REPLY TO WALSH ET AL.:

Hexagonal patterns of Australian fairy circles develop without correlation to termitaria

Stephan Getzin[a,2], Hezi Yizhaq[b,c], Bronwyn Bell[d,1], Todd E. Erickson[e,f], Anthony C. Postle[g], Itzhak Katra[h], Omer Tzuk[i], Yuval R. Zelnik[b], Kerstin Wiegand[j], Thorsten Wiegand[a,k], and Ehud Meron[b,i]

Bare-soil gaps in arid grasslands often appear in conjunction with termites or ants (1, 2), but should this common correlation (3) automatically infer a causal relationship? To the unfamiliar, it may be difficult to realize that plant populations can organize themselves into geometric order so as to optimize their access to scarce soil water (4–6). Based on the preliminary data obtained by excavating two gaps from the fairy circle (FC) area near Newman, Walsh et al. (7) claim that subterranean termitaria are the sole cause of the Australian FCs (8). This claim is unjustified for several reasons.

Although erosion of pavement mounds may lead to local bare-soil gaps, the resulting large-scale pattern is heterogeneous. This pattern has been shown for *Drepanotermes* harvester termites in the study of Noble et al. (9). Similarly, our mapping of termite nests found aggregated and nonordered distributions at the gap edges that are fundamentally different from the extremely regular and homogeneous pattern of FCs (8). In figure 1B of ref. 7, Walsh et al. also show nonordered signs of termite activity elsewhere in Australia.

Erosion of pavement mounds typically occurs in a symmetrical pattern around the mound in the center of the small gap (compare figure 2A in ref. 9). However, when termite (and ant) mounds were present in the FC area near Newman, then they occurred primarily at the edges of the large gaps, indicating a general insect preference for these favorable microenvironments (8). Thus, mound erosion can hardly explain the circular shape, and especially not the fact that significantly higher clay contents were found in the gap center compared with the gap edges (8).

We verified in the field that mechanical crusts resulting from soil weathering were easily distinguishable from crusts potentially resulting from pavement mounds (8). Mechanical crusts are only a few millimeters to a few centimeters thick, and when they were removed, loose sand was found underneath them (Fig. 1 *A* and *B*).

Most importantly, Walsh et al. (7) have not examined our field areas L1 and L2 (8), where actively forming, irregularly shaped gaps can be witnessed. Especially in area L2, large gaps are developing on loose sand with relatively young, and hence very thin, crust layers. Unlike "very hard pavements, withstanding road grader blades" (7), these thin crusts can be removed easily by hand. Clearly, below-ground pavements may sometimes be covered by a shallow layer of loose soil (10) but should be detectable "within 5 cm of the surface" (7). We excavated the soil in the gap center and at the edge to a depth of circa 30 cm but did not find any signs of hard pavements (Fig. 1 *C* and *D*). The fact that plants could still partly survive on sand in these gaps, and that these FCs were forming in the absence of termitaria (Fig. 1 *E* and *F*), falsifies the claim that Australian fairy circles would be primarily caused by pavement termites.

Finally, localized termitaria explain neither the very large bare-soil areas adjacent to gaps (Fig. 1*G*) nor the co-occurrence of labyrinthine (Fig. 1*H*) and gap patterns in the same location (4, 8).

[a]Department of Ecological Modelling, Helmholtz Centre for Environmental Research–UFZ, 04318 Leipzig, Germany; [b]Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boker Campus, Beer Sheva 84990, Israel; [c]The Dead Sea and Arava Science Center, Tamar Regional Council, Israel; [d]Environmental Management, Rio Tinto, Perth, 6850 WA, Australia; [e]School of Plant Biology, The University of Western Australia, Crawley, 6009 WA, Australia; [f]Kings Park and Botanic Garden, Botanic Gardens & Parks Authority, Kings Park, 6005 WA, Australia; [g]Private address, Cairns, 4870 QLD, Australia; [h]Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel; [i]Physics Department, Ben-Gurion University of the Negev, Beer Sheva 84105, Israel; [j]Department of Ecosystem Modelling, University of Goettingen, 37077 Goettingen, Germany; and [k]German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, 04103 Leipzig, Germany

Author contributions: S.G., H.Y., and B.B. designed research; S.G., H.Y., and T.E.E. performed research; H.Y., O.T., Y.R.Z., and E.M. contributed new reagents/analytic tools; S.G., H.Y., A.C.P., I.K., K.W., T.W., and E.M. analyzed data; and S.G., H.Y., T.E.E., A.C.P., I.K., and E.M. wrote the paper.

The authors declare no conflict of interest.

[1]Present address: Private address, Cloisters Square, 6850 WA, Australia.

[2]To whom correspondence should be addressed. Email: stephan.getzin@ufz.de.

www.pnas.org/cgi/doi/10.1073/pnas.1611877113

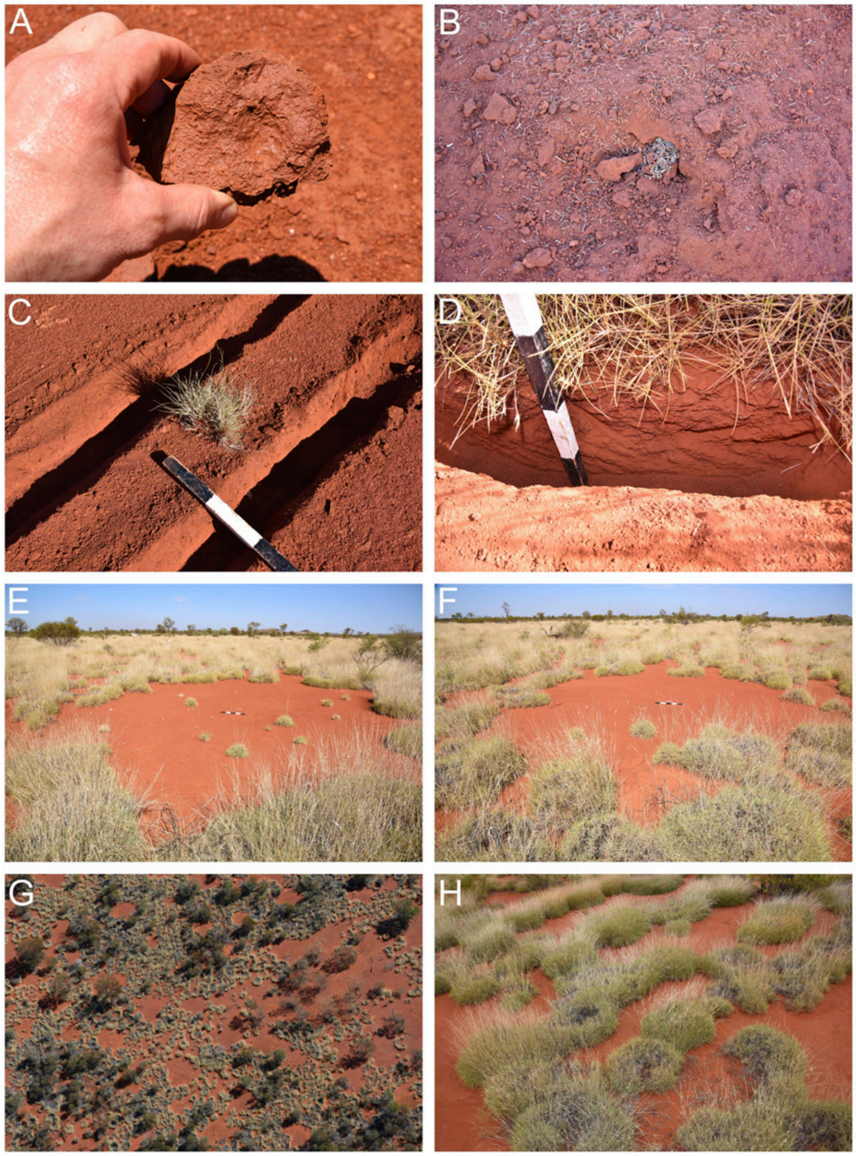

Fig. 1. Soil crusts resulting from mechanical weathering are only up to a few centimeters thick (*A*), whereas hard pavement crusts with termite galleries underneath reach deep into the ground (*B*). Also, the elemental composition differs between these crusts as our analysis with the electron microscope has shown (8). (*C* and *D*) In the fieldwork area L2, the excavation of the soil around several plants did not reveal any termite galleries or underground termitaria (ghosts) to a depth of circa 30 cm. Mechanical crusts there were still relatively young and thin, and individual plant survival was not yet fully inhibited. (*E* and *F*) These actively forming large gaps (Ø 6.0 m, 5.2 m) have no sign of above- or below-ground pavements and are not yet completely circular; thus, water can largely escape into the matrix. However, with increasing time after a fire and mechanical crust building, it is assumed that the individual grass clumps form a circle, because a circle has the smallest circumference-to-area ratio. This geometric structure optimizes their exclusive per-capita use of access run-off water from the gap center. *F* reproduced from ref. 8. (Scale bar, 0.5 m.) (*G* and *H*) Large bare-soil areas adjacent to round gaps have the same plant-inhibiting mechanical crusts. (*G*) They cannot be explained by localized termitaria, but by infiltration contrasts resulting from mechanical weathering. (*H*) Also, only the population-level response of the spinifex plants to water stress adequately explains the labyrinthine or striped patterns that coexist with gaps in the same areas.

1 Crist TO, Wiens JA (1996) The distribution of ant colonies in a semiarid landscape: Implications for community and ecosystem processes. *Oikos* 76:301–311.

2 Getzin S, et al. (2015) Adopting a spatially explicit perspective to study the mysterious fairy circles of Namibia. *Ecography* 38(1):1–11.

3 Tschinkel WR (2015) Experiments testing the causes of Namibian fairy circles. *PLoS One* 10(10):e0140099.

4 Deblauwe V, Couteron P, Lejeune O, Bogaert J, Barbier N (2011) Environmental modulation of self-organized periodic vegetation patterns in Sudan. *Ecography* 34(6):990–1001.

5 Getzin S, et al. (2015) Clarifying misunderstandings regarding vegetation self-organization and spatial patterns of fairy circles in Namibia: A response to recent termite hypotheses. *Ecol Entomol* 40(6):669–675.

6 Meron E (2015) *Nonlinear Physics of Ecosystems* (CRC, Boca Raton, FL).

7 Walsh FJ, Sparrow AD, Kendrick P, Schofield J (2016) Fairy circles or ghosts of termitaria? Pavement termites as alternative causes of circular patterns in vegetation of desert Australia. *Proc Natl Acad Sci USA* 113:E5365–E5367.

8 Getzin S, et al. (2016) Discovery of fairy circles in Australia supports self-organization theory. *Proc Natl Acad Sci USA* 113(13):3551–3556.

9 Noble J, Diggle P, Whitford W (1989) The spatial distributions of termite pavements and hummock feeding sites in a semi-arid woodland in eastern Australia. *Acta Oecol-Oec Gen* 10(4):355–376.

10 Abensperg-Traun M, Perry DH (1998) Distribution and characteristics of mound-building termites (Isoptera) in Western Australia. *J R Soc West Aust* 81(4):191–200.