Strong interaction between plants induces circular barren patches: fairy circles

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Vast landscapes extending from southern Angola, Namibia, and South Africa exhibit localised barren patches of vegetation called fairy circles. They consist of isolated or randomly distributed circular areas devoid of any vegetation. They are surrounded by fringes of tall grasses and are embedded in a sparse grassland on sandy soils. When the aridity increases, the size of the fairy circles increases and can reach diameters up to 10m. Although several hypotheses have been proposed, the origin of this phenomenon remains unsolved. We show that a simple non-local model of plant ecology based on realistic assumptions provides a quantitative explanation of this phenomenon. Fairy circles result from strong interaction between interfaces connecting two uniform covers: the uniform grassland and the bare states, and their stabilisation is attributed to the Lorentzian-like non-local coupling that models the competition between plants. The cause of their formation in thus rather inherent to the vegetation dynamics. Our analysis explain how a circular shape and fringes are formed, and how the aridity level influences the size of the fairy circles. In agreement with field observation, these theoretical findings, provide a link between a strong non-local interaction of plants and the formation of stable fairy circles. Finally, we show that the proposed mechanism is model-independent: indeed, it also applies to the reaction-diffusion type of model that emphasises the influence of water transport on the vegetation dynamics.

When ecosystems are subject to limited resources such as water and nutrients, they adopt a periodic [1]-[5] or aperiodic [6]-[8] distribution of densely vegetated and bare soil areas. In order to fight against drought, every plant struggles to spread its roots so that they outgrow the size of the aerial structure by an order of magnitude, for greater water uptake. However, this adaptation increases plant-to-plant competition between neighbouring plants, and at plant communities level, via non-local interaction, favours the self-organisation phenomenon [1]. Other modelling approaches that underline either the role of water transport by below ground and above ground run-off [4], or the role of constructive influence of the environment randomness [9] have been proposed to explain the formation of vegetation patterns. A well-documented example of non-uniform spatial distribution of biomass is localised barren patches of vegetation often called fairy circles (FCs), but their origin is still a subject of debate. These circles can be either isolated, or randomly distributed in space. They are embedded in a sparse grassland as shown in Fig. 1. The term "grass" refers to any grass or herbaceous species. This phenomenon is visible from either aerial and satellite photographs or on ground level in vast territories in southern Angola, Namibia, and South Africa [10, 11]. In these arid territories, the annual rainfall ranges between 50 and 100 mm. The size of barren patches increases from South to North where the climate [12] becomes more and more arid. Their average diameter ranges from 2 m to 10 m [13]. Several hypothesis attributing the formation of FCs to factors external to the vegetation have been suggested [11]-[19]. All these external factors can not explain the orgin of the circular shape of FCs [13, 20]. Recently, a detailed description of fairy circle structures, of their life span and range of variation in multiple habitats has been provided [21]. How Mathematical modelling of the vegetation growth constitutes an important tool toward the understanding of arid ecosystems. To explain the origin of this ecological phenomenon, we take a strictly homogeneous (flat) territory and isotropic environmental conditions. This corresponds to a reasonable approximation for a large territory compared to typical sizes of FCs and for a small territory compared to the geographical scale. We use the generic interaction-redistribution model [1]. When the
water resources are scarce, in order to survive plants increase the size of their roots structure. The size of the roots in dryland can reach ten times the size of the aerial structure (see Fig. 7 of Ref. [10]). In this arid climatic condition, plants should then compete for the extraction of water.

The purpose of this Letter is to report on the occurrence of stable FCs with an intrinsic dynamical nature. The size of the FC is determined by the strong non-local competitive interaction between plants mediated by a Lorentzian type of kernel function, and under bistability between spatially homogeneous covers of arid ecosystems. The size of the FCs is thus determined rather by the system’s dynamical parameters and not by external factors and/or boundary conditions. In agreement with field observations, we show that the diameter of a FC increases with the aridity parameter, and that each isolated FC exhibits a fringe with high biomass density. In order to show that our mechanism is model-independent, we incorporate the Lorentzian-like non-local coupling in the reaction-diffusion type of model that includes water transport [4], and we also show that this model supports stable FCs. Finally, we show that when FCs diameter exceeds a given maximum size, i.e., maximum aridity, they present a deformation of their circular shape. However, when the aridity is lower than a given threshold, fairy circles shrink and disappear. The spatial distribution of all plants is described by the vegetation density \( b = b(x, t) \) at time \( t \) and at the point \( x = (x, y) \). It is defined as the plant biomass per unit area. We consider a single dominant species forming a plant community that occupies a flat territory [1, 22]. The growth and death processes are modelled by the following logistic equation governing the time-space evolution of the biomass [23]

\[
\partial_t b = b [1 - b] M_f - \mu b M_c + \nabla^2 b. \tag{1}
\]

The first term expresses the rate at which the biomass density increases and saturates. This is the biomass gain that corresponds to the natural production of plants via seed production, dissemination, germination and development of shoots into new mature plants. The second term models the biomass losses which describes death or destruction by grazing, fire, termites, or herbivores. The parameter \( \mu \) measures the resources scarcity, i.e., the aridity parameter. The Laplacian \( \nabla^2 b \) expresses the vegetation spatial propagation through seed dispersion, production and germination, which we assume to be a simple random walk or brownian motion. When the water becomes scarce, plants adapt their roots systems to fight against water scarcity. They strive to maintain their water uptake by increasing the length of their roots. They thus compete with other plants on long distance \( L_c \).

This is a negative feedback that tends to reduce the biomass density modelled by the function \( M_c \). In contrast with previous mathematical models of plant ecology, we incorporate a strong non-local interaction by using a Lorentzian-like kernel. The term ”strong” refers to the class of spatial kernel functions that decreases slower for large distance \( r' \) than the exponential distribution [26]. The major ingredient that needs to be incorporated in Eq. (1) is the competition by a Lorentzian-like kernel \( M_c \). This function reads

\[
M_c = \exp \left[ \frac{\xi_c}{N_c} \int \frac{b(r + r', t)}{1 + (r'^2/L_c^2)} \, dr' \right], \tag{2}
\]

where \( N_c \) is the normalisation coefficient. The facilitative interaction between plants is modelled by the function \( M_f \) which expresses the positive feedback which favours the vegetation development. We focus on the limit where the length of the facilitation is negligible \( L_f \approx 0 \). Then the mean field function \( M_f \approx \exp(\xi_f b) \). The parameters \( \xi_c \) and \( \xi_f \) model the interaction strength associated with the competitive and facilitative. In the absence of non-local interaction (\( \xi_c, f = 0 \)), Eq. (1) becomes the F-KPP equation, that is a paradigm in the study of front propagation [27, 28]. Note that, at the F-KPP equation level
there is no bistability between stable spatially uniform states. When non-local interaction is included, however, it is possible to find two coexisting spatially uniform stable states: the bare solution corresponding to a territory totally devoid of vegetation \( b_0 = 0 \); and a uniformly vegetated state \( b_s > 0 \). This phenomenon has been studied in Refs.\[23, 25\] as well as a pattern forming instability.

Considering a regime far from any pattern forming instability, we focus on the parameters where the bistability between the bare and the uniformly vegetated states takes place. To generate FCs, we need to connect these two homogeneous states. This connection is referred to as front. Depending on the choice of the non-local coupling function, front interaction between vegetated and bare states can be either strong or weak \[26\]. All ecol 1 models used a weak non-local coupling such as a Gaussian or an exponential function \[1, 4, 8\], which decay asymptotically faster than the Lorentzian distribution.

When considering a weak front interaction, domains of bare state embedded in the uniformly vegetated state are unstable: they either shrink or broaden. This type of non-local coupling involves short range interaction which is always attractive. However, when considering a strong non-local coupling mediated by a Lorentzian type of function, this leads to the stabilisation of FCs. Contrary to weak nonlocal coupling, strong competitive interaction induces long-range interaction that can be either repulsive or attractive. This allows for a confinement of the barren state domain inside a uniformly vegetated state. There is then a balance between strong competitive interaction and the tendency of grass to populate the barren zone. Indeed, numerical simulations of Eq. \( (1) \) with periodic boundary conditions allow us to obtain stable FCs as shown in Figures 2b and 2c. Photos and areal views of the pro-Namibia fairy circles are shown in Figures 2a, 2b. These long-lived permanent circular structures neither shrink in spite of available free space, nor grow in spite of adverse conditions. In agreement with long-term observations, Van Rooyen et al. \[13\] show that several marked fairy circles are stable more than 20 years later. In order to show that bistability together with strong non-local coupling is responsible for the stabilisation of fairy circles, we use the reaction-diffusion model [see Eqs. \( (1) \) in Ref \[4\]], replacing the non-local coupling \( g(r+r', t) \) by a Lorentzian like function. This model emphasizes the role of water transport by below ground and/or above ground run-off. The results of numerical simulations of this model are illustrated in Figs. 2e and 2f. These results show that the formation of stable FCs are model-independent. Equation \( (1) \) can help to understand the behaviour of FCs, not only the stationary regime, where fronts interaction leads to the uniformly curved circular shape, but also the way that an initial perturbation evolves toward a circular shape. Suppose we start with non-uniformly curved bare state, numerical simulation of Eq. \( (1) \) shows that, in the course of time, the space-time dynamics leads to the formation of uniformly curved circular domain (see Fig. 3). The circular shape results from fronts interaction mediated by Lorentzian-like non-local coupling. The cross section along the \( x \) direction shows occurrence of fringes characterised by larger biomass density. These fringes appear clearly on the natural FCs shown in Figures 2a, 2b. They possess a stable plateau (see the cross section along the \( x \) direction Fig. 3) and the minimum biomass density is zero, corresponding to the bare state.

As the aridity parameter \( \mu \) increases, the environment becomes more and more arid and the size of FCs broadens as illustrated in Fig. 4. Stable FCs occur in the range of \( \mu_{min} < \mu < \mu_{max} \). This explains why the FCs’ average diameter increases with the aridity. Indeed field measurements indicate that the FCs’ average diameter varies in the range of 2 m-10 m from the South to the North where the aridity increases \[13\]. This provides a ratio between the maximum and minimum average diameter equal to 5. The estimation by numerical simulations of the diameter shows that this ratio is of the order of 4 (see Fig. 4). Note, however, that the results obtained in this Letter are different from those generated in the pattern forming regime \[25\]. Indeed, in this regime, the size of spots does not vary with the aridity and spots do not exhibit a plateau. Therefore, the spots obtained in the pattern forming instability are not sufficient to explain the fairy circles. For \( \mu > \mu_{max} \), FCs become unstable, and lose their circular shape through a curvature instability. The diameter of FCs grows, and on a long-term evolution they exhibit a radial deformation. However, when \( \mu < \mu_{min} \), the diameter of FCs decreases, so that FCs shrink and disappear through a transition toward the uniformly vegetated state.

Two ecological models are used to understand the for-
systems with strong non-local coupling such as metama-
cussed. Our theoretical mechanism is applicable to other
modelling. Quantitative interpretation of observations
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geneous covered states. Second, the strong competitive
should operate in the bistability region between homo-
bilisation to two main ingredients. First, the ecosystem
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formation of fairy circles. We attribute their stabilisation to two main ingredients. First, the ecosystem
should operate in the bistability region between homogeneous covered states. Second, the strong competitive
interaction between plants should be incorporated in the
modelling. Quantitative interpretation of observations
and of the predictions provided by the theory are discussed. Our theoretical mechanism is applicable to other
systems with strong non-local coupling such as metamaterials, and populations dynamics [29].

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[1] Lefever R., Lejeune O., On the origin of tiger bush, Bulletin of Mathematical biology, 59, 263-294 (1997).
[2] Kluasmeier C.A., Regular and irregular patterns in semi-arid vegetation, Science 284, 1826-1828 (1999).
[3] von Hardenberg J., Meron E., Shachak M., and Zarmi Y., Diversity of Vegetation Patterns and Desertification, Physical Review Letters, 87, 198101-198105 (2001).
[4] Gilad E., von Hardenberg J., Provenzale A., Shachak M., Meron E., Ecosystem engineers: from pattern formation to habitat creation, Physical Review Letters, 93, 098105-098108 (2004).
[5] Sherratt J. A., An analysis of vegetation stripe formation in semi-arid landscapes. J. Math. Biol. 51, 183-197 (2005).
[6] Lejeune O., Tlidi M., Couteron P., Localized vegetation patches: A self-organized response to resource scarcity, Physical Review E, 66, 010901-010904 (2002).
[7] Rietkerk M., Dekker S.C., de Ruiter P.C., van de Koppel J., Self-organized patchiness and catastrophic shift in ecosystems, Science, 305, 1926-1929 (2004).
[8] Meron E., Yizhaq H., Gilad E., Localized structures in dryland vegetation: forms and functions, Chaos, 17, 037109 (9 pages) (2007).
[9] Ridifi L., D’Odorici P., and Laio F., Noise induced phenomena in the environmental sciences (Cambridge University Press, 2011).
[10] Albrecht C., Joubert J.J., De Rycke P.H., Origin of the enigmatic, circular barren patches (‘Fairy rings’) of the pro-Namib, South African Journal of Science, 97, 23-27 (2001).
[11] Becker T., Getzin S., The fairy circles of Kaokoland (North-West Namibia), Origin, distribution, and characteristics. Basic and Applied Ecology, 1, 149159 (2000).
[12] The term climate contains the statistics in a given region over long periods of temperature, humidity, precipitation, and other meteorological elemental measurements.
[13] van Rooyen M.W., Theron G.K., van Royen N., Jankowitz W.J., Matthews W.S., Mysterious circles in the Namib Desert: review of hypothesis on their origin, Journal of Arid Environments, 57, 467-485 (2004).
[14] Tschinkel W. R., The Foraging Tunnel System of the Namibian Desert Termite, Baucalitermes hainesi, Journal of Insect Science 10, 1-17 (2010).
[15] Picker M.D, Ross-Gillespie V., Vlieghe K., Moll E., Ants and enigmatic Namibian fairy circles–cause and effect, Ecological Entomology, 37, 33-42 (2012).
[16] Fraley L., Response of shortgrass plains vegetation to gamma radiation. III. Nine years of chronic irradiation. Environmental and Experimental Botany, 27, 193-201 (1987).
[17] Jankowits W.J., Van Rooyen M.W., Shaw D., Kaumba J.S., N. van Rooyen, South African Journal of Botany, 74, 332-334 (2008).
[18] Naude Y., van Rooyen M.W., Rohwer E.R., Evidence for geochemical origin of the mysterious circles in the Pro-Namib desert. J. Arid Environ. 75, 446456 (2011).
[19] Norbert Juergens, The Biological Underpinnings of Namib Desert Fairy Circles, Science 339, 1618-1621 (2013).
[20] Sabine Grube, The fairy circles of Kaokoland (Northwest Namibia) is the harvester termite Hodotermes mosaicus the prime causal factor in circle formation?, Basic and Applied Ecology, 3, 367370 (2002).
[21] Tschinkel W., The life cycle and life span of Namibian fairy circles, PLoS ONE 7(6), e38056 (2012).
[22] Greig-Smith P., Pattern in vegetation, The Journal of Ecology, 67, 755-779 (1979).
[23] Lefever R., Barbier N., Couteron P., Lejeune O., Deeply vegetation patterns: On crown/root allometry, criticality and desertification”, Journal of Theoretical Biology, 261, 194-209 (2009).
[24] Lefever R., Turner J. W., A quantitative theory of vegetation patterns based on plant structure and the non-local F-KPP equation, Comptes Rendus Mécanique, 340, 818-828 (2012).
[25] Dissipative Solitons: From Optics to Biology and Medicine, Lecture Notes in Physics, Vol. 751 edited by N. Akhmediev and A. Ankiewicz (Springer, Berlin, 2008), Chapter by Tlidi M., Lefever R., Vliminov A., pages 381-402.
[26] Escaff D., Non-local defect interaction in one-dimension: weak versus strong non-locality. Eur. Phys. J. D 62, 33-38 (2011).

[27] Fisher R.A, The use of multiple measurements in taxonomic problems, Ann. Eugenics 7, 335-369 (1937).

[28] Kolmogorov A., Petrovsky I., Piskunov N., Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique, Bull. Univ. Moscow Ser. Int. A 1, 1-25 (1937).

[29] Fernandez-Oto F., Clerc M.G., Escaff D., and Tlidi M., Strong Nonlocal Coupling Stabilizes Localized Structures: An Analysis Based on Front Dynamics, Phys. Rev. Lett., 110, 174101 (2013).