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GÖTTINGEN

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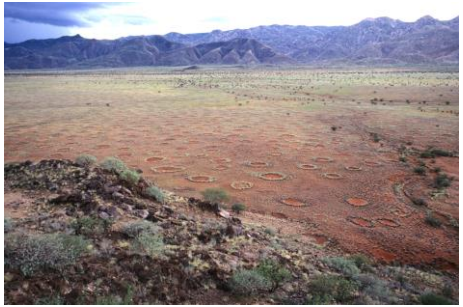
DFG Deutsche Forschungsgemeinschaft
German Research Foundation

# Plant water stress, not termite herbivory, causes Namibia's fairy circles

Stephan Getzin[1,2]

[1]University of Göttingen, Dept. of Ecosystem Modelling, Germany
[2]Gobabeb Namib Research Institute, Namibia



Marienfluss 2000

2009

2009

2021

# Latest results published 20th October 2022

Perspectives in Plant Ecology, Evolution and Systematics 57 (2022) 125698

Contents lists available at ScienceDirect

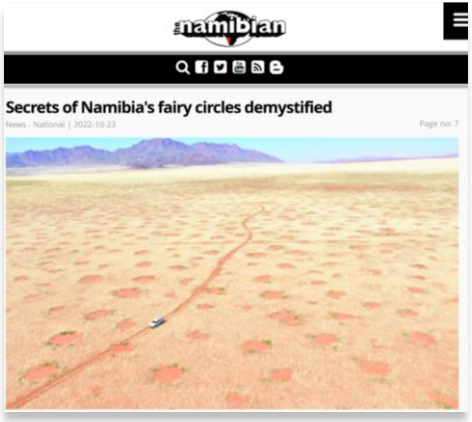
Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

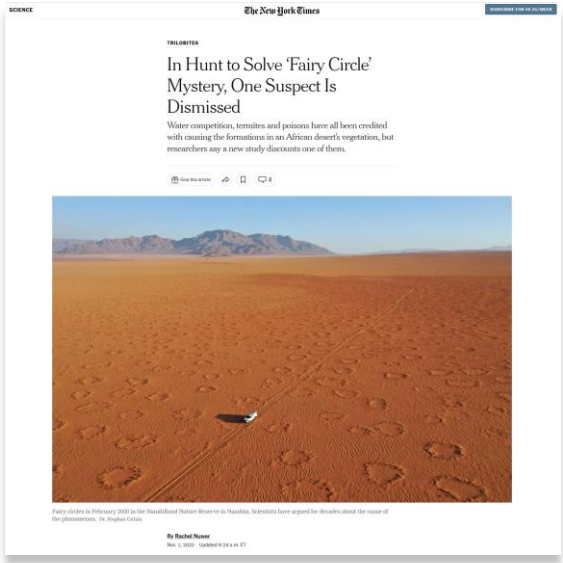
Research article

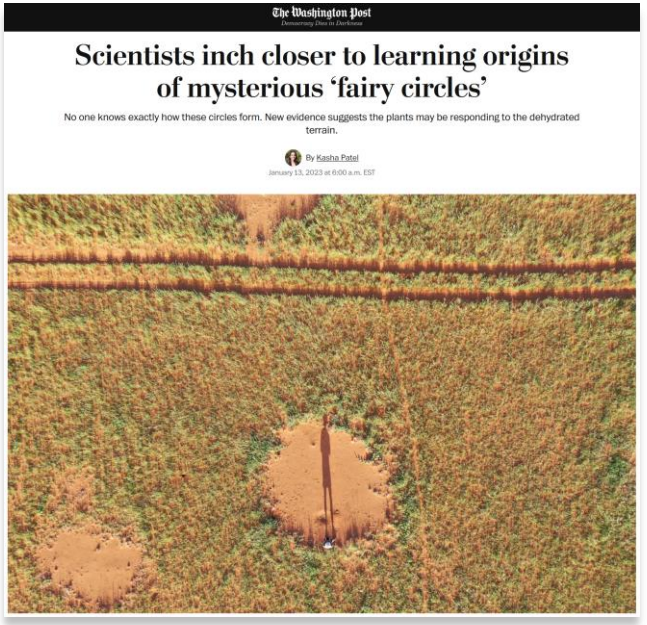
## Plant water stress, not termite herbivory, causes Namibia's fairy circles

Stephan Getzin [a,b,c,*], Sönke Holch [a], Hezi Yizhaq [d], Kerstin Wiegand [a]







# Collaboration partners and co-authors

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Prof. Hezi Yizhaq
Ben-Gurion University
Israel

Dr. Todd Erickson
The University of
Western Australia
Australia

Dr. Miriam Muñoz-Rojas
UNSW Sydney
Australia

Sönke Holch
University of Göttingen
Germany

Ailly Nambwandja
Gobabeb, NUST
Namibia

Prof. Walter Tschinkel
Florida State University
USA

Prof. Mike Cramer
University of Cape Town
South Africa

Dr. Gillian Maggs-Kölling
Gobabeb
Namibia

Dr. Eugene Marais
Gobabeb
Namibia

# Some facts about me

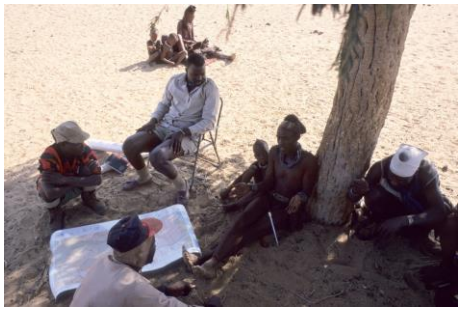
1997-2000, B.Sc. at University of Namibia

African Journal of Ecology

The suitability of the degradation gradient method in arid Namibia

Stephan Getzin

1998-1999, voluntary work with IRDNC in Kunene -> fairy circles



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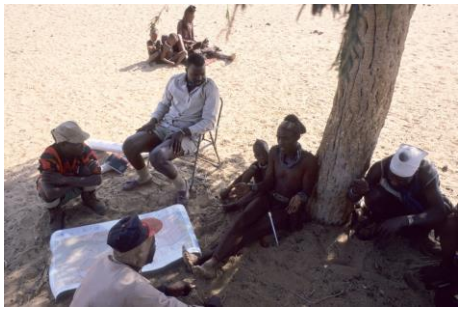
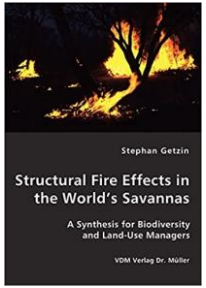
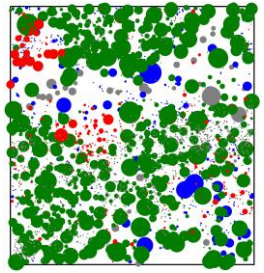


2000-2002, M.Sc. University of Potsdam thesis on “fire structures in savannas”




2003-2007, Ph.D. University of Jena thesis on “spatial ecology/statistics”



# Some facts about my fairy circle research

2000, first paper on the “fairy circles”, which established that term in scientific literature

Basic Appl. Ecol. 1, 149–159 (2000)
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Basic and Applied Ecology

## The fairy circles of Kaokoland (North-West Namibia) – origin, distribution, and characteristics

Thorsten Becker[1], Stephan Getzin[2]

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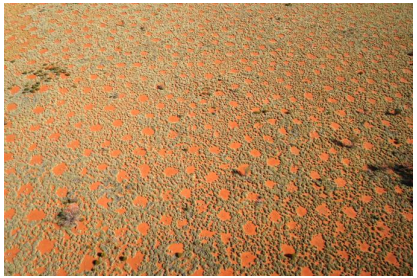

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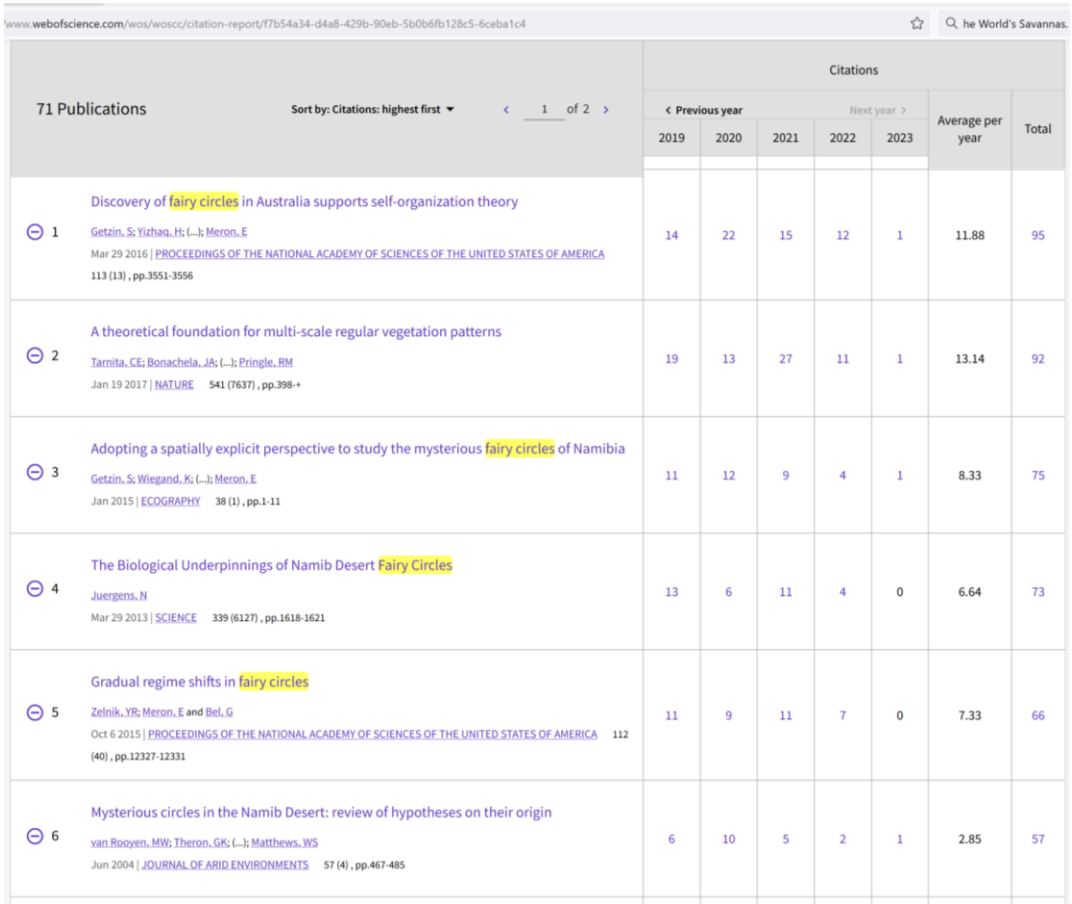
8 papers on Namibian fairy circles,
5 papers on Australian fairy circles
-> 2 papers among the 3 most cited papers



www.webofscience.com/wos/woscc/citation-report/f7b54a34-d4a8-429b-90eb-5b0b6fb128c5-6ceba1c4

he World's Savannas.

71 Publications | Sort by: Citations: highest first | 1 of 2

| | | Citations | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | < Previous year | | | | Next year > | Average per year | Total |
| | | 2019 | 2020 | 2021 | 2022 | 2023 | | |
| 1 | Discovery of fairy circles in Australia supports self-organization theory<br>Getzin, S; Yizhaq, H; (...); Meron, E<br>Mar 29 2016 \| PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA 113 (13) , pp.3551-3556 | 14 | 22 | 15 | 12 | 1 | 11.88 | 95 |
| 2 | A theoretical foundation for multi-scale regular vegetation patterns<br>Tarnita, CE; Bonachela, JA; (...); Pringle, RM<br>Jan 19 2017 \| NATURE 541 (7637) , pp.398-+ | 19 | 13 | 27 | 11 | 1 | 13.14 | 92 |
| 3 | Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia<br>Getzin, S; Wiegand, K; (...); Meron, E<br>Jan 2015 \| ECOGRAPHY 38 (1) , pp.1-11 | 11 | 12 | 9 | 4 | 1 | 8.33 | 75 |
| 4 | The Biological Underpinnings of Namib Desert Fairy Circles<br>Juergens, N<br>Mar 29 2013 \| SCIENCE 339 (6127) , pp.1618-1621 | 13 | 6 | 11 | 4 | 0 | 6.64 | 73 |
| 5 | Gradual regime shifts in fairy circles<br>Zelnik, YR; Meron, E and Bel, G<br>Oct 6 2015 \| PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA 112 (40) , pp.12327-12331 | 11 | 9 | 11 | 7 | 0 | 7.33 | 66 |
| 6 | Mysterious circles in the Namib Desert: review of hypotheses on their origin<br>van Rooyen, MW; Theron, GK; (...); Matthews, WS<br>Jun 2004 \| JOURNAL OF ARID ENVIRONMENTS 57 (4) , pp.467-485 | 6 | 10 | 5 | 2 | 1 | 2.85 | 57 |

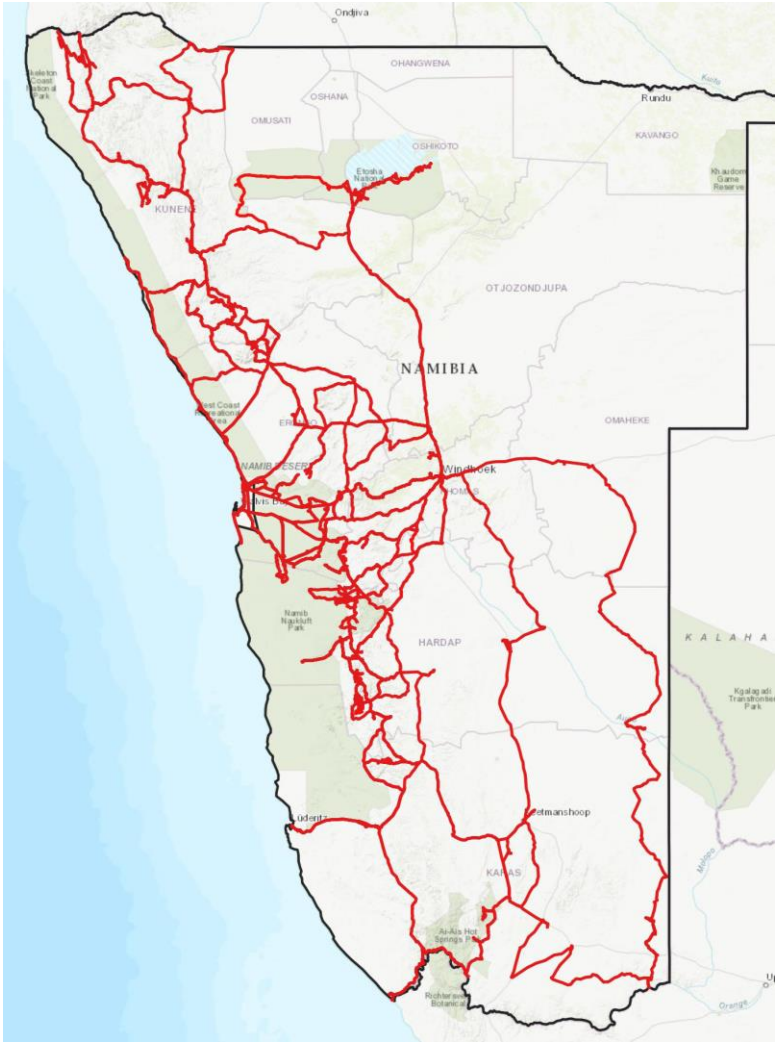
# Some facts about my fairy circle research

2000, first paper on the “fairy circles”, which established that term in scientific literature

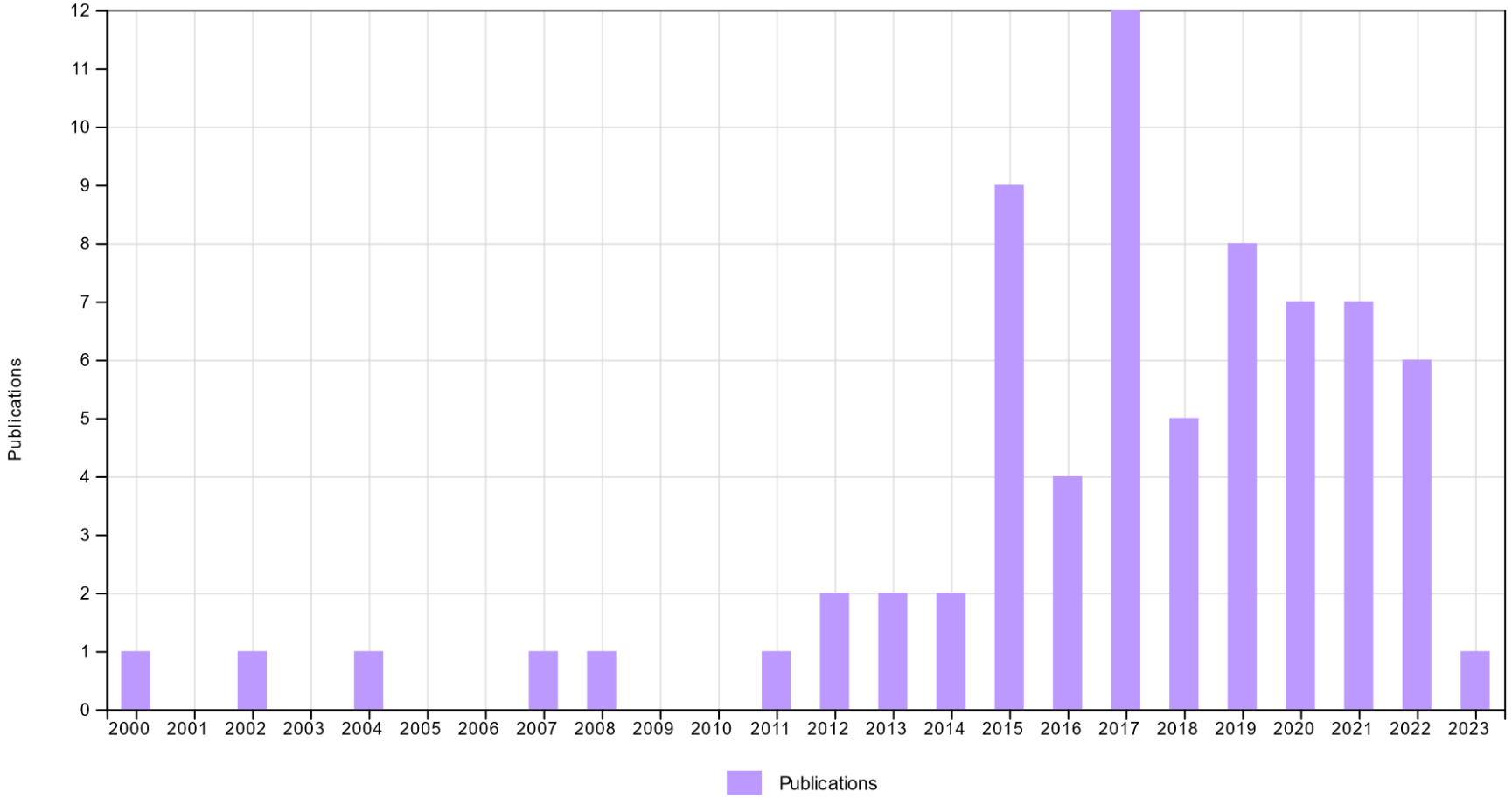
2014, discovery of fairy circles in Australia

8 papers on Namibian fairy circles,
5 papers on Australian fairy circles
-> 2 papers among the 3 most cited papers

Since 2015 every year in the Namib, driving 50 000 km

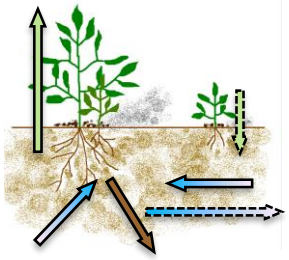


# *Web of Science*: Number of publications on search topic “fairy circles”



Correlation with fairy circles

## Plant self-organization



Tschinkel 2012/15
Cramer & Barger 2013
Getzin et al. 2015/16/22
Zelnik et al. 2015
Cramer et al. 2017
Ravi et al. 2017
Grabovsky 2018

## Euphorbia poisoning

Theron 1979, Meyer et al. 2015/20

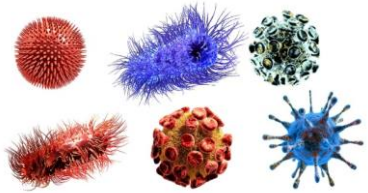
## Burrowing rodents

Cox 1987

## Harvester termites

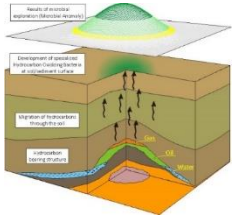
Moll 1994, Becker & Getzin 2000

## Microbial communities



Ramond et al. 2014, van der Walt et al. 2016

## Abiotic gas



Naude et al. 2011

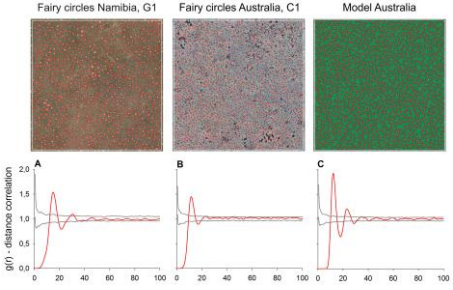
## Ants

Picker et al. 2012

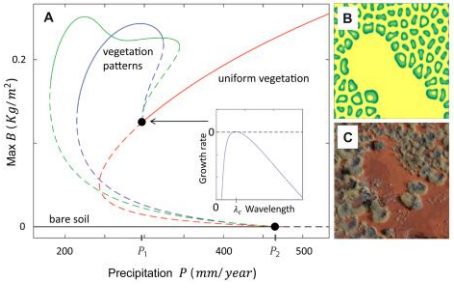
## Sand termites

Juergens 2013, Juergens et al. 2015
Vlieghe et al. 2015, Tarnita et al. 2017

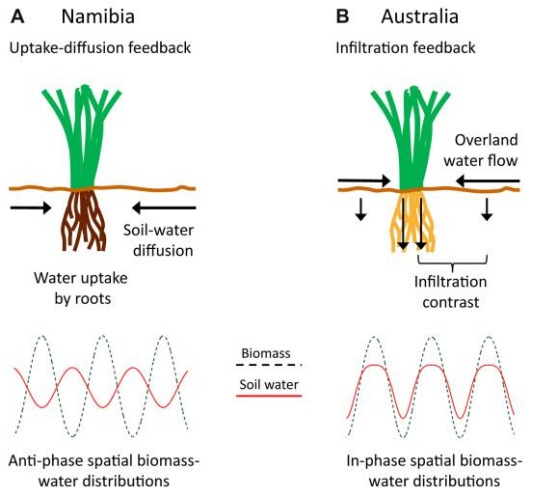
## Pattern-process inference



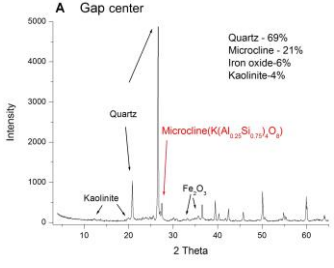

## Process-based models




## Testing processes in field

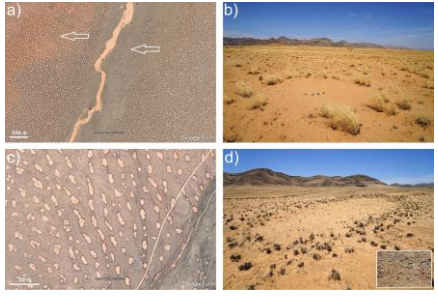



## Soil analysis




## Which mechanism explains all characteristics?

## Boundary conditions




## Excavations

## Manipulation experiments

# Background – Namibian fairy circles

- Fairy circles (FCs) occur mainly from 70 to 120 mm MAP along Namib Desert, disappear at 150 mm

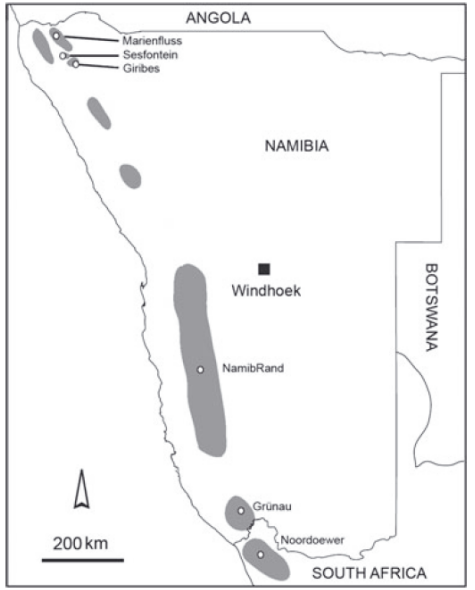



**Fig. 2.** Study sites (open circles) in Namibia and South Africa, and distribution of fairy circles (grey shading; after Becker & Getzin, 2000; augmented, to include all known records).

Picker et al. 2012

# Historic overview & three main hypotheses

Euphorbias

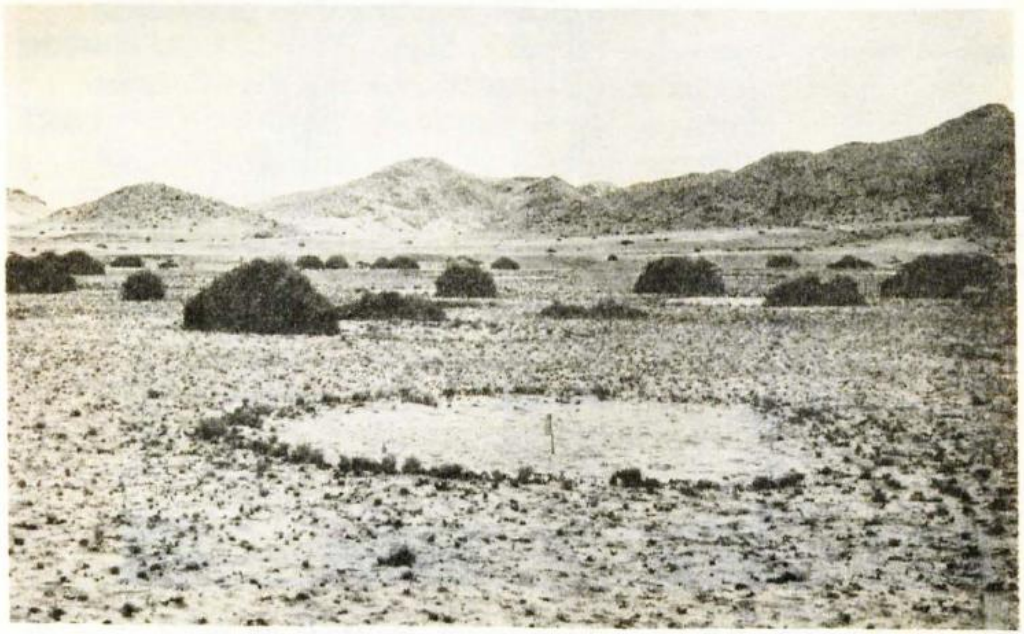
Termites

Plant self-organization

# The Euphorbia hypothesis

# First research done by Theron (1979)

- In southern Giribes and Marienfluss
- *Euphorbia damarana* could poison the soil and form fairy circles
- He marked dead Euphorbias and fairy circles in 1978
- Euphorbia hypothesis was “reactivated” by Meyer et al. (2015, 2020)



*Jl. S. Afr. biol. Soc. 20(1979)*

**DIE VERSKYNSEL VAN KAAL KOLLE IN KAOKOLAND, SUIDWES-AFRIKA**

*G K THERON*
DEPARTEMENT PLANTKUNDE, UNIVERSITEIT VAN PRETORIA

Meyer et al. BMC Ecol (2020) 20:45
https://doi.org/10.1186/s12898-020-00313-7

BMC Ecology

RESEARCH ARTICLE Open Access

The allelopathic, adhesive, hydrophobic and toxic latex of *Euphorbia* species is the cause of fairy circles investigated at several locations in Namibia

J. J. Marion Meyer[1,3*], Christiaan E. Schutte[1,2], Jan W. Hurter[1], Nicole S. Galt[1], Petunia Degashu[1], Greg Breetzke[2], Denis Baranenko[3] and Nicole L. Meyer[1]

# Euphorbia hypothesis cannot explain FCs – Reason 1

- Dead Euphorbias did not form fairy circles and marked FCs did not change over four decades
- Grass growth is not inhibited around dead Euphorbias

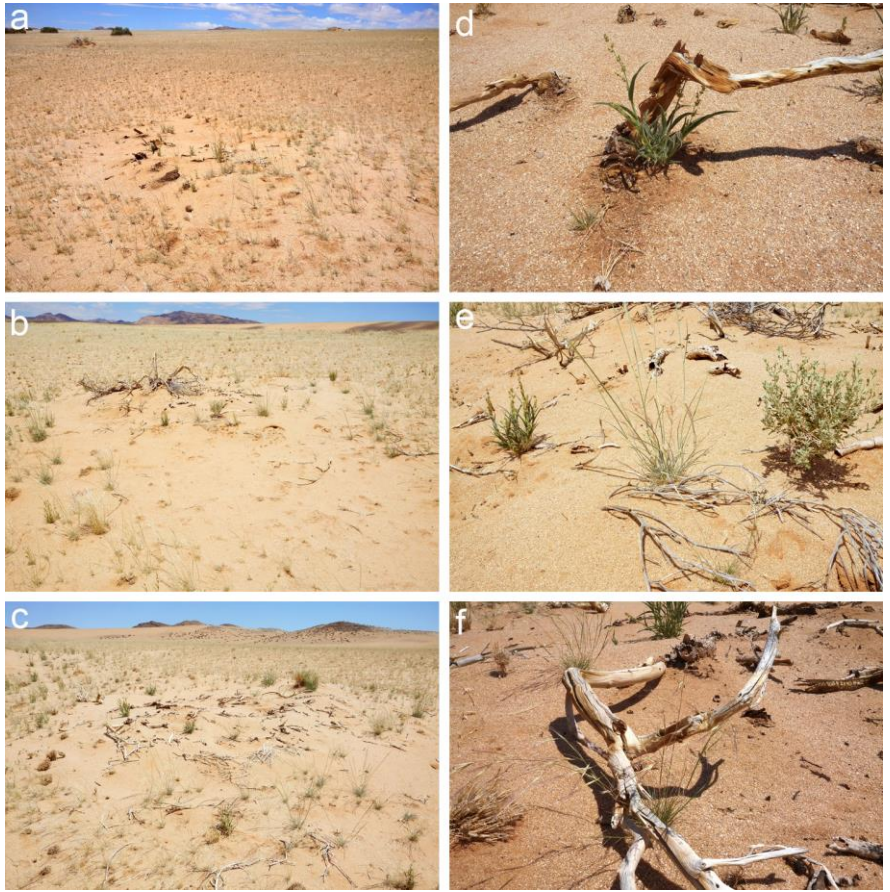
Giribes 2022

Drone images 2020, Google satellite 2009

# Euphorbia hypothesis cannot explain FCs – Reason 1

- Grass growth is not inhibited under *E. damarana* at Brandberg or under *E. gummifera* at Garub

Brandberg 2022

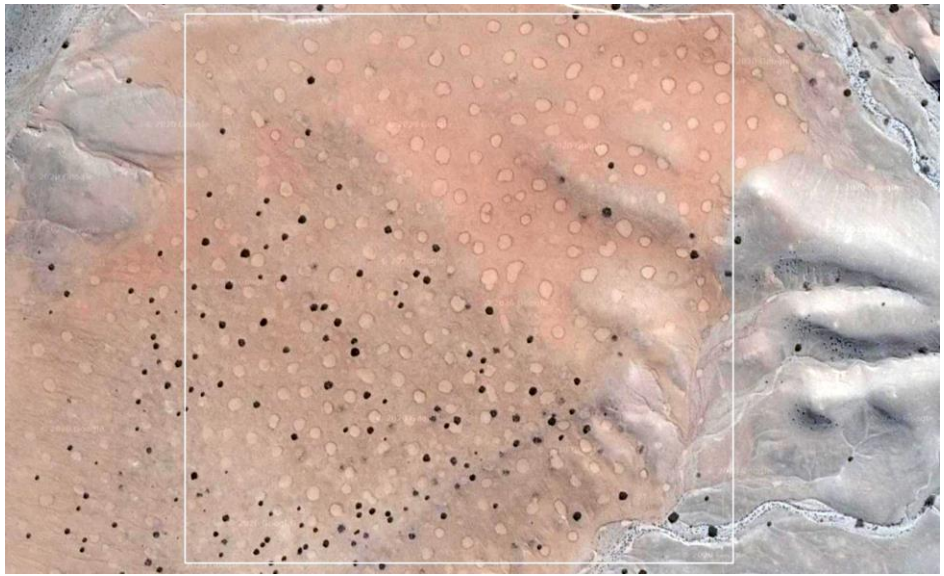


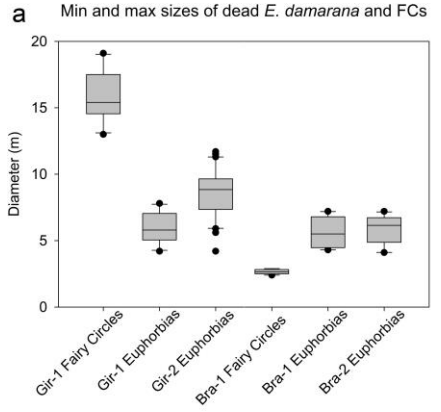

Garub 2021

# Euphorbia hypothesis cannot explain FCs – Reason 2

Drone images 2020, Google satellite 2009

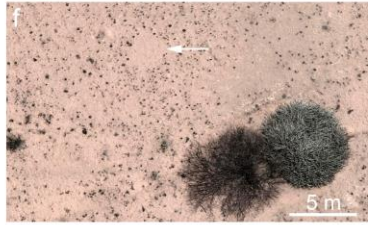
- FCs at Giribes ranged in diameter from 13-19 m, but dead Euphorbias only from 4-12 m
- At Brandberg, we found small FCs with 2-3 m, but the dead Euphorbias ranged in size between 4-7 m







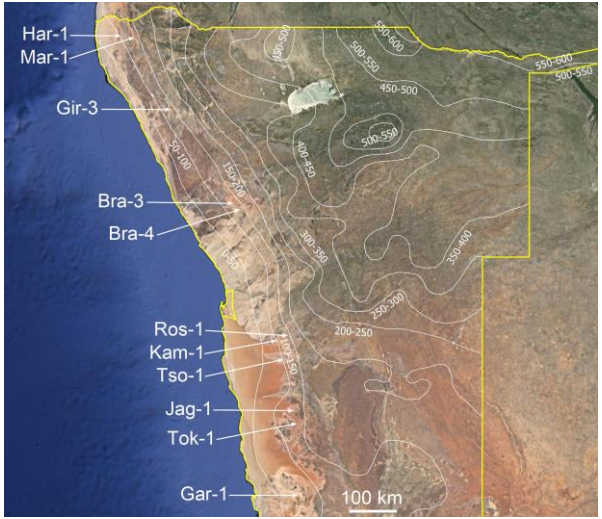


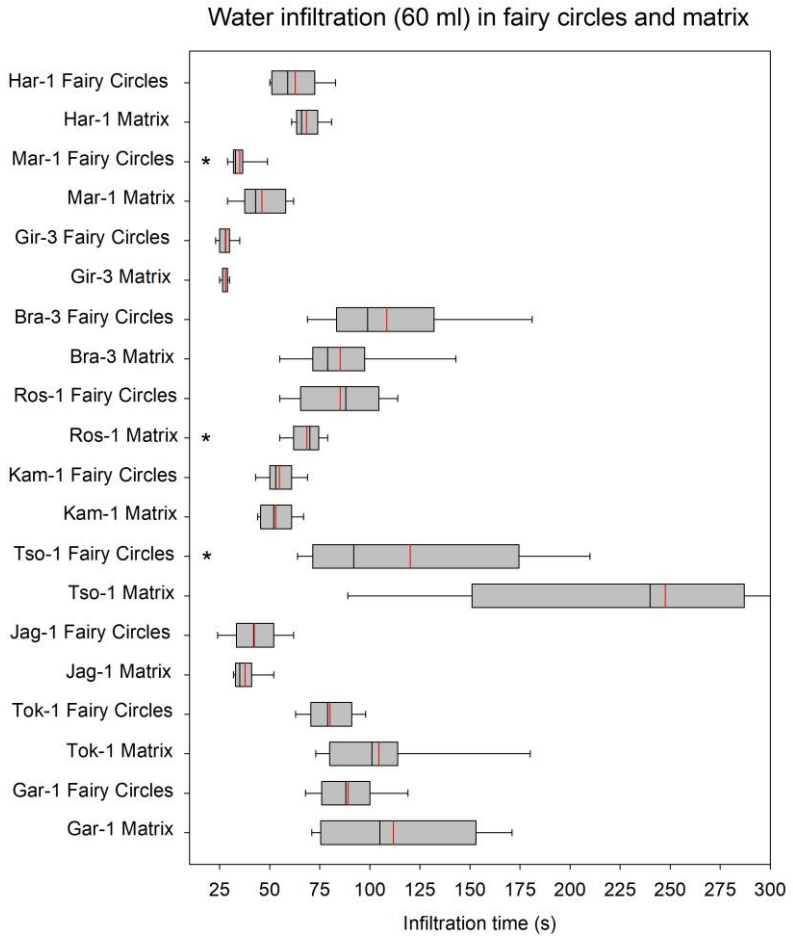




# Euphorbia hypothesis cannot explain FCs – Reason 3

- Meyer et al. (2020) claimed “Hydrophobic properties and faster infiltration rates could be introduced to matrix soil by coating it with Euphorbia latex”
- But our infiltration measurements from 10 FC regions found no systematic faster infiltration in FCs vs matrix

Getzin et al. 2021, 2022



# Euphorbia hypothesis cannot explain FCs – Reason 4

- In four out of five plots the spatial patterns differed significantly
- FCs were regularly distributed while Euphorbias were predominantly clustered
- The process that causes FCs does not match Euphorbias

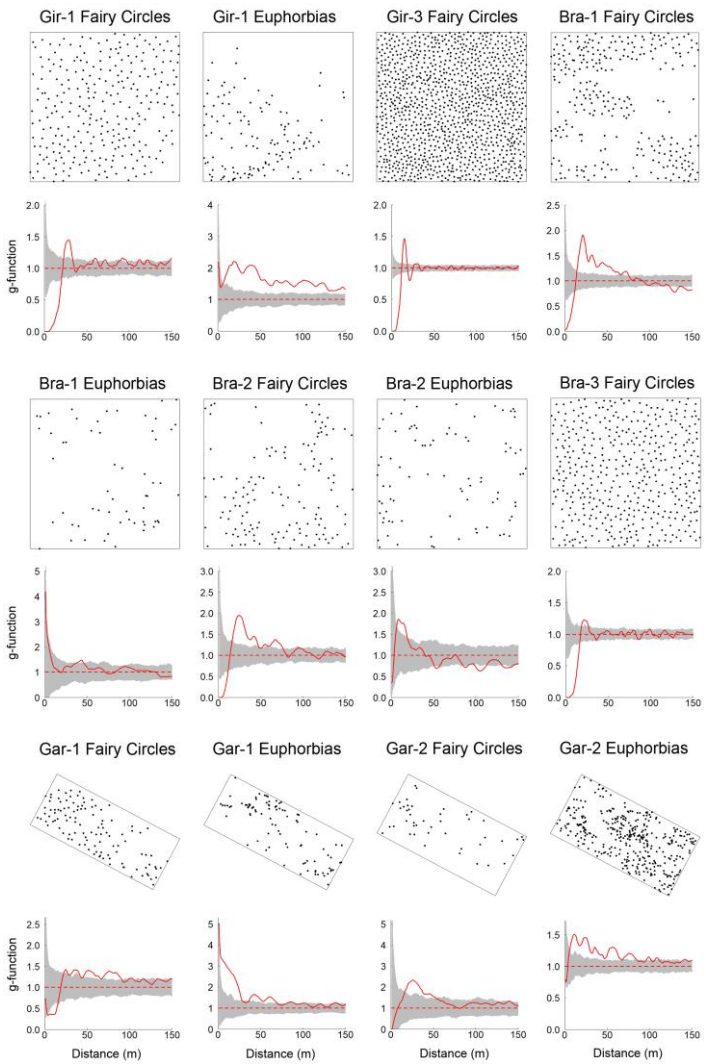
Getzin *et al. BMC Ecol Evo* (2021) 21:102
https://doi.org/10.1186/s12862-021-01834-5

BMC Ecology and Evolution

RESEARCH ARTICLE Open Access

## Revisiting Theron's hypothesis on the origin of fairy circles after four decades: Euphorbias are not the cause

Stephan Getzin[1,2*], Ailly Nambwandja[3], Sönke Holch[1] and Kerstin Wiegand[1]



# The termite hypothesis

# First mentioning by Tinley (1971) but no data collected

- Refers to an image of Marienfluss Valley
- The fairy circles could be fossil termite mounds

TINLEY

## ETOSHA AND THE KAOKOVELD

(323)

Supplement to "African Wild Life", Vol. 25, No. 1. March 1971

The Marienfluss Valley in the northern Kaokoveld-Namib region adjoining the Kunene River. On the right are the Otjihipaberge and in the background is the beginning of the Baynes Mountains, which attain an altitude of over 2 333 m (7 000 ft.). **The circular bare patches in the foreground are probably fossil termite mounds**, now truncated, from a geological period when this region received a higher rainfall. These grasslands are perennial only if rain occurs consecutively in the same area for several years. Otherwise the ground is completely bare.

# Harvester-termite hypothesis goes back to Moll (1994) but again, no data collected in support

- He worked in 1989 in Kunene and all other FC regions along the Namib
- "Despite the fact that *H. mossambicus* were not collected from fairy rings…it could be responsible for the formation of rings"

J.H. Seyani & A.C. Chikuni, Proc. XIII[th] Plenary Meeting AETFAT, Malawi, 2: 1203-1209 (1994).



## THE ORIGIN AND DISTRIBUTION OF FAIRY RINGS IN NAMIBIA

Eugene J.Moll

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## THE ORIGIN AND DISTRIBUTION OF FAIRY RINGS IN NAMIBIA

Eugene J.Moll

- **For nearly 30 years the termite hypothesis was not based on concrete data evidence**
- It's popular because it's so easy to explain

# Harvester-termite hypothesis goes back to Moll (1994) but again, no data collected in support

- He worked in 1989 in Kunene and all other FC regions along the Namib
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J.H. Seyani & A.C. Chikuni, Proc. XIII[th] Plenary Meeting AETFAT, Malawi, 2: 1203-1209 (1994).



THE ORIGIN AND DISTRIBUTION OF FAIRY RINGS IN NAMIBIA

Eugene J.Moll



- In 2000, nothing was known about FCs
- Becker & Getzin (2000) found harvester termites and supported Moll's idea

**Fig. 7.** *Hodotermes mossambicus* feeding on *Stipagrostis uniplumis* (Marienfluss).

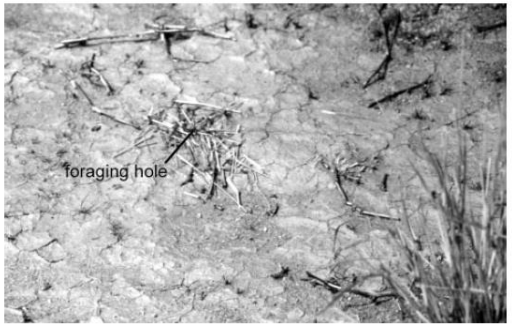
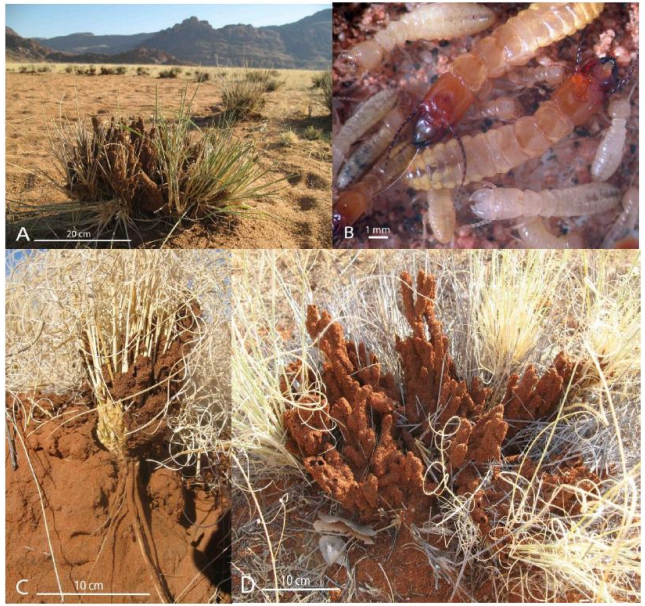



**Fig. 8.** Foraging hole of *Hodotermes mossambicus* surrounded by pieces of *Stipagrostis uniplumis* (Marienfluss).

# The sand termite hypothesis goes back to Juergens (2013)

- Juergens (2013) claimed that the fairy circles would be a "termite-generated ecosystem" caused by *P. allocerus*
- "The generation of a perennial water supply facilitates the survival of termites...even in extreme drought years"
- Mechanism: "their foraging on the roots of freshly germinated grasses kills them and keeps the bare patch free of vegetation"
- "In 80 to 100 % of FCs, *P. allocerus* nests and underground tunnel-like galleries….were found a few centimeters to decimeters underneath the bare patch…"

**The Biological Underpinnings of Namib Desert Fairy Circles**
Norbert Juergens
*Science* **339**, 1618 (2013);
DOI: 10.1126/science.1222999



# First Fairy Circle Symposium in 2015 at Wolwedans

- None of the fairy circle researchers in the room agreed with the sand termite hypothesis

**Fairy circle symposium leaves the mystery unanswered**

News - National | 2015-03-12 Page no: 0

the namibian

# The termite hypothesis

Termites cannot explain the patterns of fairy circles

JGR Biogeosciences

RESEARCH ARTICLE
10.1029/2019JG005393

# Contrasting Global Patterns of Spatially Periodic Fairy Circles and Regular Insect Nests in Drylands

**Key Points:**
- Regular spatial patterns are

Stephan Getzin[1,2], Hezi Yizhaq[3], Michael D. Cramer[4], and Walter R. Tschinkel[5]

## Termites cannot explain the patterns of fairy circles

Research

EDITOR'S CHOICE

Ecography 38: 1–11, 2015
doi: 10.1111/ecog.00911

Subject Editor: Miguel Araújo. Accepted 9 April 2014

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

Stephan Getzin, Kerstin Wiegand, Thorsten Wiegand, Hezi Yizhaq, Jost von Hardenberg and Ehud Meron

Ecological Entomology

*Ecological Entomology* (2015), **40**, 669–675
DOI: 10.1111/een.12267

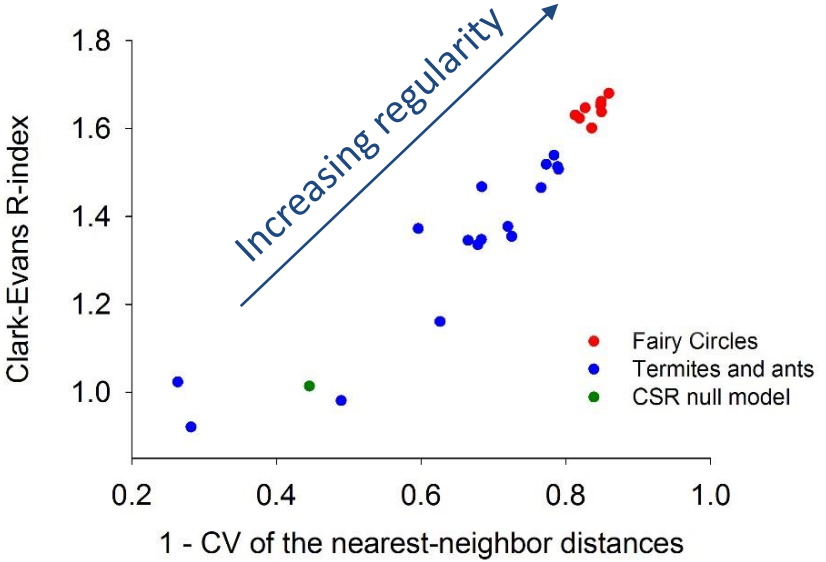
OPINION

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

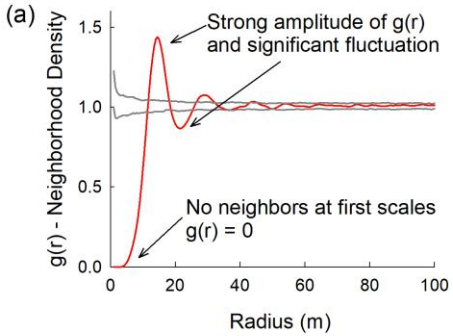
STEPHAN GETZIN,[1] KERSTIN WIEGAND,[2] THORSTEN WIEGAND,[1] HEZI YIZHAQ,[3,4] JOST VON HARDENBERG[5] and EHUD MERON[3,6] [1]Department of Ecological Modelling, Helmholtz Centre for Environmental Research – UFZ,

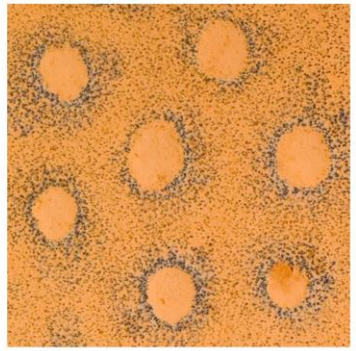
# Termites cannot explain the patterns of fairy circles

- FCs attain extremely regular (*spatially periodic*) patterns with six neighbours of equal distance
- But termite nests of the global drylands typically show less ordered patterns

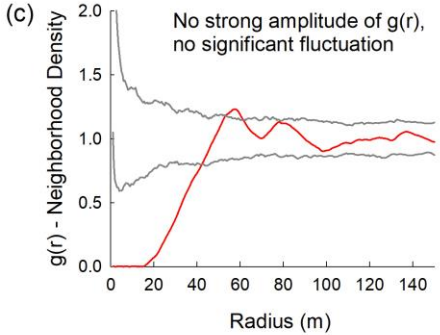


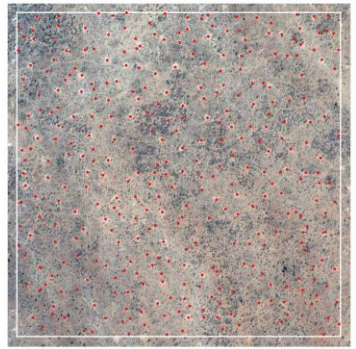

Above fairy circles, below Macrotermes mounds near Outjo




Spatially periodic fairy circles (above), regular termite circles (below)



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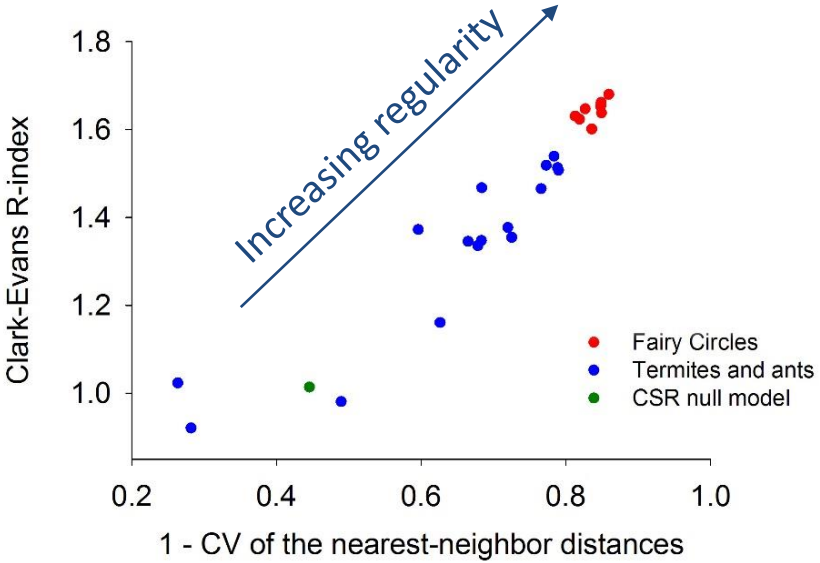
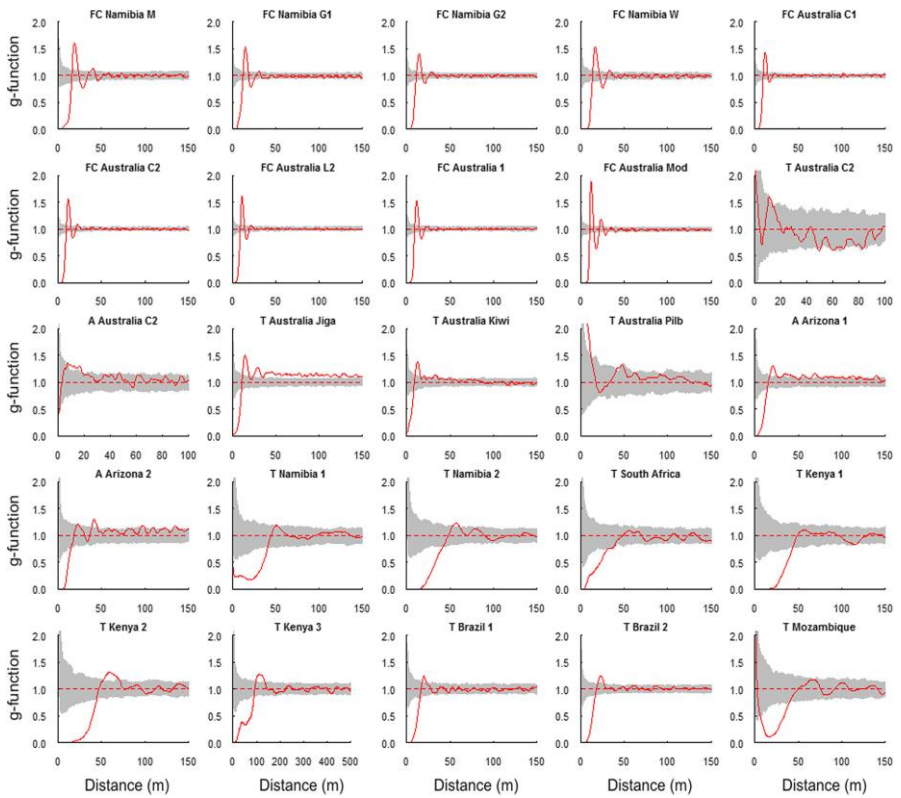



25 global patterns of fairy circles, termites and ants



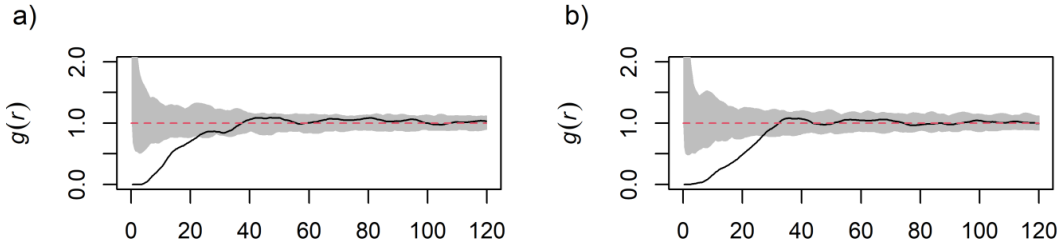
# Termites cannot explain the patterns of fairy circles

- Also harvester termite nests in southern Angola show merely regular patterns but never spatially periodic patterns like FCs
- Unlike fairy circles, they always have a typical nest in the center
- According to the “Definition of fairy circles”, these circles were classified as “common vegetation gaps” but not as fairy circles

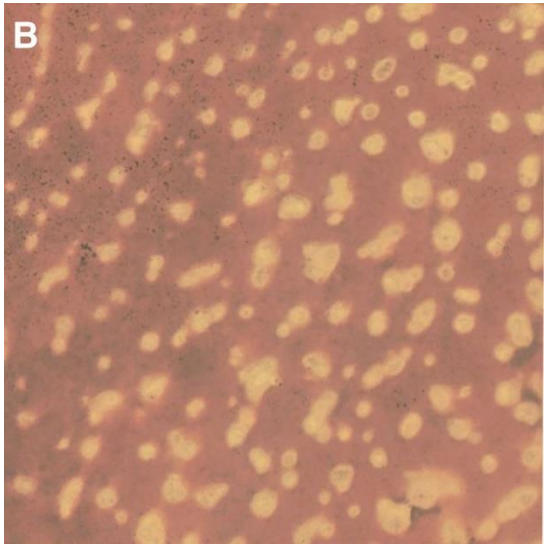
Received: 5 February 2021 | Revised: 20 September 2021 | Accepted: 18 October 2021
DOI: 10.1111/jvs.13092
Journal of Vegetation Science
SYNTHESIS

**Definition of “fairy circles” and how they differ from other common vegetation gaps and plant rings**

Stephan Getzin[1,2] | Hezi Yizhaq[3] | Walter R. Tschinkel[4]




Juergens et al. 2021




Juergens et al. 2021

# Termites cannot explain the patterns of fairy circles



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

Received: 5 February 2021 | Revised: 20 September 2021 | Accepted: 18 October 2021
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Journal of Vegetation Science IAVS

SYNTHESIS

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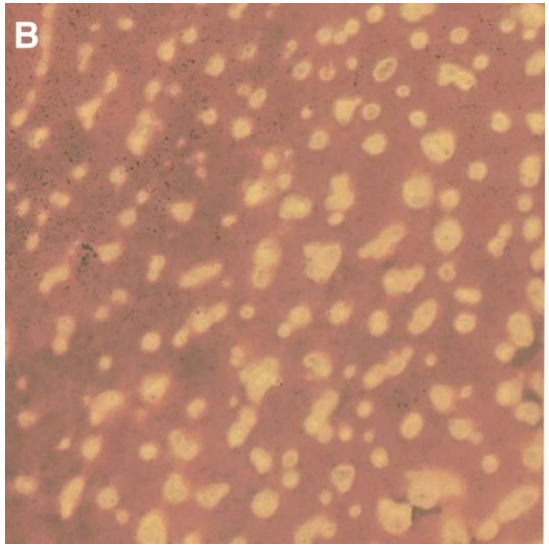



Juergens et al. 2021

# The termite hypothesis

Most fairy circle researchers did not find sand termites in fairy circles

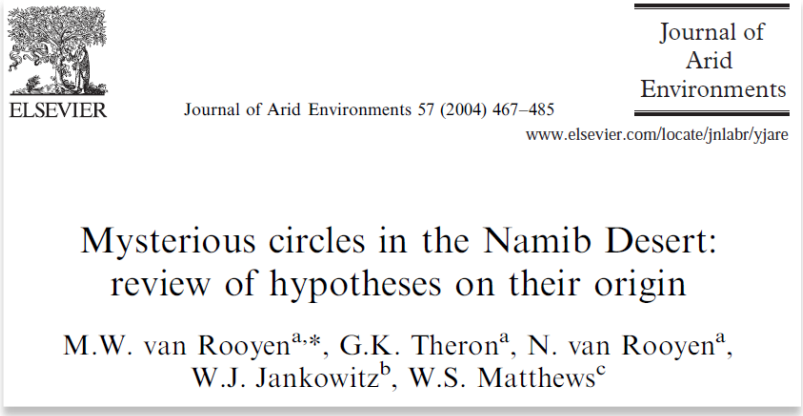
3 examples for the absence of correlation

# Most fairy circle researchers did not find sand termites in fairy circles

- van Rooyen et al. (2004) excavated the FCs in Hartmann's Valley, Marienfluss, Giribes, Brandberg, Khan, Escourt Experimental Farm, Sesriem, Namtib Guest Farm and Rooiduin

- 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

- "none of the trenches revealed any termite tunnels" and "the presence of termite nests beneath the circle has yet to be demonstrated"



ELSEVIER

Journal of Arid Environments 57 (2004) 467–485

Journal of Arid Environments

www.elsevier.com/locate/jnlabr/yjare

Mysterious circles in the Namib Desert: review of hypotheses on their origin

M.W. van Rooyen[a,*], G.K. Theron[a], N. van Rooyen[a], W.J. Jankowitz[b], W.S. Matthews[c]

# Most fairy circle researchers did not find sand termites in fairy circles

"It took us about three days to establish, without a doubt, that termites were absolutely nothing to do with this" (Tschinkel 2014, BBC)



## Walter R. Tschinkel

From Wikipedia, the free encyclopedia

**Walter R. Tschinkel** is an internationally renowned myrmecologist, entomologist and Distinguished Research Professor of Biological Science and R.O. Lawton Distinguished Professor emeritus at Florida State University. He is the author of the Pulitzer Prize nominated book *The Fire Ants* (Harvard University/Belknap Press 2006), and more than 150 original research papers on the natural history, ecology, nest architecture and organization of ant societies; chemical communication in beetles; and the mysterious fairy circles of the Namib desert. His casts of ant nests and botanical drawings appear in numerous museums of art and natural history, from Hong Kong to Paris.

Walter Tschinkel standing near a cast of a harvester ant nest

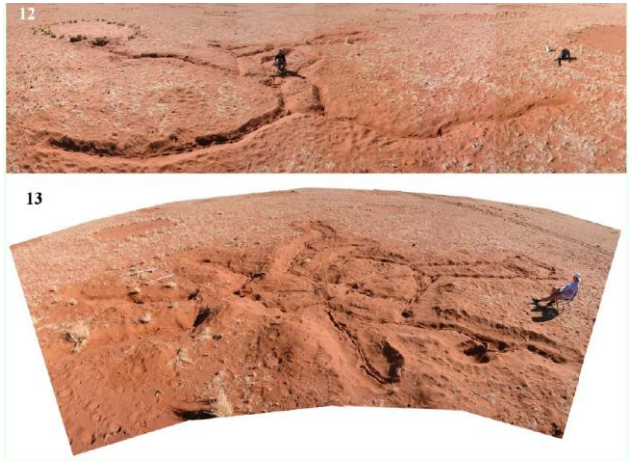
Tschinkel is known for his thorough and inventive experimental design, often involving the construction of special contraptions (stimulatorium,[1] trash can kiln,[2] ice nests [3]) and re-purposing methods from other fields of inquiry. In 1991, he coined the term "insect sociometry" to describe an under-emphasized method, involving the detailed physical and numerical description of social insect colonies;[4] which he views as superorganisms. He is an advocate of scientific natural history and the "bottom-up" approach to biological research, noting that, "…empirical evidence is the horse that pulls the cart of theory through testing, and the three move along the road to understanding." [5] He suggests that novel and meaningful research questions are best derived from extensive observation, familiarity and careful experimentation.

Professor Tschinkel has written extensively on education [6] and gained a reputation as a stern yet inspirational lecturer who places special emphasis on knowing the basics. During his 43 years at Florida State University, he developed and taught numerous university courses including Animal Behavior, Animal Diversity and Insect Biology. He also served as a major professor and mentor to 22 Masters and PhD students, and more than 71 undergraduate researchers. In 2013, Dr. Tschinkel retired from teaching. Today he remains active in research, with field sites in Florida's Apalachicola National Forest and Namibia. In addition to numerous professional honors and accolades, Walter Tschinkel is a fellow of the Entomological Society of America, co-founder of the environmental advocacy group, Friends of The Apalachicola National Forest, and a committee member for The Nierenberg Prize for Science in the Public Interest. In his spare time he enjoys writing, creating botanical artwork, photography, hiking, wood working and reading mystery novels. He is capable of a breath-hold dive to the depth of 60 ft.

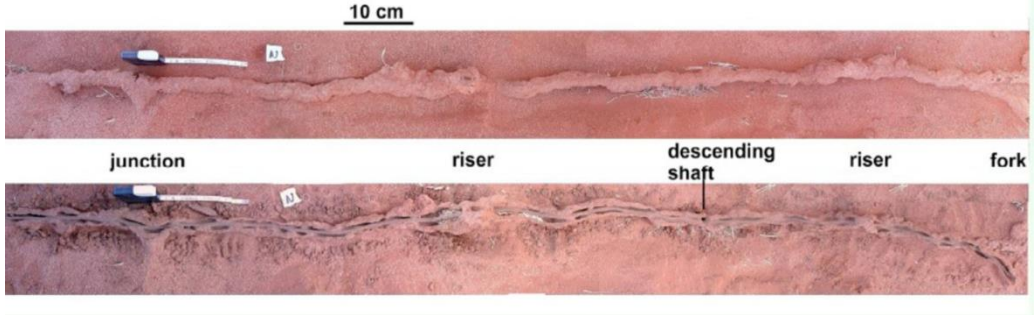
# Most fairy circle researchers did not find sand termites in fairy circles

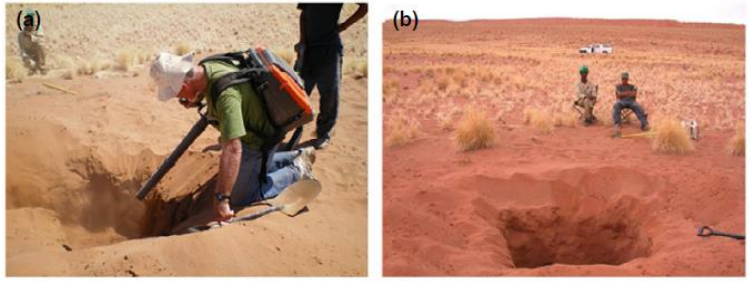
- Walter Tschinkel was the first entomologist who excavated the fairy circles with a leaf blower to reveal all possible galleries

- 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”




(Tschinkel 2010)



# Most fairy circle researchers did not find sand termites in fairy circles

- Namibia‘s leading entomologist, Eugene Marais, looked specifically for sand termites in several FC regions of Namibia (Ravi et al. 2017)
- “We have not found 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”

**Journal of Geophysical Research: Biogeosciences**

**RESEARCH ARTICLE**
10.1002/2016JG003604

**Key Points:**
- We provide experimental evidence for the ecohydrological interactions within fairy circles in the Namib Desert

## Ecohydrological interactions within “fairy circles” in the Namib Desert: Revisiting the self-organization hypothesis

**Sujith Ravi[1], Lixin Wang[2], Kudzai Farai Kaseke[2], Ilya V. Buynevich[1], and Eugene Marais[3]**

# Most fairy circle researchers did not find sand termites in fairy circles

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- “We have not found 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”
- This absence cannot be “excused” with sand termites disappearing in the dry season because:
- “The ecosystem-engineer hypothesis rests on the proposition that the sand termites will still exploit the higher moisture source in the center”
- “At present, empirical data on termite tunnel structures within fairy circles that may favor niche construction by sand termites are not yet available”

# The termite hypothesis

Grasses within fairy circles died without termite herbivory

Perspectives in Plant Ecology, Evolution and Systematics 57 (2022) 125698

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Research article

Plant water stress, not termite herbivory, causes Namibia's fairy circles

Stephan Getzin [a,b,c,*], Sönke Holch [a], Hezi Yizhaq [d], Kerstin Wiegand [a]

# No magnifying glass is necessary to see root damage…

- In 2013, Juergens showed in the appendix one picture with yellow grasses having no roots
- Is this typical detritus feeding of termites? -> Hence we also photographed the death of grasses….


Fig. S9A: Young FC of probably 2 or 3 years of age. This estimation is based on comments by local managers and on comparisons with photos taken in the years before). S9B: Various states of root damage of young grass plants. S9C: Typical *Psammotermes* burrows with partly visible black tapetum (1) and termite worker (2) near the damaged roots of a young grass plant.

# Grasses within fairy circles died without termite herbivory

- After rainfall, the quickly dying grasses within FCs showed no sign of termite herbivory
- This was observed in 2021 at NamibRand (a,b), Garub (c,d) and Brandberg (e,h and below)


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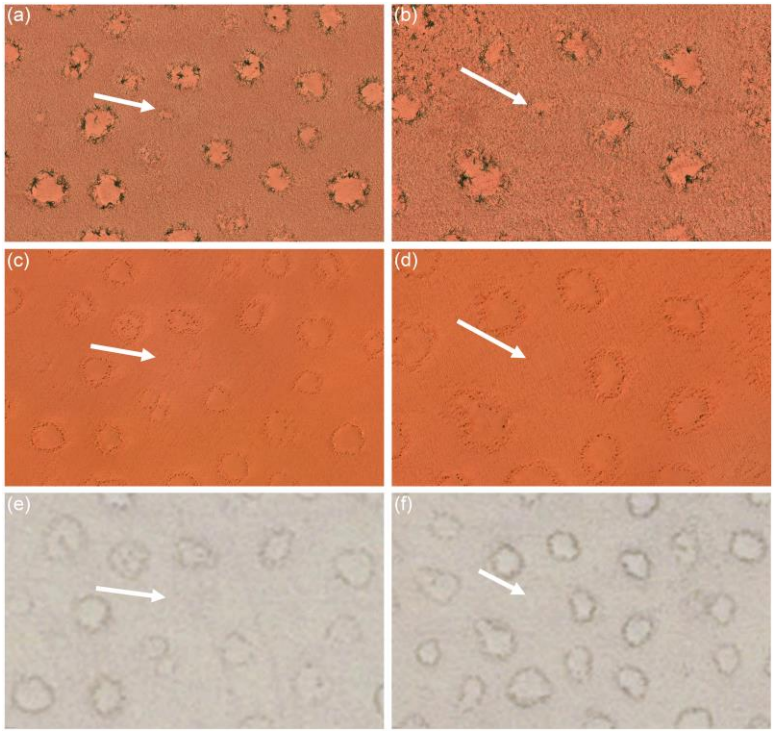
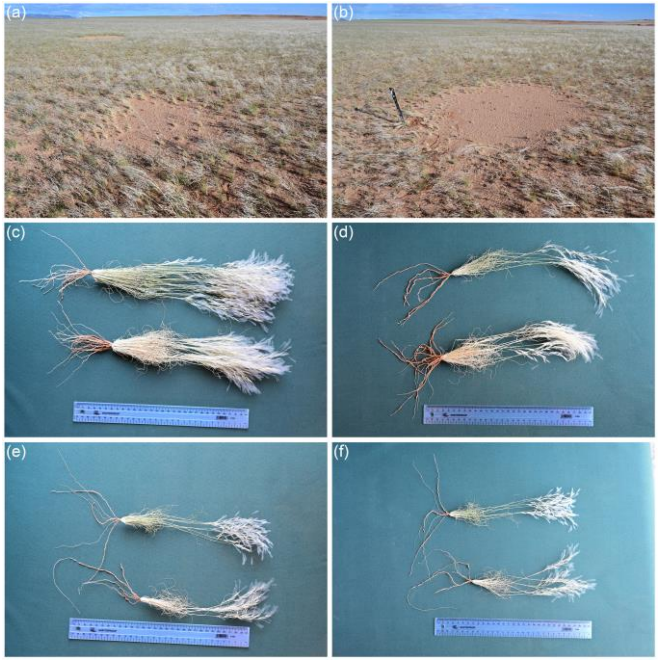
# Grasses within fairy circles died without termite herbivory

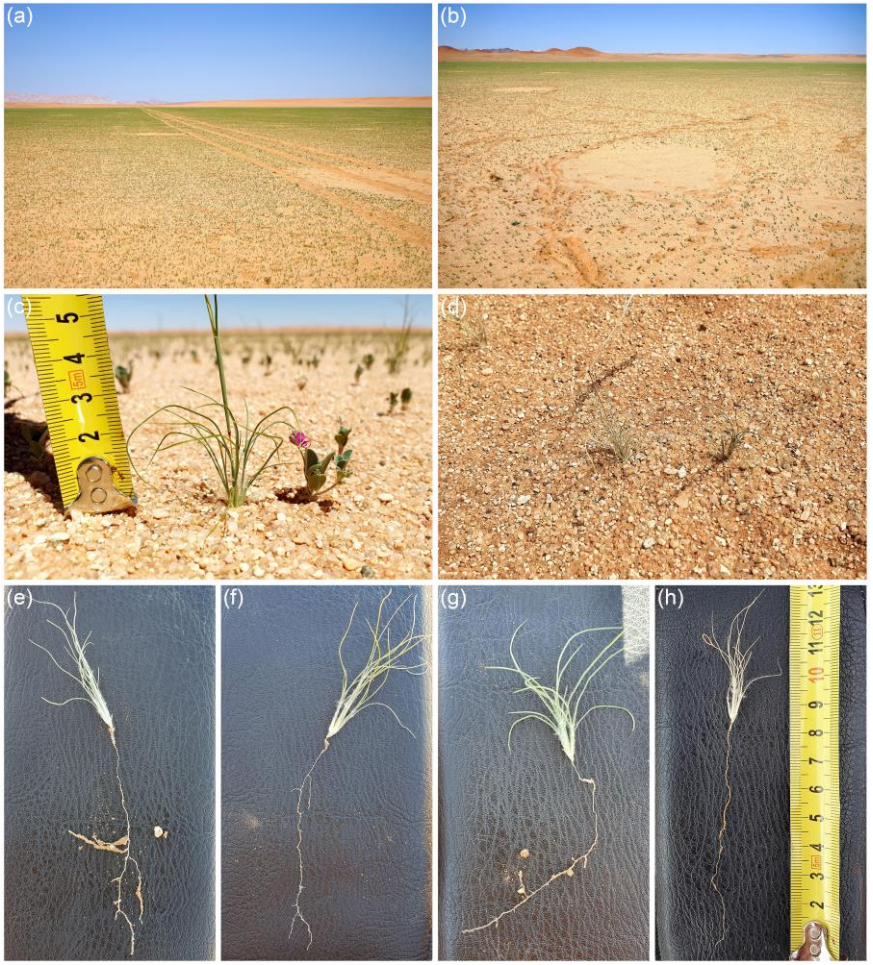
- Also in “new” fairy circles (top images) at NamibRand, the grasses died without termite herbivory




# Grasses within fairy circles died without termite herbivory

- No root herbivory at Kamberg in 2020 (right) and during the strong rainy season in 2022 (below)
- Roots often had intact rhizosheath (below)



# Grasses within fairy circles died without termite herbivory

- 3-5 weeks after rainfall, 100 % of all dead FC grasses showed no sign of root damage

| Plot properties | Kam-1 FC | Kam-1 Matrix | Jag-1 FC | Jag-1 Matrix | Gar-1 FC | Gar-1 Matrix | Bra-3 FC | Bra-3 Matrix | Bra-4 FC | Bra-4 Matrix |
|---|---|---|---|---|---|---|---|---|---|---|
| Number of days after triggering rain | 19-20 | 19-20 | 53 | 53 | 59 | 59 | 47 | 47 | c. 35 | c. 35 |
| Number of excavated grasses | 50 | 90 | 50 | 60 | 50 | 60 | 50 | 60 | 10 | 10 |
| Median shoot length (cm) | 3.0 | 3.5*** | 8.0 | 9.8** | 3.3 | 4.5*** | 4.0 | 5.0*** | 4.5 | 6.5*** |
| Median root length (cm) | 9.0 | 9.0 | 8.5 | 15.0*** | 8.5 | 14.0*** | 8.0 | 11.3*** | 12.5*** | 9.8 |
| Median root-shoot ratio | 3.2** | 2.7 | 1.1 | 1.6*** | 2.6 | 3.3** | 2.3 | 2.4 | 3.1* | 1.6 |
| Percent grass roots without damage (%) | 100 | 100 | 74 | 100 | 82 | 100 | 68 | 100 | 100 | 100 |
| Median soil-water content at grasses (%) | 1.9 | 2.0 | 3.1*** | 2.5 | 4.0 | 5.0*** | 3.0*** | 1.9 | 3.8 | 4.4*** |

# Grasses within fairy circles died without termite herbivory

- Only later, 7-8 weeks after rainfall, 18-32 % of all dead FC grasses showed signs of root damage
- Termites prefer to feed on dead plant material

| Plot properties | Kam-1 FC | Kam-1 Matrix | Jag-1 FC | Jag-1 Matrix | Gar-1 FC | Gar-1 Matrix | Bra-3 FC | Bra-3 Matrix | Bra-4 FC | Bra-4 Matrix |
|---|---|---|---|---|---|---|---|---|---|---|
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# Grasses within fairy circles died without termite herbivory

- Termites are detritus feeders which explains the increase in root damage with time after rain

- *Psammotermes allocerus* classified as:

  "wood and litter feeder" Zeidler 1997
  "detritus feeder" Crawford & Seely 1994

- In the dry Namib **"*Psammotermes* selectively grazes the outer grey layer of the stems"** Jacobson et al. 2015


**Fig 2. Termites (*Psammotermes allocerus*) consume fungal-colonized litter.** Perennial *Stipagrostis ciliata* litter cast has been removed, showing termites (arrows) stripping the grey outer layer, leaving the golden-yellow interior (2

# The long roots of dead grasses reject termite herbivory as a causal mechanism

- Dead grasses within FCs had even longer roots than the vital grasses outside
- Large root-to-shoot ratios indicate plant water stress -> grasses invest into root biomass to find water

| Plot properties | Kam-1 FC | Kam-1 Matrix | Jag-1 FC | Jag-1 Matrix | Gar-1 FC | Gar-1 Matrix | Bra-3 FC | Bra-3 Matrix | Bra-4 FC | Bra-4 Matrix |
|---|---|---|---|---|---|---|---|---|---|---|
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# Comments of fairy circle experts on our new study

*Contrary to popular belief, termite activity does not cause the fairy circles.*

(Dr. Yvette Naudé, University of Pretoria)

*The new study showed "conclusively" that termites were not a factor.*

(Dr. Marion Meyer, University of Pretoria)

*The support for the hydrodynamic explanation is now very strong, and the support for the termite cause is very weak.*

(Dr. Walter Tschinkel, Florida State University)

The New York Times

TRILOBITES

In Hunt to Solve 'Fairy Circle' Mystery, One Suspect Is Dismissed

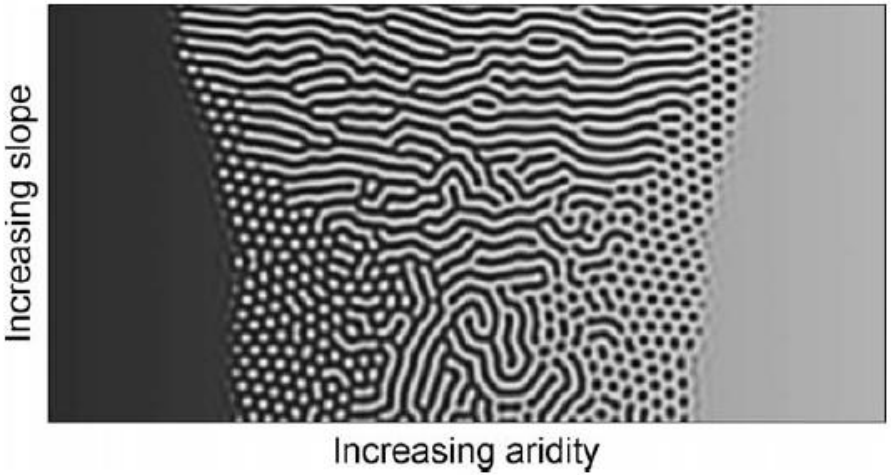
Water competition, termites and poisons have all been credited with causing the formations in an African desert's vegetation, but researchers say a new study discounts one of them.

# The plant self-organization hypothesis

The most plausible working hypothesis

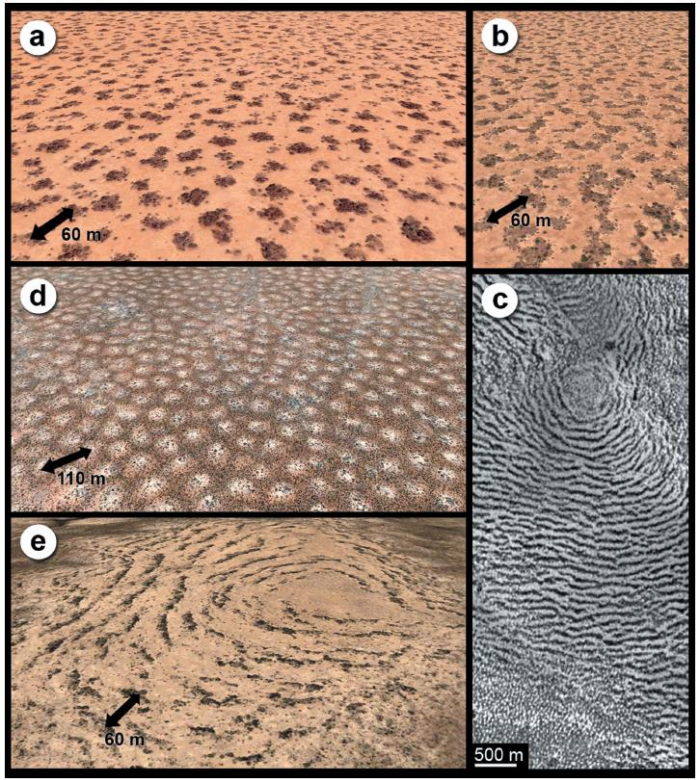
# What is plant self-organization?

- Occurs worldwide in arid environments, where annual rainfall is too low to allow continuous vegetation cover
- Only one or two plant species dominate -> clear patterns
- Spatially periodic bare soil = scale of water shortage




(Deblauwe et al. 2008, 2011)

a) Spots, Sudan
b) Labyrinths, Sudan
c) Stripes, Sudan
d) Gaps, eastern Africa
e) Stripes, Baja California

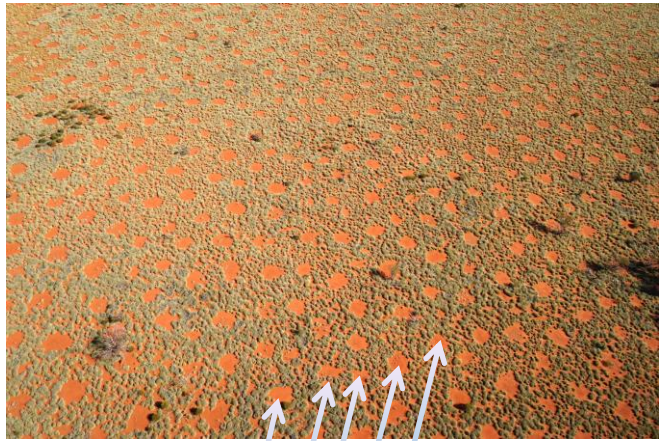


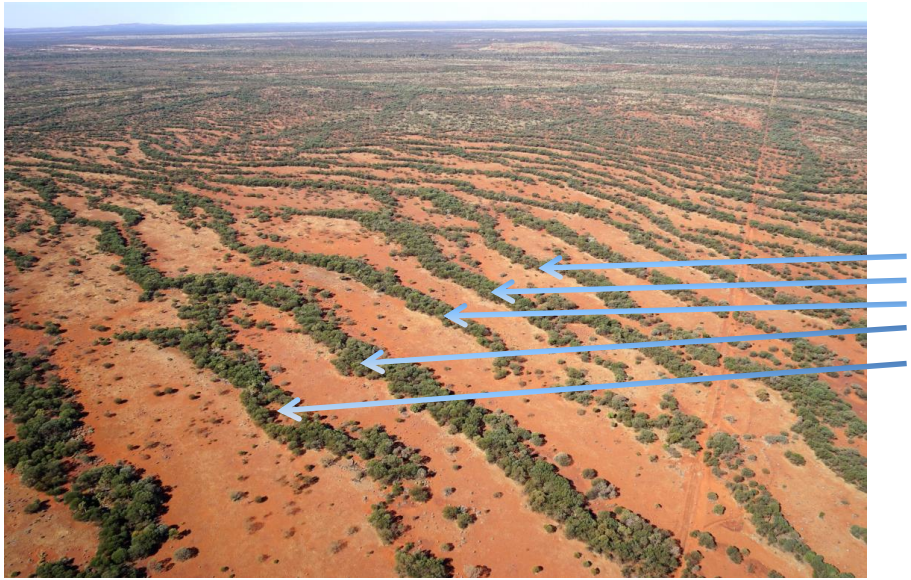
# What is plant self-organization?

- *Festuca* grasses in Andes form stripes on slopes or rings on level terrain (below) -> phenotypic plasticity
- Stripes of *Salsola* & *Melobium* bush on slope 40 km west of Maltahöhe (right)

# What is plant self-organization?

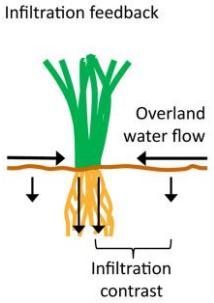
- Examples of fairy circles in Australia and *Acacia* stripes on a slope 10 km away from the circles
- Circles form in flat areas, where competition for water is equal over 360°

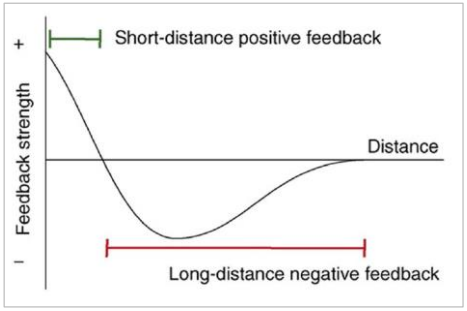




Consistent spacing of bare soil & plants results from homogeneous lack of water

# What is plant self-organization?




- 50 m between stripes are necessary to accumulate enough rain water to sustain a next stripe with trees

A self-enhancing positive feedback loop acts at small scales

- More water infiltration due to roots loosening the soil crusts
- Falling leaves and branches block water
- Shade facilitates germination and survival of new recruits

The building of barriers creates large-scale negative feedback = bare soil

# What is plant self-organization?

- Plants are actively redistributing scarce water and thereby modify the abiotic environment with barriers

**Plants act as “ecosystem engineers”**
and build dams just like the beaver

www.earth.com

VOLUME 93, NUMBER 9 PHYSICAL REVIEW LETTERS week ending 27 AUGUST 2004

**Ecosystem Engineers: From Pattern Formation to Habitat Creation**

E. Gilad,[1,2] J. von Hardenberg,[3] A. Provenzale,[3,4] M. Shachak,[5] and E. Meron[2,1]

# What is plant self-organization?

- Depending on prevalent soil type and plant architecture, three biomass-water feedbacks exist
- The “uptake-diffusion feedback” may dominate in Namib sands: large edge plants transpire and strongly draw water

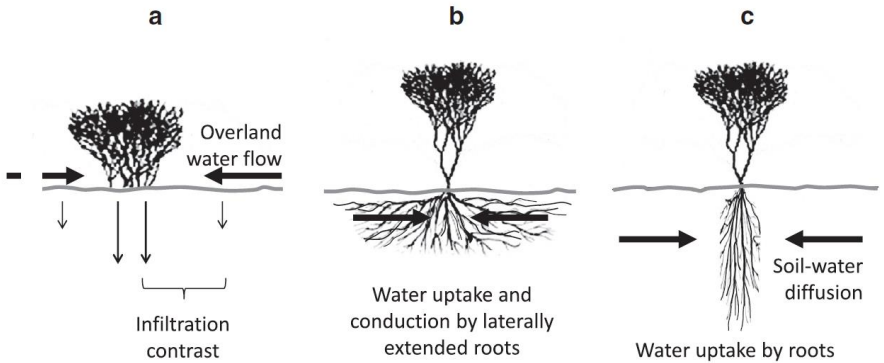
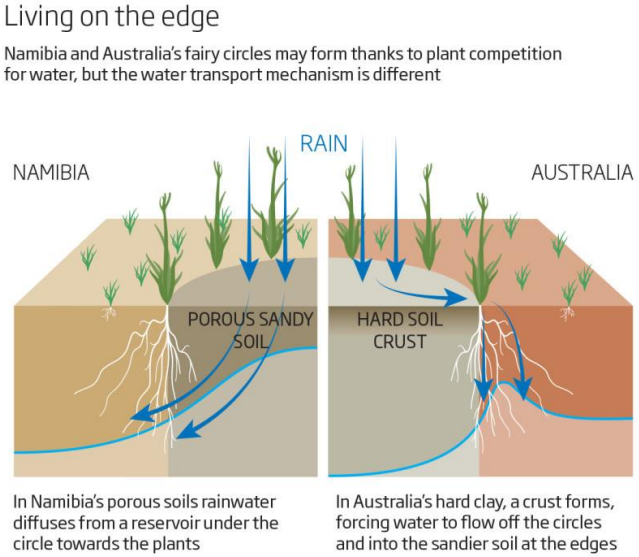



**Fig. 3.** Schematic illustrations of three modes of water transport capable of inducing pattern-forming feedbacks in water-limited vegetation: (a) overland water flow induced by an infiltration contrast (infiltration feedback), (b) water uptake and conduction by laterally extended root systems (root-augmentation feedback), (c) fast soil-water diffusion relative to biomass spread (soil-water diffusion feedback). From [12].

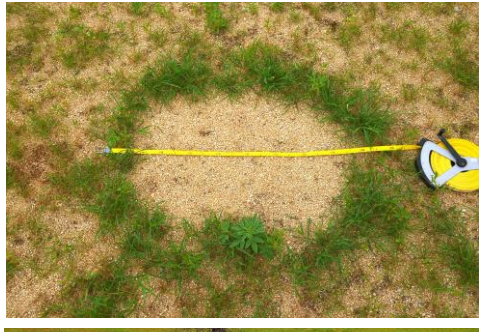
(Meron 2016)




(New Scientist 2016)

# What is plant self-organization?

- In Namibia, many plant species form circles or rings
- 3 days after rainfall, soil moisture within *Schmidtia* rings was 3.6% but outside 5.3% -> depletion of $H_2O$



After rainfall, annual *Schmidtia kalahariensis* + *Crotalaria podocarpa* form rings at Donkerhuk

*Stipagrostis* fairy circle near Nubib Mtn.

Annual forb *Limeum argute-carinatum* at NamibRand

# What is plant self-organization?

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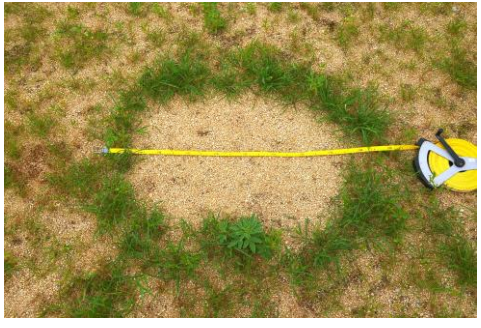


After rainfall, annual *Schmidtia kalahariensis* + *Crotalaria podocarpa* form rings at Donkerhuk

*Stipagrostis* fairy circle near Nubib Mtn.

- Grasses form rings and circles to maximise uptake of water from circle
- A circle has the smallest circumferene-to-area ratio
- For a given circle area, least plants have to share the water

# Many papers support plant self-organization, including several field studies

- van Rooyen MW et al. (2004) Mysterious circles in the Namib Desert: review of hypotheses on their origin. J. Arid Environ.
- Tlidi M et al. (2008) On vegetation clustering, localized bare soil spots and fairy circles. Lect. Not. Phys.
- Tschinkel WR (2012) The life cycle and life span of Namibian fairy circles. PLoS One
- Cramer MD & Barger NN (2013) Are Namibian 'fairy circles' the consequence of self-organizing spatial vegetation patterning? PLoS One
- Getzin S, Wiegand K, Wiegand T, Yizhaq H, von Hardenberg J & Meron E (2015) Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia. Ecography
- Getzin S, Wiegand K, Wiegand T, Yizhaq H, von Hardenberg J & Meron E (2015) Clarifying misunderstandings regarding vegetation self-organization and spatial patterns of fairy circles in Namibia: a response to recent termite hypotheses. Ecol. Entomol.
- Zelnik YR, Meron E & Bel G (2015) Gradual regime shifts in fairy circles. PNAS
- Tschinkel WR (2015) Experiments testing the causes of Namibian fairy circles. PLoS ONE
- Getzin S et al. (2016) Discovery of fairy circles in Australia supports self-organization theory. PNAS
- Ravi S, Wang L, Kaseke KF, Buynevich IV & Marais E (2017) Ecohydrological interactions within "fairy circles" in the Namib Desert: revisiting the selforganization hypothesis. J. Geophys. Res. Biogeosci.
- Cramer MD, Barger NN & Tschinkel WR (2017) Edaphic properties enable facilitative and competitive interactions resulting in fairy circle formation. Ecography
- Getzin S et al. (2021) Bridging ecology and physics: Australian fairy circles regenerate following model assumptions on ecohydrological feedbacks. Journal of Ecology

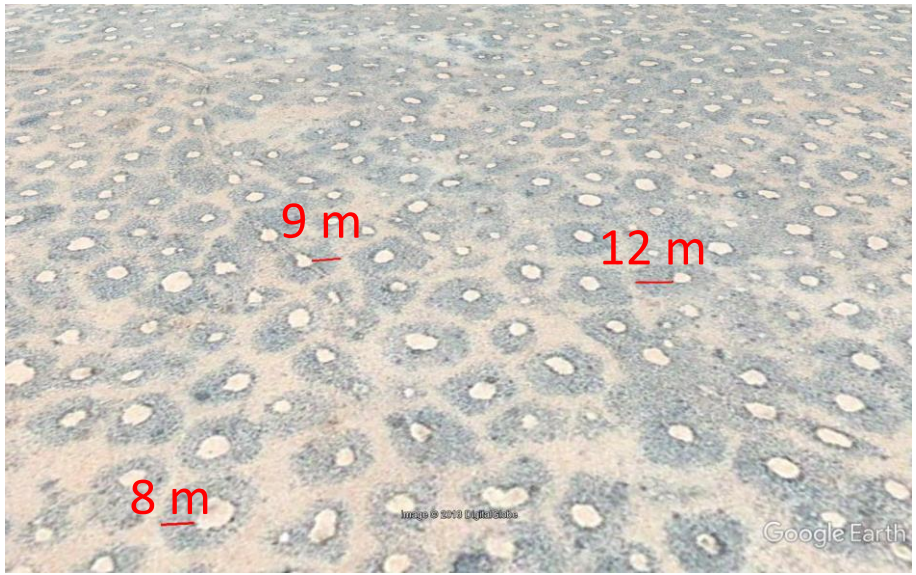
# Field studies strongly support plant self-organization – FCs are hydrologically connected

- "Water- and $^{15}N$-pulse experiments showed that edaphic resources were highly mobile, moving up to 7.5 m over a period of 1–3 weeks" (Cramer et al. 2017)

**Edaphic properties enable facilitative and competitive interactions resulting in fairy circle formation**

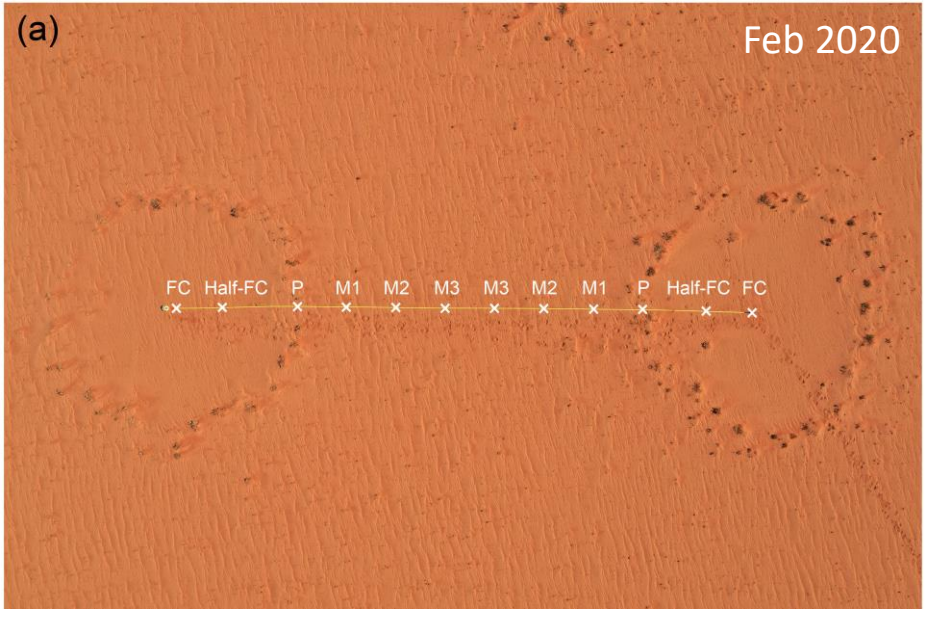
Michael D. Cramer, Nichole N. Barger and Walter R. Tschinkel

Halos show FC benefit to grasses for many meters



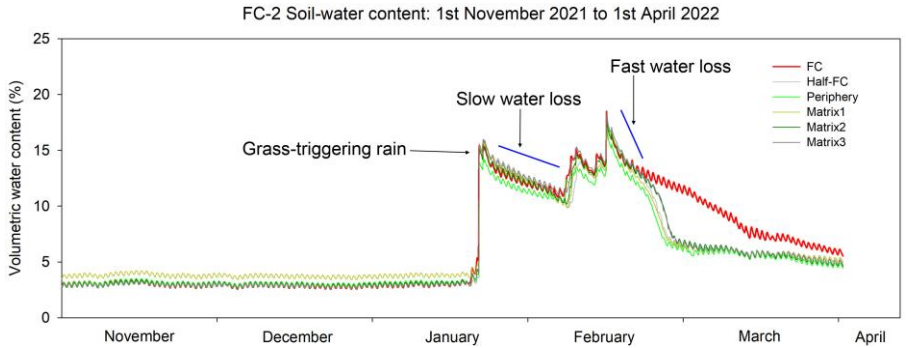
# Continuous soil-moisture measurements 2020-2022


- In 2020, we benefitted from a drought period, enabling us to see how the new grasses in 2021 and 2022 modified the soil water
- What will happen to the soil water at 20 cm depth, once all grasses are out, transpire, and draw water by diffusion?

# Continuous soil-moisture measurements 2020-2022 - NamibRand

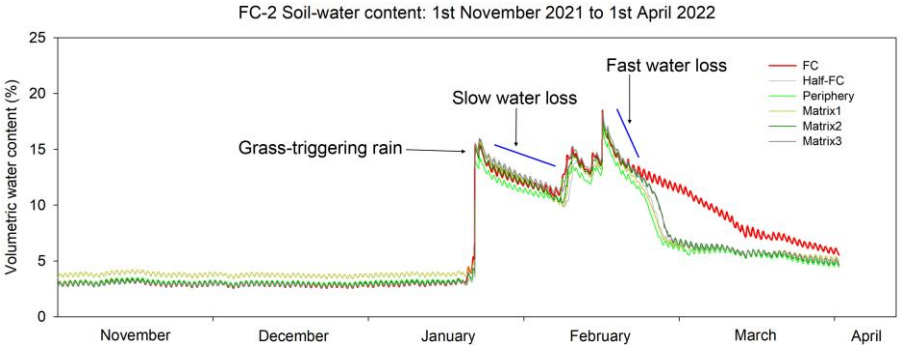
- Without dense grasses, the water loss within 1 week is the same in FC and matrix (-1.4%,-1.3%)




| | | | Mean SWC (%) | | Change in SWC (%) | |
|---|---|---|---|---|---|---|
| | | Vegetation status | Fairy circle | Matrix | Fairy circle | Matrix |
| End of dry season | (01/11/21) | No grasses in FC & matrix | 2.7 | 2.7 | | |
| 1 week after 1st rainfall | (28/01/22) | No grasses in FC & matrix | 12.5 | 12.5 | 9.8 | 9.8 |
| 2 weeks after 1st rainfall | (04/02/22) | **No** grasses in FC, thin matrix grasses | 11.1 | 11.3 | -1.4 | -1.3 |
| | | | | | | |
| | | | | | | |

# Continuous soil-moisture measurements 2020-2022 - NamibRand

- Without dense grasses, the water loss within 1 week is the same in FC and matrix (-1.4%,-1.3%)
- With dense matrix grasses, the water loss from the FC is **suddenly 2.7 times higher** in 1 week
- Since no grasses exist/transpire water in the FC, only the matrix grasses can have drawn that FC water via diffusion

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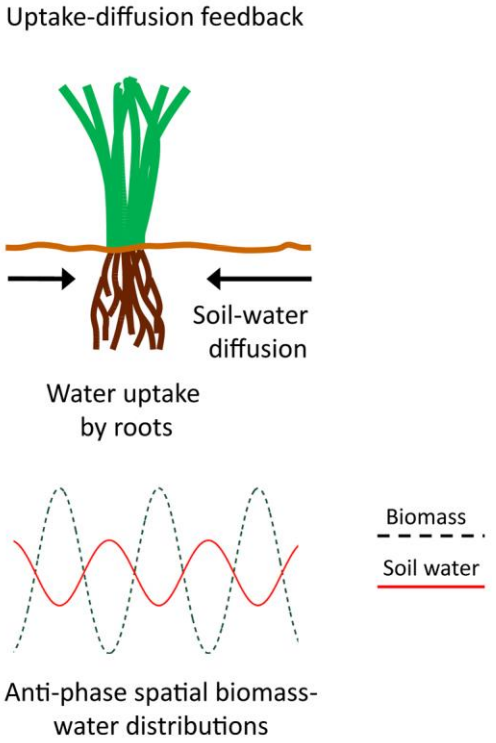
| 1 week after 2nd rainfall | (21/02/22) | **No** grasses in FC, **dense** matrix grasses | 12.8 | 12.7 | 1.6 | 1.4 |
| 2 weeks after 2nd rainfall | (28/02/22) | **No** grasses in FC, **dense** matrix grasses | 8.9 | 6.7 | **-3.8** | **-6** |

# Continuous soil-moisture measurements 2020-2022

- Absolute moisture values at 20 cm depth may be higher in the FC due to effects from higher moisture at soil depth > 30 cm
- But the large peripheral grasses and the matrix grasses induce critical loss of FC water and outcompete grasses within FCs
- Particularly the upper 10 cm of soil, where grasses germinate and establish, is crucial for plant survival or mortality



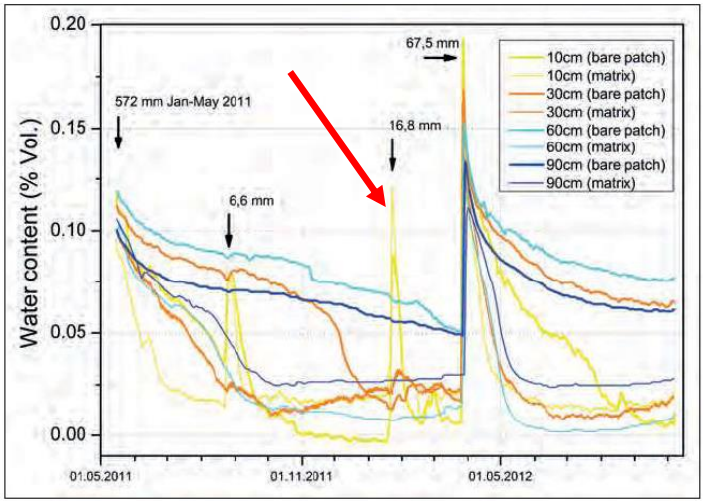
# Soil moisture at 10 cm depth is most important to grass establishment

- Young dying grasses invested biomass into roots, rather than shoots, as they suffered strongly from lack of water at 10 cm depth
- Empirical data show that critical water stress exists in the upper 10 cm

Outside 17.4 mm vs. inside 12.9 mm water at 10 cm

| 10 Feb 2008 (5 days after first good rains of the season (ca. 25mm) | | | | | | | |
|---|---|---|---|---|---|---|---|
| Depth[cm]\Position | Matrix | Per. Belt | Half radius | Center | Half radius | Per. Belt | Matrix |
| 10 cm | 8.9 | 8.5 | 5.2 | 7.7 | | | |
| 20 cm | 5.2 | 5.9 | 5.9 | 6.2 | | | |
| 30 cm | 3.4 | 4.9 | 5.5 | 6.8 | | | |
| 40 cm | 3.4 | 3.6 | 5.3 | 5.1 | | | |
| 50 cm | 4 | 4 | 5 | 6.8 | | | |
| 60 cm | 4.2 | 4.3 | 6.3 | 7.3 | | | |
| 70 cm | 4 | 4.1 | 6.2 | 7.6 | | | |
| 80 cm | 4.1 | 3.9 | 7.0 | 6.5 | | | |
| 90 cm | 4.5 | 4.3 | 7.1 | 7.4 | | | |
| 100 cm | 4.5 | 4.3 | 7.1 | 7.4 | | | |
| ∑$H_2O$[mm] in 0-100cm: | 48.4 | 49.9 | 59.65 | 68.95 | | | |

Juergens 2013

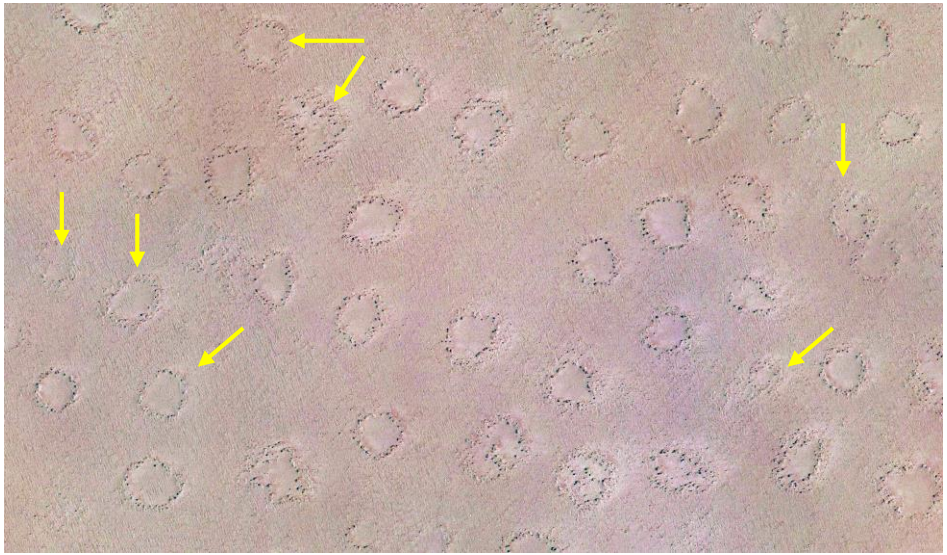



Gröngröft & Juergens 2022

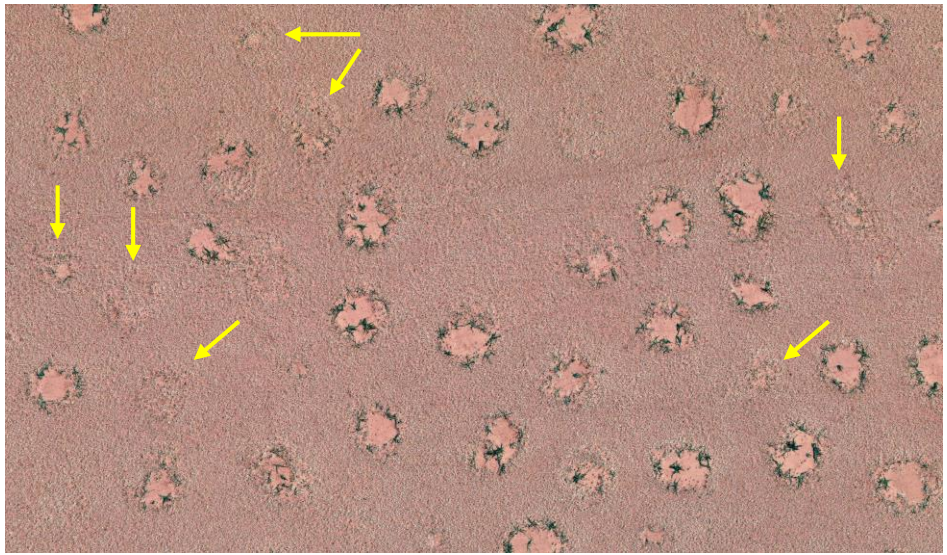
# Appearance and disappearance of fairy circles is driven by water availability

- We mapped three 25-ha plots at Jagkop, NamibRand with 732, 987, and 822 fairy circles
- FCs strongly closed (≥ 2/3 grass cover) or died (100% grass cover) in 2021 with abundant rainfall

15 February 2020

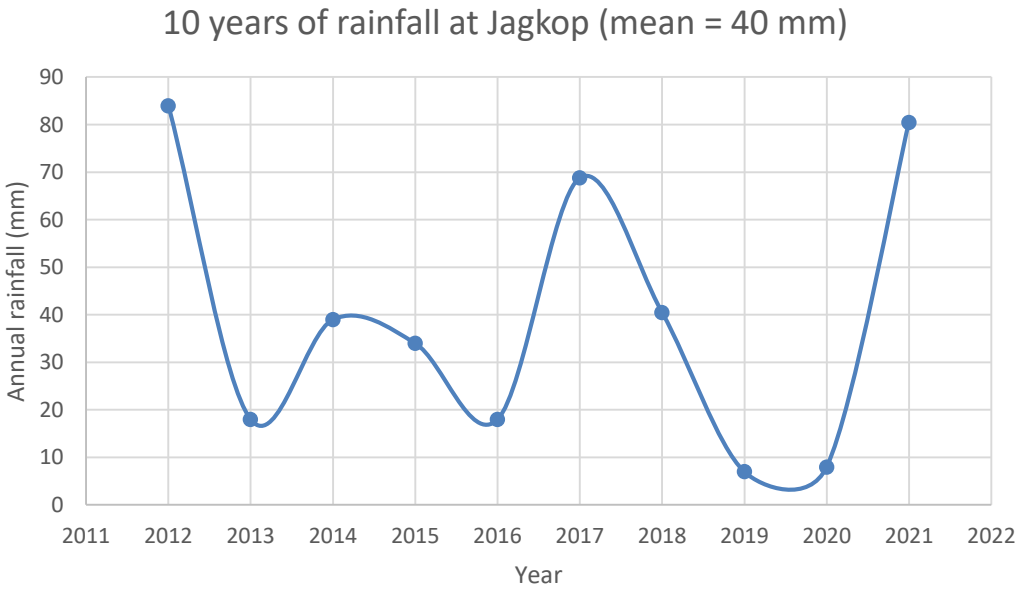


23 February 2021



# Appearance and disappearance of fairy circles is driven by water availability

- 58%, 44%, and 34% of FCs disappeared during good rainfall year 2021 (rain = 80.5 mm)
- Only 9, 0, and 6 new FCs formed in the three plots during that wet year
- **Biomass-water feedbacks are the main driver!**

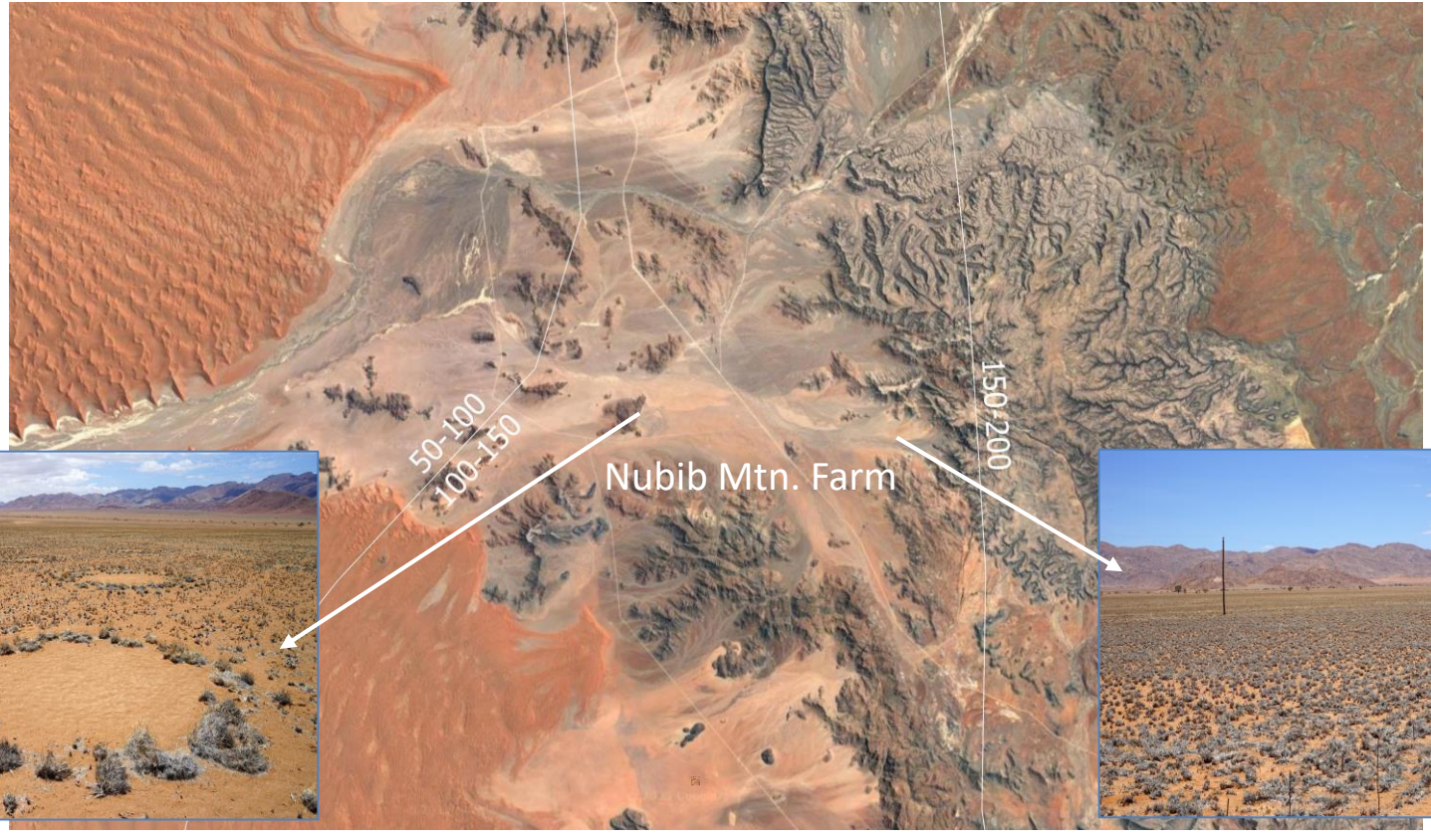



| Kategorie | Jag-1 | Jag-2 | Jag-3 |
|---|---|---|---|
| mature | 299 | 531 | 510 |
| closing | 336 | 392 | 252 |
| dead | 73 | 31 | 8 |
| new | 9 | 0 | 6 |
| reappearing | 15 | 33 | 46 |
| | | | |
| mature [%] | 42,232 | 55,660 | 66,234 |
| closing [%] | 47,458 | 41,090 | 32,727 |
| dead [%] | 10,311 | 3,249 | 1,039 |
| | | | |
| reappearing [%] | 2,119 | 3,459 | 5,974 |
| new [%] | 1,271 | 0,000 | 0,779 |
| Total_new [%] | 3,390 | 3,459 | 6,753 |

B.Sc. thesis, Sönke Holch 2021

# Only subtle degrees of water dependency can explain the vanishing of FCs at 150 mm MAP

- 10-12 mm rainfall is enough to cause a green grass layer...and the disappearance of FCs at 150 mm



# Concluding remarks & take home message

- Timing in fieldwork is critical -> grasses died quickly in fairy circles, before any termites arrived
- Need to study more the subtle degrees of water availability and how plants redistribute that scarce water via competition and self-organization
- Plants are “stupid” but the spatial pattern they develop to cope with water stress is “intelligent”
- At the end, fairy circles are merely an expression that there is not enough water along the Namib to sustain a continuous vegetation layer

# Thanks to NamScience!

## German Research Foundation
## &
## NCRST, NCAA, MEFT, Gobabeb, NamibRand, and many more

GEORG-AUGUST-UNIVERSITÄT GÖTTINGEN

NCRST

NCAA

REPUBLIC OF NAMIBIA
MINISTRY OF ENVIRONMENT, FORESTRY AND TOURISM

GOBABEB

NamibRand Nature Reserve

Funded by DFG Deutsche Forschungsgemeinschaft German Research Foundation