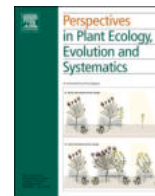


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Sand termite herbivory causes Namibia's fairy circles – A response to [Getzin et al. \(2022\)](#)

Norbert Jürgens^{a,*}, Alexander Gröngröft^b

^a Institute of Plant Sciences and Microbiology, University of Hamburg, Hamburg, Germany

^b Institute of Soil Science, University of Hamburg, Hamburg, Germany

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ABSTRACT

In parts of Angola, Namibia and South Africa the sparse vegetation at the margin of the Namib Desert is often dotted with roughly circular bare patches. The origin of these “fairy circles” (FC) is subject of an ongoing debate. In a recent article in PPEES, Getzin et al. (2022) provided assessments of grasses and termites combined with soil moisture measurements, in and near to fairy circles in several areas in Namibia. In their interpretation they state that termite herbivory is not causing this grass death as the plants had undamaged roots. Instead they propose that the matrix grasses severely depleted the water in FCs. Here, we use a comprehensive, detailed body of measurements and assessments collated during the last 14 years to propose an alternative interpretation. We structure our interpretation with four statements, each of them based on shown evidence: (1) Long-term soil moisture measurements confirm that the soil beneath the dry topsoil of the bare patch of fairy circles contains an equal or, especially during the biologically active season, higher amount of moisture than the surrounding matrix, at any given time. The grasses of the fairy circles bare patch die during the moist phase of the first weeks after a rain, before even the soil beneath the matrix vegetation gets depleted by transpiration. (2) Within the sandy soils of fairy circle landscapes, there is no sufficiently strong “uptake–diffusion feedback” that could cause a horizontal movement of soil moisture over several meters within a few days. (3) The grasses of the fairy circles bare patch first die at the centre of the bare patch and later towards the margin. (4) The grass in the bare patch of fairy circles dies because of damage to roots due to herbivory by sand termites.

1. Introduction

[Getzin et al. \(2022\)](#), in their article entitled “Plant water stress, not termite herbivory, causes Namibia's fairy circles”, invested time and effort to investigate the role of termites and the soil moisture at and next to fairy circles in the Namib Desert. Thanks to the recent publication in ppees, the debate on the origin of the bare patches that occur in great number in grasslands at the Namib Desert margin was once again brought to the attention of the scientific community.

During 2020–2022, Getzin et al. studied the status of grass seedlings that germinated at fairy circles, triggered by a rare precipitation event at several places in Namibia. In addition, they measured the course of soil moisture with automatic TDR-sensors during the rainy season within and next to fairy circles. In their final discussion, the authors conclude that (a) termite herbivory is not causing the grass death as they couldn't find damaged roots, and (b) plant water stress causes the death of grasses within the bare patch of fairy circles.

Our response is partly based on the results of five years of soil moisture measurements, already published in [Jürgens \(2013\)](#), and partly on new data sampled since 2009 until 2022. In our response, we will show that key measurements and observations published in [Jürgens \(2013\)](#) are confirmed by key measurements and observations made by [Getzin et al. \(2022\)](#). However, the interpretation differs fundamentally.

With the following four statements, all based on shown evidence, we propose an alternative view of the course of the soil moisture, the temporal and spatial dieback of the grasses and the observations and statements regarding the presence and functional role of termites.

2. Material and methods

Our material and methods have been described in [Jürgens \(2013\)](#), for the observation sampled since 2009 until 2022 in [Jürgens et al. \(2022\)](#): http://www.biodiversity-plants.de/biodivers_ecol/vol7.php.

* Correspondence to: Institute of Plant Sciences and Microbiology, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany.

E-mail address: Norbert.juergens@uni-hamburg.de (N. Jürgens).

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3. Results and discussion

Statement 1.

The soil beneath the dry topsoil of the bare patch of fairy circles contains an equal or, especially during the biologically active season, higher amount of moisture than the surrounding matrix at any given time. Thus the grasses in the bare patch of the fairy circles do not die due to soil drought.

Getzin et al. (2022) present moisture measurements of the soil beneath the bare patches and matrix of fairy circles, using time domain reflectometry (TDR) sensors at 20 cm soil depth only. A typical course of soil moisture is presented in Fig. 1 (Fig. 1. in Getzin et al., 2022). The measurement convincingly shows that during the last days of February 2022, the soil moisture beneath the matrix vegetation (shown in green) differs from the soil moisture beneath the bare patch of the fairy circle (shown in red). The soil beneath the bare patch (in red) remains much moister because there are no grasses that consume the soil moisture. To explain this difference, Getzin et al. (2022), in the “highlights” of the publication) suggest that “Soil-moisture data indicate that the matrix grasses severely depleted the water in FCs.” In section 4.4. Getzin et al. add: “While we have not directly measured lateral water flow, our data suggest that these matrix grasses have drawn the water from the FCs and induced water stress to the desiccating grasses within the circles ...”.

Getzin et al. (2022) do not mention that their measurements repeat and confirm the more detailed soil moisture measurements published in Jürgens (2013). Those measurements of soil moisture beneath the bare patch and the matrix of fairy circles span five years from January 2008 until the end of 2012, including the effects of quite different amounts of precipitation. These measurements report the speed of infiltration and percolation of the rain water at 10, 30, 60 and 90 cm depth (Fig. 2, was Fig. 2 in Jürgens, 2013). In total, 10 precipitation events and the resulting moisture pulses were captured and shown. For two precipitation events, the increase and subsequent decrease of soil moisture for both the fairy circle bare patch and the matrix were presented (Fig. 2B in Jürgens, 2013).

An extreme amount of rain (>500 mm) fell during January to May 2011, followed in the next year by a single strong rainstorm with 67.5 mm in early April 2012. The water content beneath the bare patch is moister than the soil beneath the surrounding matrix at any given time water content is higher (not moister).

Despite the high moisture in the soil beneath the bare patch, the young grass plants died within the first five weeks after the triggering rains. During these periods, the soil moisture levels beneath the bare patch of the fairy circle were higher than 5 vol%, well above the permanent wilting point at ca. 2 vol%.

The dieback within the moist phase during the first five weeks after the triggering rainfall was confirmed during the continued observation from 2013 until 2022. A soil hydrological analysis of the soil moisture monitoring data spanning more than a decade is presented in Gröngröft and Jürgens (2022).

From all the above data, it can be summarized that the soil beneath

the dry topsoil of the bare patch contains a higher or similar amount of moisture than the surrounding matrix at any given time. Both soils are equally moist or dry shortly after a rain or during extreme droughts of longer than a year. This result is equally based on the measurements presented by Jürgens (2013) and the data shown by Getzin et al. (2022).

Consequently, the above statement in the highlights of Getzin et al. (2022), “Soil-moisture data indicate that the matrix grasses severely depleted the water in FCs”, is not supported by the measured evidence.

With regard to the timing of the death of the grasses within the fairy circles bare patch, Getzin et al. (2022) confirm the observations made in Jürgens (2013): The grasses die early, during the first few weeks when the soil beneath the bare patch is still moist. Getzin et al. (2022) explicitly write: „we noticed that the few grasses that were able to germinate within the FCs started wilting already a week after rainfall. By less than three weeks after rainfall, all grasses within FCs were desiccated and dead while the matrix grasses were still vital.” (Section 4.1).

In their interpretation, Getzin et al. (2022), in the “highlights” of the publication) state: “After grass-triggering rainfall, new grasses within FCs die instantly due to wilting.”

This statement is in obvious contradiction to their own interpretation, discussed above. As the data show (see red line in Fig. 1), the instant death of the grasses cannot be caused by a lack of water, as the soil moisture even in 20 cm depth is still high.

During these “three weeks after rainfall”, even the vegetation in the matrix outside the fairy circle is still alive and enjoys high soil moisture, despite the fact that here the plants take up soil water with their roots and transpire the water with their leaves.

It is even less possible to explain the death of grass in the bare patch to have been caused by a lack of water because the measurements from 2008 to 2012, as well as the measurements in Getzin et al. (2022), prove that there are sufficient moisture levels.

Consequently, the early death of the grass plants within the bare patch must have another cause.

Statement 2.

Within the sandy soils of fairy circle landscapes, there is no sufficiently strong “uptake–diffusion feedback” that could cause a horizontal movement of liquid or vaporized soil moisture over several meters within a few days.

Getzin et al. (2022) introduce a key process for the hypothesis of the self-organization of vegetation patterns by stating: “Proponents of the vegetation self-organization theory argue that the gaps remain bare because the ecohydrological feedback between grasses that surround the FCs are depleting the soil moisture to an extent that revegetation of the gap interior is hardly possible due to critical plant water stress. In the Namib, the pattern-forming feedback is caused by a high rate of water uptake by the plants and by fast lateral soil-water diffusion, relative to biomass expansion (Zelnik et al., 2015). Given that the permanently transpiring *Stipagrostis* grasses with their laterally confined roots create “soil-moisture vacuums” around the root zone, the so called “uptake-diffusion feedback” leads to antiphase spatial biomass-water distribution and thus vegetation gaps in the sandy soils of the Namib (Kinast et al., 2014; Getzin et al., 2016).”

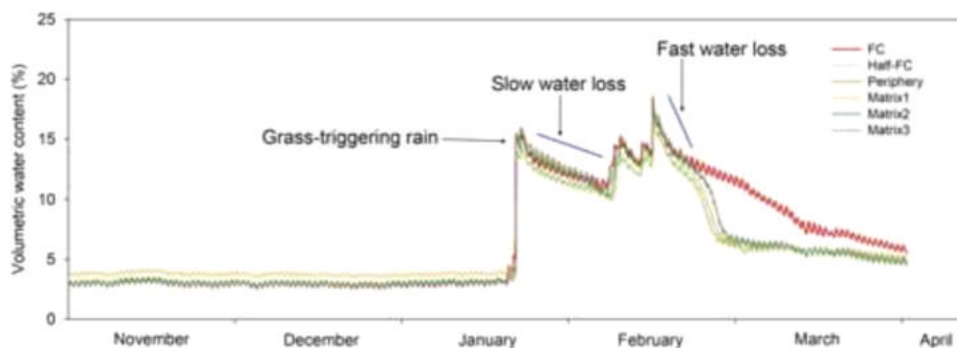


Fig. 1. taken from Fig. 1 in Getzin et al. (2022): “Two main rain events occurred in 2022: one on 21st January and one on 14th February. Two minor rain events occurred in between. Data were recorded until the 1st of April 2022. Without matrix grasses after initial rainfall, the drop in soil-water was very slow at all sensor positions (left blue line). But with a dense cover of transpiring grasses in the matrix a month later, the water loss in the unvegetated FC and in the matrix was very fast (right blue line).”

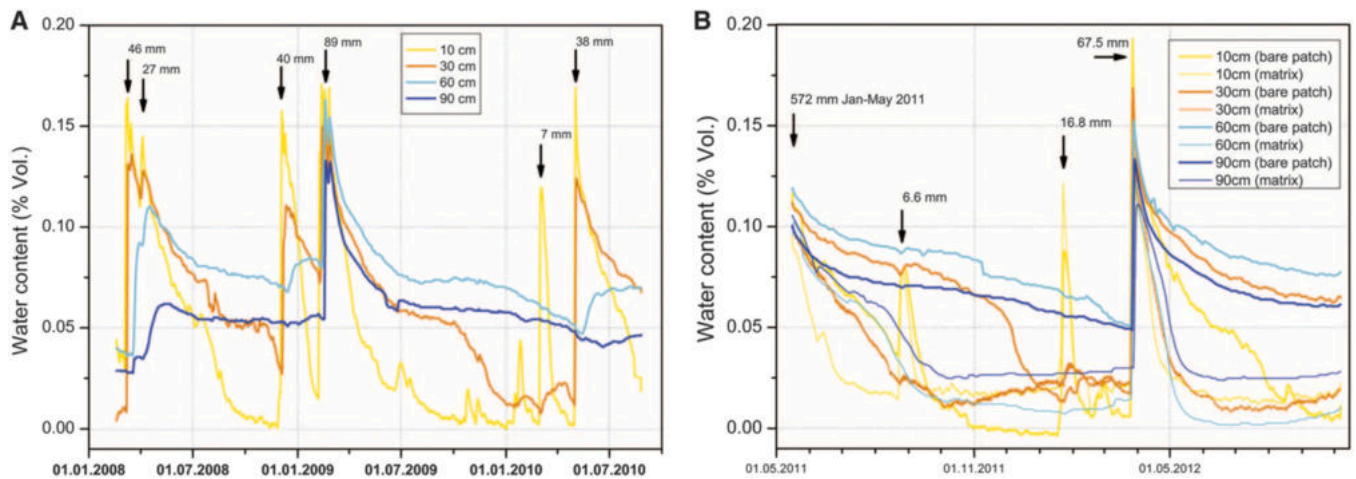


Fig. 2. A: Water content of the soil beneath the bare patch of the Fairy Circle F15 in Dieprivier in four depths. Rainfall event (black arrows) and amounts (numbers in mm) (Figure from Jürgens, 2013). B: Water content in the soil of the Fairy Circle F15 in Dieprivier beneath the bare patch (bold lines) and under the matrix at 2 m distance to the perennial belt (thin lines) (Figure from Jürgens, 2013).

The theory of the “uptake-diffusion feedback” is proposed by Kinast et al. (2014), and empirical evidence in support of this hypothesis was presented by Cramer et al. (2017).

Here, we challenge whether the hypothesis of “uptake-diffusion feedback” with lateral moisture flows by “diffusion” in the range of meters within unsaturated sandy soils is supported by the established knowledge developed in soil hydrology. Based on Buckingham (1907), who found the flow rate related to suction gradients, and the pioneer works of Richards (1931), the flows of liquid water through unsaturated porous media is described by differential equations comparable to heat flow and includes the law of Darcy. In one-dimensional form, the flow follows:

$$v = -k_u \frac{\delta\psi}{\delta x}$$

with v = the rate at which water flows perpendicular to the flow direction through a unit area, k_u = the unsaturated hydraulic conductivity, ψ = soil water potential, x = flow direction. The negative sign indicates that the flow is contrary to the gradient of the potential $\delta\psi/\delta x$. The unsaturated hydraulic conductivity is strongly related to the water

content of the soils: with ongoing desiccation, the conductivity reduces by orders of magnitude (Fig. 3).

In addition, the hydraulic properties of the soil are temperature dependant. For a calculation of the liquid water flows according to the above-given equation, the gradients of the potential as well as the unsaturated hydraulic conductivity are essential. Models to relate soil water content, soil water potential, and hydraulic conductivity have been developed by different authors (see Simůnek et al., 2012). The liquid water flow through unsaturated material may be hysteretic.

The soil hydraulic properties of pure sands that dominate the landscape with fairy circles can be characterized by.

- a high hydraulic conductivity at and near saturation,
- thus a high infiltration rate,
- a low water content at field capacity,
- a very low water content at the permanent wilting point and
- a steep decline of k_u with decreasing water content.

Additionally, these soils mostly occur in the single grain structure. The development of aggregation is, if at all, rather weak, and thus, soil properties are equal in the vertical and horizontal directions. Under the arid conditions of the Namib, the combination of the above soil hydraulic properties have significant consequences:

- the infiltration capacity is fairly high, so that surface ponding and potential run-off or run-on are restricted to rare rain events with extreme short-term intensity.
- following the gravitational gradient, the infiltrated water seeps into deeper layers, leaving only small amounts of water (field capacity) in the topsoil.
- the depth of soil moistening depends on the amount of rain; the dry deeper subsoil stays dry.
- water in the topsoil evaporates within a few days, thus developing an almost dry layer at the soil surface.
- this layer develops because the evaporation is usually larger than the capillary uplift of water due to the gradient of the water potential.
- through the almost dry topsoil, water flow takes place in the vapor phase. These flows follow diffusion laws and are driven by vapor pressure gradients (Wang, 2015).
- the flow resistance of this layer protects the underlying soil from further drying by evaporation (Wang, 2015).

In the fairy circle systems with spots of stored soil moisture in the subsoil of the bare patches, there are horizontal water potential

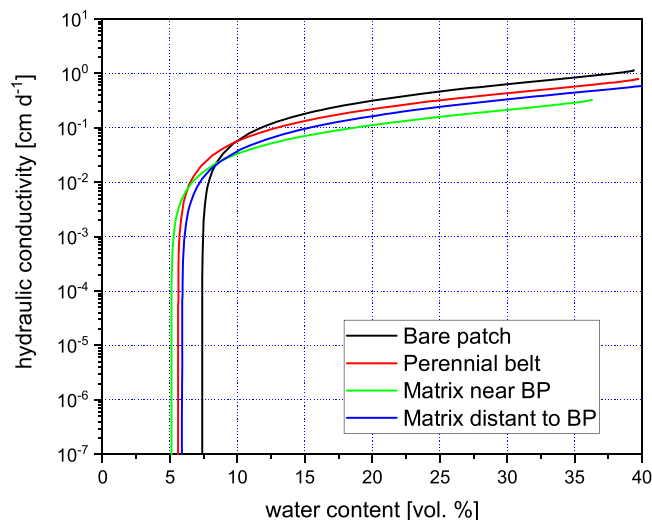


Fig. 3. Relation between soil water content and hydraulic conductivity of four samples from a fairy circle landscape (Dieprivier). Methods see Gröngröft & Jürgens (2022).

gradients producing vectors of liquid moisture movement to the dry surrounding matrix. However, the low unsaturated hydraulic conductivities ($k_{u,i}$) and the long distance (meters) restrict the water flow to very small amounts (see Gröngroft and Jürgens, 2022).

Keeping these soil hydrological properties in mind, there is no evidence that a “fast lateral soil-water diffusion” (Getzin et al., 2022; Zelnik et al., 2015) from the bare patch to the surrounding matrix is possible, neither in the liquid nor in the vapor phase. The proposed “uptake-diffusion feedback” (Getzin et al., 2022) may result in zones of low soil water potential in the rhizosphere, a narrow space around the roots (Carminati, 2012). However, in the here-discussed sandy soils, there is no evidence that this feedback acts in the dimension of meters.

The low vertical movement of soil moisture in the case of topsoil desiccation proves that liquid and vapor transport phenomena in dry sandy soils are restricted with regard to water mass. The hypothesis of self-organization of vegetation patterns, as proposed by Getzin for the fairy circles of the Namib, thus lacks a theoretical foundation and factual measured evidence.

Getzin et al. (2022) refer to a water-pulse experiment by Cramer et al. (2017), in order to provide empirical evidence for the assumed rapid hydraulic water transport in the soil. Cramer et al. (2017) applied 20 l of water at Namibrand into a 50 cm deep augured hole in a centre of a FC. Within 10 days they report an increase in moisture in 7.5 m distance of about 1.8 vol%. The water volume to generate a circular increase in soil moisture as registered is more than 300 l. Obviously it is not possible to explain the registered increase in 7.5 m distance with hydraulic transport.

We acknowledge that in theory a fast lateral water extraction from the bare patch to the surrounding grasses would be possible, if those grasses were able to expand their rooting space into the bare patch. However, numerous excavations and measurements of root lengths revealed, that this is not the fact and the observed water storage in the subsoil of the bare patches prove, that this extraction does not take place.

Statement 3.

The grasses in the bare patch of the fairy circles first die in the center and later at the margin.

Getzin et al. (2022) state that „Given that the grasses are permanently transpiring under the strong heat, this small loss in soil moisture cannot have sustained their demand for water. While we have not directly measured lateral water flow, our data suggest that these matrix grasses have drawn the water from the FCs and induced water stress to the desiccating grasses within the circles ...”. They also state that „... this strong decline in soil water within the FC is due to the uptake-diffusion feedback, whereby the transpiring grasses strongly pull laterally water from their surroundings because soil water in these coarse sand at Namibrand does diffuse relatively quickly over distances of more than 7 m (Cramer et al., 2017).”

This interpretation is in contradiction with the observed (a) temporal and (b) spatial course of the dieback of the grasses within the bare patch of a fairy circle.

- (a) It is in contradiction with the timing (compare statement 1). If we follow the course of the measured soil moisture beneath the bare patch (Figs. 1 and 2), for many weeks and sometimes months, the moisture content below 20 cm depth is high enough to support plant life. Death of grasses caused by insufficient moisture may occur after many weeks or even months. However, in reality, the grasses in the bare patch already died very early after the triggering rain event, during the first two to five weeks. It should be noted that Getzin et al. (2022) only measured the soil moisture of the topsoil at 20 cm depth, which quickly desiccates due to evaporation.
- (b) Our own observations of the dieback of the grasses within the bare patch of fairy circles in Angola, Namibia, and South Africa equally show that the dieback always starts in the center of the bare patch (Fig. 4). As additional evidence we here add a time-



Fig. 4. The dieback of grasses starts in the center of the bare patch and later progresses towards the margin. 10.04.2011, Dieprivier, Namib Desert Park (= Fig. S11A in Jürgens, 2013).

lapse video that shows the dieback from the centre to the margin during the weeks after a rainfall triggering germination (FC F99 at Dieprivier).

In summary, the observed temporal and spatial sequence of the dieback of the grasses, which always starts early and at the center of the bare patch and later progresses towards the margin, rebuts the interpretation proposed by Getzin et al. (2022).

Statement 4.

The grass in the bare patch of fairy circles dies because of damage to the grass roots caused by localized herbivory by sand termites.

Getzin et al. (2022), in the “highlights” of the publication) state: “Termite herbivory is not causing this grass death as the plants had undamaged roots.” In detail, the authors report for their Kamberg study site: “Careful inspection of the grasses and of potential termite activity revealed that neither grass roots of the dead plants inside the FCs nor of the matrix outside of FCs showed any sign of termite damage as proposed by Juergens (2013), and no termite individuals or nests were found under or nearby the excavated grasses...”. They also state “In summary, we found no termites or their nests around the investigated grasses, and we also found no such termite activity during additional soil excavation, when we dug several trenches ... at Namibrand.”

The latter statement that denies any presence of sand termites at Namibrand is astonishing because it stands in sharp contrast to the results of a thoroughly conceptualized PhD study of the Department of Biological Sciences at the University of Cape Town that was carried out at the same place: Namibrand, by Kelly Vlieghe, supervised by the entomologist Mike Picker. Vlieghe et al. (2014); Vlieghe (2016); and Vlieghe and Picker (2019) found a clear correlation between sand termites and fairy circles, especially young ones. Also, Jürgens (2013); Jürgens et al. (2015); Gunter et al. (2022a,b); Jürgens (2022) report observations and collections of sand termites at Namibrand FCs. Looking beyond Namibrand, evidence for the statement that grasses in the bare patch of fairy circles get killed by localized herbivory at the roots has been provided by numerous publications (Jürgens (2013); Vlieghe et al. (2014); Jürgens (2015); Jürgens et al. (2015); Vlieghe (2016); Vlieghe and Picker, 2019; Gunter et al. (2022a,b,c); Jürgens (2022); Jürgens and Henschel et al. (2022)). In the northernmost Namib in Angola, north of the Rio Curoca, a different type of very large fairy circles is established by a newly discovered termite species of the family Hodotermitidae (Jürgens et al., 2021b).

How can such a contradiction be resolved?

First of all, sand termites operate in the shadows for most of their life. During unfavorable periods it requires quite an effort to find the faint

tracks of their activities. Only very careful examination enables the detection of the fragile tunnels. Living animals are best observed in the early morning hours. The videos attached to [Getzin et al. \(2022\)](#) portray rough methods of excavation. Jürgens (2022) offers a practical guide to observations that indicate termite activity.

Secondly, [Albrecht et al. \(2001\)](#) and [Van Rooyen et al. \(2004\)](#) report an inhibitory effect of sand sampled from the bare patch on the germination and growth of grasses in laboratory or greenhouse tests. Such an effect is not obvious in the field. However, we cannot exclude that under certain conditions, inhibitory effects of the soil may play a role, perhaps related to semivolatile organic compounds, interpreted by [Jürgens \(2015\)](#) as a product of *Psammotermes*, in response to [Naude et al. \(2011\)](#).

Thirdly, the damage to grass roots is not always visible to the naked eye. It often requires a magnifying lens to see finer damage, especially at the karyopsis ([Jürgens, 2022](#), in chapter 5). It should be investigated whether minor termite bites can cause a fatal infection with plant pathogenic microorganisms found in the termite nests ([Yurkov et al., 2022](#)).

With regard to periods of time much longer than the weeks after a strong precipitation event, it should be noted that sand termite colonies are mortal, and the above-ground vegetation patterns, like the perennial belt and the circular bare patch, remain visible for many years, even when the termite colony died. For example, the fairy circles between Gobabeb and Mirabib still had green perennial belts and freshly used tunnels in 2012 ([Jürgens, 2022](#), Chapter 6.9, Figure 6.9.1 and 6.9.2). However, because of a long drought period, by 2015 and 2016 it was no longer possible to find living termites, as stated by [Ravi et al. \(2017\)](#). In addition, it is likely that reproductive individuals survive medium-strength drought periods in a refuge in deeper soil layers ([Tasaki et al., 2021](#)).

However, with the exception of such phases of extreme drought, we always found colonies, structures and activities of *Psammotermes* (living animals, nests, soil dumps, tunnels or galleries) within all fairy circles inspected by us in all landscapes containing fairy circles, from the Iona National Park in Angola to the Richtersveld in South Africa, to date accumulating to a record of 1.799 confirmed *Psammotermes* verifications within fairy circles ([Jürgens, 2022](#), chapter 7).

In a similar debate regarding so-called “fairy circles” in Australia ([Getzin et al., 2016](#)), Aboriginal traditional knowledge and soil excavation data suggest that these regularly spaced, bare and hard circles in grasslands are pavement nests occupied by *Drepanotermes* harvester termites ([Walsh et al., 2023](#)). [Walsh et al. \(2023\)](#) dug trenches in plots, examined before and interpreted as products of self-regulation, not termites, by [Getzin et al. \(2019\)](#). They found *Drepanotermes* chambers in 100% of the trenches.

In addition to the large body of evidence regarding the presence of *Psammotermes* colonies in fairy circles in the Namib, we provided detailed evidence for the process how the annual death of freshly germinated grasses within the bare patches following summer rains of at least 10–20 mm is caused by the sand termites. Already 11 days after the triggering rain, sand termites damaged the grass seed at the point where the plumula exits the karyopsis ([Jürgens, 2022](#), chapter 5, microscope images).

As additional evidence we here add a second time-lapse video that shows the spatial correlation between sand termite tunnels (indicated by soil dumps at the tunnel opening) and the subsequent dieback during the weeks after a rainfall triggering germination (FC E91, Giribesvlakte).

[Tarnita et al. \(2017\)](#) showed theoretically that not only can both the two hypothesized pattern-forming mechanisms produce the same pattern (and can even co-occur at different scales in the same system), and [Pringle and Tarnita \(2017\)](#) emphasized the need for manipulative experiments. Therefore, we set up experiments in several study sites in Namibia and South Africa to exclude sand termites from the topsoil of FC by adding borax and carbaryl to the uppermost 5 cm of the soil. This treatment was also applied to five replicates and not applied to five

control plots in the Giribesvlakte in 2017. The experiment resulted in strong grass growth in the five treated FC while five untreated controls had almost no grass ([Jürgens, 2022](#), chapter 4.2).

Not only the application of toxic chemicals, but also a severe drought can be regarded as a “natural” experiment, because the drought kills a proportion of the sand termite colonies. This was the case in the Giribesvlakte, where rainfall for five years (2012–2016) was below average. A light rain in early 2016 triggered germination of grass and provided the opportunity for a snapshot comparison of the state in 2016 with the state in 2011: About one-third of the examined fairy circles ceased to show sand termite activity and those fairy circles were revegetated with grass ([Jürgens, 2022](#), chapter 5.4).

4. Conclusions

The title of the publication of [Getzin et al.](#) in PPEES “Plant water stress, not termite herbivory, causes Namibia’s fairy circles” suggests a final conclusion in the debate on the origin of the fairy circles of the Namib Desert. However, this is not the case. The data presented in [Getzin et al. \(2022\)](#) rather prove the opposite with regard to the role of water stress. Furthermore, the paper ignored earlier published and more detailed measurements on the soil moisture of fairy circles. Similarly, the paper omitted the majority of publications from southern African entomologists and the Jürgens team that provided evidence for the causative role of termites. Therefore, here we present the opposite conclusion: Sand termite herbivory causes Namibia’s fairy circles.

Regarding statement 1, concordant measurements prove that the soil beneath the bare patch below 20 cm depth of the fairy circle contains an equal or higher amount of moisture than the surrounding matrix at any given time. Consequently, the death of the grasses in the bare patch cannot be caused by plant water stress. Concordant observations prove that the grasses in the bare patch of the fairy circle die early, during a period when even the topsoil has a high moisture content. Consequently, the death of the grasses in the bare patch must be caused by a different reason than plant water stress.

With regard to statement 2, we show that under arid conditions, the sandy soils of the fairy circles do not enable the *fast lateral soil-water diffusion*, as assumed by [Getzin et al. \(2022\)](#).

With regard to statement 3, the observed temporal and spatial sequence of the dieback of the grasses, which always starts early and at the center of the bare patch and later progresses towards the margin, rebuts the interpretation proposed by [Getzin et al. \(2022\)](#) that the transpiring grasses of the surrounding matrix vegetation would – at a later stage – pull water out of the bare patch and thereby desiccate the bare patch soil and ultimately the grasses.

With regard to statement 4, southern African entomologists and experienced desert ecologists published numerous papers showing the presence of termites and associated localized herbivory at several sites also visited by [Getzin](#) and his co-authors. Microscopic images of the early attacks on grass seedlings by sand termites and time-lapse videos provide additional evidence for the processes by which sand termites damage grass roots.

In conclusion, there is clear evidence supporting the presence and causative role of sand termites in Namibia’s fairy circles. Measurements and observations first published by [Jürgens \(2013\)](#) and repeated by [Getzin et al. \(2022\)](#), as well as basic soil hydraulic properties ([Gröngröft and Jürgens, 2022](#)), conclusively rule out and falsify the self-organization hypothesis for these systems.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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References

- Albrecht, C.F., Joubert, J.J., De Rycke, P.H., 2001. Origin of the enigmatic, circular, barren patches ('Fairy Rings') of the pro-Namib. *South Afr. J. Sci.* 97, 23–27.
- Buckingham, E., 1907. Studies on the movement of soil moisture. *Bull. USDA Bureau of Soils*, Washington, DC, 38.
- Carminati, A., 2012. A model of root water uptake coupled with rhizosphere dynamics. *Vadose Zone J.* 11, vzj2 011, 0106.
- Cramer, M.D., Barger, N.N., Tschinkel, W.R., 2017. Edaphic properties enable facilitative and competitive interactions resulting in fairy circle formation. *Ecography* 40, 1210–1220.
- Getzin, S., Yizhaq, H., Bell, B., Erickson, T.E., Postle, A.C., Katra, I., Tzuk, O., Zelnik, Y.R., Wiegand, K., Wiegand, T., 2016. Discovery of fairy circles in Australia supports self-organization theory. *Proc. Natl. Acad. Sci.* 113, 3551–3556.
- Getzin, S., Yizhaq, H., Muñoz-Rojas, M., Wiegand, K., Erickson, T.E., 2019. A multi-scale study of Australian fairy circles using soil excavations and drone-based image analysis. *Ecosphere* 10 (e02620), 2019.
- Getzin, S., Holch, S., Yizhaq, H., Wiegand, K., 2022. Plant water stress, not termite herbivory, causes Namibia's fairy circles. *Perspect. Plant Ecol., Evol. Syst.* 57, 125698.
- Gröngroft, A., Jürgens, N., 2022. Soil moisture and hydrology of fairy circles. In: Schmiedel, U., Finckh, M. (Eds.), *Fairy Circles of the Namib Desert. – Ecosystem engineering by subterranean social insects*, 7. *Biodiversity & Ecology*, pp. 185–198. DOI: 10.7809/b-e.00368.
- Gunter, F., Oldeland, J., Picker, M.D., Henschel, J.R., Jürgens, N., 2022a. Cryptic subterranean diversity: regional phylogeography of the sand termite *Psammotermes allocerus* Silvestri, 1908 in the wider Namib region. *Org. Divers. Evol.* 1–12.
- Gunter, F., Henschel, J.R., Picker, M.D., Oldeland, J., Jürgens, N., 2022b. Phylogeny of the sand termite. In: Schmiedel, U., Finckh, M. (Eds.), *Fairy Circles of the Namib Desert. – Ecosystem engineering by subterranean social insects*, 7. *Biodiversity & Ecology*, pp. 51–54. <https://doi.org/10.7809/b-e.00364>.
- Gunter, F., Oldeland, J., Henschel, J.R., Picker, M.D., Jürgens, N., 2022c. Reproduction of sand termites and local genetic patterns. In: Schmiedel, U., Finckh, M. (Eds.), *Fairy Circles of the Namib Desert. – Ecosystem engineering by subterranean social insects*, 7. *Biodiversity & Ecology*, pp. 54–55. DOI: 10.7809/b-e.00365.
- Henschel, J.R., Jürgens, N., 2022. Animals. In: Schmiedel, U., Finckh, M. (Eds.), *Fairy Circles of the Namib Desert. – Ecosystem engineering by subterranean social insects*, 7. *Biodiversity & Ecology*, pp. 229–249. DOI: 10.7809/b-e.00369.
- Jürgens, N., 2013. The biological underpinnings of Namib Desert fairy circles. *Science* 339, 1618–1621.
- Jürgens, N., 2015. Exploring common ground for different hypotheses on Namib fairy circles. *Ecography* 38, 12–14.
- Jürgens, N., et al., 2022. Fairy Circles of the Namib Desert. – *Ecosystem engineering by subterranean social insects (= Biodiversity & Ecology, 7)*. Klaus Hess Publishers, Göttingen & Windhoek, p. 376. DOI: 10.7809/b-e.vol.07.
- Jürgens, N., Vlieghe, K.E.P., Bohn, C., Ermi, B., Gunter, F., Oldeland, J., Rudolph, B., Picker, M.D., 2015. Weaknesses in the plant competition hypothesis for fairy circle formation and evidence supporting the sand termite hypothesis. *Ecol. Entomol.* 40, 661–668.
- Jürgens, N., Gunter, F., Oldeland, J., Gröngroft, A., Henschel, J.R., Oncken, I., Picker, M.D., 2021b. Largest on earth: discovery of a new type of fairy circle in Angola supports a termite origin. *Ecol. Entomol.* 46, 777–789.
- Kinast, S., Zelnik, Y.R., Bel, G., Meron, E., 2014. Interplay between Turing mechanisms can increase pattern diversity. *Phys. Rev. Lett.* 112, 078701.
- Naude, Y., Van Rooyen, M.W., Rohwer, E.R., 2011. Evidence for a geochemical origin of the mysterious circles in the Pro-Namib desert. *J. Arid. Environ.* 75, 446–456.
- Pringle, R.M., Tarnita, C.E., 2017. Spatial self-organization of ecosystems: integrating multiple mechanisms of regular-pattern formation. *Annu. Rev. Entomol.* 62, 359–377. <https://doi.org/10.1146/annurev-ento-031616-035413>.
- Ravi, S., Wang, L., Kaseke, K.F., Buynevich, I.V., Marais, E., 2017. Ecohydrological interactions within "fairy circles" in the Namib Desert: revisiting the self-organization hypothesis. *J. Geophys. Res.: Biogeosciences* 122, 405–414.
- Richards, L.A., 1931. Capillary conduction of liquids through porous mediums. *Physics* 1, 318–333.
- Šimůnek, J., Genuchten, Van, Šejna, M., M.T., 2012. The HYDRUS software package for simulating the two- and three-dimensional movement of water, heat, and multiple solutes in variably-saturated porous media. *Tech. Man., Version 2*, 258.
- Tarnita, C.E., Bonachela, J.A., Sheffer, E., Guyton, J.A., Coverdale, T.C., Long, R.A., Pringle, R.M., 2017. A theoretical foundation for multi-scale regular vegetation patterns. *Nature* 541, 398–401. <https://doi.org/10.1038/nature20801>.
- Tasaki, E., Takata, M., Matsuura, K., 2021. Why and how do termite kings and queens live so long? *Philos. Trans. R. Soc. B* 376, 20190740. <https://doi.org/10.1098/rstb.2019.0740>.
- Van Rooyen, M.W., Theron, G.K., Van Rooyen, N., Jankowitz, W.J., Matthews, W.S., 2004. Mysterious circles in the Namib Desert: review of hypotheses on their origin. *J. Arid Environ.* 57, 467–485.
- Vlieghe, K., 2016. The ecology of Namibian fairy circles and the potential role of sand termites (*Psammotermes allocerus* Silvestri) in their origin. PhD dissertation. University of Cape Town. open.uct.ac.za.
- Vlieghe, K., Picker, M., 2019. Do high soil temperatures on Namibian fairy circle discs explain the absence of vegetation? *Plos One* 14, e0217153.
- Vlieghe, K., Picker, M.D., Ross-Gillespie, V., Ernie, B., 2014. Herbivory by subterranean termite colonies and the development of fairy circles in SW Namibia. *Ecol. Entomol.* 40, 42–49.
- Walsh, F., Bidu, G.K., Bidu, N.K., Evans, T.A., Judson, T.M., Kendrick, P., Michaels, A.N., Moore, D., Nelson, M., Oldham, C., Schofield, J., Sparrow, A., Taylor, M.K., Taylor, D.P., Wayne, L.N., Williams, C.M., Martu elders and experts, 2023. First peoples' knowledge leads scientists to reveal 'fairy circles' and termite linyji are linked in Australia. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-023-01994-1>.
- Wang, X., 2015. Vapor flow resistance of dry soil layer to soil water evaporation in arid environment: an overview. *Water* 7, 4552–4574.
- Yurkov, A., Pascual, J., Sikorski, J., Geppert, A., Gunter, F., Huber, K.J., Jürgens, N., Overmann, J., 2022. Evidence for *Psammotermes allocerus* termite nests as refugium for plant pathogenic microbes: a contribution to generation and maintenance of fairy circles in the Namib Desert. *Biodivers. Ecol.* 7, 154–273.
- Zelnik, Y.R., Meron, E., Bel, G., 2015. Gradual regime shifts in fairy circles. *Proc. Natl. Acad. Sci.* 112, 12327–12331.