Модель самоорганизации растительного покрова в условиях дефицита ресурсов: сравнение наблюдаемых и модельных пространственных паттернов "ведьминых кругов"

Грабовский В.И., Грабарник П.Я.

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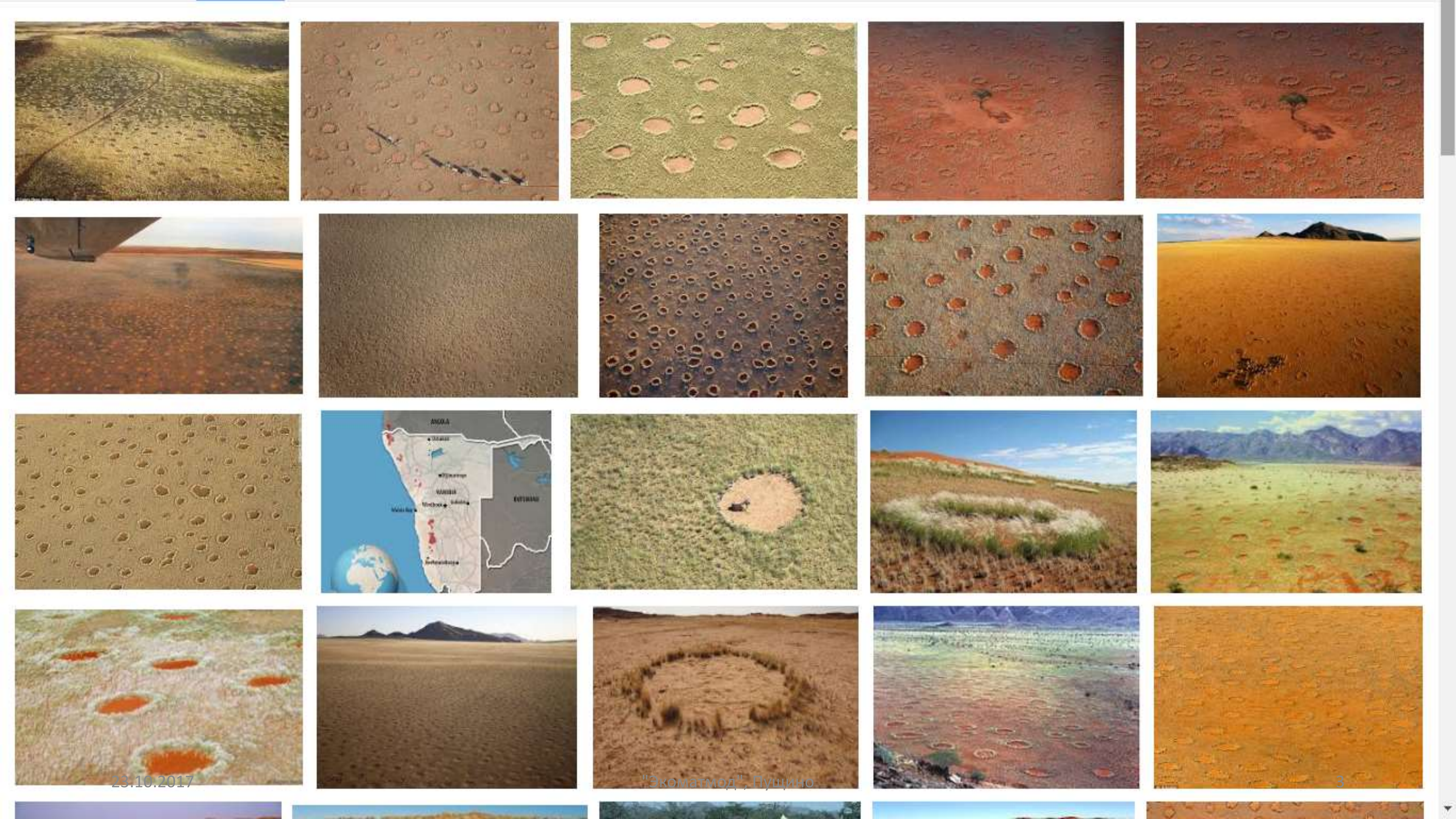

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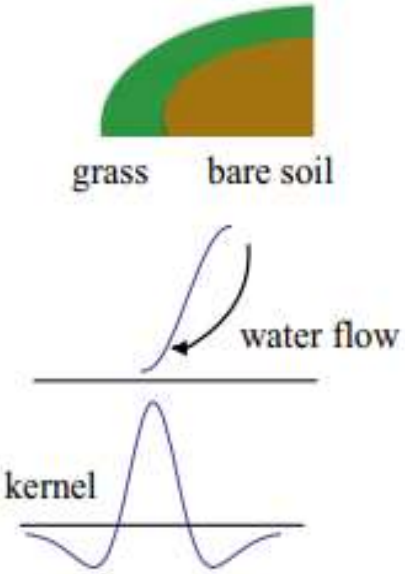
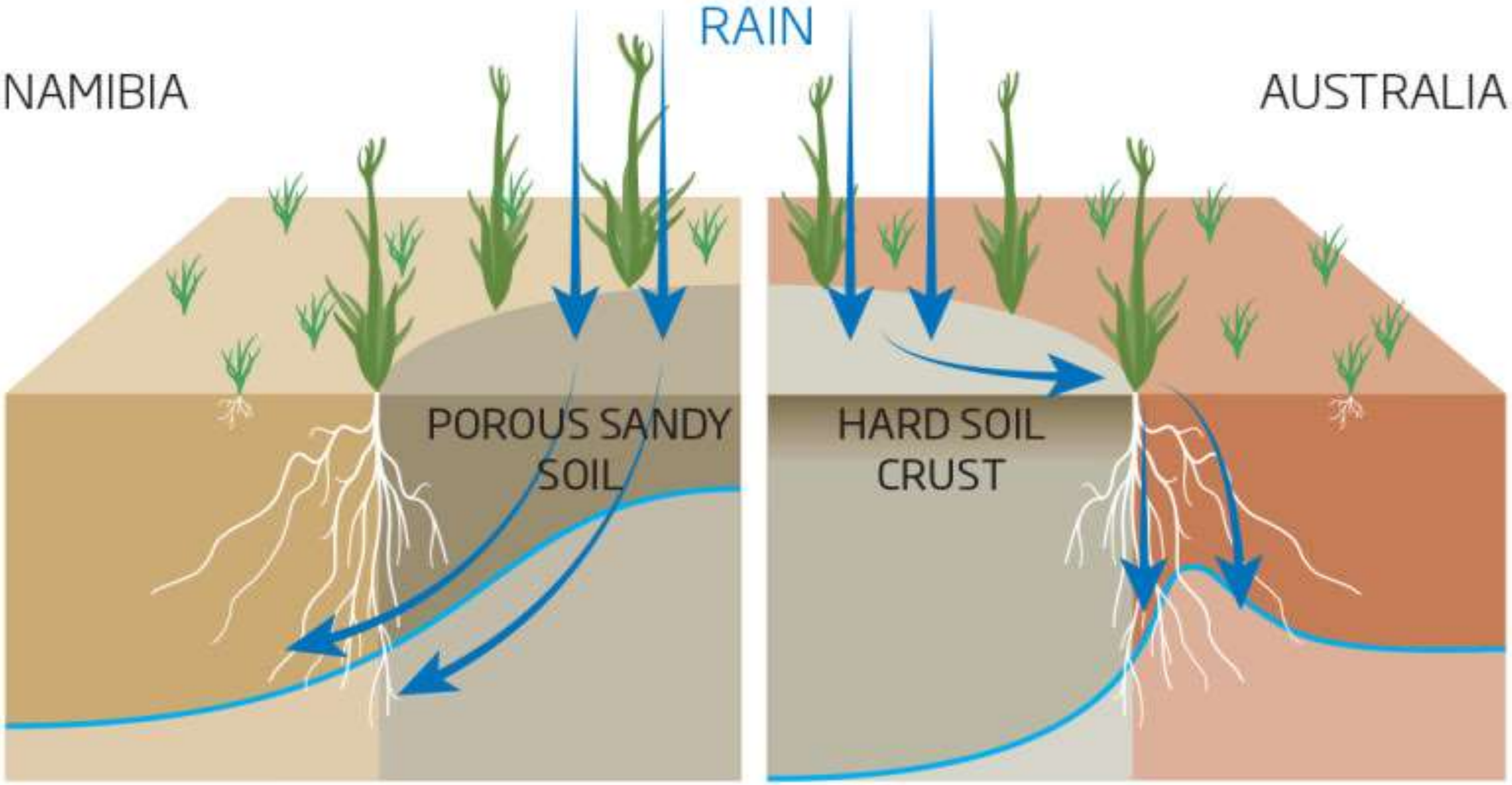
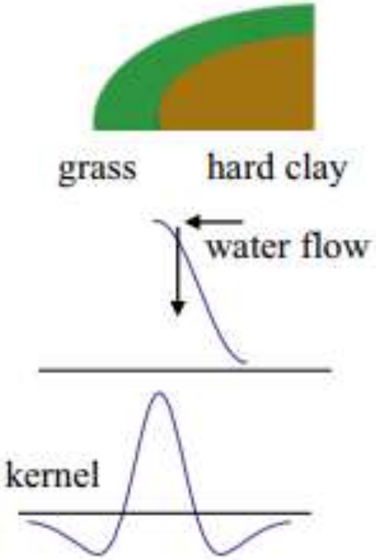
Living on the edge

Namibia and Australia's fairy circles may form thanks to plant competition for water, but the water transport mechanism is different





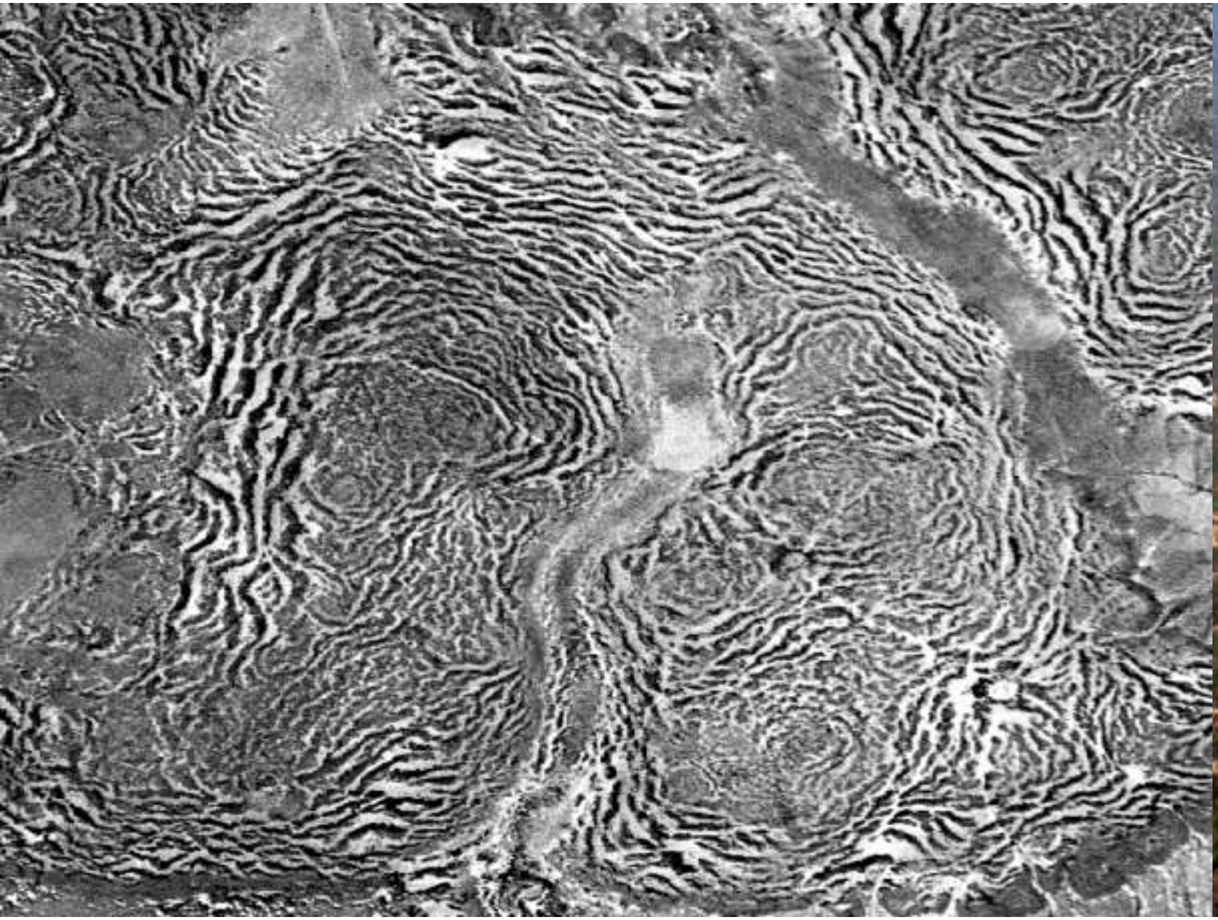


In Namibia's porous soils rainwater diffuses from a reservoir under the circle towards the plants

In Australia's hard clay, a crust forms, forcing water to flow off the circles and into the sandier soil at the edges

https://www.newscientist.com/article/2080615-mysterious-fairy-circles-now-discovered-in-australias-desert/

Варианты двухфазной мозаики: тигровый (слева) и дырчатый буш в Нигерии



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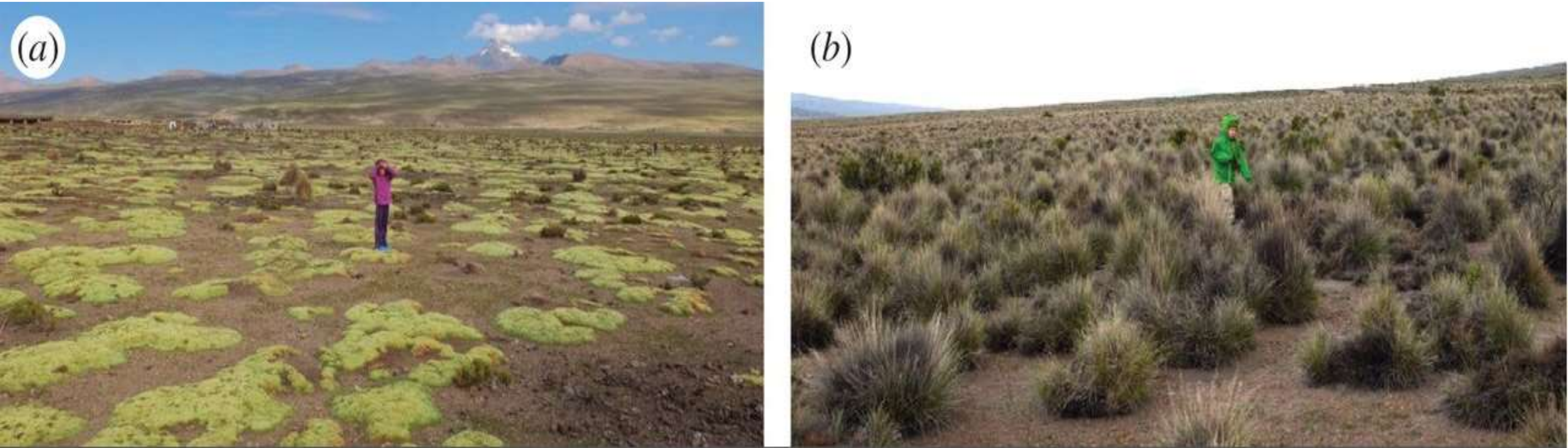
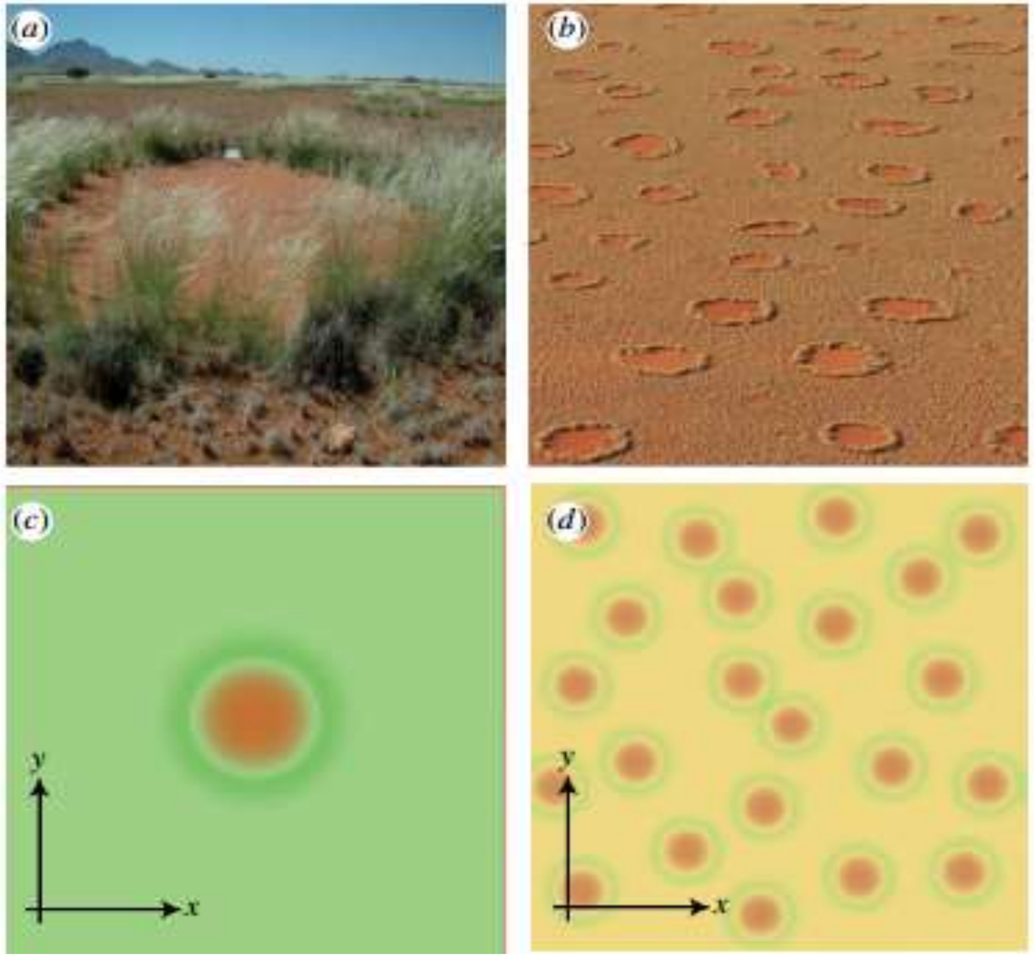
Варианты двухфазной мозаики растительного покрова в Саямском национальном парке (Боливия)



The two vegetation systems under study. Both display strong contrasts between bare ground and vegetation structures. (*a*) The cushion plant *Pycnophyllum tetrastichum*. (*b*) *Festuca orthophylla* also known as paja brava. Photos: F. Anthelme. (Online version in colour.)

Couteron P, Anthelme F, Clerc M, Escaff D, Fernandez-Oto C, Tlidi M. 2014 Plant clonal morphologies and spatial patterns as self-organized responses to resource-limited environments.Phil. Trans. R. Soc. A 372: 20140102. http://dx.doi.org/10.1098/rsta.2014.0102

Самоорганизация или насекомые?



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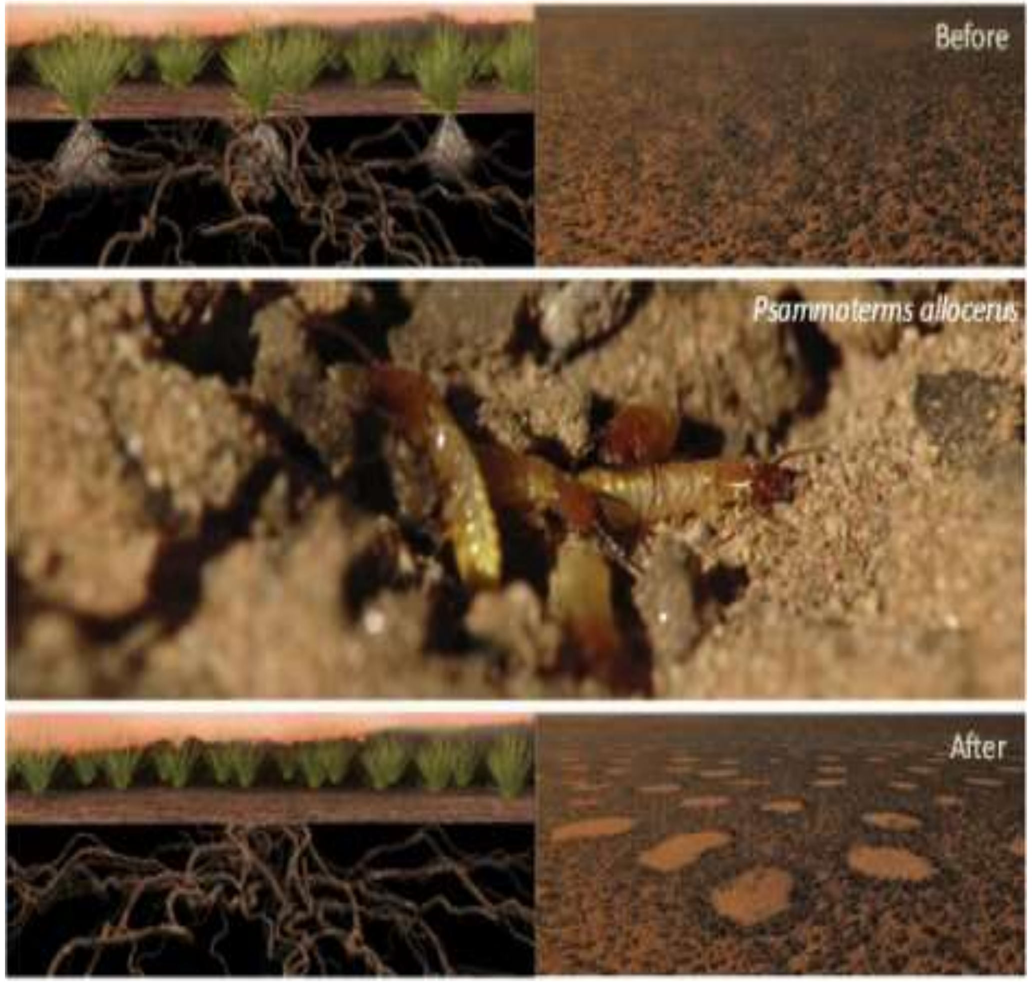

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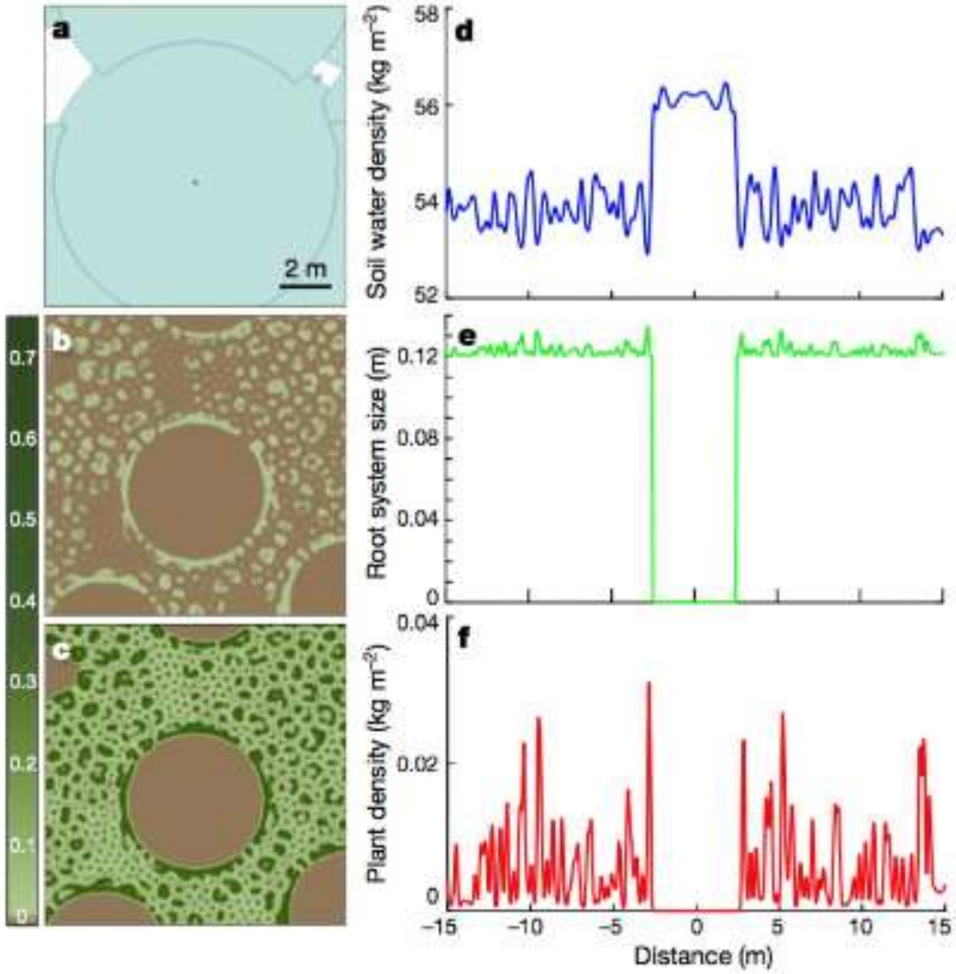

Figure 2 | Simulation of FC emergence from termite engineering and vegetation feedbacks. a, Termite nest (blue dot) with roughly circular foraging territory. **b, c,** Characteristic FC vegetation arising around nest site after (**b**) dry and (**c**) wet seasons; brown, soil; green, vegetation; darker green indicates greater biomass according to colour-gradient bar on the left (units are kilograms per square metre). **d–f,** Model-predicted soil moisture, root-system size, and plant-density profiles along 30-m transects through simulated FCs (0, nest centre). Parameterization in Extended Data

Что требуется объяснить.

1. Паттерн пространственного распределения ВК
    1. регулярное распределение,
    2. увеличение регулярности при увеличении общей плотности распределения ВК
2. Динамику системы:
    1. появление ВК в матриксе (рождение),
    2. продолжительное существование ВК (стазис),
    3. исчезновение ВК (зарастание)
3. Экологические условия возникновения ВК (дефицит воды)

Диффузионная модель генерирует пространственное распределение ВК близкое к природе (Намибия, Австралия)

Discovery of fairy circles in Australia supports self-organization theory

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Edited by Alan Hastings, University of California, Davis, CA, and approved February 18, 2016 (received for review November 9, 2015)

Vegetation gap patterns in arid grasslands, such as the "fairy circles" of Namibia, are one of nature's greatest mysteries and subject to a lively debate on their origin. They are characterized by small-scale hexagonal ordering of circular bare-soil gaps that persists uniformly in the landscape scale to form a homogeneous distribution. Pattern-formation theory predicts that such highly ordered gap patterns should be found also in other water-limited systems across the globe, even if the mechanisms of their formation are different. Here we report that so far unknown fairy circles with the same spatial structure exist 10,000 km away from Namibia in the remote outback of Australia. Combining fieldwork, remote sensing, spatial pattern analysis, and process-based mathematical modeling, we demonstrate that these patterns emerge by self-organization, with no correlation with termite activity; the driving mechanism is a positive biomass-water feedback associated with water runoff and biomass-dependent infiltration rates. The remarkable match between the patterns of Australian and Namibian fairy circles and model results indicate that both patterns emerge from a nonuniform stationary instability, supporting a central universality principle of pattern-formation theory. Applied to the context of dryland vegetation, this principle predicts that different systems that go through the same instability type will show similar vegetation patterns even if the feedback mechanisms and resulting soil-water distributions are different, as we indeed found by comparing the Australian and the Namibian fairy-circle ecosystems. These results suggest that biomass-water feedbacks and resultant vegetation gap patterns are likely more common in remote drylands than is currently known.

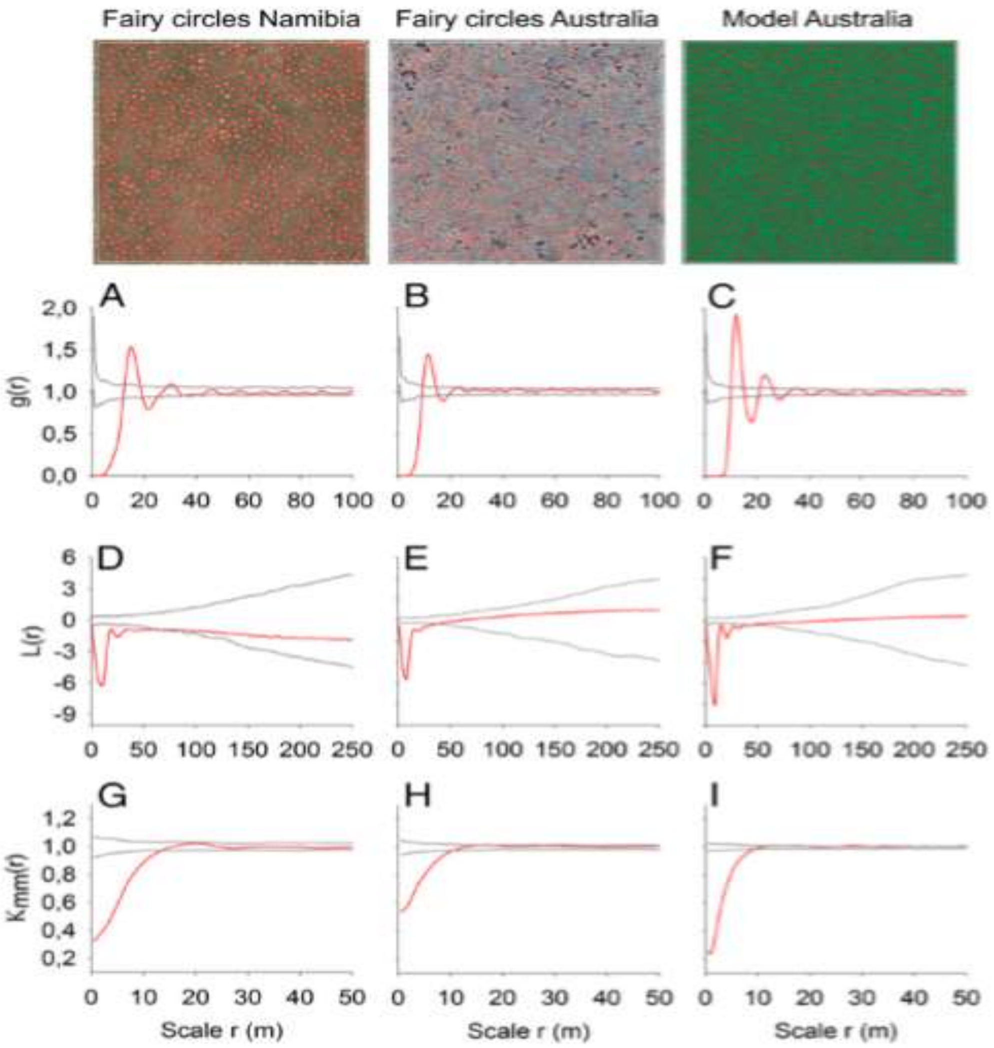
drylands | spatial pattern | *Triodia* grass | Turing instability | vegetation gap

patches is very rare. The archetype of such a gap pattern is that of the fairy circles (FCs) of Namibia, which cover vast areas in a narrow range of climatic conditions (13, 14). However, the origin of the Namibian FCs is still unknown. Several competing hypotheses exist ranging from vegetation self-organization (13–17), termite-induced activity (18), and *Euphorbia* poisoning (19) to abiotic gas leakage (20). Among these, vegetation self-organization stands out as the most solid mechanism that explains the emergence of large-scale order (15, 16) and the strong dependence of fairy-circle distribution on mean annual precipitation (13). Furthermore, only self-organized biomass–water feedbacks can explain the shrinking in size and disappearance of fairy circles after above-average rainfall years and the typical enlargement and increased appearance of FCs after below-average rainfall years (21).

According to pattern-formation theory, the large-scale order that emerges from a uniform state obeys a universal pattern whose particular form is dictated by the instability that the uniform state undergoes (8, 22). The fairy-circle gap pattern observed in Namibia (15) is likely an example of a universal hexagonal pattern that, according to pattern-formation theory, is induced by a nonuniform stationary instability (3, 21–24). The mechanisms inducing the instability may differ among ecosystems, but the resulting hexagonal order of the pattern is the same. This suggests that gap patterns similar to the Namibian FCs should be observable in other water-limited landscapes, even if the mechanism of their formation is different. Also, the opponents of the

Significance

Pattern-formation theory predicts that vegetation gap patterns, such as the fairy circles of Namibia, emerge through the action of pattern-forming biomass-water feedbacks and that such pat-



Временная динамика – результат межсезонных вариаций объема осадков

PNAS

Gradual regime shifts in fairy circles

Yuval R. Zelnik[a], Ehud Meron[a,b], and Golan Bel[a,1]

[a]Department of Solar Energy and Environmental Physics, Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus 8499000, Israel and [b]Department of Physics, Ben-Gurion University of the Negev, Beer Sheva 8410501, Israel

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved August 19, 2015 (received for review March 4, 2015)

Large responses of ecosystems to small changes in the conditions—regime shifts—are of great interest and importance. In spatially extended ecosystems, these shifts may be local or global. Using empirical data and mathematical modeling, we investigated the dynamics of the Namibian fairy circle ecosystem as a case study of regime shifts in a pattern-forming ecosystem. Our results provide new support, based on the dynamics of the ecosystem, for the view of fairy circles as a self-organization phenomenon driven by water–vegetation interactions. The study further suggests that fairy circle birth and death processes correspond to spatially confined transitions between alternative stable states. Cascades of such transitions, possible in various pattern-forming systems, result in gradual rather than abrupt regime shifts.

fairy circles | regime shifts | pattern formation | hybrid states | vegetation self-organization

The response of ecosystems to climate variability and anthropogenic disturbances is a fundamental aspect of ecology. Much attention has been devoted recently to large responses of ecosystems to small environmental changes or disturbances. Such responses, often termed "catastrophic regime shifts," are conceived of as abrupt transitions between two alternative stable states that occur uniformly across the ecosystem (1). Spatially extended systems can respond in different ways to varying conditions, including pattern formation (2–4) and spatially confined transitions to alternative stable states (5). When one of the alternative stable states is spatially patterned, a multitude of additional stable states can appear, each a mosaic of fixed domains that alternate between the ecosystem, with an empirical data analysis, to account for fairy circle dynamics in the NamibRand Nature Reserve from the years 2004 to 2013, thereby accomplishing two goals. The first goal is to substantiate the view of fairy circles as a pattern-formation phenomenon by complementing the current statistical evidence (11, 15, 17) with evidence based on the dynamics of the NFC ecosystem. The second goal is to demonstrate the feasibility of gradual regime shifts in the NFC ecosystem as cascades of unidirectional transitions across hybrid states.

Model

The model we use is based on the Gilad et al. vegetation model (21, 23), which captures three different mechanisms of vegetation pattern formation (24). However, applying the model to the NFC ecosystem (sandy soil, confined root zones) results in a simplified model describing the dynamics of aboveground biomass (B) and soil-water (W) areal densities. The simplified model captures a single pattern-forming feedback associated with the high rate of water uptake by the perennial grasses and the fast soil-water diffusion (relative to biomass expansion) in sandy soils. This mechanism leads to higher soil-water content in the bare fairy circles compared with the vegetation matrix (24), in agreement with reported observations (14, 15). The model equations read

$$\partial_T B = \Lambda W B(1 - B/K)(1 + EB)^2 - MB + D_B \nabla^2 B, \qquad [1]$$

$$\partial_T W = P - N(1 - RB/K)W - \Gamma W B(1 + EB)^2 + D_W \nabla^2 W.$$

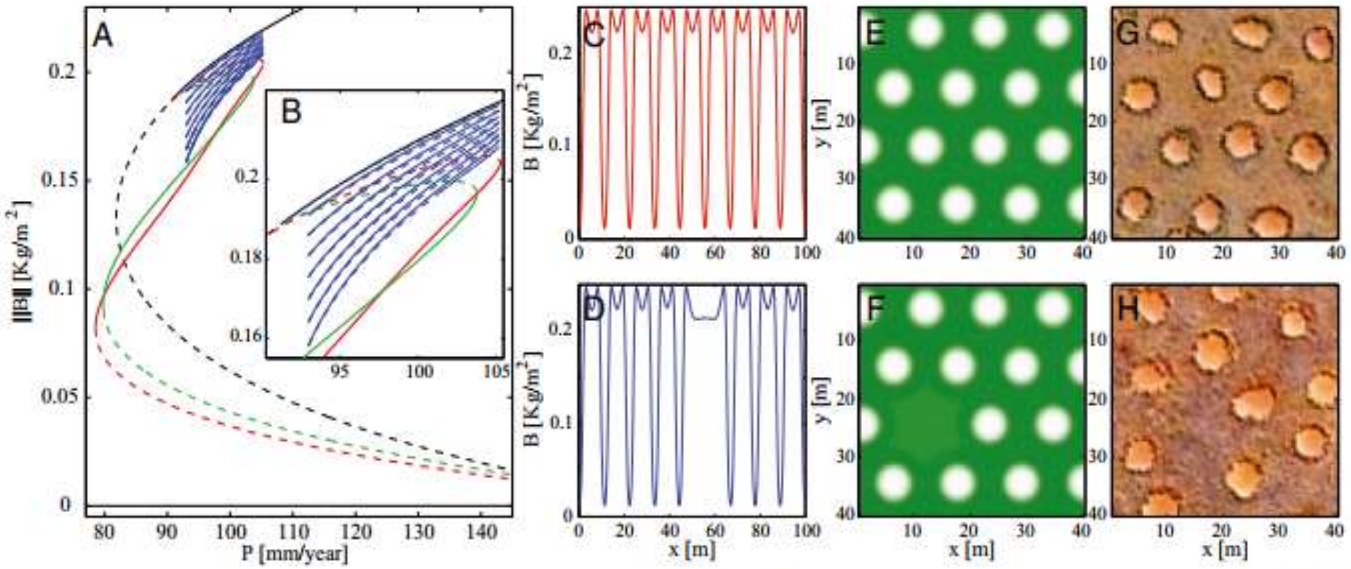
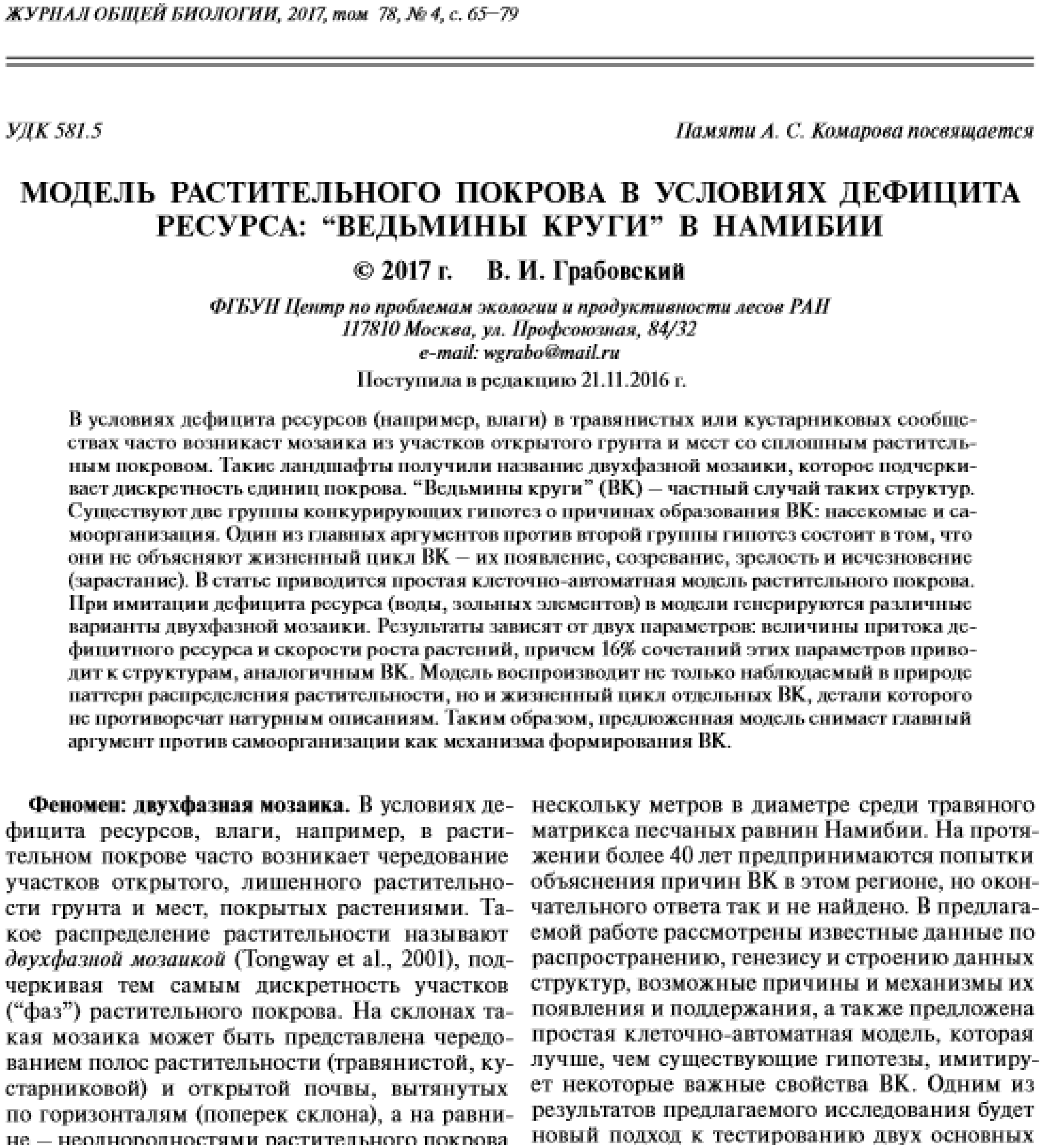


Fig. 1. Steady states of the model. (*A*) Partial bifurcation diagram for a 1D system, showing the L^2 norm of the biomass vs. the precipitation rate. The steady states shown include two uniform solutions of bare soil and uniform vegetation (black), two periodic solutions of gap patterns with different wavelengths (red and green) spanning the bistability range of uniform vegetation and patterned states, and hybrid solutions representing uniform vegetation with an increasing (as the branch snakes down) number of gaps (blue). The solid (dashed) lines in the diagrams represent stable (unstable) solutions. (*B*) Blowup of the hybrid-state range. (*C*) The periodic solution corresponding to the red branch in *A*. (*D*) A hybrid solution corresponding to the lowest blue branch in *B* (a single missing gap) obtained with $P = 102$[mm/y]. (*E* and *F*) The 2D versions of the solutions shown in *C* and *D*. (*G* and *H*) Corresponding fairy circle patterns, obtained from the 2013 satellite image.

Наша модель в одном параметрическом поле адекватно воспроизводит и пространственный и временной паттерны ВК, наблюдаемые в природе



ЖУРНАЛ ОБЩЕЙ БИОЛОГИИ, 2017, том 78, № 4, с. 65–79

УДК 581.5

Памяти А. С. Комарова посвящается

МОДЕЛЬ РАСТИТЕЛЬНОГО ПОКРОВА В УСЛОВИЯХ ДЕФИЦИТА РЕСУРСА: “ВЕДЬМИНЫ КРУГИ” В НАМИБИИ

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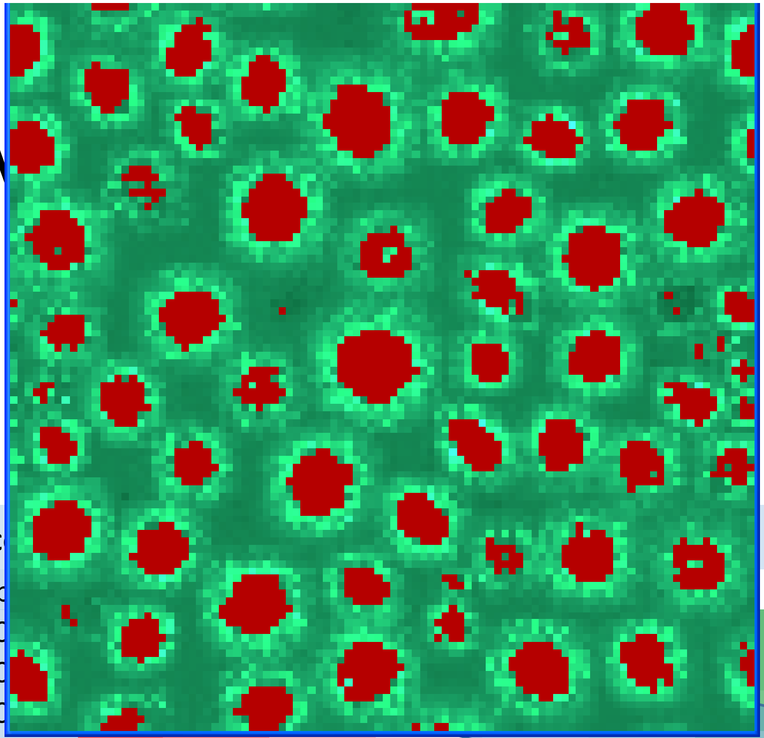
Поступила в редакцию 21.11.2016 г.

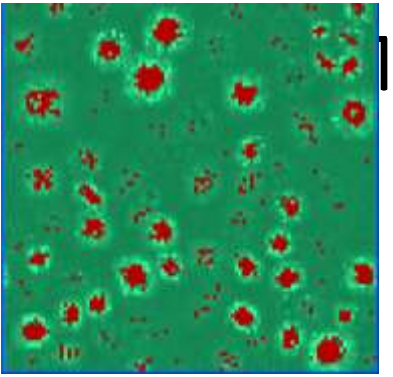
В условиях дефицита ресурсов (например, влаги) в травянистых или кустарниковых сообществах часто возникает мозаика из участков открытого грунта и мест со сплошным растительным покровом. Такие ландшафты получили название двухфазной мозаики, которое подчеркивает дискретность единиц покрова. “Ведьмины круги” (ВК) – частный случай таких структур. Существуют две группы конкурирующих гипотез о причинах образования ВК: насекомые и самоорганизация. Один из главных аргументов против второй группы гипотез состоит в том, что они не объясняют жизненный цикл ВК – их появление, созревание, зрелость и исчезновение (зарастание). В статье приводится простая клеточно-автоматная модель растительного покрова. При имитации дефицита ресурса (воды, зольных элементов) в модели генерируются различные варианты двухфазной мозаики. Результаты зависят от двух параметров: величины притока дефицитного ресурса и скорости роста растений, причем 16% сочетаний этих параметров приводит к структурам, аналогичным ВК. Модель воспроизводит не только наблюдаемый в природе паттерн распределения растительности, но и жизненный цикл отдельных ВК, детали которого не противоречат натурным описаниям. Таким образом, предложенная модель снимает главный аргумент против самоорганизации как механизма формирования ВК.

Феномен: двухфазная мозаика. В условиях дефицита ресурсов, влаги, например, в растительном покрове часто возникает чередование участков открытого, лишенного растительности грунта и мест, покрытых растениями. Такое распределение растительности называют *двухфазной мозаикой* (Tongway et al., 2001), подчеркивая тем самым дискретность участков (“фаз”) растительного покрова. На склонах такая мозаика может быть представлена чередованием полос растительности (травянистой, кустарниковой) и открытой почвы, вытянутых по горизонталям (поперек склона), а на равнине – неоднородностями растительного покрова

нескольку метров в диаметре среди травяного матрикса песчаных равнин Намибии. На протяжении более 40 лет предпринимаются попытки объяснения причин ВК в этом регионе, но окончательного ответа так и не найдено. В предлагаемой работе рассмотрены известные данные по распространению, генезису и строению данных структур, возможные причины и механизмы их появления и поддержания, а также предложена простая клеточно-автоматная модель, которая лучше, чем существующие гипотезы, имитирует некоторые важные свойства ВК. Одним из результатов предлагаемого исследования будет новый подход к тестированию двух основных

Парам ртре и





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0,6	100	100	85	70	56	48	37	31	25	19	12	6	4	2
0,7	100	100	96	79	65	55	46	38	32	28	23	17	9	6
0,8	100	100	98	87	73	63	54	47	39	33	30	24	20	16
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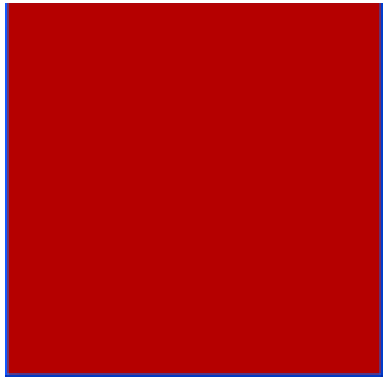
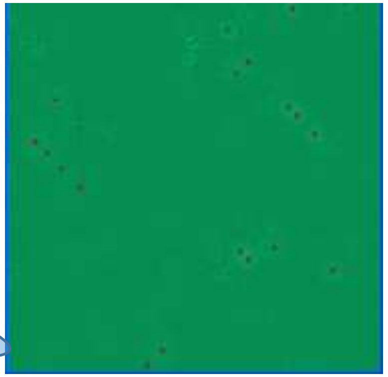
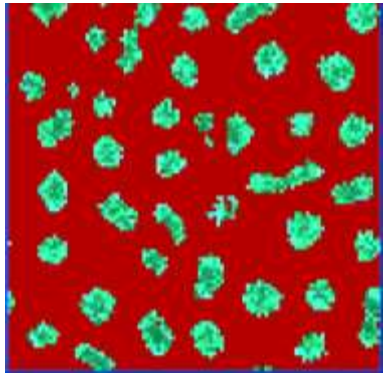






Устойчивость (робастность) модели

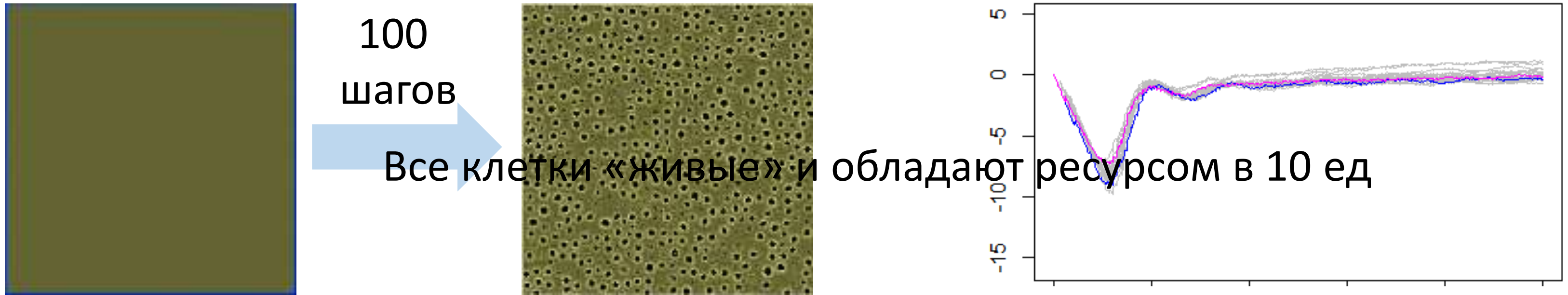
Изменяемая характеристика	По умолчанию	Тест 1	Тест 2	Тест 3
Начальное распределение	Все клетки «живые» и обладают ресурсом в 10 ед.	Лишь 10% клеток «живые» и обладают ресурсом в 10 ед.	Все клетки «живые» и обладают ресурсом в 100 ед.	Все клетки «живые» и обладают ресурсом в 10 ед.
Формула расчета порога выживания (TL)	Порог не зашумлен	Порог не зашумлен	Порог не зашумлен	Порог зашумлен (добавлена случайная составляющая)

На старте

L-test

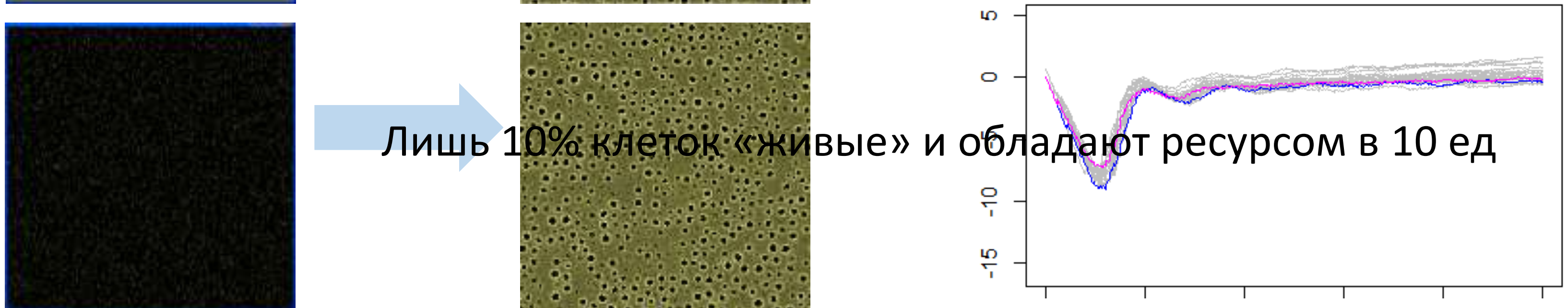
100 шагов

По умолчанию



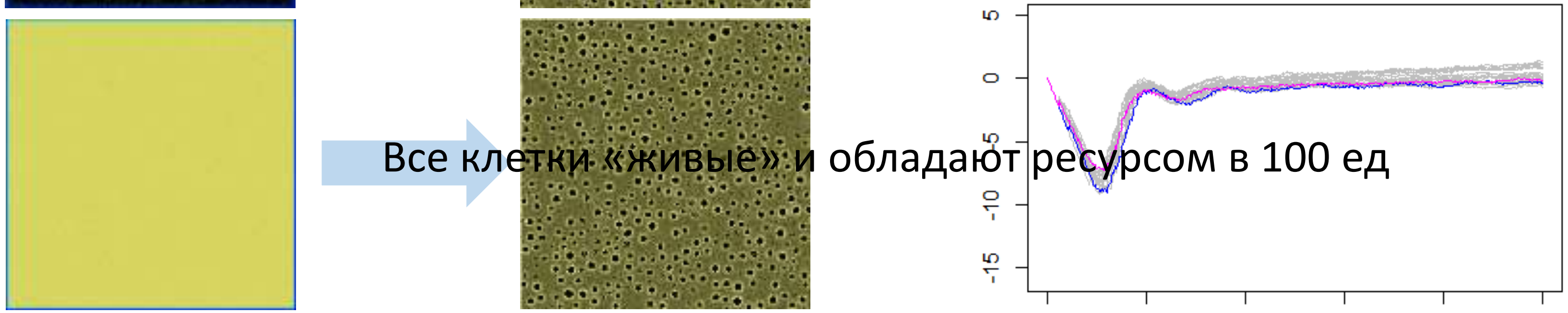
Все клетки «живые» и обладают ресурсом в 10 ед

Тест1



Лишь 10% клеток «живые» и обладают ресурсом в 10 ед

Тест 2



Все клетки «живые» и обладают ресурсом в 100 ед

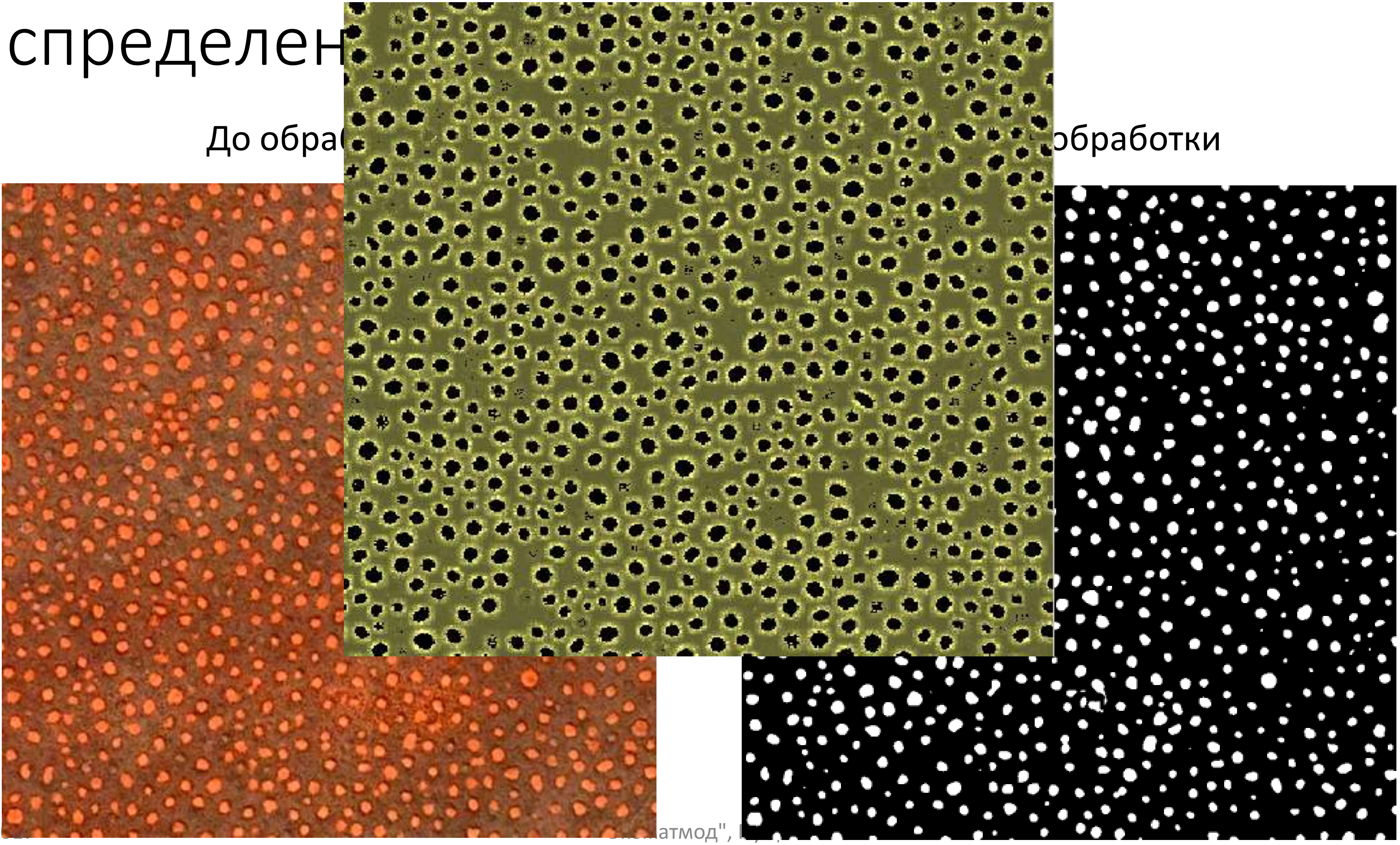
Тест 3

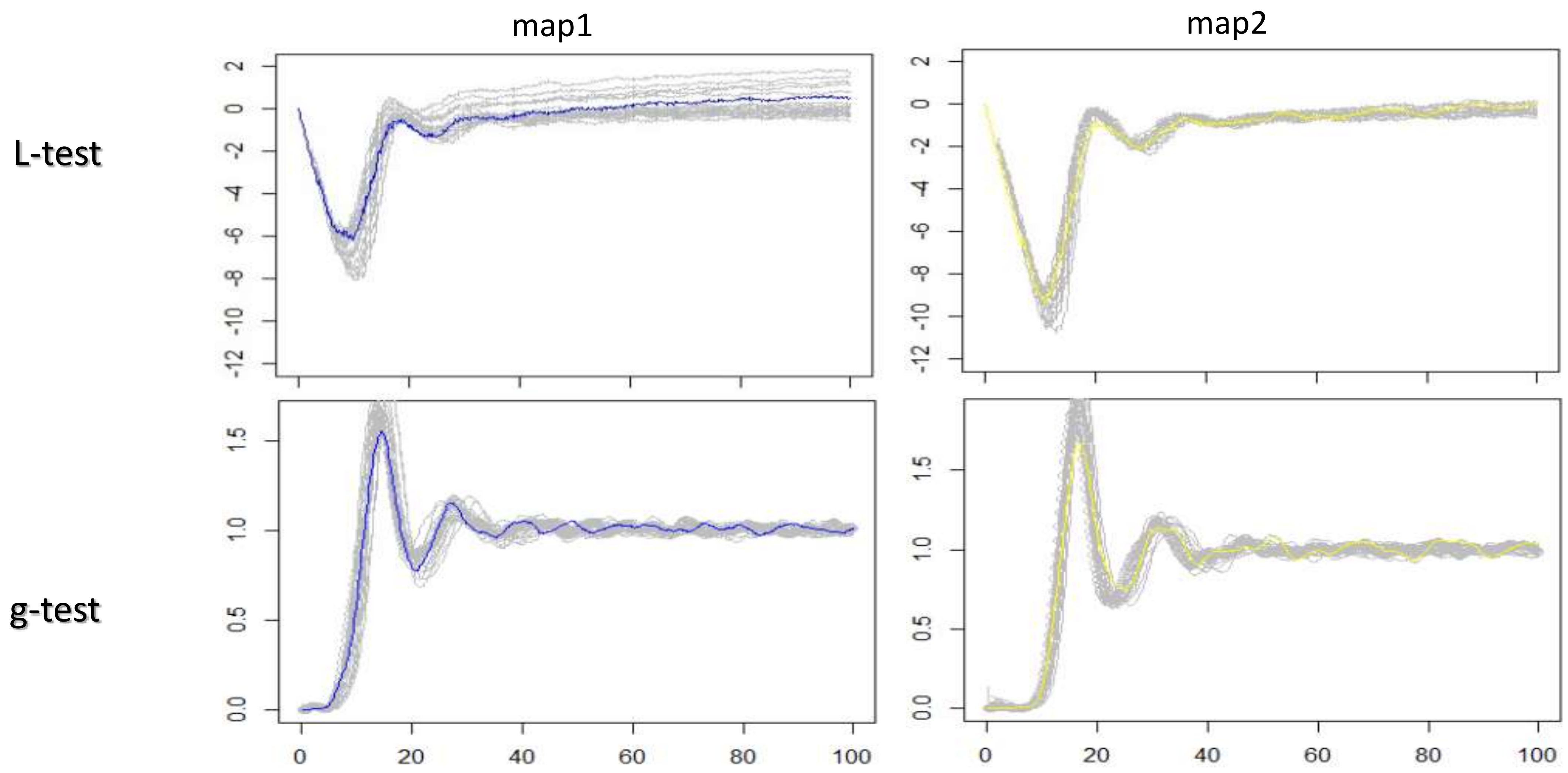
Порог зашумлен (добавлена случайная составляющая)

Подготовка карт из Гугл для оценки параметров распределен

До обра

обработки

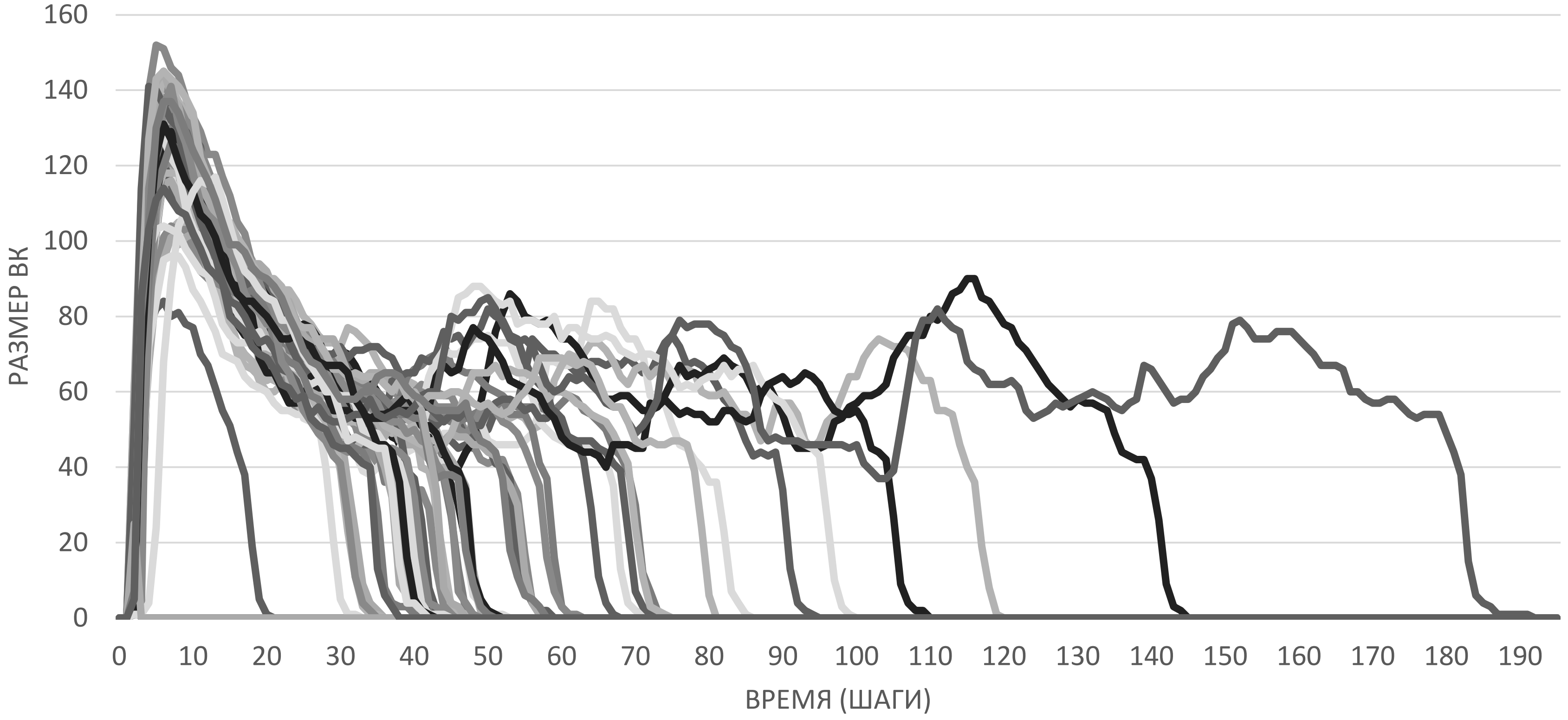




Source	N	Dist	Rad	% of open Graund	Size	Coordinates
map1	523	7,73 m	3,42 m	12,41	400x400m	24°57'00.0"S 15°55'48.0"E
map2	754	5,28 m	3,29 m	16,83	400x400m	19°02'11.9"S 13°20'25.1"E
Rad1_6	771	5,6 units	3,42 units	19,45	400x400units	model
Rad2_6	631	6,45 units	3,94 units	19,78	400x400units	model

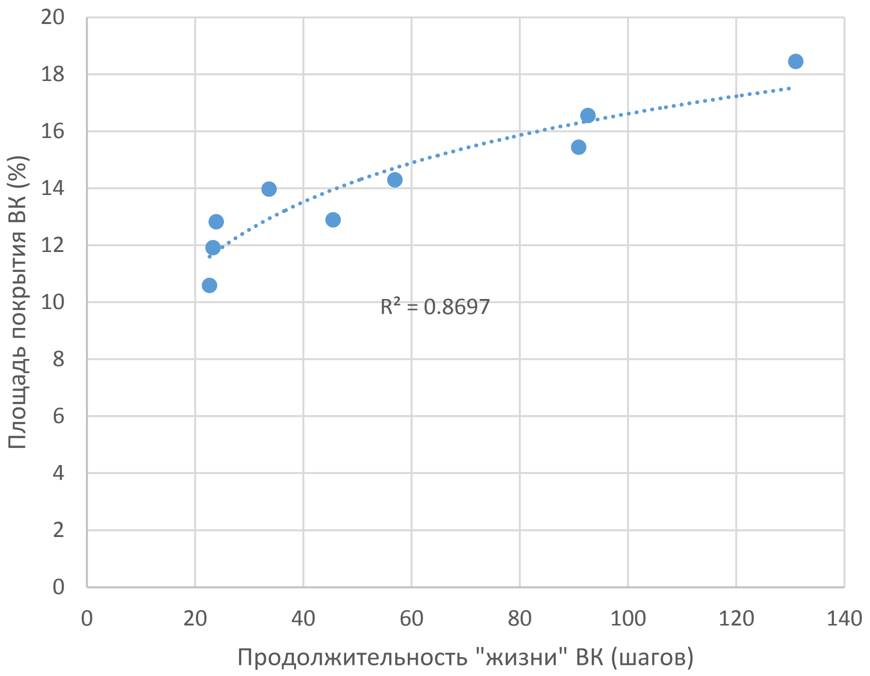
Жизненный цикл ВК:

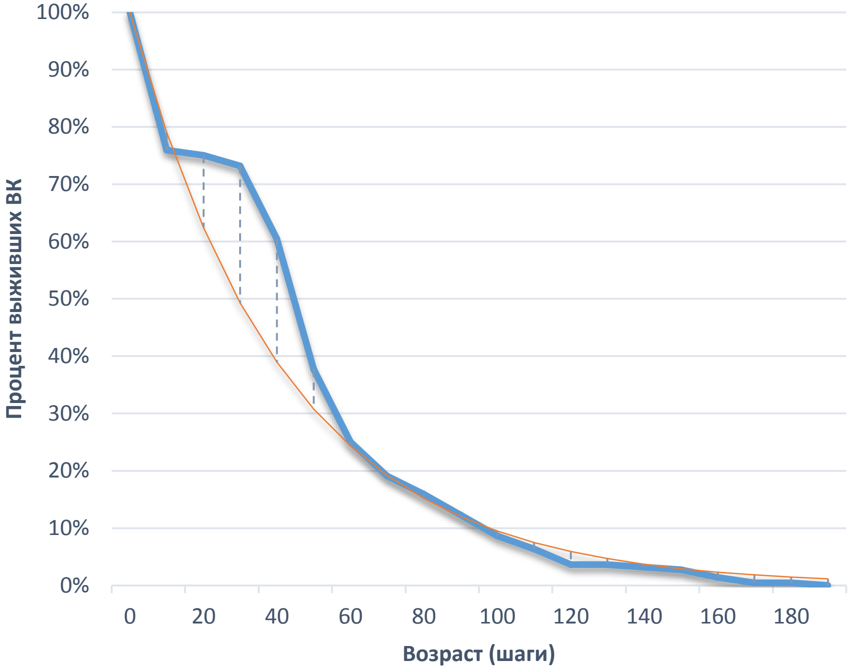
Связь размеров (площади) ВК с продолжительностью жизни



Зависимость размеров первых 50 ВК от возраста (моменты "рождения" для удобства сравнения сведены в одну точку – нулевой шаг времени). Параметры Income = 2, mtbRate = 0.1. Оттенки серого на графике маркируют индивидуальные ВК.

Связь продолжительности жизни ВК с площадью покрытия (слева) и демографическая кривая ВК (справа)





Похоже, не правда ли?