the circle distance is shorter there is less competition as most plants have long enough roots to benefit from nearby circles and take up water. As a consequence, the vegetated matrix area can expand, making the circle areas up to $r = 13$ m smaller than the average for the entire study plot.

In this context, it is important to note that field surveys revealed higher soil-moisture contents at mean depth larger than 32 cm within fairy circles as compared to the matrix (Picker et al. 2012) and Juergens (2013) showed in detail that fairy circles act as important water traps. Thus, due to the absence of transpiration by grasses and also due to the concave surface structure, fairy circles provide essential moisture reservoirs for the surrounding vegetation and are

likely attractive to other organisms such as the abundant sand termites (Juergens 2013). While our model emphasizes competition for water, it is likely that a resource shortage does also apply to nutrient availability. Although differences in chemical properties are only small between soils of the fairy circles and the matrix, the lower soil organic carbon, N, and K found inside circles indicates that nutrient depletion is another mechanism that may be involved in the emergence of fairy circles (Cramer and Barger 2013).

Overall, our study supports the view that fairy circles appear as a result of a non-uniform instability of a uniform vegetation state that is induced by water stress. This competition for water as a central process is also evident from aerial images provided in the Supplementary material Appendix 1, Fig. A3 and A4 show that the density of circles strongly declines in moister site conditions along drainage lines because water supply is sufficient for sustaining pure matrix vegetation. This equals the uniform vegetation state of the model which is stable at high precipitation rates (cf. Fig. 2; values $p > p_2$). Notably, at these relatively high precipitation rates $p > p_2$) or moist habitats at the transition to uniform grassland vegetation, the self-organized typical pattern of fairy circles may shift from regular to random spacing with an overall strong decline in density of circles. These are potentially the transitional rainfall areas where MAP is above 120 mm, which is thus outside the core isohyet range of their occurrence (see also Cramer and Barger 2013). However, these geographically confined areas with a very narrow band of isohyets are not typical for the periodic gap pattern and are thus not treated here.

Conclusion

In this study we analyzed the spatial pattern of the fairy circles at scales up to 25 ha with spatially explicit correlation functions to provide the research community with a precise description of their properties and to invite scientists to conduct future research to propose mechanisms that can explain how their favoured hypothesis can generate such patterns. We already did an initial step in this direction and adapted a model of vegetation self-organization to the conditions of our study areas. Our model was indeed able to produce spatial patterns that are in remarkable quantitative agreement with the observed patterns (i.e. showing a gap pattern with a regular hexagonal structure and similar critical spatial scales, negative correlation of the circle areas, and complete homogeneity at larger scales). However, future research should test the ability of self-organization models to match the birth- and death dynamics of fairy circles (e.g. revealed by Tschinkel 2012 and Juergens 2013) and their regional patterns in the density and size with respect to environmental gradients. In order to improve our understanding of the modelled processes and parameterizations it is also necessary to undertake further field research. For example, little is known about the horizontal and vertical extent of the root system of *Stipagrostis uniplumis* or the soil moisture content at various depths and times of the year for a variety of circle sizes. Furthermore, low-cost unmanned aerial vehicles could be used to map fairy circles of selected study sites

on a monthly basis (Getzin et al. 2012, Koh and Wich 2012). This would enable us to accurately monitor the duration of their emergence and the change of their diameter and shape at high temporal and spatial resolutions.

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Supplementary material (Appendix ECOG-00911 at <www.ecography.org/readers/appendix>). Appendix 1.

Ecography

Supplementary material

Appendix 1

Figure A1 Artificially created random and clustered point patterns

Figure A2 Aerial image of the two digitized Giribes plots G1 and G2

Figure A3 Aerial image of the effect of drainage channels on the distribution of fairy circles (1st example)

Figure A4 Aerial image of the effect of drainage channels on the distribution of fairy circles (2nd example)

a) Random pattern   b) Clustered pattern   c) Observed pattern
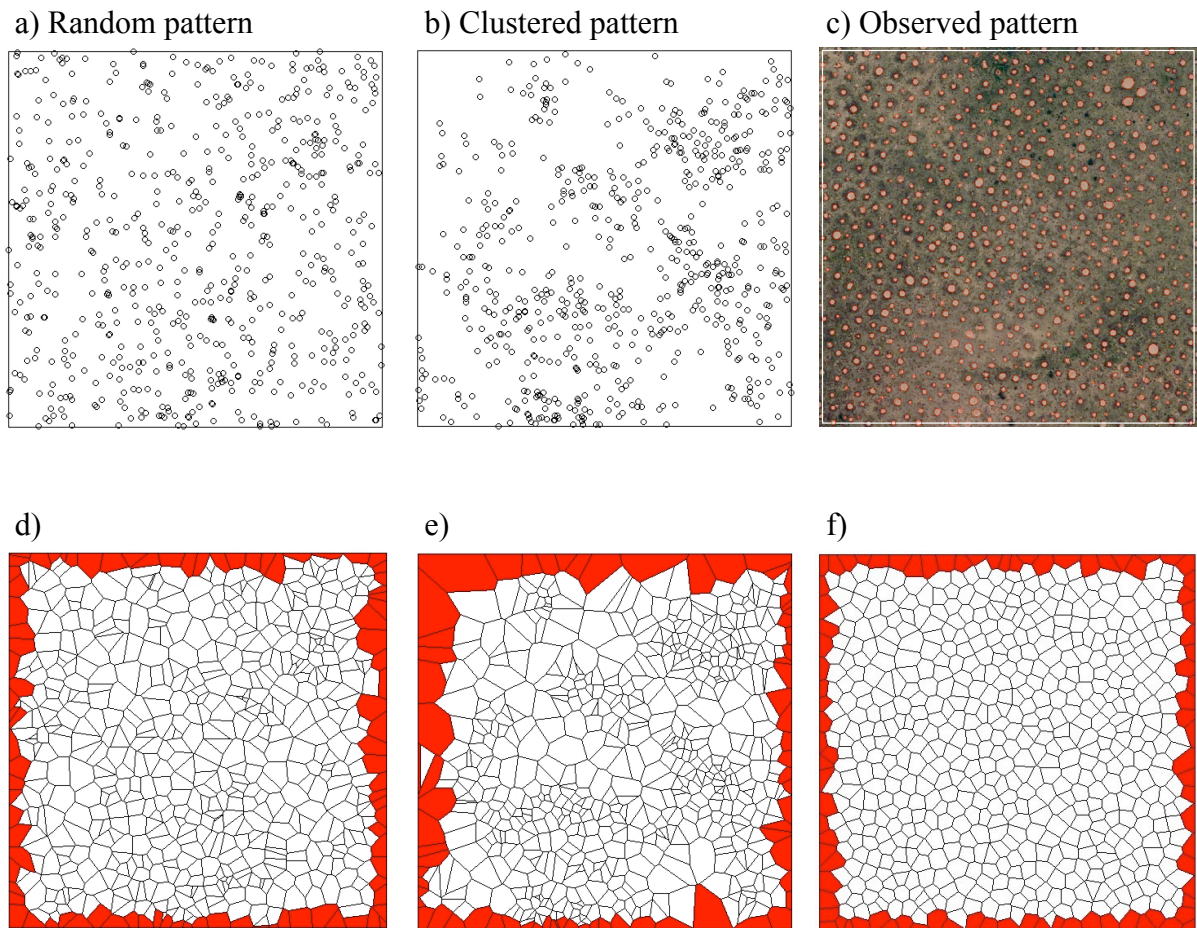
d)   e)   f)

Fig. A1. For comparative reasons, we artificially created random a) and clustered point patterns b) with 630 points, which equals the amount of fairy circles of the Marienfluss plot c). Voronoi tessellations, with edge tiles (red) removed for the random d), the clustered e), and the regular point pattern of the Marienfluss f). A tile for each point seen in a-c) is the region of space which is closer to that point than to any other point in the neighbourhood. For the random and clustered patterns, the percentage of tiles with six corners made up only 27% and 29%, respectively (see results section) as opposed to 43% to 46% for the observed patterns.
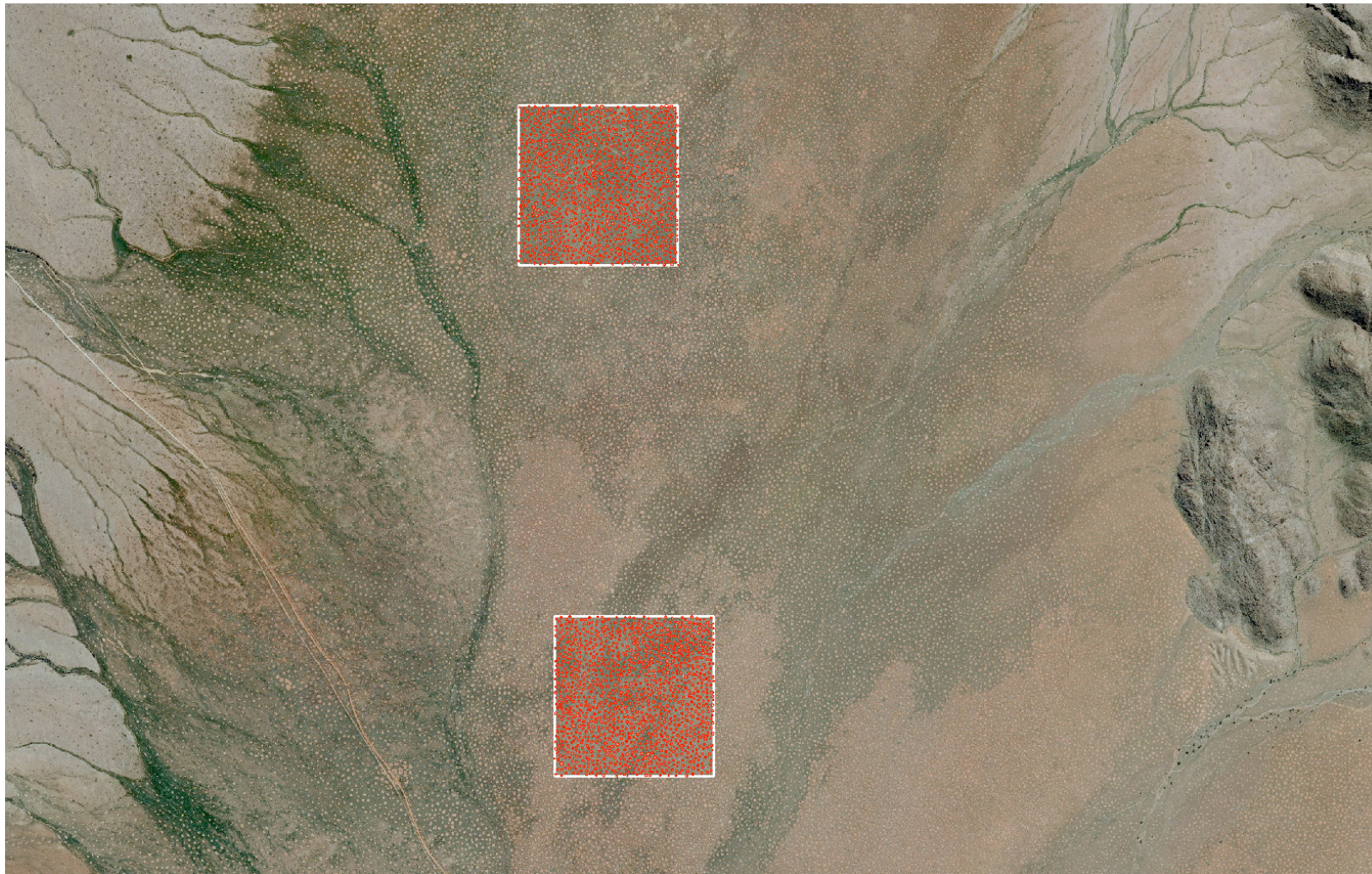
Fig. A2. Aerial image of the two digitized Giribes plots G1 and G2. The upper G1-plot had 1079 and the lower G2-plot 1217 fairy circles, respectively. These 500 m × 500 m plots were placed at homogenous locations and were thus not affected by dry riverbeds, roads or rock outcrops.

Fig. A3. Aerial image of the effect of drainage channels on the distribution of fairy circles (1st example, Giribes Plain). A very low density of circles around the drainage channel indicates better water supply and thus reduced competition for water. Consequently, more matrix vegetation can grow.
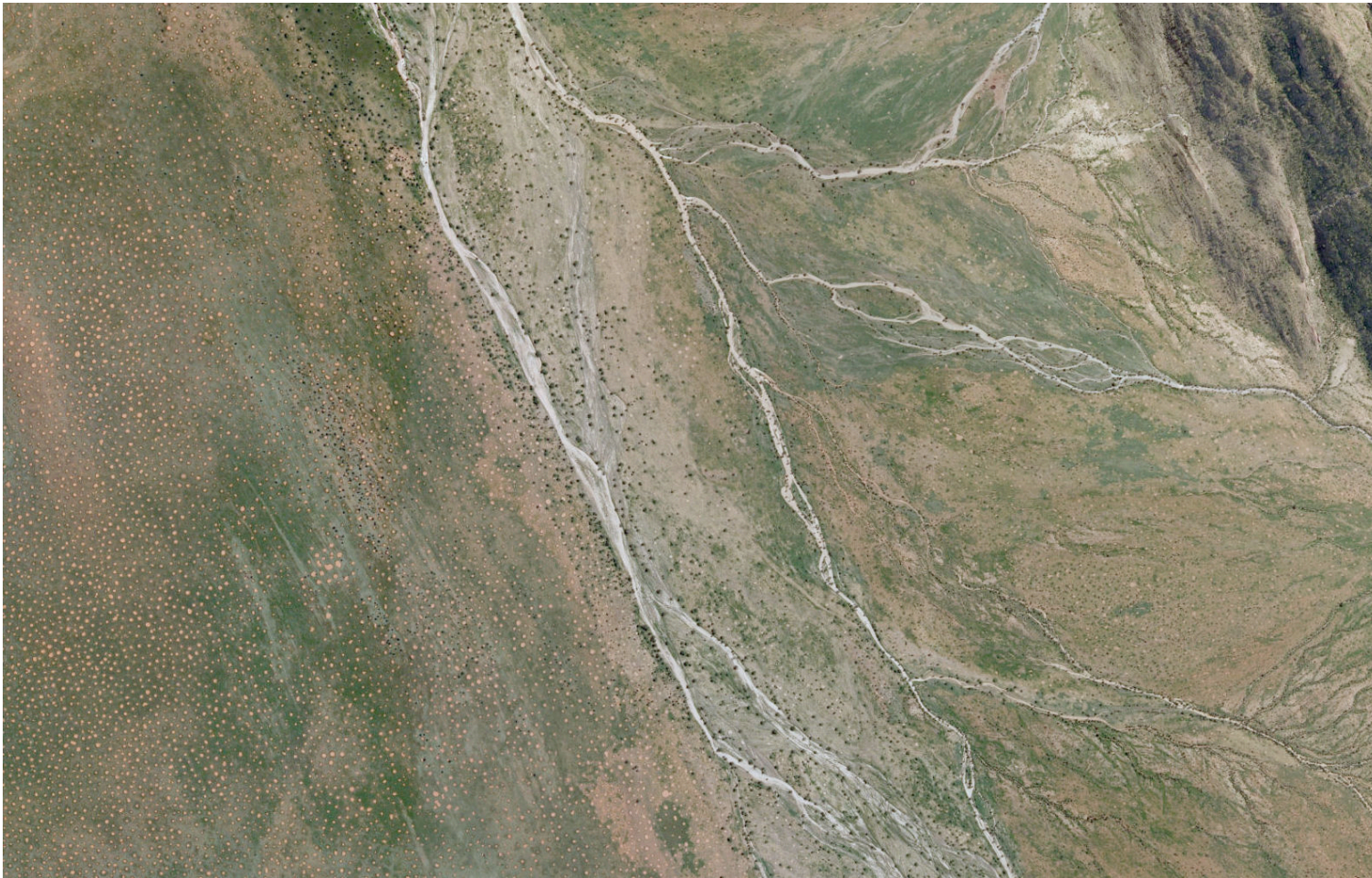
Fig. A4. As Fig. A3 but 2nd example (Marienfluss Valley). Similarly to example 1, here in example 2 there is a very low density on the right side of the main drainage channel due to increased water supply coming from the eastern mountains.