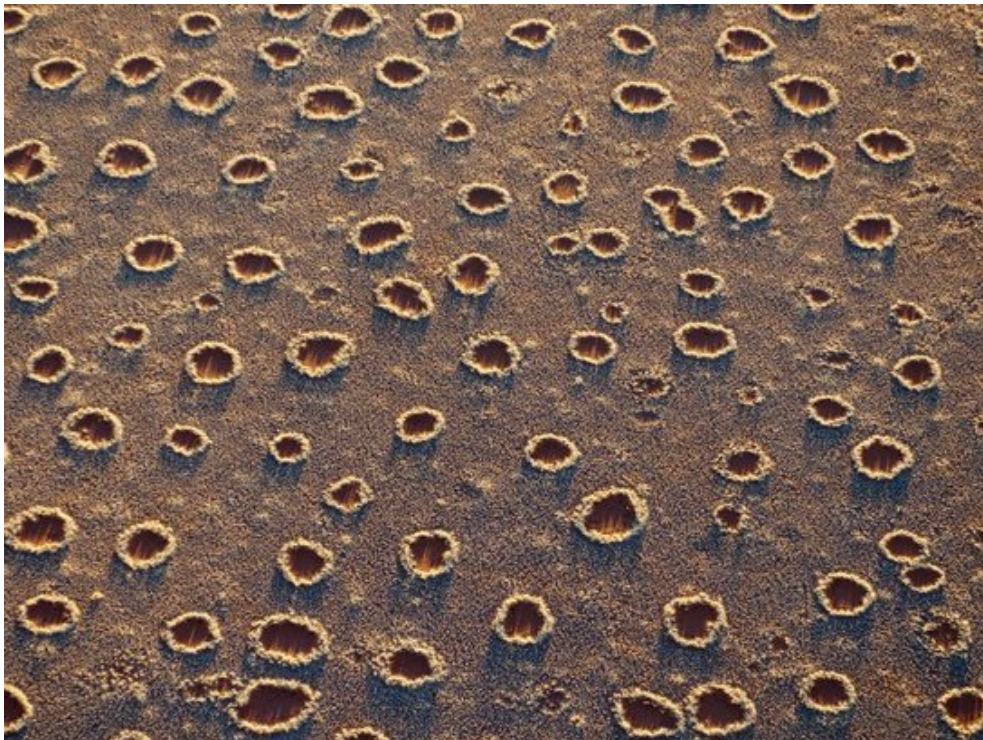


The persistent enigma of the Namibian desert fairy circles.

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fairy circles aerial view, photo by Frans Lanting

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Abstract

Fairy circles is the name given to the localised bare spots which pepper the otherwise vegetated landscape of the pro-Namib transition zone to the Namib desert in western Namibia, Africa. While conjectures on the causes of this pattern abound, there is no scientific consensus about their origin. In this study we review the literature published on the subject at hand, and highlight the convergence of the field to certain candidate propositions, namely the possible role of termites as ecosystem engineers[1], and the resource competition of plants for water leading to emergence of spatial patterns[2]. Concomitantly, we formulate a new hypothesis on the origin of fairy circles based on differential condensation of water between the barren and vegetated areas, that could occur during nighttime. As a proof of principle we demonstrate, by means of numerical simulations of a spatially explicit model, that this effect can create patterns resembling the fairy circles. We furthermore propose a simple experiment which can test this hypothesis at the field.

1 Introduction

The Namib desert is one of the oldest deserts in the world, with continuous arid conditions been present for the last 20 million years[3]. Situated on the southern-west coast of Africa, it spans the territories of Angola, Namibia and South Africa. The coastal part of the desert, consisting of sand dunes, is known for its frequent fog events, (roughly 88% chance of fog occurring every month[4]) the only reliable source of water for the organisms living there[3]. East of the sand dunes, roughly 60 to 120 km inland[5], on the gravel planes of the desert, an interesting phenomenon can be observed. As vegetation becomes more frequent due to the increasing (over longitude) mean annual precipitation rate (MAP), plant cover of the planes is non-homogeneous, leaving barren circular spots, at regular intervals, devoid of any plant life (figure 1). These spots, the fairy circles (FCs), have a mean diameter of 5 meters (SE=0.2m) and have a mean distance of 14m (SE=1) between each other[6, 7]. Between the fairy circles the ground is populated by plants, called the matrix vegetation. At the periphery of the FCs plants tend to become more lush, or be of a different species, creating a crown of higher biomass that can be perennial in a landscape of mostly annual grasses. This formation is known as the perennial belt (PB) of the FCs (figure 1B).

The plant species populating the areas where FCs are present are usually of the genus *Stipagrostis* (Nees) of the Poaceae. The matrix vegetation has been observed to consist of only *Stipagrostis uniplumis*[8, 9], *S.obtusa*[10] or even *Schmidtia kalahariensis*[9]. Perennial belt (PB) formation is not present in all the sites of FCs[11]. PB vegetation is usually lush and taller (for example 0.5m tall PB in an otherwise 0.2m tall matrix[6]). It consists of *S.giessii* or *S.ciliata*[6, 9] and in some cases *S.obtusa*.

1.1 What we know

The macroscale(where FCs occur) and mesoscale(how they are spaced, mean area etc.) distribution characteristics of the FCs have been the subject of in-depth study[6] and are suggested to be indicative of the processes giving rise to them[7]. FCs in the Namib occur roughly between the 50mm and the 100mm (MAP) isohet[10] (figure 2B). They appear only in this narrow band, but the plant species the matrix vegetation consists of have a much wider distribution[6]. The local presence of FCs has been accurately predicted by a boosted regression tree model using only MAP, temperature seasonality and a measure of vegetation biomass[6].

Mesoscale characteristics of the FCs include a small variation in size (which is anti correlated with MAP[6]) and the fact that they are evenly spaced. Fairy circles, in most places, are not dispersed over the field at random (figure 2A). To study how their dispersion departs from a random one, some researchers have used the R-value metric[12], which describes the arrangement of points on a plane based on the nearest neighbour distance for each point. The R-value formula is

$$R = \frac{\bar{d}}{\bar{d}_e} = \frac{2\bar{d}}{\sqrt{\frac{A}{n}}} \quad (1)$$

where \bar{d} is the observed mean distance to the nearest neighbour, \bar{d}_e is the expected mean distance to the nearest neighbour calculated for a randomly dispersed pattern of the same density, A is the 2D area and n is the number of points. When $R < 1$ it denotes a clumped distribution, when it is close to 1 a random one, and when $R > 1$ the points are overdispersed (maximum value possible is 2.149 for the hexagonal packing configuration). The FCs have an R -value ranging from 0.58 (clumped) to 1.68[8] with an average of 1.20 [6]. As such, the FCs have been characterised as "overdispersed" [7, 13, 11]. Other metrics (for example based on the Voronoi tessellations of FCs) have been used for measuring the spatial characteristics of the FCs and reach to the same conclusion, namely that they can exhibit high regularity (nearly a hexagonal array) in

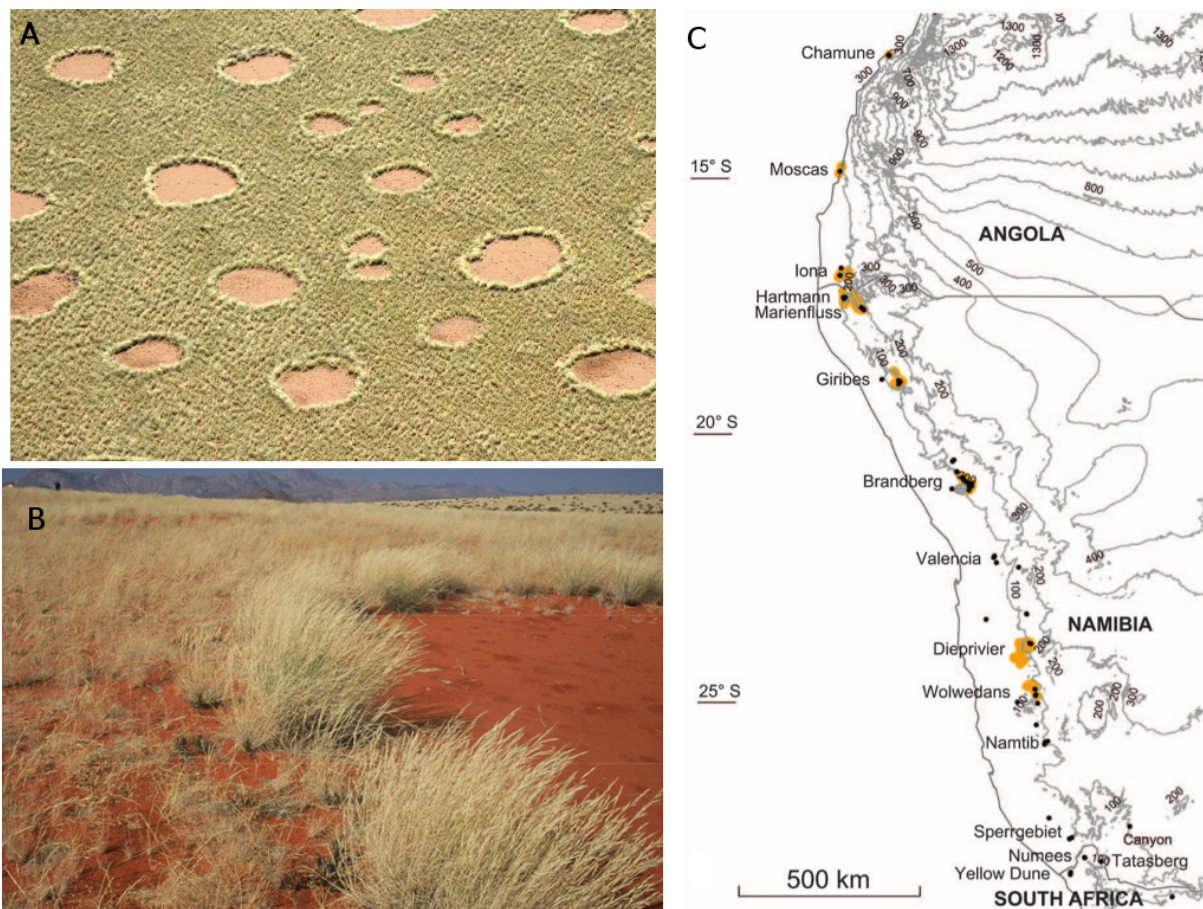


Figure 1: Fairy circles are localised spots of barren land of a characteristic size, that occur amidst the lightly vegetated gravel planes of the Namib desert, Africa. **A** birds eye view of the fairy circles. **B** close up of the periphery of an FC. The distinct states the vegetation assumes are visible: on the left side short matrix vegetation, in the middle the tall plants the perennial belt consists of, and on the right the barren interior of the FC. Photo by N. van Rooyen, adapted from [9]. **C** map depicting the distribution of FCs in western Africa, adapted from [1]. Black dots and yellow areas are sites were FCs occur. Note the association of FCs with the 100mm isohet.

the way they are positioned in respect to each-other[7]. There is also a connection between the distance between neighbouring FCs and their size. FC areas are correlated negatively with inter-FC distance up to 13 meters, as nearest neighbours FCs closer to each other than average tend to be smaller[7]. The life cycle of FCs consists of three phases: birth, where there is a collapse of plant life over an area close to the final size of the FC, the maturation phase in which the FC widens somewhat and in most cases grows a PB, and death, where plants relatively quickly repopulate the FC. The average lifespan of the FCs is from 40 to 60 years, depending on size[11].

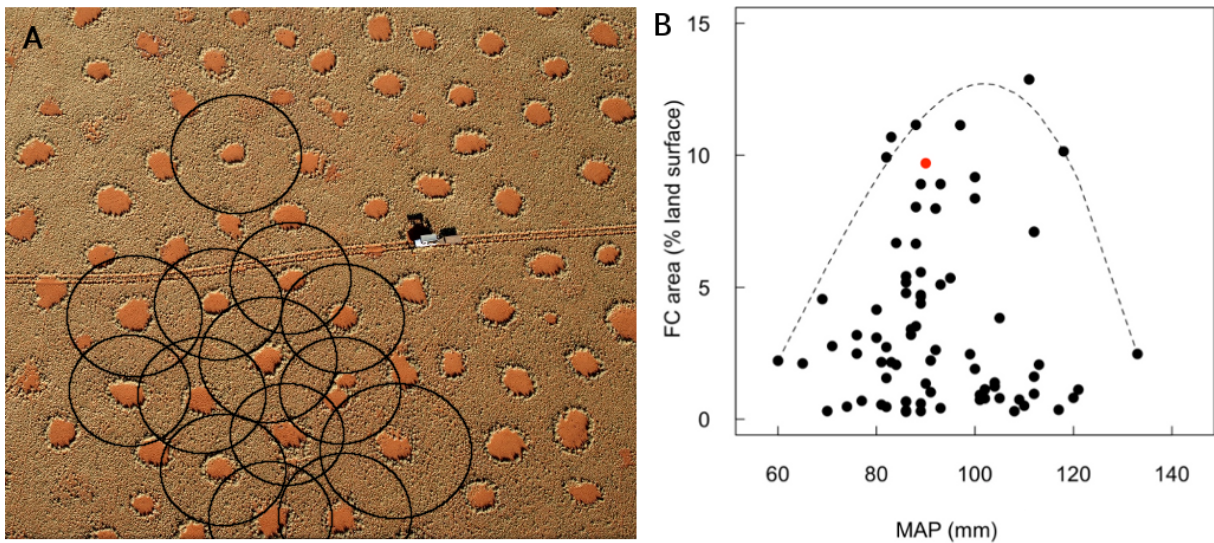


Figure 2: The FCs have striking spatial characteristics. **A** aerial photo where circles have been plotted for some FCs, with radius equal to the distance of FCs to the nearest neighbouring FC. One can appreciate the spatial regularity under which the FCs exist. Photo by Bruno Kaesling-kuemmelberg. **B** plot depicting the relationship between mean annual precipitation and FC land occupancy (cumulative FC area/total area measured) for a number of independent measurements throughout the FC range, adapted from [6]. FCs appear at a specific MAP range.

The relative importance of biogenic factors on FCs is a subject of considerable debate[11, 14, 1, 6, 7]. In one study, Juergens[1] presents a strong correlation of the termite *Psammotermes allocerus* activity and the FC barren interior. He presents detailed statistics on where the termites forage, based on the small soil dumps the workers create when cleaning the underground burrows during night-time and morning hours (figure 4). These suggest this species of termites is active inside FCs and to a lesser degree in the matrix, leaving the PB intact. In the same study the presence of *Psammotermes allocerus* is shown to co-occur with FCs in the whole range of the phenomenon, in contrast to all the other ant and termite species observed in FCs *in natura*. However, other studies on the putative faunal aspect of FCs have been inconclusive[14] or suggest different species of insects as causative agents[15, 13]. For example, the ant species *Anoplolepis steingroeveri* (Forel) has been shown to be spatially correlated with

the FCs, and these ants are observed in the PB to tend to *Meenoplidae* bugs that feed on roots and produce honeydew[13] (figure 4D).

Apart from ants and termites, a second interesting biological aspect of FCs is the difference of soil microbiome inside and outside the FCs. Vesicular-arbuscular mycorrhizae are consistently shown to be absent in soil or roots of invading plants from inside the FCs, and the same trend holds for general microbiome population density and diversity[9, 10, 16]. The anaerobic bacteria in contrast, have a higher activity inside the FCs and lower in the matrix-PB[16, 9, 8]. Both results indicate a substantial shift in microbiome composition in the two microhabitats.

Fairy circles are perplexing when viewed in terms of their physicochemical aspects. The soil of the FCs is significantly inferior in sustaining plant life, in comparison to soil coming from the PB-matrix as measured by potting trials [8, 6, 5, 9, 10], where soil is extracted at regular intervals from the FC center to the matrix, and used as a medium for germinating seeds. One might argue this result has to do with resource availability, for example water. However, all experiments on FCs agree there is a 2.3-fold [6] to 5-fold[8] higher soil moisture in the FCs[13, 1] (figure 3). Nutrient analyses of soil in areas where FCs occur reveal extremely nutrient impoverished conditions. Comparisons of soil nutrient abundances inside and outside FCs have revealed relatively few statistically significant differences, or none[10, 9]. One report shows that soil inside FCs has lower [K], total [N] and organic carbon, and higher available P(Olsen) than the PB and the matrix[6]. The same study also shows that, in the macroscale, matrix soil total [N] between different sites where FCs occur is related to spatial properties of the FCs. Specifically, [N] was found to be anti correlated with individual FC area and FC area as a percentage of land surface, and correlated with the distance between FCs, FCs been absent when [N] is above a certain value. Total [N] however was also correlated with MAP, making [N] difficult to assess as a resource-competition candidate.

The FCs have been subjected to a series of tests for natural gas microseepage[17]. These have shown CO gas emissions of an episodic nature in the FCs. In addition, new forming FCs were found enriched in alkenes.

2 Review of proposed hypotheses

An attribute of the fairy circles is their dual capacity to invoke human inquisitiveness and at the same time baffle the exegetical tendencies of scientists and people of other walks of life alike. Here we will review the hypotheses proposed explicitly in the scientific literature, following a chronological order, and present the existing evidence for and against each one.

The hypothesis of fossil termitaria

Tinley[18], back in 1971, proposed FCs are the remains of fossil termitaria, created during wetter conditions in the past. This hypothesis, which is the first historically, can be easily refuted in its original form because FCs have been observed to come into existence in recent long term studies by Tschinkel[11]. As

such, fossil remains of termitaria are not the causative agent of the formation of FCs. The role of termites, on the other hand, is much more general hypothesis which still stands to scrutiny, as we will discuss later in this section.

The allelopathy hypothesis

Theron[19], in 1979, hypothesized on possible allelopathy between the matrix vegetation (ex. *Stipagrostis*) and the plant *Euphorbia damarana*, a medium sized bush known for its toxicity. By allelopathy here we mean the inhibition

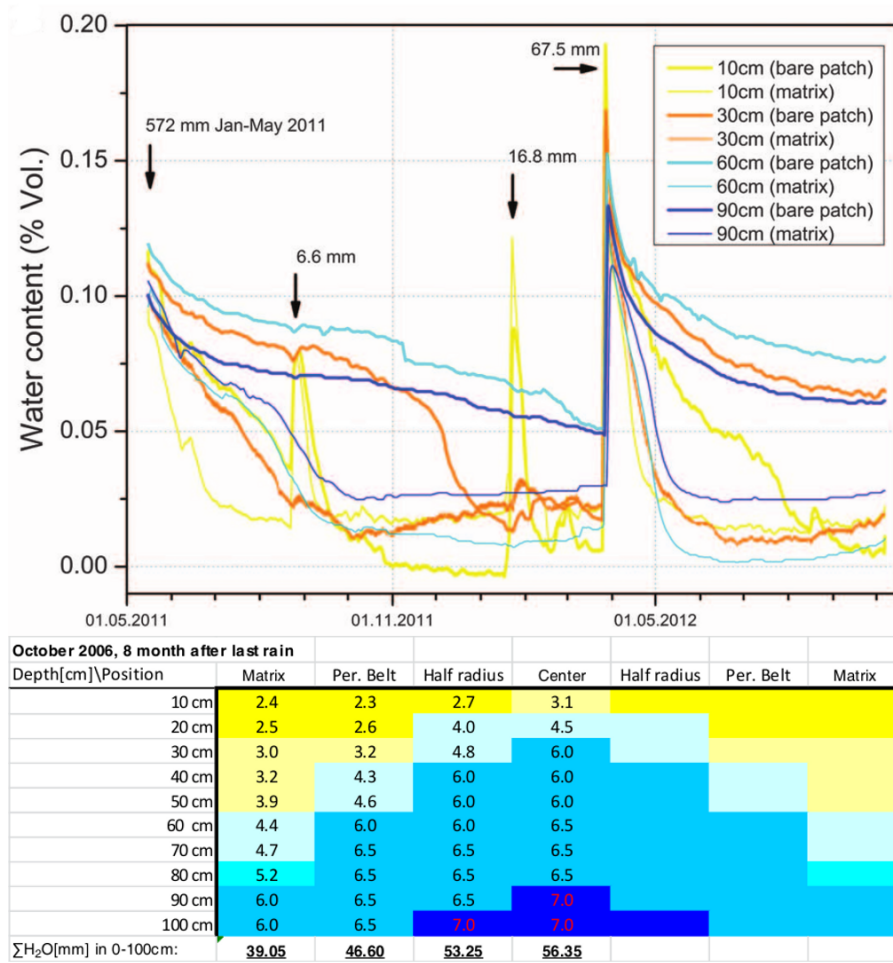


Figure 3: water spatial and temporal dynamics in FCs, figures adapted from [1]. **Top** time series over one and a half years, depicting the water content of the soil at different depths, for two arrays of sensors, one inside the FC (solid lines) and one outside (at the matrix, thin lines). Water content is expressed as volume percent, $\frac{m^3}{m^3} \cdot 100$. Rain events are depicted by arrows. Note the lower water content outside the FC. **Bottom** volumetric soil water content at various depths in and around an FC of 3-meters diameter. The measurements have been color-coded and extended for better visual inspection. Information about the methods used to obtain the measurements can be found in [1].

of germination and/or growth of plants by compounds *E.damarana* produces, directly or by biosynthesizing their precursors. A fairy circle thus might form where an *E.damarana* plant once lived. Initially, in the absence of long term studies on FCs, this hypothesis seemed plausible, since *E.damarana* average diameter is close to the diameter of FCs (ca. 6 meters)[8]. The allelopathy hypothesis has been given considerable attention by a number of experimenters. Van Rooyen *et al* , in a long term study[10], plotted on scale a specific area's FCs and *E.damarana* plants and revisited the same location 21 years later. He did not find FCs forming near alive or long before dead *E.damarana* plants. In addition, he compared in potting trials the germination of seeds in soil coming from directly under *E.damarana* plants, to the germination of seeds potted in matrix, PB and FC soil. The surprising results where that germination and subsequent growth was significantly higher in soil coming from under *E.damarana*, in both cases of the plant being alive or dead. In a follow up study, Joubert[9] found that crude extract (using ethanol) coming from *E.damarana* did in fact significantly inhibit germination of seeds, the only result supporting the idea of this succulent plant containing growth inhibiting compounds. The hypothesis of allelopathy however, has other shortcomings, the most important in our opinion being that it proposes no mechanism for the overdispersion of FCs. If we assume a random distribution of *E.damarana* plants, the resulting FCs should also be randomly distributed over the field. A second shortcoming is the fact that FC formation has been documented[11, 1, 17] but the respective teams did not report any *E.damarana* plants, dead or alive, present in the new circles, something they surely would have noticed, since the decomposition rate is slow in the planes. In conclusion, this hypothesis lacks convincing supporting experimental results.

The hypothesis of social insects as ecosystem engineers

The first time the role of living social insects on the formation of FCs was investigated was by Moll back in 1989[20, 8]. By digging trenches through a number of FCs, he provided evidence of sparse termite activity of the species *Baucaliotermes hainsei* and *Psammotermes allocerus*, leading him to propose that one of these two species or *Hodotermes mossambicus* is responsible for the gaps in the Namibian vegetation. This work branched into a number of studies assessing the role of termites and ants in FC formation. Postulated mechanisms by which insects create FCs can be divided into two groups. First we have direct mechanisms, like the foraging of seeds, seedlings and adult plants from inside FCs by insects. Second we have indirect effects, like the production of inhibitory agents by active termite nests, affecting the growth of plants above them.

Foraging by termites is notoriously difficult to document, as these species live below ground in sandy soils that easily collapse over their tunnels. It is perhaps because of this fact that although direct foraging by termites has been explicitly studied by a number of separate groups [15, 1, 13, 10, 14], the results have been largely mutually inconsistent, with some of the studies reporting no correlation of termite or ant activity and the FCs [10, 14], some reporting that seed collecting ants (*Anoplolepis steingroeveri*) generate the pattern [15, 13] and only one presenting detailed and clear statistics of the activity of *Psammotermes allocerus* in FCs[1] (figure 4).

Indirect effects of termites on FCs have been studied, specifically the case of

abiosis factors the termite nests might produce[8, 13]. Albrecht *et al*[8] has indicated, by soil sample methanol extract analysis using HPLC, that there are some chemicals in the FCs that are not present in the matrix. In a follow up study, alkenes have been detected to be present in newly forming FCs[17]. Picker *et al* have argued that these alkenes could be coming from the Dufour's glands of ants, and are used for chemosignaling. All these results are circumstantial evidence that aim to relate possible abiosis factors to the consistently tested inferior growth of plants in FCs. Specifically, they aim to address the result of Jankowitz *et al*[5] which shows that perforation of soil containers (making holes in the pots) significantly inhibits growth of potted plants positioned by researchers in the center of FCs.

We would like to point out that termite activity, if it does happen preferentially in FCs, could indirectly lead to a catastrophic (in relation to vegetation) long term shift in the soil microbiome, for example the eradication of mycorrhizae. This by itself could be a substantial limiting factor to the soil retention of nutri-

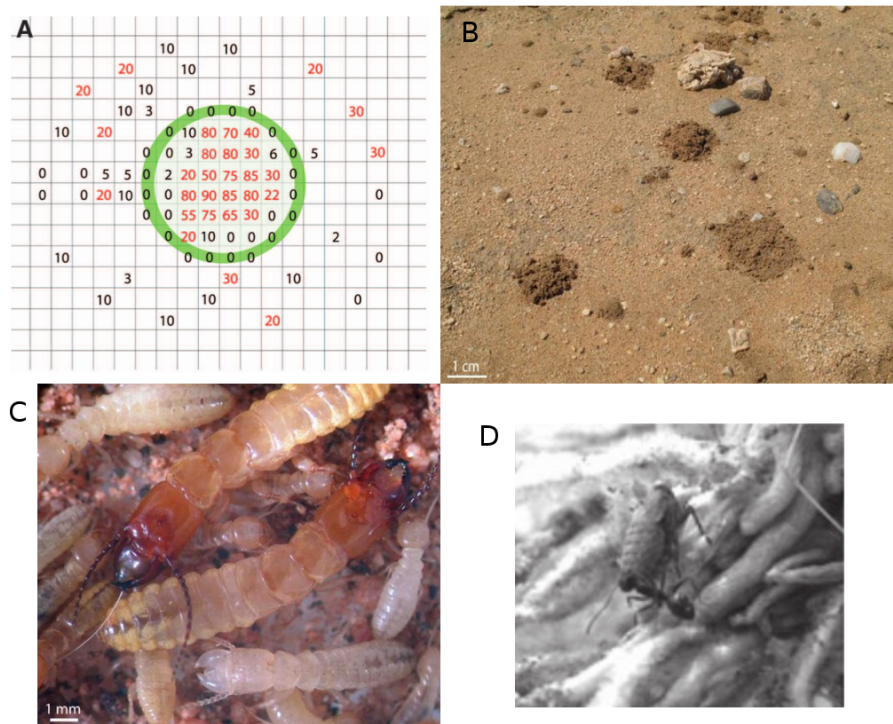


Figure 4: Activity of social insects in FCs. **A** soil dumps of termites per square meter, measured on a grid of $1m^2$, centered on an FC. The green ring represents the perennial belt. Matrix measurements were conducted at random, empty cells were not counted. Figure adapted from Juergens[1](also the two following pictures), who uses this measurement as a proxy for termite activity, and postulates a causal relationship with FCs. **B** soil dumps made by termites[1]. **C** *Psammotermes allocerus* workers and soldiers[1]. **D** *Anoplolepis steingroeveri* worker, guarding a Meenolipidae bug that feeds on roots of *S.obtusa*. Photo taken from Picker[13], who puts forward the hypothesis that these ants create the FCs.

ents (explaining, for instance, the depletion of N[6] inside FCs), to the presence of VAM, and thus to the survivability of seedlings inside FCs.

Although more experimental results are needed for the independent confirmation of the correlation between termite activity and FC formation, we would like at this point to recognize the multiple ways by which termites might contribute to FC patterning. Termite literature meta-analysis has shown that they are able to create spatial heterogeneities in resources[21]. In the case of FCs, if termites were attracted to water and forage where water is, there is a positive feedback between termite presence and the water supply, since barren land is shown to have higher water content than vegetated one, in the area where FCs occur[1]. Moreover, intraspecific competition for space between different colonies of termites can create overdispersion of nests[22, 21], although the reported R-values for such situations are lower than those of FCs[13, 6]. In conclusion, termites do make a compelling case as factors of FC formation and maintenance. To elucidate their relative importance, an experiment involving a pesticide with a long half-life and the monitoring of FCs just after the rain events could be an interesting approach.

The hypothesis of ring formation by clonal plants

A different explanation proposed for FCs which has not been studied extensively is that they are ring formations resulting from radial propagation of clonal plants. Originally proposed by Danin *et al*[23], this idea stems from the general observation that growth of several different classes of organisms, when it happens on a roughly planar surface, results in the death of the founder members in the center due to depletion of resources and competition, and a radially symmetrical growth front (figure 5). It is this front we perceive as a population of clonal individuals arranged in a ring. Models and experiments on the field have consistently shown how ring formation occurs[24, 25]. Danin *et al*, in an article published in 1995[23], presented his observations on ring formation of clonal *Stipagrostis ciliata* and *S.obtusa* (note here that they are the species most related to the PB formation of FCs) in the Negev desert in Israel (figure 5A). Although the rings he documented are of smaller size than mature FCs (in the order of 1 meter in diameter) he argued that this process, in conjunction with the longer timescales of homogeneous undisturbed conditions the Namib desert is known for, gives rise to the large diameter rings (FCs).

The adoption of this idea leads to a number of contradictions with recent literature. Firstly, it is directly at odds with the scrupulous research on the FC life-cycle by Tschinkel[11]. He documented that new FCs appear close to their final size, and that the process takes less than 4 years, something ring formation cannot possibly account for. Secondly, it does not give reasons as to why FCs are to such a high degree evenly spaced, and coherent in size variations in each area[6, 7]. By itself, we believe the ring formation hypothesis lacks explanatory power, and thus it can in the present time be refuted as an all encompassing answer to this enigma[26].

The hypothesis of gas microseepage

The next hypothesis we will discuss is possible radioactivity and/or microseepage of gases coming from the soil. During the formation of a new FC, vegetation

dies locally in unison, with no easily discernible cause (figure 5D). This is why observers most of the times believe there is some kind of poison acting on the local scale, for example the *E.damarana* speculated herbicide we discussed earlier. Along these lines of thought, radioactivity was historically proposed as an FC inducer[8], but subsequently found to not increase in FCs by experiments[10]. In recent years, research on this possible mechanism has led to the discovery of gas microseepage that is present inside FCs, by Naudé *et al*[17]. Although the

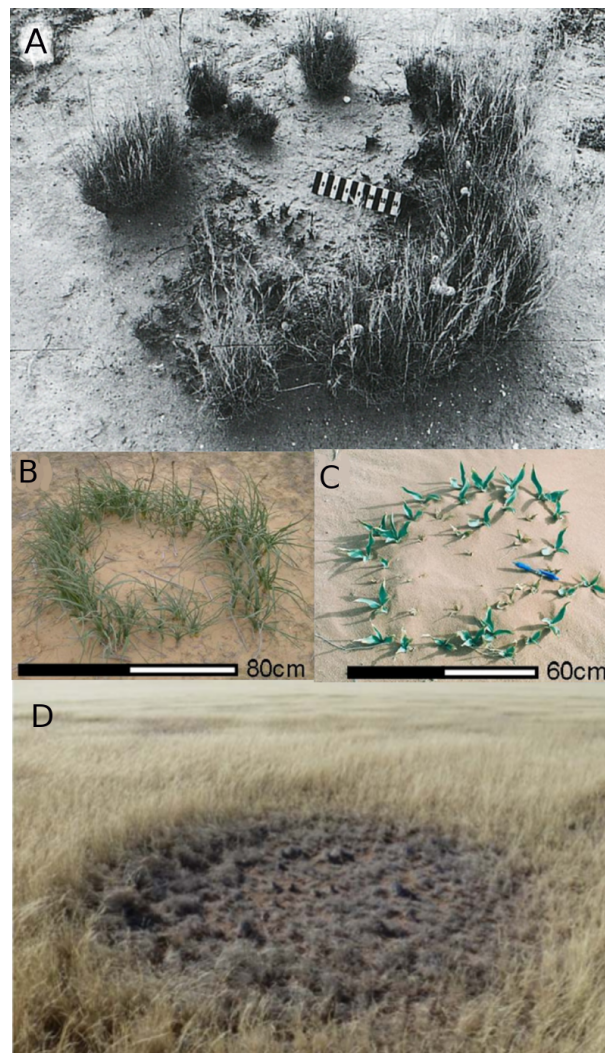


Figure 5: Ring formation resulting from clonal propagation of plants. **A** a circle of *S.ciliata* in the Negev desert. All plants are ramets of a long dead central progenitor. Bar=15cm. Photo by Danin *et al*[23]. **B-C** ring formation in arid conditions of *Asphodelus ramosus* and *Urginea maritime*. Photo adapted from Sheffer *et al*[25]. **D** newly formed FC. Notice the difference in size in comparison to the previous pictures of ring formation. Photo by Denis Hesemans (Namib Sky Balloon Safaris), adapted from Tschinkel[11].

exact nature of the gasses involved is not found yet (except the alkane-alkene fraction, and the CO emission), they argue that hydrocarbon microseepage is the primary causal agent for FC formation. As is the case for previously discussed hypotheses, the criticism here stems from the fact that although ample evidence exists on how hydrocarbon seepage leads to plant death, this generally happens heterogeneously at the landscape scale, and thus it is difficult to explain how this can come about at an evenly spaced manner. Cramer *et al*[6], as well as Tschinkel[11] have given elaborate arguments along these lines, and agree this hypothesis is not viable, as it does not propose a patterning process for the subterranean point sources.

The hypothesis of vegetation patterning

We chose to leave for the last place in this review of hypotheses the one we believe bears the most significance and at the same time the most debate about its viability as an explanation for the fairy circles (it is also the most recent proposed). It is the hypothesis of the self-organised patchiness of the Namibian vegetation. One can imagine a situation where the resources needed for the survival of plants over a given field are not enough to support individuals of a full life-cycle in all available positions. In this sparsely populated field, any form of non-local resource competition, for example for water (by root water uptake), can lead to pattern formation. By this we mean the plants may, for example, form local cohorts of more than one individual, due to short-scale facilitation of co-existence, and deplete the surroundings of water, inhibiting plant life in the longer scale. This kind of interactions have been studied extensively by spatial ecologists, and linked to other fields of study, as these patterning processes are abundant in nature and can be described using the same array of mathematical formalisms. This type of thinking about emergent pattern formation can be traced back to the seminal work on reaction-diffusion chemical systems by Turing[27], who showed how a set of spatially explicit chemical equations can produce strikingly regular patterns from a near-homogeneous initial state. In recent years, a bonanza of different mathematical models has been formulated in order to capture the defining principles of pattern formation in diverse ecological settings. This includes the study of vegetation patterns, in the most general theoretical sense as well as specific ones that appear for example in arid ecosystems[28], like the vegetation stripes or "tiger bush" (modeled by Thiery *et al*[29]), labyrinthine patterns, spotted vegetation and gapped vegetation (figure 6, two models which produce all of the above patterns can be found in [2, 30]). It is due to the remarkable similarity FCs have with the gapped patterns these models produce that a number of theoretical biologists propose the hypothesis of fairy circles being an emergent phenomenon arising from competition between plants for the available resources[31, 7, 2, 32, 33, 34]. However, the defining processes each researcher proposes as the ones giving rise to the pattern are not always the same, and also (in most of the cases) not mutually exclusive.

Due to the general observation of "Turing patterns" appearing in arid and semi-arid ecosystems (figure 8C-F, examples can also be found in [30]), models exist that aim to theoretically approach all of them together, without the FCs as an explicit target[36, 37, 2, 38, 39, 40, 35, 33, 28, 30, 41]. Although a number of them give great insight to vegetation patterning processes which could occur at FC formation, here we will review only the models the authors proposed for

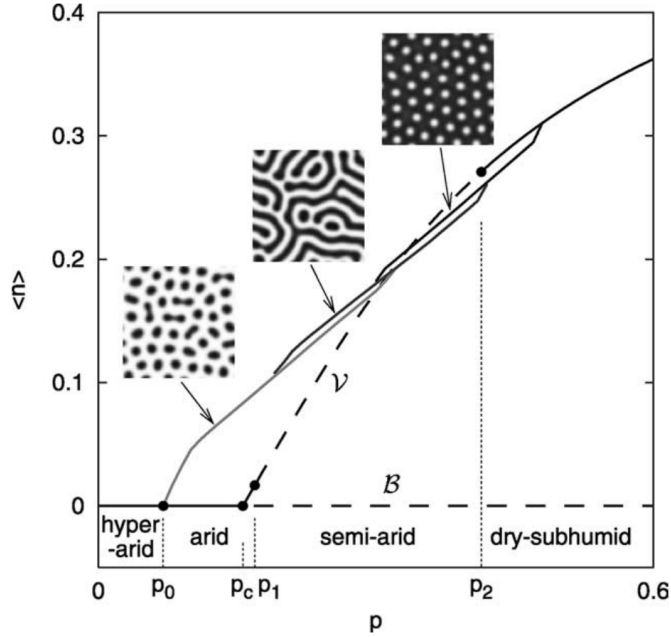


Figure 6: Turing patterns emerging from a model of vegetation patterning by Meron *et al*[35](adapted unchanged). Plot of the spatially averaged biomass n versus the precipitation p , as determined by numerical simulations. The insets are typical non-uniform solutions of the system for different precipitation rates.

FC research.

An interesting approach spanning multiple articles is the one by Gilad, Getzin *et al*[2, 7]. They put forward a continuum model of vegetation patterning consisting of 3 partial integro-differential equations representing the vegetation biomass per unit area $B(x, y, t)$, the soil water $W(x, y, t)$, and the surface water $H(x, y, t)$ that can undergo surface runoff. For the mathematically inclined, the equations are[2]:

$$\begin{aligned}\frac{\partial B}{\partial t} &= G_B B \left(1 - \frac{B}{K}\right) - MB + D_B \nabla^2 B \\ \frac{\partial W}{\partial t} &= IH - N \left(1 - R \frac{B}{K}\right) W - G_W W + D_W \nabla^2 W \\ \frac{\partial H}{\partial t} &= P - IH + D_H \nabla^2 (H^2) + 2D_H \nabla H \cdot \nabla Z + 2D_H H \nabla^2 Z\end{aligned}$$

In the first equation, G_B is the biomass growth rate (given by a separate equation which includes a root augmentation feedback to water uptake), K is the maximum biomass, M is the rate of biomass loss and the last term represents seed dispersal. In the second equation, I is the infiltration rate of surface water to the soil. This is also given by a separate equation and is positively influenced by the local biomass. The parameter N is the water evaporation rate, R is how the evaporation rate is lowered due to shading (a third water-biomass feedback), G_W is the soil water consumption rate, and the last term represents water percolation. In the third equation, P is the precipitation rate, D_H is the bottom

friction coefficient, and the rest of the terms stem from shallow water theory modeling of water runoff, with $Z(x, y)$ being the ground surface height for non flat topologies. This model resembles earlier models by Rietkerk *et al*[28, 30], and has been reviewed in terms of applications by Meron[33]. It is capable of Turing pattern formation, and depending on the parameter values (for example the precipitation rate P) transitions from gapped patterns to stripes and eventually to spotted vegetation. Getzin *et al* used this model to explain FC formation by minimising the infiltration feedback I (as the FCs happen in sandy soil where there is no big difference in infiltration between barren and vegetated land) and maximising the root augmentation feedback, that retains water under high vegetation biomasses (figure 8A-B). They showed that statistical attributes of the gapped pattern they produce resemble surprisingly well results from multiple field observations. The result we find most convincing is that when looking at the size of closest neighbouring FCs in relation to the distance from each other, both model and observations alike reveal a strong negative correlation up to a distance of 13m, which means, crudely speaking, that FCs closer together than average tend to be also smaller than average. The general approach has been criticised to ignore seasonality of rain events[38], as the precipitation rate is constant, and simply imposing seasonal precipitation events eliminates any pattern formation. Our additional criticism for this approach is that the profile for soil water the model produces in most cases is qualitatively different from field observations showing higher water content inside FCs[1] (figure 7C-D).

Another model applicable to FC formation is the one by Kyriazopoulos *et al*[32]. This model is based on the one we just discussed[2], but focuses on the dynamics of two species of plants, one evolved to be better in capturing sunlight and a second better in capturing soil water (higher root to shoot ratio). The model, in a specific parameter regime, gives rise to spatial coexistence of the two species, producing localised structures which resemble FCs in terms of the species spatial distribution, by a process of "front pinning" which is well researched in other dynamical systems. It is interesting to note that in this model the inclusion of non-homogeneous precipitation and other external heterogeneities is connected by the authors to the widening of the parameter range where bistability occurs. Our only point of possible criticism in the application of this model in FCs is its strong dependence on the competition for light for bistability. One can argue that light is not a limiting growth factor in the Namib, where plant growth dynamics are extremely slow due to other resource restrictions[42].

A second line of theoretical research on FCs can be traced in the work of Tlidi *et al*[34] and Fernandez *et al* [31], both extensions of earlier models by Lefever *et al* that focus on the application of the F-KPP front propagation equation on vegetation dynamics (for information, read [40]). The Fisher-Kolmogorov-Petrovskii-Piskunov equation was originally put forward by Fisher to describe the spatial spread of an advantageous allele, and is known for its traveling wave solutions. Here it is used to model the vegetation dynamics under facilitation and competition interactions without calling for other state variables like soil water. In the work by Tlidi *et al*, the equation for the spatio-temporal evolution of normalised plant biomass b at a point \mathbf{r} reads:

$$\partial_t b(\mathbf{r}, t) = k_1 b(\mathbf{r}, t) - k_2 b(\mathbf{r}, t) + D \int \left[\Phi_{in}(|\mathbf{r}'|) b(\mathbf{r} + \mathbf{r}', t) - \Phi_{out}(|\mathbf{r}'|) b(\mathbf{r}, t) \right] d\mathbf{r}'$$

The first term of the equation represents the gains in biomass due to natural growth of the plants, and the second term the losses due to decay. The third term represents the propagation of the plants over the field, and can be interpreted as seed dispersion and/or any other process the plants use. D is the rate of propagation of the vegetation, while dispersion kernels Φ_{in} and Φ_{out} weight the inbound and outbound seed fluxes that happen between neighbouring points, depending on their separation $|r'|$. The k_1 and k_2 are kinetic coefficients which take into account the communal feedbacks between plants, be it positive (short range facilitation in k_1) or negative (long range inhibition in k_2). Tlidi analyses FCs as localised structures that are stationary waves (dissipative solitons) which can emerge in a special case of this alternative short-range facilitation, long-range competition reaction diffusion system. These localised structures do not need to be part of a regular pattern, but rather they are stable mesoscale patterns themselves, and an arbitrary number of them can exist depending on the initial conditions (figure 7A-B). These localised structures interact with each other with repulsive and attractive forces, and can form bound states. This model could explain, if the hypothesis of emergent vegetation pattern formation holds true, why FCs, in some specific areas near the transition to the homogeneous vegetated state, are randomly dispersed, fewer in number, and farther apart. The model, however, has only one variable, namely the normalised plant biomass, and thus most of its parameter values are difficult to infer-verify experimentally, as they represent phenomenological attributes of the system like the facilitative and competitive feedbacks between plants.

Along the same lines of mathematical reasoning, Fernandez *et al* [31] argues that the FCs are emergent phenomena of an intrinsically dynamical nature, arising from non-local strong competitive interactions between plants, mediated by a Lorentzian type of kernel function. The Lorentzian function belongs to a class of spatial functions that decrease slower over longer distances in comparison to the exponential distribution (it has fatter tails). The model they use is a simplified version of the model by Tlidy *et al*:

$$\partial_t b = b[1 - b]M_f - \mu b M_c + \nabla^2 b$$

where

$$M_f = \exp(\xi_f b) , \quad M_c = \exp\left[\frac{\xi_c}{N_c} \int \frac{b(\mathbf{r}+\mathbf{r}', t)}{\left(1 + \frac{|\mathbf{r}'-\mathbf{r}|^2}{L_c^2}\right)^n} d\mathbf{r}'\right]$$

The parameter μ is the aridity parameter (as water scarcity is the foremost death process in the Namib). M_f is the short-scale positive feedback of plant biomass in plant development, M_c is the Lorentzian-like kernel, N_c is the normalisation coefficient and ξ_f, ξ_c are the interaction strengths of the two feedbacks. The authors report on the stabilisation effect the Lorentzian-type feedback has on the diameter of FCs: by using it, the FCs acquire a dynamically stable specific size, that is increasing with the aridity parameter μ , in agreement with field observations[6]. Numerical model simulations also show the formation of a ring of higher plant biomass around the bare center of the emergent localised structures. The innovation of this work however, lies in the successful attempt to bridge these results with the work by Gilad *et al* we discussed earlier (the first model of vegetation patterning we described). The Lorentzian-like kernel was inserted in a reaction diffusion model that explicitly describes water dynamics[43]

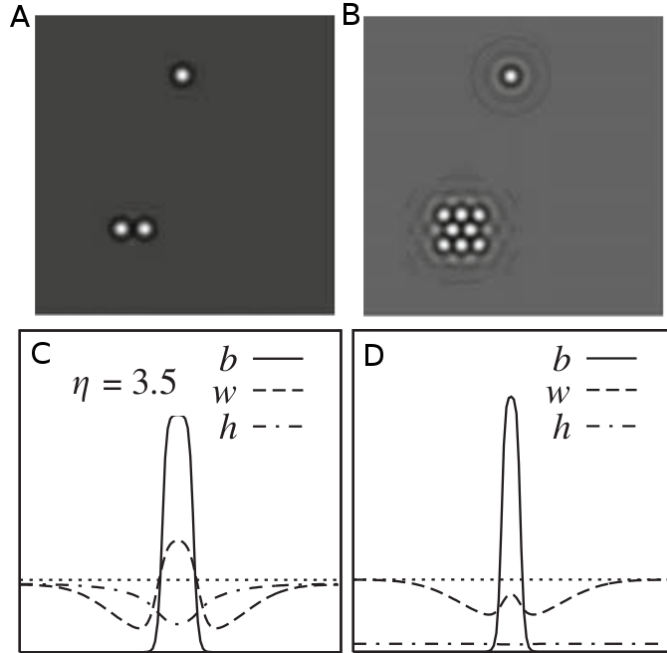


Figure 7: **A-B** localised bare spots (solitons) the model by Tlidi *et al* produces[34]. The two pictures are different timepoints of the same simulation. Notice how the interaction between the two solitons at the bottom facilitates the emergence of others nearby, in a hexagonal configuration. Figure adapted from [34] **C-D** spatial profiles of biomass (b), soil water (w) and surface water (h), cross-sections of two-dimensional simulations of the model by Gilad *et al* (adapted from [2]). The uptake feedback parameter η is the same for both pictures, whereas the infiltration feedback f is low in the first picture (0.1, meaning that the soil can have significant crusting and surface runoff) and high in the second (0.9, meaning there is little difference between barren and vegetated soil infiltration). We present these results for comparison to the observed water profile of FCs (figure 3).

and the behaviour of the model changed as to include stable localised structures which are not part of a regular pattern and can exist by themselves, in an otherwise vegetated field. This approach strengthens the view that FC formation could be the result of vegetation-resource dynamics even if the pattern we observe does not have characteristic distances between its constituent structures. At the same time, it tempts us to ponder upon the biological interpretation of the Lorentzian-type kernel, and the robustness of the results under similar kernels.

As we have just seen, work on the conceptualisation of FCs as emergent properties of vegetation dynamics has been extensive and connected to general vegetation patterning studies attempting to capture the defining principles for all the patterns that arise in arid ecosystems (spots, bands, gaps, depicted in figure 8). The models proposed more or less take into consideration the specific attributes on the FC ecosystem (ex. the non-crusting, sandy soil) and produce patterns emphatically close to the ones observed[7]. To date, they are the only

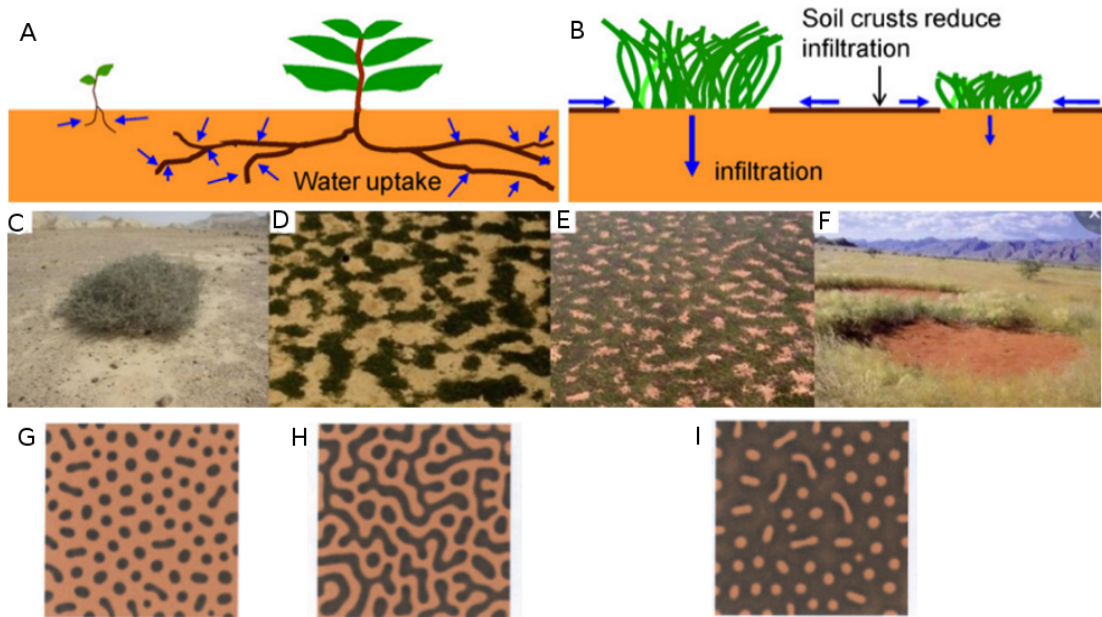


Figure 8: different feedbacks and emergent vegetation patterning (adopted from Meron[33](A-F) and Rietkerk *et al*[28](G-I)). **A** schematic representation of the root augmentation feedback, where plants of higher biomass can recruit water from a much larger area due to higher root-to-shoot ratio. **B** the infiltration feedback, where water infiltration on non-vegetated soil, due to crust formation, is inhibited in favour of surface runoff. **C** a spot of vegetation (isolated shrub) in the Negev. **D** spots and labyrinths of woody vegetation in Niger. **E** woody vegetation with gaps, also in Niger. **F** Gapped vegetation (fairy circles). **G-I** the corresponding to the above pictures vegetation patterns arising from a general model of vegetation-water dynamics[28].

explanation for FCs which can account for the changes in individual FC size depending on MAP (Fernandez *et al*, in comparison to data by Cramer *et al* [6]) as well as distance to nearest neighbour (Getzin *et al*[7], in comparison to field measurements produced in the same study). At the same time, the hypothesis of vegetation patterning accommodates easily other aspects of the FCs, like the formation of a perennial belt, the high R-values indicating a circle packing arrangement and the confinement of the pattern between specific MAP isohets. Evaluating this hypothesis is a difficult task. As a starting point, it must be pointed out that there are numerous processes which can create Turing patterns, so considerable attention must be given to find the one dominating the dynamics of FC formation, if one exists. Positive feedbacks between biomass - water infiltration and biomass - water retention due to shading can both produce bistability, but their presence in FCs has been questioned[7]. At the same time, the root augmentation (uptake) feedback (figure 8B), proposed to be the dominant FC formation force[31, 7], is far from verified by the inconsistent field observations of root length [1, 6]. Another point of criticism is the differences between the profile for water content the models produce and observation. Although FCs have higher water content than the matrix[6, 8, 13, 1], only special cases of model parameters ranges give analogous simulation results[2, 33] (figure

7C-D). It is interesting to note however that these parameter settings minimize the infiltration feedback and augment the uptake feedback[2]. Lastly, an argument against this hypothesis stems from our personal observation, by means of online satellite pictures, of the transition zone between FCs and barren land. All models predict that as the aridity parameter increases, the patterns should transition to labyrinthine-banded vegetation and then to vegetation spots. We did not observe any labyrinthine patterns around the domain of FC occurrence. An in-depth study of how FC patterning behaves at the transition zones could be a valuable addition to the FC literature.

Social insects and self-organised vegetation patchiness are, at this time, the two hypotheses for FC formation that are supported (or at least do not raise serious opposition) by field experiments. Consequently it is not surprising the two can be combined without the creation of contradictions. Central to this line of reasoning is the premise that insect activity and nest creation is under strong positive feedback with soil water content (water to attract insects). The presence of an FC creates an area effect of higher water availability for plants to survive the long dry season, due to water percolating into deeper layers after a rain event, effectively making the FC a local well. Whereas some authors introduce the termites-ants as the ecosystem engineers[1, 13], capable to single-handedly redistribute the available resources as to increase the local biodiversity, others do the same for the plants[43, 2, 33, 30]. In recent years, the view that insects might contribute to FC maintenance irrespective of the cause of the pattern has been put forward [6]. We believe experiments devised specifically for gauging the relative importance of faunal and floral dynamics must be designed.

Our hypothesis of differential water condensation

Studies of the water cycle in the areas where FCs are present have been focused on the soil water content of the FCs[6, 8, 13, 1], and its connection to rain events[1]. The coastal Namib desert however, with its tall sand dunes, is known for its frequent fog events[3, 44, 45, 42], and the remarkable ways by which the local species have adapted to air moisture harvesting[3, 45]. The occurrence of fog in the gravel planes where FCs are (inland of sand dunes), has not been the subject of independent study, but is certainly lower if it does indeed exist (Tschinkel, personal communication). Infrequent fog co-occurrence with some of the FC sites can be derived by the studies of Eckardt *et al* ([44], found in an insert of figure 1 of that article) and Rooyen *et al*[10](reporting fog can be present 80km inland, referring to two older studies). Studies of dew formation in FCs are also absent from the literature. Be that as it may, dew has been indicated as an important moisture contributor in arid ecosystems, and in some years dewfall can even exceed rainfall ([46], referring to the Negev desert). For all these reasons, we became interested in the possible contribution of dew and fog to the water cycle of the FC ecosystem.

In the absence of direct measurements of dew formation in the gravel planes, we contacted the NamibRand nature reserve administration[47], who kindly provided us with high resolution meteorological data from their weather station (Davis instruments Vantage Pro 2, located at 24 54' 00" S, 16 00' 00" E), which is in relative proximity to the area in the reserve where FCs occur (2.3km away from fairy circles as measured using online satellite images). The data

were uninterrupted measurements for the year 2008, including measurements of temperature and dew point. By comparing the lowest recorded temperature for each report interval (30 minutes) to the dew point, we found that 8 times during the year 2008 (mostly nights) the dew point exceeded the lowest temperature. In addition, we found that 66 nights of the year the lowest temperature was within 2.5 degrees of the dewpoint. Given these results we believe that a significant contribution of dew to the water economy of the FCs is plausible.

Our hypothesis stems from the idea that differences in soil cover by plants can create differences in the water influx to the soil-plants system. This can of course be due to rain being able to percolate quickly to deeper soil in FCs[1], thus avoiding evaporation from the top soil, but also can be due to differential dew formation related to the faster cooling of non-covered top soil, during each night, and diffusion towards the surroundings either by air or by ground (a similar effect has been reported for the presence-absence of trees and dew formation here [48]). These effects have not been tested by theoretical models for their emergent behaviour. We thus formulate the hypothesis that FCs are the result of vegetation patterning arising from differential water influx to the soil, dependent on the local vegetation cover (figure 9A). We use a simple model that has these features to test how a plant community would respond under these conditions of resource availability. Crucially, our model is an interesting juxtaposition to the models proposed for FC vegetation patterning, as it proposes a qualitatively different mode of plant-resource interaction. Whereas all models presented here assume a positive feedback between water redistribution and plant biomass, in our model the plants completely inhibit the local influx of water, as we will shortly describe.

3 Model description

It is evident from the hypothesis we propose that the emergent population dynamics of plants might be rather counterintuitive: When plants populate a specific space, due to their mere existence they deprive themselves from local condensation of water. The survival of these plants is dependent on water percolation from elsewhere, and thus the existence of barren land in the vicinity of the patch. It is for this reason we choose to investigate how plants would behave in the field by means of simulating a spatially explicit model capturing, in a simple way, the processes of plant propagation, water condensation in barren land, and water percolation in the soil.

To describe plants existing and propagating over the desert field, we use the stochastic cellular automaton model formalism [49, 29, 30] that uses discrete space (a square grid), discrete states (values each square takes) of this space to indicate if plant life exists there, and discrete time. This is a model in two spatial dimensions, and the spatial resolution is chosen to be 1 meter. Our model has two states, state "0" representing a barren parcel of land, and state "1" that represents a parcel that has plant life. Each timestep for this part of our model is selected to correspond to 1 day in the field. Our model has periodic boundary conditions.

Plant propagation in our model is described as a stochastic process. That is, each new timestep there is a small chance each square on our grid of state 0 (barren) gets populated by plants, if by randomly picking out one adjacent square on the grid (of the Moore neighbourhood [49] consisting of all 8 neighbours) we find it is of state 1 (vegetated). The probability a square of state $A_{x,y}(t) = 0$ becomes 1 at the next timestep ($A_{x,y}(t+1) = 1$) is

$$P_{x,y}(t) = \sum_{k=-1}^1 \sum_{l=-1}^1 A_{x+k,y+l}(t) \cdot b_1 \quad (2)$$

where the double series essentially gives the number of vegetated direct neighbours of the barren spot, and b_1 is a parameter expressing the probability each one of the neighbouring vegetated squares has in invading the barren spot.

Each vegetated patch in our model has a variable $S_{x,y}(t)$ associated with it depicting the drought stress level of the patch. This variable is a simple counter that takes the value of how many timesteps ("days") the patch has survived without meeting its water needs. The counter gets fully reset every time there is enough water for the plants in the parcel of land under consideration to fill their daily needs (supplementary figure 11). The plant death process in our model is based only on drought stress. If the plants have exceeded their limits in terms of drought tolerance, they die leaving behind barren land. Thus in our model we have the following processes taking place:

$$S_{x,y}(t) = \begin{cases} 0 & \text{if } W_{x,y}(t) \geq w_1 \\ S_{x,y}(t-1) + 1 & \text{otherwise} \end{cases} \quad (3)$$

$$A_{x,y}(t) = 0 \text{ if } S_{x,y}(t) > t_1 \quad (4)$$

The variable $W(x, y, t)$ is the water content of the soil at the start of each day (after condensation and percolation has occur), and the parameter w_1 is the amount of water each square patch needs to overcome drought stress. The parameter t_1 is how many consecutive days the plant patch can survive under drought stress.

Water percolation dynamics are much faster than plant propagation dynamics. Hydraulic conductivities of sandy soils are reported to be *circa* $1\text{cm}\cdot\text{min}^{-1}$, one of the largest values compared to different soil compositions[50]. For this reason, we modeled the influx and percolation of water by using the same lattice representation but a much smaller timestep (in the order of 1 hour). Simulation of water influx-percolation takes place in between each timestep of the cellular automaton, for a number of sub-timesteps representing the night time hours we hypothesize this process occurs (figure 9B). We implement water dynamics using a simple forward Euler numerical integration of a PDE model of water creation-diffusion. Put formally, the model we implement is based on Fick's law of diffusion:

$$\frac{\partial W}{\partial t} = \begin{cases} D\nabla^2 W + p & \text{if } \sum_{k=-1}^1 \sum_{l=-1}^1 A_{x+k,y+l}(t) = 0 \\ D\nabla^2 W & \text{otherwise} \end{cases} \quad (5)$$

where the $D\nabla^2 W$ term describes the water percolation in 2 dimensions with D being the "diffusion" coefficient and ∇ is the gradient operator. The parameter D is crucial in our opinion for understanding the emergent dynamics of FCs, and we shall discuss its role in depth in the discussion section. The parameter p is the influx of water from outside the system we describe, and is present when the parcel of land has no populated direct neighbours. This is the exact part of the model where our hypothesis of differential condensation of water is taking place, in a rather extreme form: water only appears in barren land that is away from vegetation.

In the end of each "night", after the profile of water content W has being computed, it is compared with the needs for water the plants have (w_1) in each patch, to determine the stress level (equation 3-4) of each patch. After, we assume that during the next "day" in our simulation all water that went in the system the previous "night" gets lost completely by the processes of evapotranspiration, evaporation, and percolation to deeper soil. Thus our model is an attempt to capture only what happens on and in the top soil, using simple functions and processes (figure 9B).

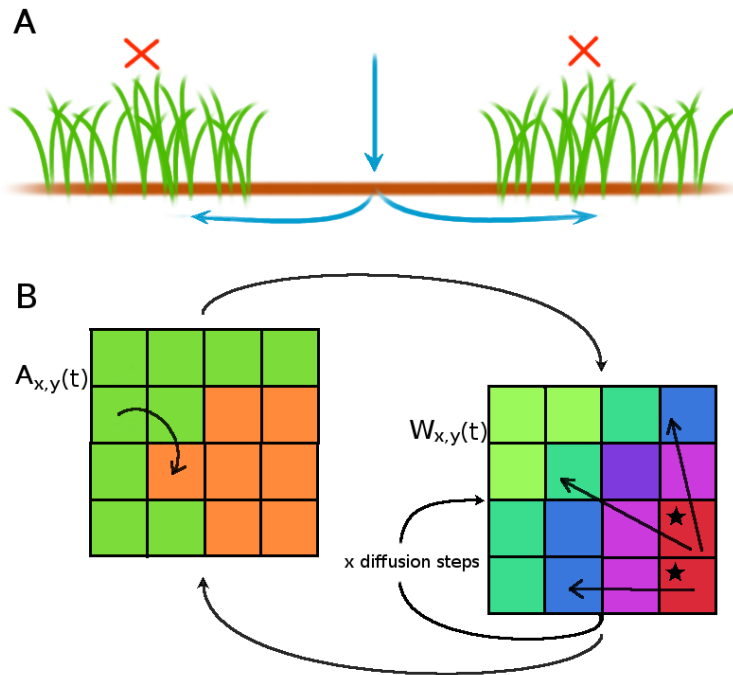


Figure 9: **A** schematic representation of the differential condensation feedback. Dew formation is facilitated in barren land that is away from plants (vertical blue arrow), and is inhibited in vegetated patches (red crosses). Water then percolates to surrounding areas where it sustains plant life. **B** simplified diagram of our cellular automaton model. On the left, we have the daily dynamics of plant birth and death processes (vegetated state in green, barren in brown). On the right, we have the multiple in-between steps of water production and diffusion (green=low water content, blue=medium, red=high water content). Water production only happens in cells with no vegetated direct neighbours, indicated here by a star. Water percolates away from sites of production (straight black arrows). Based on the final profile of water, the next daily step of plant dynamics gets evaluated. In the end of the day, all water disappears from the field.

4 Results

Numerical simulations of this model prove very interesting in terms of how the vegetation populates the field. An example can be seen in figure 10. Expanding plant communities have as a consequence the depletion of water from their central parts, leading to localised death of plants, and the creation of structures resembling FCs. At the dynamic equilibrium of transitions between barren and vegetated states, each of these structures persist for a large amount of simulation time, more than the rate of plant propagation would allow, but are not permanent, some of them getting populated by plants and losing their ability to provide water (supplementary figure 14A). Intuitively, these structures can be thought of as providers of water for the nearby vegetation that encircles them, that are semi-stable, because any invading plants are short lived. This is because those particular plants are killing their water supply while at the same time being very far away for other barren structures to support them with water (supplementary figure 13). Another interesting observation in the simulations is that new FCs are spontaneously created by the concerted death of many closely packed parcels of land. In many cases this birth of a new FC happens at the site of a recent collapse (by invasion by plants) of an older one, a "back from the dead"- "Lazarus" effect. These attributes of the behaviour of our model are in striking agreement with observations of the real phenomenon in the field[11].

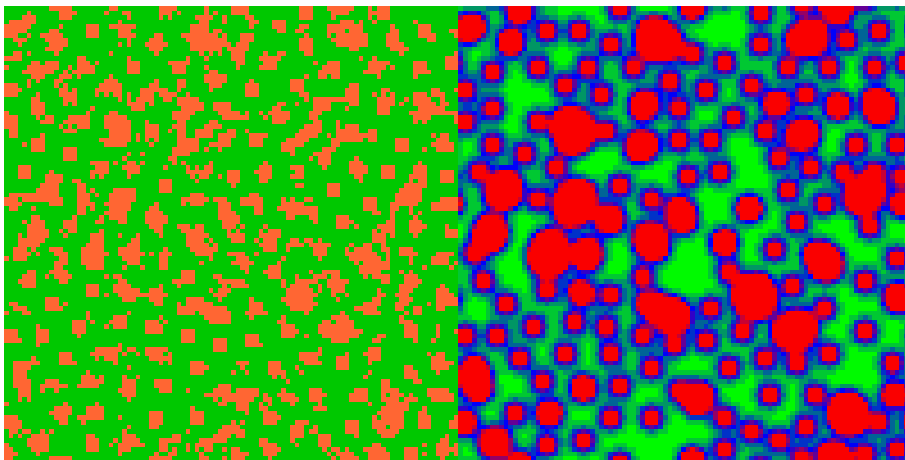


Figure 10: Simulation results at 10000 years of simulation time (dynamic equilibrium between barren and vegetated states is reached ca. 5 years into the simulation). The lattice dimensions are 100 by 100 meters (lattice sites). **Left:** vegetation dynamics on a homogeneous surface resembling the Namibian desert (green=vegetated, brown=barren). **Right:** the water dynamics over the same surface (green=low water, red= high water content)

Next, we calculated the distribution characteristics of the localised bare spots our model produces. We used the R-value as a metric of the dispersion of the spots (equation 1), in order to be able to compare our results with the existing literature. We devised a specialised algorithm to find the centroids of bare spots, and we used them to find the euclidean distance to the nearest neighbour. Our

model robustly produced significantly overdispersed bare spots, with R-values ranging as high a value as 2, dependent on various model parameters (water influx p , water percolation rate D , plant birth parameter b_1). A plot depicting the R-value of the bare spots over simulation time can be seen in figure 11. This result is comparable with previous calculations of the R-value of real fairy circles[8].

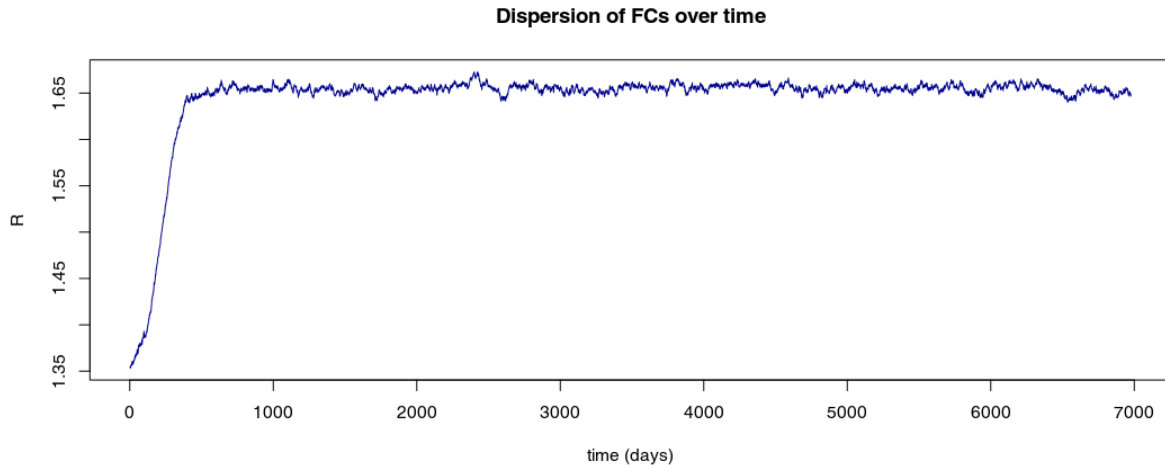


Figure 11: R-values of localised bare spots over simulation time. The simulation producing these results is performed over a lattice of dimensions 1000 by 1000 meters. Although the lattice is initialised with random plant cover, the R-value is not calculated at the start to be at 1, due to an artifact of the centroid calculation algorithm, which goes away when the gaps in vegetation appear.

4.1 Inclusion of a second species of plants

The formation of a perennial belt of plants around FCs, although not always present[11], is a characteristic attribute of the pattern. Using our model, we tried to highlight conditions under which PB formation is possible, by including a second variant of vegetation cover. This second variant approximates the higher biomass perennial vegetation, and in our cellular automaton takes the form of a third possible state of the automaton's cells ($A_{x,y}(t) = 2$). The second variant depicts the maturation of matrix vegetation under conditions of higher water availability, and has distinct parameter values for its drought stress tolerance and daily water needs. The probability of a vegetated parcel of land ($A_{x,y}(t) = 1$) to make the transition to perennial vegetation ($A_{x,y}(t+1) = 2$) is

$$M_{x,y}(t) = \begin{cases} b_2 & \text{if } W_{x,y}(t) \geq w_2 \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

where b_2 is the maturation probability and w_2 is the daily water needs of the perennial vegetation. The stress and death process for the perennial vegetation is identical to the one of regular matrix vegetation (equations 3-4) except for

the parameters w_2 and t_2 , which is the tolerance in days the perennial vegetation has to suboptimal water availability. Aiming to differentiate as faithfully as possible the perennial state vegetation from the regular one, we chose to set the water needs of the perennial vegetation higher ($w_2 > w_1$) but also make the perennial vegetation more hardy to drought conditions ($t_2 > t_1$). These additions to the model proved sufficient to produce a ring of the new cellular automaton state around the localised bare spots (figure 12).

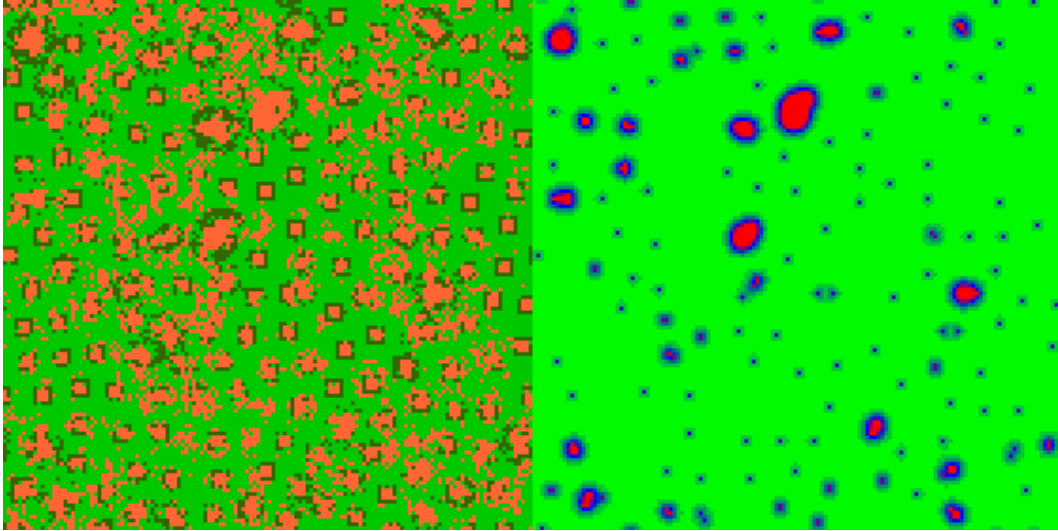


Figure 12: Inclusion to the cellular automaton model of a third possible state resembling in behaviour a second variant of plant vegetation. The state $A_{x,y}(t) = 2$ (in this simulation depicted as deep green colour) has higher water demands than the ordinary vegetation state and higher tolerance to drought. We observe rings of the new state around barren spots, resembling the perennial belt of FCs. The simulation grid is 280 by 280 meters. Parameter settings can be found in supplementary table 1.

5 Discussion

The theoretical outcome of our hypothesis, judged by our model simulation results, can be argued to be in good agreement to the nature of FCs. The model creates overdispersed bare spots, transient in nature, which have a higher water content than the surroundings. Our model however, is a simplistic representation of reality: It is coarse grained in its depiction of vegetation, the water dynamics completely ignore the third dimension of deeper soil layers, and water influx to the system is a bimodal function of vegetation cover. In addition, due to time constrains, we did not bridge our water condensation-diffusion parameter settings to existing literature on water soil dynamics, something crucial for identifying which exact process might give rise to a pattern of such a characteristic wavelength as the fairy circles. For example, the diffusion of water droplets might be through the layer of air directly above the soil and not through the soil itself (a presumably faster process). Another possibility is that the timescales of the model are completely wrong and the same process actually takes place in a yearly cycle, the water of the model being the fraction of rainwater that achieved infiltration to deeper soil and thus long term storage. As such our theoretical results need to be taken "with a grain of salt" as to how much they are descriptive of the conditions on the field. The contribution of our work on this hypothesis to the existing knowledge on the subject should thus be limited to the theoretical observation that if you couple barren land with water influx in the system under consideration (an open field) , overdispersed gaps robustly emerge to vegetation that attempts to populate it.

Evaluating the possible basis of our hypothesis on dew formation is rather straight-forward. Using an array of soil surface pyrometers (thermometers) and microlysimeters[46] (measuring moisture coming from fog-dew formation) from the center of the FC to the matrix between them, differences in local temperature and dewfall can be analysed for statistical significance, and be used to support or disprove differential dew formation in FCs. This experiment can easily be part of studies like the one proposed by Eckardt[44], who postulates a significant, higher than expected, ambient sub-surface humidity in the Namibian planes, and calls for experiments on this general subject with detailed instrumentation. Finding the cause of the FCs (or eliminating possible ones) is crucial in the face of global warming and rising night temperatures, in order to assess the susceptibility of this ecosystem to environmental change[51].

So what is the cause of fairy circles? Is it termites or maybe vegetation patterns? In our model barren areas provide water to the system and the interplay between them via water diffusion gives rise to the overdispersion. If indeed termites are the culprits for FC formation and maintenance, and they do it for providing themselves with sufficient water[1], we incidentally showed here that the overdispersion of their nests might not be due to intraspecific competition, but rather by a form of vegetation patterning that depends on how water percolates away from their nests, and how far it can get and support plant life. Such is the interplay between the possible effects of termites and vegetation patterning, that at this time pointing to one and refuting the other in our opinion can not be substantiated by any of the results in the literature. Experiments on the long term effects of exclusion of termites from FCs (for example by using

an insecticide with an exceptionally long half life), as well as experiments aiming to find how water circulates between FCs and the matrix and how plants affect this, can clarify the relative importance of these two leading hypotheses. In addition, fairy circles do not behave as expected by vegetation patterning studies in the transition zone to full desert environment or homogeneous full cover vegetation, so an in-depth study of how FC patterning behaves at the transition zones could be a valuable addition to the FC literature, possibly clarifying the exact role of social insects (indicated already by Juergens[1], figures S1B, S6, S7).

6 Summary

The fairy circles are large discs of barren land, that appear, in equal distances between them, in the low vegetation of the gravel plains of the Namibian desert. Their origin is a hotly debated subject, and only recently we begin to understand what the possible causes might be. By reviewing the literature, we present here the two leading hypotheses, which are that either insects make them, or plants, via competition for resources. Inspired by the finding that water is more abundant in them, we postulated fairy circles act as water condensers, attracting dew formation in the night-time, and providing water to their surrounding vegetation. Forming a theoretical model which does exactly that we found attributes of the FCs like their strikingly regular spacing can be explained by such a simple system. We thus put forward this variant of the vegetation patterning hypothesis for field tests, and discuss how it relates to the other ideas about fairy circle formation. Under our explanation, fairy circles can be thought of as water providers for their surrounding vegetation, and any given plant has the surrounding fairy circles for help with its water needs. They are stable, because invading plants die off, as they deprive themselves from long term water by killing the water creating capacity of the FC, and at the same time they are far away for any other FCs to support them. This leads to long term alterations in the soil of the FCs, attraction of termites, and other changes that further stabilise their presence. We invite interested students of dynamical systems to observe the pattern in satellite pictures provided online, and appreciate how excellent a subject it is for pedagogical studies of pattern formation in biological systems.

7 Supplementary material

parameter	value	motivation
b_1	0.001	slow vegetation dynamics in the Namib[42], the FCs more stable for slower dynamics
b_2	0.001	
w_1	0.001 arbitrary water units/day	
w_2	0.05 arbitrary water units/day	PB vegetation needs more water
t_1	20 days	
t_2	30 days	PB plants more hardy than matrix
p	1 arbitrary water units/timestep	
D	$2.5m^2 \cdot hour^{-1}$	

Table 1: Parameter values for the results presented in this study.

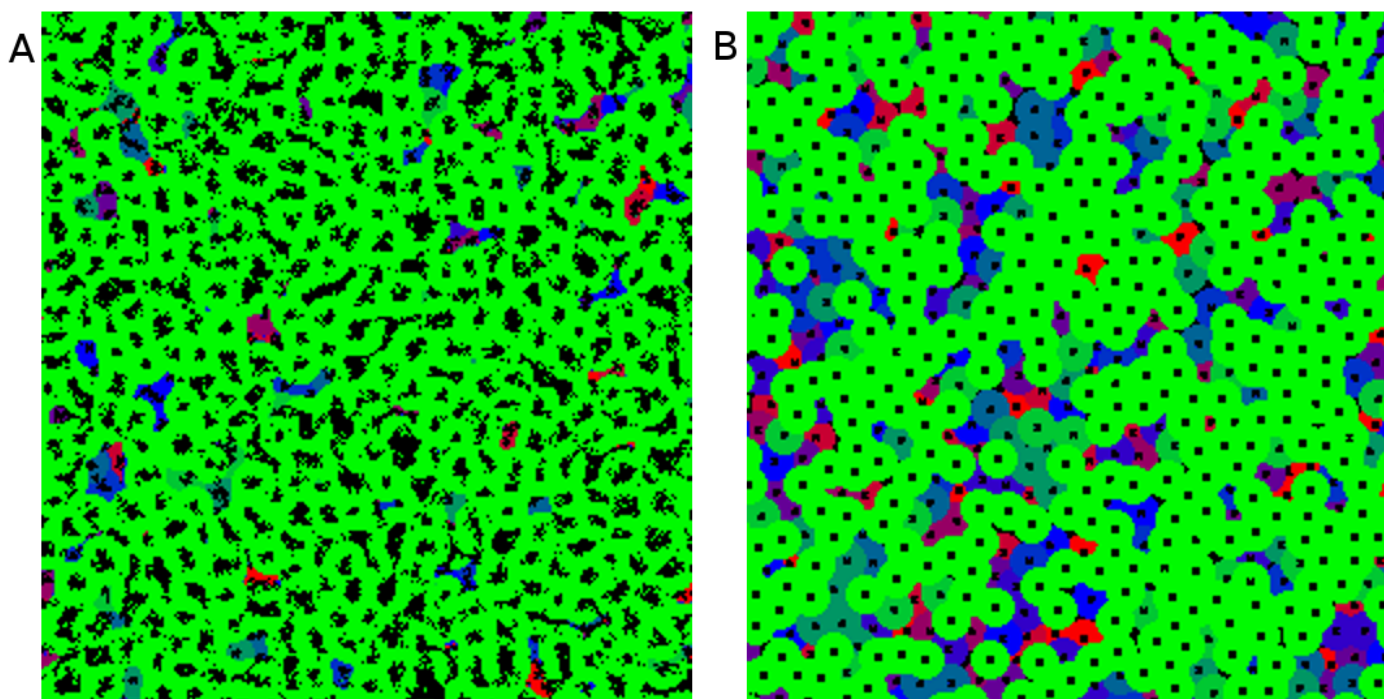


Figure 13: Stress levels of plants in two types of long term simulations. Green denotes healthy plants, and a gradient from blue to red denotes increasing stress levels. Notice how the fairy circles have overlapping domains where they affect the stress levels of plants, and how plants next to recently invaded FCs are under high stress. **A** simulation of the simple model, with a high birth rate ($b=0.01$). **B** simulation of the exact same model, with the addition of the rule that plants do not invade a square cell unless there is enough water (w_1) in it to fulfill their needs.

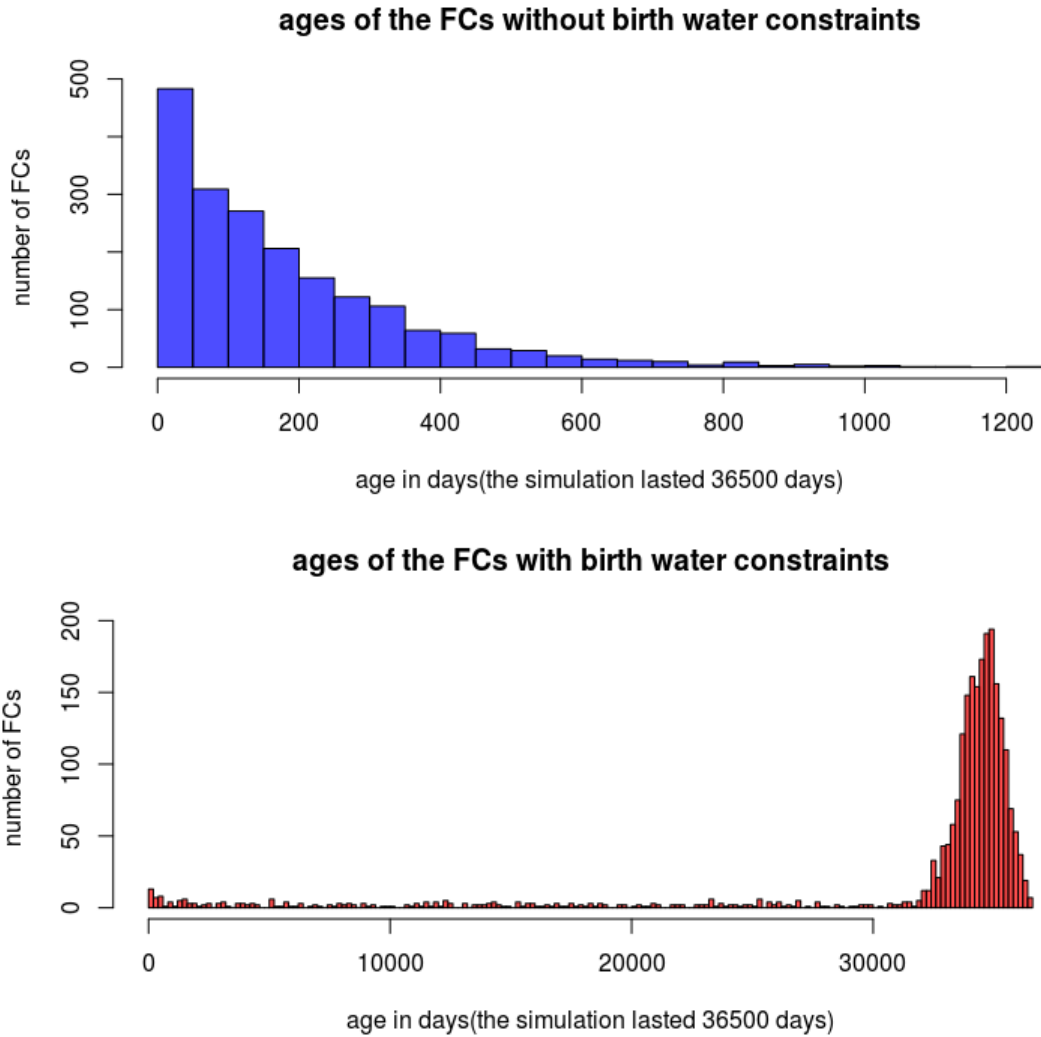


Figure 14: histograms of the ages of fairy circles for the two simulations of supplementary figure 13. **top** distribution of ages for the localised barren structures for the simple model. Notice how the fairy circles have a life cycle (are transient in time). **bottom** distribution of ages of localised barren spots. In this simulation we added the rule that plants cannot invade a cell if there is not enough water to support them in it. The distribution of ages changes drastically, and the fairy circles, although not completely stable in time, can attain arbitrarily high lifespans.

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