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Definition of "fairy circles" and how they differ from other common vegetation gaps and plant rings

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Abstract

Aims: The fairy circles along the Namib Desert in southern Africa are round grassland gaps that have puzzled scientists for about 50 years. With the discovery of fairy circles in Australia in 2016, the debate on the origin of the circles has been extended to a new continent. Research interest on the topic has since then risen strongly but so has the use of the term "fairy circle". This term has become more imprecise and, by analogy, has been applied to circular vegetation gaps or plant rings that are largely unrelated to fairy circles. For this reason, we define the concept of fairy circles by identifying their three main characteristics based on in situ field observations and soil excavations to larger-scale spatial patterns, and regional-scale distribution.

Results: Following this approach, fairy circles are defined by: (a) being "empty gaps" in grassland without a central insect-nest structure; (b) their ability to form spatially periodic patterns, which are regular hexagonal patterns with an extraordinary degree of spatial ordering; and (c) their strongly regional distribution confined within a narrow arid climatic envelope. In these combined traits, fairy circles differ from other common vegetation gaps which, for example, always have a central insect-nest structure and may occur across broad climatic gradients on continents. Also plant rings have their own specific characteristics that largely differ from the combined attributes of genuine fairy circles.

Conclusions: There are many other vegetation-gap patterns in arid lands but if such gaps cannot jointly show the three characteristics defining the fairy circles, they should be carefully discussed on their own, rather than mixing them up with fairy circles. Our synthesis provides a new etymology for the different types of vegetation gaps and rings, aiming to guide the reader through various classes of circular plant patterns.

KEYWORDS
aridity, collective plant rings, fairy circles, fungal fairy rings, hexagonal grid, Namib Desert, nearest neighbor, rainfall, spatial periodicity, tussock rings, vegetation gaps, Western Australia

1 | INTRODUCTION

So-called "fairy circles" (FCs) are roughly circular barren patches with mean diameters ranging mostly between 4 m and 10 m, and are found in arid grasslands along the Namib Desert in southern Africa (van Rooyen et al., 2004). The majority of FCs are found in Namibia around the 100 mm rainfall isohyet, with some in northern South Africa or southern Angola. More recently, similar FCs have also been discovered in a small part of Western Australia (Getzin et al., 2016a). These are widely accepted as genuine FCs across research disciplines (Maestre et al., 2021; Saha & Galic, 2018; Sahagian, 2017; van der Walt et al., 2016).

FCs have long been recognized as a mysterious phenomenon whose origin is still subject to lively debate (Sahagian, 2017). Early hypotheses on the cause of the FCs in Namibia related fossil nests of termites (Tinley, 1971), allelopathic chemicals originating from extinct poisonous *Euphorbia* plants (Theron, 1979) or rodent activity (Cox, 1987) to the distribution of the barren patches. Later, Moll (1994) suggested that FCs were caused by harvester termites of the species *Hodotermes mossambicus*. In the new millennium, new research papers on FCs were stored in digital repositories such as the Web of Science in which the first publication on the search topic "fairy circles" appeared (Becker & Getzin, 2000). This study from 2000 was the first scientific article that established the term "fairy circles" more than 20 years ago. All research articles before either used the term "circular bare patches" (Tinley, 1971), the Afrikaans word "kaal kolle" (Theron, 1979) or that term together with the English translation "bare patches" (Eicker et al., 1982), "vegetation circles" (Cox, 1987) or "fairy rings" (Danin & Orshan, 1995; Moll, 1994). These words are not in use anymore to describe FCs and between the years 2000 to 2020 in total 57 studies used the term "fairy circles" instead (Appendix S1).

Until 2000, very little was known about the FCs and research data were hardly available. During the next 10 years only five studies on FCs were published. However, during the following 10 years from 2011 until today, research interest in FCs has risen tremendously. Various additional hypotheses on the origin of FCs have been proposed, including a geochemical origin (Naude et al., 2011), activities by ants (Picker et al., 2012) or sand termites (Juergens, 2013; Vlieghe et al., 2015), a potential microbial (Ramond et al., 2014) or allelopathic (Meyer et al., 2020) cause, and self-organization by competing plants in water-limited ecosystems (Cramer & Barger, 2013; Getzin et al., 2015a, 2015b; Ravi et al., 2017; Zelnik et al., 2015). Until 2015, all the studies focused solely on the original Namib FCs and confined the term "fairy circle" to this particular gap pattern.

However, the discovery of FCs near the town of Newman in Western Australia in 2016 broadened the perspective on the phenomenon, because those FCs have identical spatial patterns, size properties and other characteristics as their Namibian sister circles (Getzin et al., 2016a). Unintentionally, this expansion of the term "fairy circles" to a vegetation-gap pattern being found on a different continent and 10,000 km away from the Namib FCs subsequently led other scientists to use this term interchangeably for a variety of other gap patterns that have nothing in common with genuine FCs. For example, common grassland gaps that are obviously created by harvester termites and that can be found in many regions of the Australian continent have been synonymously called FCs (Walsh et al., 2016), despite the fact that these nest-associated gaps differ significantly in many structural and spatial characteristics from the genuine FCs (Getzin et al., 2016b, 2019a, 2021a). Recently, plant rings have been mixed up with FCs (Ross & Moles, 2021; Zhao et al., 2021), despite the fact that both are different phenomena. Also, underwater structures in Mediterranean seagrass (Ruiz-Reynés et al., 2017) and even the microscopic nanostructures of carbon-based graphene and graphite surfaces (Phan et al., 2019) have also been called FCs. Moreover, superficial circular depressions resulting from hydrogen escaping from sedimentary basins in Russia, the USA or Brazil have been recently called FCs (Prinzhofer et al., 2019), despite the fact that such disordered and globally common gaps with diameters of up to several 100 m are merely circular but otherwise share nothing with the famous Namib FCs or the Australian FCs. This opportunistic use of the term "fairy circles" culminated in two related follow-up studies on hydrogen seepage where the term has been repeatedly used in geochemical research (Frery et al., 2021; Myagkiy et al., 2020). Although the established term "fairy circles" may attract more readers, we wonder what such completely unrelated structures really have in common with the real FCs — a unique and rare ecological phenomenon that has puzzled scientists for several decades? This immediately leads to the important question of what FCs actually are and what they are not?

In the past, the mysterious FCs of Namibia received so much attention – in particular from the media (Carrington, 2014) – because of their disputed origin and their unique polka-dot patterning as revealed from the air. Although it is understandable that researchers working in other fields of science are inclined to use the attractive term "fairy circle" for all sorts of circular gap features, it will not help to solve the fundamental question of the origin of the FCs. For this reason, it is time now to draw a line between real FCs and all other common vegetation-gap structures or rings that are completely unrelated to the former.

We focus here not on the current controversial cause of the FCs but on the characteristic structure and distribution of mature FCs because these can persist for many decades (up to 75 years; Tschinkel, 2012), dominating the landscape and creating astonishing spatial patterns. For our synthesis paper, we present the established literature from the past 40 years and include literal quotations of FC researchers to describe the key characteristics of FCs. In the following, we describe three main features that qualify vegetation gaps as FCs and describe scenarios in which other gap patterns differ in those three properties. It is important to note that these key characteristics define a vegetation-gap pattern as FCs when they are in combination. In other words, FCs are genuine when and only when there is empirical evidence of the following combined three characteristics. We list the three key characteristics in a bottom-up approach, describing them first from an in situ field perspective, then the aerial view on their spatial patterns, and finally their regional-scale distribution and climatic

context. Our definition of the FC phenomenon will also include a discussion on plant rings, which differ from genuine FCs. This exemplary discussion on the detailed differences between FCs and plant rings shall demonstrate why it is so important to define the FCs and explain what are "fairy circles" and what are not.

2 | RESULTS

2.1 | Fairy circles are "empty gaps" in grassland without a central insect-nest structure

FCs are so mysterious because over the past decades numerous researchers working on them found nothing but sand during excavations inside these gaps. Hence the name, because if there is nothing but sand it was whimsically suggested that dancing fairies created the magical circles overnight.

Despite the many theories, there is overwhelming agreement among researchers that FCs are empty gaps that are not associated with insect-nest structures of termites or ants. In the following we quote the most important studies that describe the structure of excavated FCs. Already four decades ago, Theron (1979) excavated trenches through the FCs of the Kaokoveld in northwest Namibia but found no indications of past or present termite activity. Moll (1994) excavated FCs in central Namibia 0.75 m deep and up to 3 m outside in the matrix, but did not report that he found insect nests. He only found some individuals and casts of sand termites (*Psammotermes allocerus*) and *Baucaliotermes hainesi* but stated that both termite species are unlikely "responsible for fairy ring

formation". For their review, van Rooyen et al. (2004) excavated the FCs extensively in all FC-hotspot regions of Namibia such as Hartmann's Valley, Marienfluss, Giribes Plains, Brandberg, Khan, Escourt Experimental Farm, Sesriem, Namtib Guest Farm and finally Rooiduin in the far south. Trenches were dug from the center of the FCs to 0.5 m into the matrix and the depth of the trenches varied from 0.5 m to 2.2 m. As the authors summarized, "none of the trenches revealed any termite tunnels" and "the presence of termite nests beneath the circle has yet to be demonstrated". The same findings were later confirmed by Tschinkel (2010) who undertook sophisticated excavations of FCs at NamibRand Nature Reserve (Figure 1a–c). He used a leaf-blower, enabling him to gently reveal even the finest nest and tunnel structures that may potentially occur within and around FCs (Figure 1a,c). But Tschinkel (2012) stated that he "found no association between the nests or underground foraging tunnels of the endemic termite *B. hainesi* and fairy circles, nor have other termite species been found to be associated with fairy circles". Picker et al. (2012) also found no positive association between FCs and termite activity but instead emphasized a high correlation of ants with FCs. Although these excavations did not reveal termite nests, the single-author study of Juergens (2013) claimed that most FCs would have underground *P. allocerus* nests and tunnel-like galleries "a few centimeters to decimeters underneath the bare patch". This was a surprising claim, as such nests should be easily visible to everyone. It challenged FC researchers such as the Namibian termite expert, Eugene Marais, to specifically search for nests of the sand termite *P. allocerus*. In their study, Ravi et al. (2017) investigated the FCs in the central Namib but they "did not find any indication of sand termite activity, e.g., nests, tunnel networks, or foraging cast
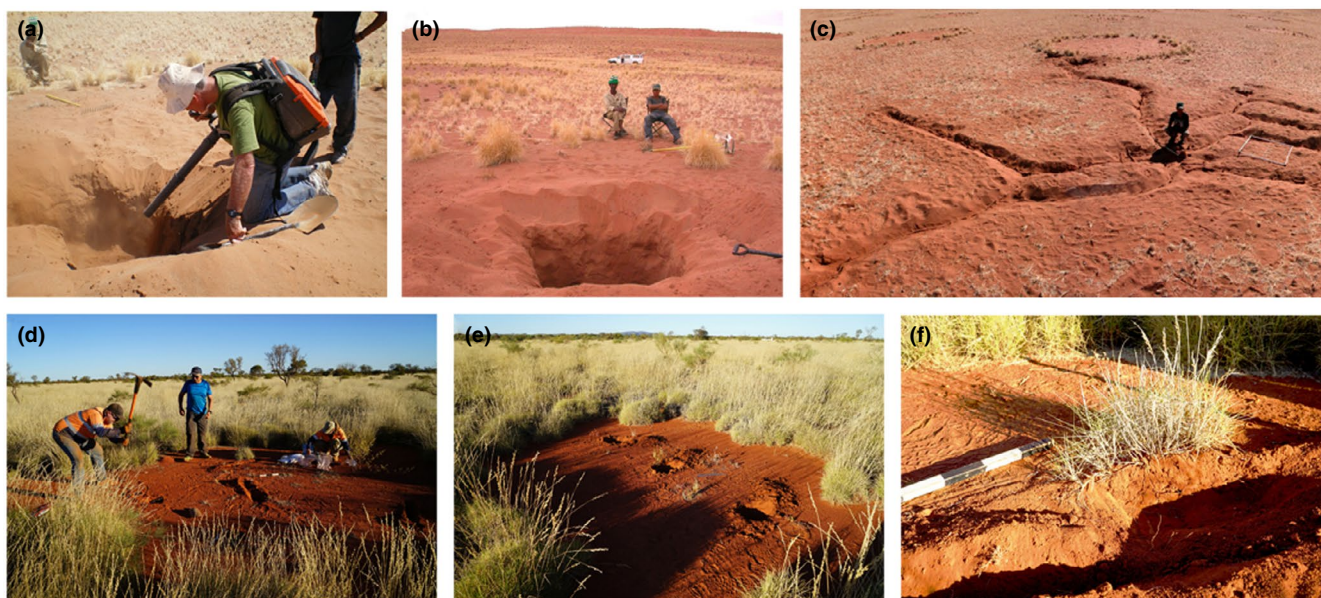
FIGURE 1 Detailed excavations of the foraging tunnels of *Baucaliotermes hainesi* undertaken by W. Tschinkel in a fairy circle landscape at NamibRand Nature Reserve (a–c). Exposure of the foraging tunnels of *Baucaliotermes hainesi* found no relation to surrounding fairy circles (c). Excavations of fairy circles near Newman in Western Australia, undertaken by S. Getzin, H. Yizhaq and T. Erickson (d–f). No insect-nest structures were found within these fairy circles and grasses can partly grow within the gaps (f)

remains within the centers or along the vegetated edges of circles." When they expanded their search for sand termites along the Namib Desert they disagreed with the claims of Juergens (2013) because they did not find "such a ubiquitous presence of sand termites at fairy circles as was suggested by Juergens (2013) when carrying out ad hoc searches throughout the fairy circle range". By contrast, the authors confirmed all earlier findings: "at present, empirical data on termite tunnel structures within fairy circles that may favor niche construction by sand termites are not yet available" (Ravi et al., 2017). Similarly, Cramer et al. (2017) emphasized that the "circles are more closely associated with a highly connective edaphic environment, rather than with particular biota" and finally, Meyer et al. (2020) who worked in many FC regions of Namibia stated that "no termite activity related to FC formation was observed in this study over several years". This widespread absence of termite nest structures is also what we found with FC and grass excavations during fieldwork along the Namib between 2016 and 2021. Whenever we dug trenches in northern Namibia such as the Giribes or in southern regions such as NamibRand, we were not able to detect insect-nest structures or foraging tunnels in FCs (Appendix S2). From these many studies on Namibian FCs over the past 40 years (Cramer et al., 2017; Meyer et al., 2020; Moll, 1994; Picker et al., 2012; Ravi et al., 2017; van Rooyen et al., 2004; Theron, 1979; Tschinkel, 2010, 2012) it is evident that mature FCs may partly correlate with various biotic and abiotic agents (Tschinkel, 2015) but lack a central nest structure, which sets them apart from all nest-associated termite circles that are commonly found around the globe.

The Australian FCs share this absence of a central insect-nest structure with their Namibian counterparts. Near the town of Newman in Western Australia there is a small, sandy to clayey flat area where genuine FCs can be found within a radius of about 10 km east to south of the Ophthalmia Dam. As in the desert margins of Namibia, this FC ecosystem in Australia has an aridity index <0.2 and is thus very arid (Getzin et al., 2016a). The grassland system is also as species-poor and the FCs are only formed by the spinifex grass *Triodia basedowii*. With more than 150 systematic excavations (Figure 1d–f), Getzin et al. (2019b) demonstrated an absence of termite nest structures in most of the FCs, emphasizing "that FCs are not trivial termite gaps and that partial correlation with termites at some sites does not imply causation".

The fact that the genuine FCs of Namibia and Australia predominantly lack a central nest structure makes them fundamentally different from all common nest-associated termite or ant circles. A typical example from Australia is the small gaps created by *Drepanotermes* harvester termites (Abensperg-Traun & Perry, 1998; Noble et al., 1989). These gaps differ from Australian FCs not only in having significantly smaller diameters, but also a slightly elevated mound and an extremely hard and cemented soil crust (Getzin et al., 2016b, 2019b). The cause of the gap is always the rock-hard, hollow-sounding termite chambers under the surface in the gap's interior (Figure 2a–c).

Worldwide, there are many examples of termite species whose mound architecture and subsequent mound erosion over many years may lead to a circular vegetation gap that superficially resembles an FC. Examples include various *Macrotermes* species of Namibia that form large mounds (Figure 2d–f; Grohmann et al., 2010; Turner et al., 2006) and the arena nests of the Kenyan fungus-growing termite species *Odontotermes fulleri* (Darlington, 2007). Likewise, *Pogonomyrmex* harvester ants in North America clear circular areas in grasslands around the nest structure in the center of the gap (Dibner et al., 2015; Nicolai et al., 2010). Similar circles with a central termite-nest structure have been recently found in southern Angola by Juergens et al. (2021). As the authors state, these are not "classic FCs" and the large circular gaps with an elevated termite nest in the center near Baba in Angola are caused by an undescribed Hodotermitidae termite species. These vegetation gaps are just another example of common nest-associated termite or ant circles, where the central nest structure always represents the spatial activity pattern of the involved insect species, and processes such as central-place foraging and/or mound erosion are responsible for the circular shape of the gap. This is in sharp contrast to genuine FCs because these empty gaps in grassland are without a central nest structure. The spatial patterns of those globally common nest-associated termite circles result from the dispersal and/or territorial behavior of the involved insect species. This leads us to describe the second key characteristic that defines FCs and that distinguishes them from common vegetation-gap patterns in water-limited arid environments.

2.2 | Fairy circles have the ability to form spatially periodic patterns

The species-poor vegetation in arid environments often forms highly regular patterns with "consistent dominant wavelengths and morphologies over extensive areas" (Deblauwe et al., 2011). Such periodic vegetation patterns, where the recurrent appearance of bare soil reflects the spatial wavelength of the lack of water in the system, occur primarily in water-limited and resource-depleted drylands with mean annual precipitation (MAP) below 400 mm (Deblauwe et al., 2008). Generally, the degree of regular vegetation patterning increases with aridity (up to a threshold precipitation value), and the Namibian and Australian FCs are "a special case of regular patterns" (Maestre et al., 2021).

The astonishing spatial patterns of FCs have been compared with other vegetation-gap patterns via aerial or satellite imagery and have shown that FCs differ from other regular gap patterns in having a much higher level of spatial ordering (Getzin et al., 2015a, 2019a). The strongly ordered patterns visible in aerial imagery show the striking, visually appealing consistency in the spacing of the vegetation. In principle, FCs have the ability to form so-called spatially periodic patterns where scale-dependent neighborhood-density functions such as the pair-correlation or $g(r)$-function show a "wave-like curve with recurrent appearances of regularity" (Getzin et al., 2015a). Figure 3a illustrates the $g(r)$-function for a spatially periodic pattern. The density of the pattern is assessed
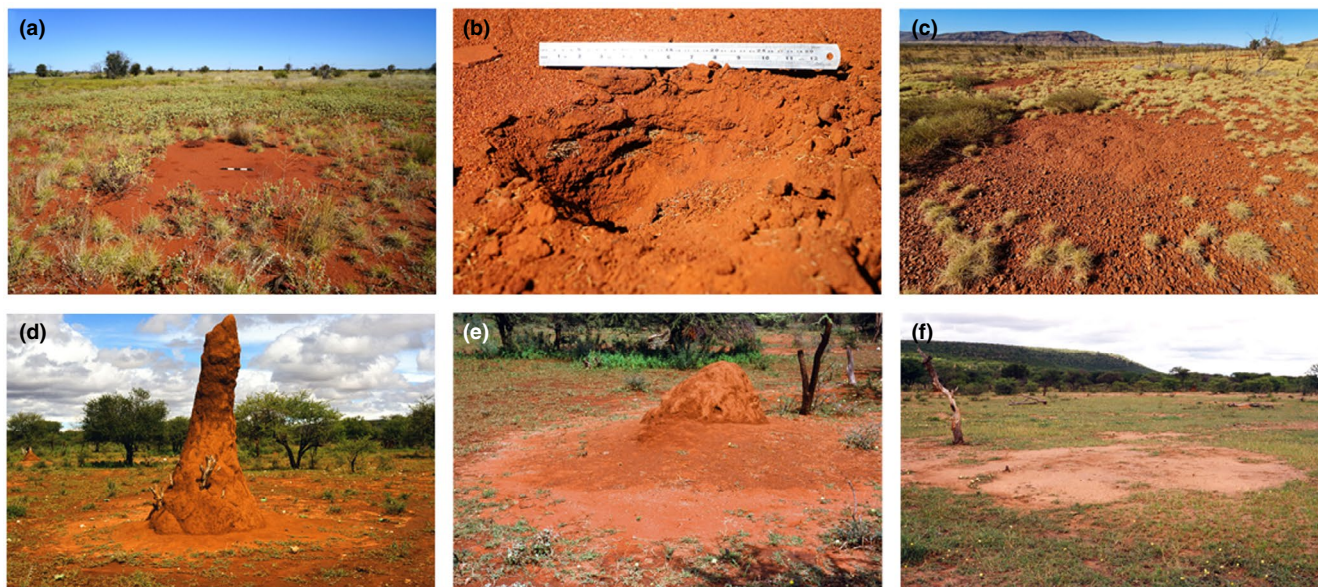
FIGURE 2 A typical small termite circle caused by *Drepanotermes* harvester termites at Jigalong Road in Western Australia. The stick in the image is 50 cm long (a). Such pavements have hollow termite chambers underneath the flat surface (b). Another example of a common termite circle at Karijini National Park in Western Australia (c). The central nest structure of the harvester termites is here more pronounced. Example of erosion of *Macrotermes* termite mounds about 100 km east of the fairy circle range in Namibia (d–f). The resultant vegetation gap is a nest-associated termite circle and has nothing in common with a fairy circle

at circular rings with radius *r*. For example, a value of $g(14) = 1.5$ (related to the first maximum in the curve) means that the point density at a radius of 14 m is 1.5 times higher than for a random distribution, which is indicated by $g(r) = 1$. The wave-like form of this neighborhood-density function and its significant positive and negative deviations from the random null-model (Figure 3a) indicates "a 'hexagonal' spatial arrangement where each FC has six nearest neighbors located at approximately the same distance from the focal circle [which] is a special form of a regular pattern with an extraordinary degree of spatial ordering" (Getzin et al., 2015b).

The dominant wavelength is consistent over extensive areas resulting in large-scale homogeneous patterns, with invariable local density of the FCs. In Namibia, such patterns can be found from the Marienfluss and the Giribes in the north, down to the NamibRand Nature Reserve 1,000 km further south. Although FCs in Namibia can locally also show more disordered and irregular patterns when substrate and habitat conditions are more heterogeneous (Cramer & Barger, 2013; Getzin & Yizhaq, 2019; Meyer et al., 2020), the fact that they exhibit significant spatial periodicity across several regions demonstrates that this ability is an inherent characteristic and thus a critical defining property. By contrast, there is no *Euphorbia* site in Namibia, for example, which demonstrates the ability to form spatially periodic patterns. For this and other reasons, the *Euphorbia* hypothesis has been recently disproven because the shrubs show significantly different spatial patterns and can thus be excluded as a causal agent of FCs (Getzin et al., 2021b).

Similar consistent spatial patterning is also found in the Australian FC area qualifying this pattern as genuine FCs (Getzin et al., 2016a).

Notably, the degree of spatial regularity (i.e., spatial periodicity) remains constant among regions despite the fact that FC diameters and hence the number of FCs per plot may strongly differ from region to region. For example, there are about 600 FCs in 25 ha in the Marienfluss Valley but about 1,200 FCs in 25 ha in the Giribes Plains, just south of the Marienfluss where the sandy substrate is as homogeneous. Despite that large difference in density, the spatial regularity of FCs is the same in the two locations (Getzin et al., 2019a), indicating that the process causing that regularity is independent of the density of the pattern.

Patterns as ordered as FCs are rare, and less-ordered patterns are far more common. Regularity is often estimated by the number of nearest neighbors (Tarnita et al., 2017), but it is important to note that merely counting the mean number of nearest neighbors alone is not a sufficient indication of a grid-like 'hexagonal' arrangement. Less-ordered, merely regular distributions are very common, and these, and even disordered random distributions (commonly used as null model), can have six nearest neighbors on average. Only spatially periodic patterns have statistically the same distance between the six neighbors (Figure 3b) which results in a consistent dominant wavelength and a hexagonal grid (Getzin et al., 2019a).

Phenomena or processes that cannot produce such highly ordered spatial gap patterns can therefore not be classified as FCs. For example, abiotic gas leakage as proposed by Naude et al. (2011) cannot result in such a high degree of regularity because there is no such regularity in the underlying geology (Getzin et al., 2015a; Tschinkel, 2012). The (mis)use of the term "fairy circle" for a completely different phenomenon in geochemical science (Myagkiy et al., 2020; Prinzhofer et al., 2019) distracts from decades of scientific research
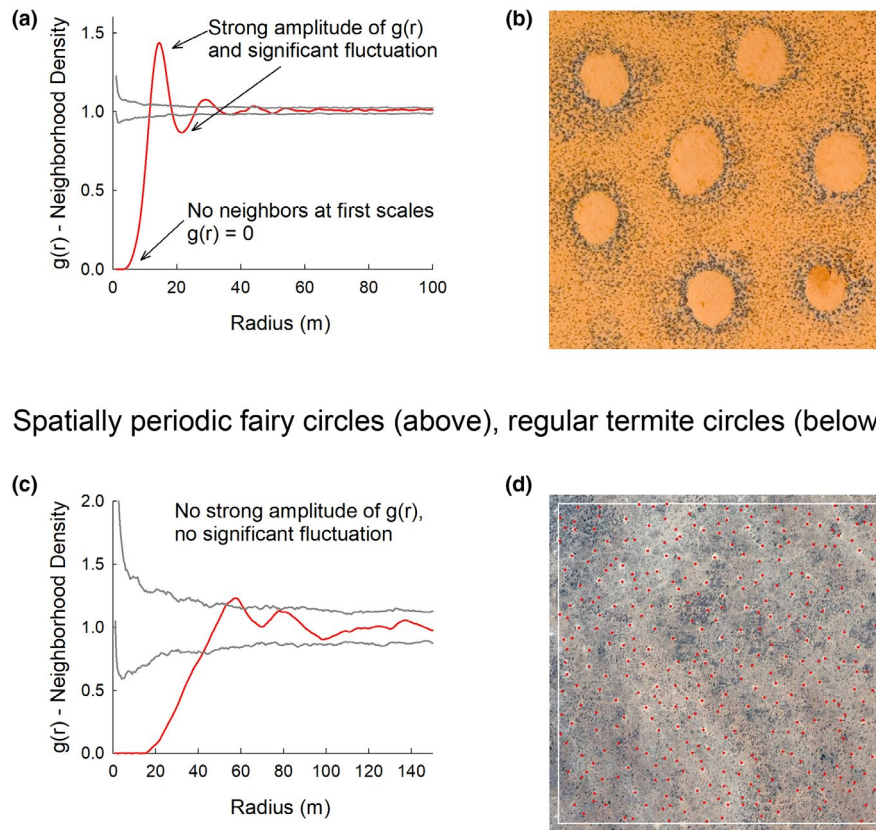
FIGURE 3 Example of the neighborhood density of Namib fairy circles at various radii (a). The gray lines indicate the upper and lower simulation envelopes of a random null model. The pair-correlation function $g(r)$ indicates a spatially periodic pattern via its strong and significant positive and negative fluctuation (red line) around the null-model envelopes. The first pronounced peak with a strong amplitude indicates the mean nearest-neighbor distance of the fairy circles. As is typical for spatially periodic patterns, the six fairy circles around a focal fairy circle have approximately the same distance, which reflects the constant wavelength of the pattern (b). The strong negative amplitude below the simulation envelope thereafter indicates the empty space between the first and second row of nearest neighbors, which is only possible because the fairy circles are periodically ordered as a hexagonal grid. By contrast, merely regular patterns are less ordered and the pair-correlation function does not significantly fluctuate around the null model, as this example for *Macrotermes* termite mounds shows (c). For better visualization, the pattern of the termite mounds is shown as red dots (d). The exemplary Namib fairy circles in (b) are from southern Angola and have diameters between 7 and 9 m. The plot size in (d) of the *Macrotermes* termite mounds near Outjo in Namibia is 1 km × 1 km

on the famous Namib FCs. This also applies to the common termite gaps of *Drepanotermes* in wide parts of Australia (Walsh et al., 2016) because such common gaps have an obvious central nest structure and do not show spatially periodic patterns. Likewise, a recent meta-analysis of 25 spatial patterns has demonstrated that there is no example known from the world's arid lands, including the same Australian FC landscape, where termites or ants have spatially periodic nest distributions (Getzin et al., 2019a). Such termite and ant nest patterns merely attain less-ordered regular distributions, as for example the *Macrotermes* termite mounds in Namibia (Figure 3c,d) and the Hodotermitidae termites at Baba in Angola (Juergens et al., 2021). These typical and globally common termite gap patterns cannot be called FCs because they violate two fundamental characteristics that jointly define genuine FCs. First, these nest-associated circles have a central termite mound that real FCs do not have. Second, as is typical for termite circles in arid and resource-poor

environments, they merely show regular but not spatially periodic distributions.

2.3 | Fairy circles are strongly confined to a narrow arid climatic envelope

Viewed on a much larger scale, Namib and Australian FCs are both strongly confined to a narrow arid climatic envelope. In Namibia, FCs dominate in the Namib Desert where rainfall ranges between 50 mm and 100 mm MAP (van Rooyen et al., 2004). At either lower or higher rainfall their density becomes very low, the patterns switch to random distributions, and they finally disappear (Cramer & Barger, 2013). Although the Namibian FCs stretch over a north–south distance of about 1,400 km, their rainfall-dependent east–west range is only about 60 km wide (Figure 4a). Long-term analysis of precipitation

(a)

(b)
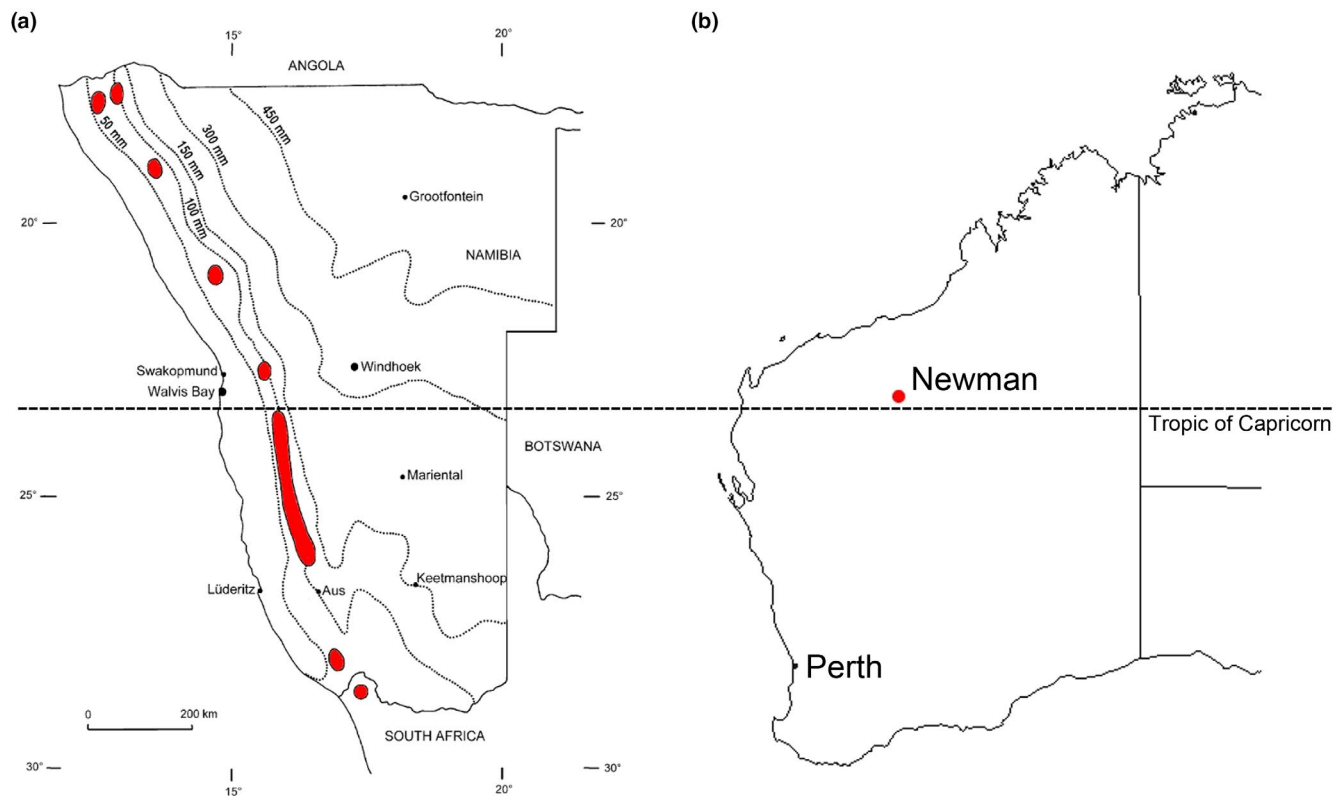
FIGURE 4 The climatic zone in which fairy circles occur is limited to a narrow band of rainfall in the Namib Desert (a). Rainfall decreases rapidly from northeast to southwest. Map in (a) after van Rooyen et al. (2004). In Australia, fairy circles occur only in an arid area east of the town of Newman (b). This area has a similar aridity index as the range of the fairy circles in Namibia

data and accompanying satellite imagery has shown that Namibian FCs are a strongly rainfall-dependent phenomenon where the dynamic appearance and disappearance of FCs depends on drought and wet cycles (Zelnik et al., 2015). Also, the spatially periodic patterns of Australian FCs occur only in a very small area east of the town of Newman (Figure 4b). This area has a MAP of 330 mm but due to the very high evaporation of about 3,200–3,400 mm, the land is as arid as in Namibia with an aridity index <0.2 (Getzin et al., 2016a, 2019b).

Whereas this narrow climatic envelope is a defining characteristic of FCs, most other vegetation-gap patterns are not as strongly confined by climate as are FCs. For example, the formation and subsequent erosion of termite mounds or flat pavements will always lead to circular vegetation gaps, irrespective of the specific climatic conditions in a region. Harvester termites in Australia induce vegetation gaps over thousands of square kilometers of the continent's interior, spanning rainfall isohyets of several hundred millimeters (Abensperg-Traun & Perry, 1998; Noble et al., 1989). In Namibia, the vegetation gaps via *Macrotermes* mound erosion span most of the country, and a climatic gradient from 250 mm to above 600 mm MAP (Turner et al., 2006). North American harvester ants clear the vegetation in circular discs in the western USA over a 200–600 mm precipitation range (Dibner et al., 2015; Nicolai et al., 2010). This is in stark contrast to the very narrow rainfall-dependent distribution of FCs. Of course, also the large gaps resulting from hydrogen seepage in Russia, the USA or Brazil (Prinzhofer et al., 2019) are not confined

to a narrow arid climatic envelope as the FCs are. Violation of this third defining FC criterion is thus another reason to draw a line between genuine FCs and unrelated vegetation gaps. The differences between FCs and other common vegetation gaps are listed for some representative examples in Table 1.

3 | DISCUSSION

With this paper we aim to restrict the original meaning of the term "fairy circle" to retain its usefulness as a descriptor of a specific and unique vegetation phenomenon. FCs have been named "fairy" because unlike all other vegetation-gap patterns, the origin of the FC phenomenon was so mysterious for decades. In recent years, too many papers have diluted the mechanistic understanding of the mysterious FCs with entirely different issues, distracting from the real scientific questions about the origin of FCs. For this reason, we have formulated three main characteristics that define FCs unambiguously. If a circular vegetation gap or any other landscape phenomenon cannot jointly show these three characteristics, it cannot qualify to be called an FC. In other words, genuine FCs should only be called as such if: (a) they are "empty gaps" in grassland without a central insect-nest structure; (b) they demonstrate an ability to form spatially periodic patterns; and (c) their regional distribution is strongly confined to a narrow arid climatic envelope.

TABLE 1 Etymology of fairy circles, other common vegetation gaps and various classes of herbaceous rings

General class of circular feature	Specific examples	Location	Literature source	Cause of the structure	Differences from fairy circles[a]
Fairy circles	*Stipagrostis* grasses	Namibia	van Rooyen et al., (2004)	Disputed	–
	Triodia basedowii grass	Australia	Getzin et al., (2016a, 2021a)	Vegetation self-organization	–
Common vegetation gaps	Harvester ant gaps	USA	Dibner et al., (2015)	Central-place foraging	1,2,3
	Macrotermes mounds	Namibia	Grohmann et al., (2010)	Central-place foraging	1,2,3
	Arena termite gaps	Kenya	Darlington, (2007)	Central-place foraging	1,2,3
	Harvester termite gaps	Angola	Juergens et al., (2021)	Central-place foraging	1,2
	Harvester termite gaps	Australia	Abensperg-Traun & Perry, (1998)	Central-place foraging	1,2,3
Tussock rings	*Triodia* grass rings	Australia	Ross & Moles, (2021)	Central dieback, pathogenic microbes	2,3
	Bouteloua grass rings	USA	Ravi et al., (2008)	Central dieback, abiotic processes	2
	Poa grass rings	Israel	Sheffer et al., (2007, 2011)	Central dieback, infiltration contrast	2
	Scirpus sedge rings	China	Zhao et al., (2021)	Central dieback, nutrient depletion	2,3
Fungal fairy rings	Multi-species grass rings	Italy	Bonanomi et al., (2012)	Radial growth of fungal mycelium	2,3
	Multi-species grass rings	Spain	Marí et al., (2020)	Radial growth of fungal mycelium	2,3
Collective plant rings	*Schmidtia* grass rings	Namibia	This study	Unknown	2
	Mixed grass-forb rings	Namibia	This study	Unknown	2
	Forb rings	Namibia	This study	Unknown	2

[a]Key differences from fairy circles: 1, no "empty gaps" but a central insect-nest structure; 2, no spatially periodic patterns; 3, not confined within narrow arid climatic envelope

3.1 | The need for more precise discussions – fairy circles are not plant rings

Our three defining criteria may help to narrow down specific working hypotheses on the origin of FCs and to be generally more precise with relating other findings from other natural phenomena to the FCs. One example of such a phenomenon is the confusion of plant rings with FCs. We are choosing this specific topic as an example for our discussion to demonstrate why there is a need to define what "fairy circles" are and what they are not.

Plant rings such as the large *Triodia* rings (or spinifex-grass rings) in Australia originate mostly from a single older plant that expands laterally over long periods, whereby mechanisms such as microbial pathogen effects in the center of the plant may induce the ring (Ross & Moles, 2021). Other reasons for plant-ring formation in arid environments are, for example, negative feedbacks between sediment deposition and vegetation growth inside the grass, which leads to central dieback in grasses of the Chihuahuan desert (Ravi et al., 2008) and in *Asphodelus ramosus* geophytes of the Negev Desert in Israel (Herooty et al., 2020; Yizhaq et al., 2019). A central dieback may also be due to increasing water uptake by newly recruited individuals at the patch

periphery, which explains ring formation in *Poa* grasses in the dry-Mediterranean climate or in creosote bushes in Californian desert (Sheffer et al., 2007, 2011). Doughnut-like ring shapes in tussocks are also known from *Festuca orthophylla* in the South American Andes, where the dynamics of grass biomass exert facilitative and competitive interactions of distinct ranges (Tlidi et al., 2018). Furthermore, nutrient depletion on the inner side of rings is also known from sedges in salt-marsh ecosystems (Zhao et al., 2021). In most of these cases it is the clonal growth of the single plant itself that forms the ring via radial extension of the ramets and subsequent central dieback (Bonanomi et al., 2014). Graminoid plants that eventually form a ring over time can be classified as "tussock rings" (Table 1). Notably, such tussock rings are not restricted to clonal growth only because obligate seeders, such as the hummock grass *T. basedowii*, also can form large rings (Getzin et al., 2016a; Ross & Moles, 2021).

Somewhat related to these plant rings are the long-known "fairy rings" (also called "elf rings"), which primarily occur from temperate grasslands (Edwards, 1984) to moss vegetation in the Arctic zone (Wilson, 1951). These concentric rings of higher plant biomass are caused by a fungal mycelium which grows radially through the soil, resulting often in visible fruiting bodies near its outer edge. These plant

FIGURE 5 The difference between Australian fairy circles (a) and tussock rings (b). Both circular structures are made up of the grass species *Triodia basedowii* but fairy circles and rings differ in several aspects (see details in the Discussion)
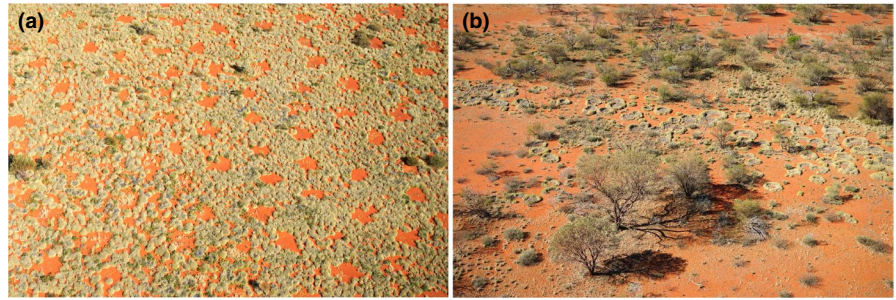
rings can be classified as "fungal fairy rings" (Table 1). For example, at a mean annual rainfall of around 950 mm, fairy rings may form in central Italy due to fungi that reduce the biomass in the mycelial zone (Bonanomi et al., 2012). A similar ring-formation mechanism under similar rainfall has been observed in pastured grassland in the eastern Pre-Pyrenees (Marí et al., 2020). In these cases of ring formation, the plant ring itself may be composed of different grass species and many individuals but the fungus does not cause a vegetation gap where grasses are dying over a circular area. Instead, the cover of grasses on the inside and outside of the fungal fairy ring is usually easily visible (Bonanomi et al., 2012; Marí et al., 2020; Wilson, 1951). All these types of grass rings are a geometrically appealing phenomenon on their own and as we outline below, caution is necessary to relate them directly to FCs.

First, in the case of tussock rings the formation of a ring is typically the result of the ongoing, mostly clonal and slow, centrifugal expansion of a single plant individual (Bonanomi et al., 2014). By contrast, the periphery of FCs is always composed of many, genetically unrelated grass individuals that jointly form the circular gap (Kappel et al., 2020). The joint circular formation of many grass individuals is the reason why the diameters of FCs can shrink or expand within one or two growing seasons, depending on the amount of fallen rainfall in previous years (Fernandez-Oto et al., 2014; Zelnik et al., 2015). Such short-term changes in diameters are not possible for tussock rings because the single plants cannot grow that quickly, and they can hardly shrink. The fact that FCs are vegetation gaps composed of many individual grasses also explains why they can be much larger in diameter than grass rings. For example, in the Giribes region of northern Namibia typical FC diameters can range between 13 m and 19 m (Getzin et al., 2021b) and in that region even so-called "mega circles" of 23 to >32 m can be locally found (Getzin & Yizhaq, 2019). In the small area of Western Australia where FCs exist, the tussock rings of *T. basedowii* commonly reach diameters of 2 m, whereas FCs at the same area have mean diameters of 4 m, and they may partly exceed 7 m (Getzin et al., 2016a). In the study of Ross and Moles (2021) the sampled *T. basedowii* rings had internal diameters from 0.3 m to 1 m and they state that large *Triodia* rings can have diameters of more than 2 m. These *Triodia* rings have nothing in common with genuine Australian FCs that have been described separately from rings (Getzin et al., 2016a). As this latter study showed, the large Australian FCs are made up of closed barriers of individual spinifex plants that arrange themselves in a circle to optimize their access to water run-off from the gap center. Therefore, the Australian FCs have green and vital grasses on the

inner periphery of the circle because they benefit from the water run-off (Getzin et al., 2016a, 2021a). By contrast, *Triodia* rings have gray and dead biomass on the inner side because they result from central dieback (Figure 5).

A second reason, why FCs are not plant rings, is related to the surrounding matrix grasses, which make them vegetation gaps or holes in a continuous layer of grasses (Figure 5a). By contrast, plant rings in arid environments are typically surrounded by bare soil but not by a continuous vegetation layer. For example, due to the recurrent and destructive bush fires in Australia, *Triodia* rings grow to very large diameters only in barren areas where the surrounding fuel load of grasses is too low to sustain fire (Figure 5b). Hence, the *Triodia* grasses can escape fire in those areas and become very old and large. However, the Australian FCs form by 3–5 years after complete destruction by fire (Getzin et al., 2021a), and the many small grass hummocks that make up the surrounding matrix vegetation around the FCs are far from old enough to form rings (Figure 5a). The short time scales of FC emergence thus work independently of the longer time scales required for plants to form tussock rings by central dieback. This is also the signature of Namibian FCs: in response to sufficient rainfall, the circular gaps emerge together with a continuous layer of annual *Stipagrostis* grasses that build the matrix (Tschinkel, 2012). Only in the dry season or after ongoing years of drought when all annuals of the matrix have died again, may the large and longer-lived peripheral grasses around the FCs appear as a ring-like structure. This happens specifically in the more arid FC areas of Namibia, such as in the central Namib near Mirabib, where rainfall variability is high and MAP is less than 80 mm (Ravi et al., 2017).

A third difference between FCs and plant rings is related to their spatial patterns. As demonstrated in the Results section, FCs have the ability to form spatially periodic patterns, where the spatial location of each FC is directly dependent on the distance to its nearest neighbors (Getzin et al., 2019a). This is in stark contrast to ring-building plants because the rings are local phenomena whose spatial occurrence is strongly habitat-driven, resulting in disordered, irregular and clustered patterns (Meron et al., 2007; Sheffer et al., 2011; Yizhaq et al., 2019; Zhao et al., 2021). In other words, whereas the location of FCs is dependent on the location of other FCs, the location of a plant ring is more independent of other plant rings and its formation is primarily driven by (micro-)habitat conditions that may or may not allow a sufficient aging and subsequent dieback of the plant center. Examples of tussock rings and fungal fairy rings and how they differ in their key characteristics from FCs are given in Table 1.

FIGURE 6 "Collective plant rings" in the Pro-Namib. At Donkerhuk farm, an 80 cm ring, composed of *Schmidtia kalahariensis* grasses and a few *Crotalaria podocarpa*, was photographed on 14 February 2021 (a). Images of similar rings with diameters of 25 cm (b) and 90 cm (c). The same ring as in (c) but photographed on 15 March 2021, long after ceasing rainfall (d). Drone image of disordered *Schmidtia* rings at Donkerhuk (e). Excavation of a 100 cm *Schmidtia* ring (f). Many *Schmidtia kalahariensis* grasses and some single *Stipagrostis ciliata* form a 70 cm ring at NamibRand (g). In the same area, the annual forb *Limeum argute-carinatum* forms a 70 cm ring (h), and numerous of these forb rings coexist together with fairy circles which can be seen in the background

3.2 | "Collective plant rings" – an unexplored class of plant rings

In most cases, the circularity of the plant ring results from a concentric pattern of the outward growing rhizomes or tillers or from the radial growth of the fungal mycelium. This category, however, does not fit new observations on grass and forb rings that have been recently recorded by us along the Namib Desert. For example, the annual grass species *Schmidtia kalahariensis* can form large rings with diameters of 20 cm to >100 cm and the ring periphery is composed of many annual grasses that appear after rainfall (Figure 6). The spatial pattern of the rings is typically disordered (Figure 6e) and excavations of five of these rings at the farm Donkerhuk West in the Pro-Namib revealed no signs of insect activity or a fungal mycelium (Figure 6f). Using 20 cm-long rods of a time domain reflectometer, we measured the soil-water content (SWC) in 15 *Schmidtia* rings on 14 February 2021, 3 days after the last rainfall event. Volumetric

SWC was 3.6%, far lower inside the rings than the 5.3% outside and about 0.5 m from the rings. Repeated measurements after ceasing rainfall revealed 0.8% SWC both inside and outside the rings on 15 March 2021 (Figure 6d) and 0.5% inside vs 0.6% outside on 15 April 2021. To date it is not known why and how these annual grasses can form such circular rings after rainfall. We name this unexplored class of rings "collective plant rings" because the many grass individuals collectively deplete the soil moisture inside the rings and their obvious benefit is gaining disproportionally higher biomass along the peripheral belt than neighboring grasses away from the rings. In that benefit, the *Schmidtia* grass rings resemble FCs which have much higher grass biomass along the circle periphery than in the matrix (Cramer et al., 2017). Interestingly, these *Schmidtia* grass rings often mix with other annual forb species such as *Crotalaria podocarpa* or *Limeum myosotis*. We also found the same type of *Schmidtia* rings at the southern NamibRand Nature Reserve where *Stipagrostis-ciliata* FCs occur also (Figure 6g). Also, numerous forb rings can be found

together with about 2 m large FCs in that area, with rings having diameters ranging between 10 cm and about 100 cm (Figure 6h). These forb rings are also composed of annual species such as mainly *Limeum argute-carinatum* (Mannheimer et al., 2008). Soil-moisture measurements on 27 February 2021 revealed lower SWC inside the *Schmidtia* rings than outside (1.4% vs 1.8%) and SWC was also lower inside the forb rings (2.5% vs 3.5%). As on Donkerhuk farm, at this arid site of the NamibRand Nature Reserve, the annual *Schmidtia* grasses and forbs seem to form a circle after rainfall to benefit collectively from exclusive access to the ring's interior moisture. The marked differences in SWC probably result from the relatively small ring-to-plant size ratios, enabling the annuals along the periphery to strongly deplete the soil water of the rings.

The mechanisms that lead to the circular form of such collective plant rings are so far unknown (but see related theoretical work by Fernandez-Oto et al., 2014; Tlidi et al., 2018). Overall, it is remarkable that very different taxa of annual plants form these up to 1 m large circles after rainfall. This leads to the fundamental question if this geometric formation is a case of "swarm intelligence" in plants (Baluška et al., 2010; Trewavas, 2014) or "ecosystem engineering", where self-organized plants modulate the soil-water distribution to enhance their survival in harsh environments (Getzin et al., 2021a; Gilad et al., 2004). To answer this question, in-depth studies on these rings are needed. For example, DNA analyses of the ring-forming individuals are required to test to what extent the herbal plants or their seeds are genetically related (Kappel et al., 2020). Although our excavations did not reveal a fungal mycelium, it needs to be clarified if bacterial or fungal microbiota, or other plant soil-biota feedbacks could be involved in ring formation (Cowan et al., 2020; Inderjit et al., 2021). Given that the annuals form the rings after rainfall, basic questions arise on whether the number of rings per area, their mean diameters and their local size variation depend on the previous rainfall characteristics or on edaphic site conditions. Also unknown is the extent to which these rings form spontaneously and whether there are rainy seasons when new grasses emerge but no rings are formed, or whether ring positions and their spatial patterns change from season to season. Although the collective plant rings were found by us only in several arid regions of the Pro-Namib, it remains to be solved whether these rings are bound to certain edaphic and/or climatic conditions and whether it is a global phenomenon in other drylands in the world. For the time being, we list the collective plant rings in Table 1 as mainly differing from FCs in their inability to form spatially periodic patterns.

4 | CONCLUSIONS

The famous FCs have puzzled scientists from various disciplines for many decades. Besides the recent mixing of unrelated phenomena with FCs, which is the rationale for this article, there are three main reasons why scientists struggle to solve this mystery.

First, FCs along the Namib Desert occur in a variety of habitats with different soil conditions such as on deep aeolian sands or on gravel plains, which is challenging for generalizations (van der Walt et al., 2016). Second, FCs as an emergent pattern are a strongly

climatically driven large landscape-scale phenomenon. This poses difficulties on experimental manipulations, because FC manipulations on the scale of 2–10 m may be too small to account for the underlying interaction scales that cause this pattern (Tschinkel, 2015). Third, FCs occur in arid conditions and rainfall along the Namib Desert is temporally and spatially variable (Henschel et al., 2005). Thus, precipitation events in these desert environments occur at erratic intervals, but only shortly after rainfall, grass seeds start germinating to form a matrix around the FCs. Because of the short growing season of the permanently transpiring grasses, the right timing of fieldwork is highly critical to narrow down plausible working hypotheses. This applies not only to research on FCs but also to the unexplored collective plant rings, where annual plants form circles in response to rainfall.

With these concluding remarks and our synthesis of the topic we intend to inspire the research community. We hope that our definition will guide future scientists to focus their research precisely on the inherent properties of FCs, without rash analogies to other merely circular gaps viewed in isolation, which otherwise have nothing in common with real and unique FCs.

AUTHOR CONTRIBUTIONS

S.G. and H.Y. conceived the study. W.R.T. contributed to the development of the ideas and provided critical feedback to the writing of the paper. All authors contributed to the writing of the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. The number of publications per year appearing in the *Web of Science* for the search topic "fairy circles"

Appendix S2. Excavations of fairy circles in the Giribes region and at NamibRand Nature Reserve