

Feedbacks between soil engineers and vegetation can increase ecosystem robustness (Emergence of multi-scale regular vegetation patterns)

Corina E. Tarnita



How do small scale interactions lead to large scale patterns?



How do small scale interactions lead to large scale patterns?

(1) what are the ecological contexts that promote self-organization and the mechanisms that implement it? how do they differ across spatial scales?



How do small scale interactions lead to large scale patterns?

(1) what are the ecological contexts that promote self-organization and the mechanisms that implement it? how do they differ across spatial scales?

(2) what are the effects of self-organization at one scale on dynamics at others?



How do small scale interactions lead to large scale patterns?

(1) what are the ecological contexts that promote self-organization and the mechanisms that implement it? how do they differ across spatial scales?

(2) what are the effects of self-organization at one scale on dynamics at others?

(3) how does self-organization influence the robustness of systems in the face of perturbation, stress, and catastrophe?



Attraction & Repulsion



Group formation



Social behavior



Multicellularity



Tissue architecture



Human cooperation



Landscape architecture





Nedium-scale patterning, Bunker Reef



Mussel Beds in the Wadden Sea

Map data: Google, © 2015 Aerodata International Surveys





Labyrinth pattern, Niger







Two Guiding Questions:

How do patterns form?

Why do patterns *matter*? What are their effects on the ecosystem?



Local Behavior Leads To Large-Scale Patterns



10 hour time-lapse of mussels on concrete substrate

Video credit: J. van de Koppel



Local Behavior Leads To Large-Scale Patterns



10 hour time-lapse of mussels on concrete substrate

Video credit: J. van de Koppel



Dense soil



Dense soil



Sandy soil



Sandy soil







Range of facilitation (+)



Range of facilitation (+)



Range of facilitation (+)



Range of



Range of Range of inhibition (–) inhibition (–) facilitation (+)



Range of

Range of Range of inhibition (-) inhibition (–) facilitation (+)



Range of

Range of Range of inhibition (-) inhibition (–) facilitation (+)





Scale-dependent Feedbacks



Short-distance positive feedback

Distance

Long-distance negative feedback

Turing, *Phil Trans B*Levin and Segel, *SIAM*Klausmeier, *Science*Rietkerk and van de Koppel, *TREE*





Turing, Phil Trans B 1952



$$\frac{\partial P}{\partial t} = c \times g_{\max} \times \frac{W}{W + k_1} \times P - d \times P + D_p \Delta P,$$

$$\frac{\partial W}{\partial t} = \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} - g_{\max} \times \frac{W}{W + k_1}$$

$$\times P - r_w \times W + D_w \Delta W,$$

$$\frac{\partial O}{\partial t} = R - \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} + D_0 \Delta O,$$

 $P + k_2$

Rietkerk et al 2002, Am. Nat.

∂t

- c = Yield coefficient for plants (water use efficiency)
- ✤ g_{max} = Maximum plant growth rate.
- * k_1 = Growth efficiency for plants growing on water as limiting nutrient.
- ✤ d = Plant mortality rate.
- * $r_w = Evaporation/loss$ rate for underground water.
- alpha = Maximum infiltration rate for the soil.
- * k_2 = Infiltration efficiency of the soil.
- \bullet W₀ = With alpha and O, minimum water infiltration in the absence of vegetation
- * D_p = Plant dispersion rate.
- * $D_w = Diffusivity of soil water$
- * $D_o = Diffusivity of surface water$























Vegetation Patterns Can Be Early-Warning Indicators

(gm⁻²)

biomass

Vegetation

10¹

10⁻¹

Rietkerk et al (2004), Science Scheffer et al (2009), Nature





• Drylands cover >40% of Earth's land surface and are home to >38% of the populace. • The robustness/resilience of drylands is an urgent concern given the importance of these systems to human livelihoods and the increased frequency/ intensity of drought expected under climate change.



Drylands Source: CRU/UEA, UNEP/GRD

Approximate equatorial scale 1:115 million



What forms these spots?

Northwestern Tanzania

. The

24

4

the

Ten 1

1

金

© 2010 Europa Technologies © 2010 Google

Q.

2

代

e

1 Martin

100

鐵

43 95

能

53.4



23

What Is Under The Vegetation Clumps?









Termites modify nutrient and moisture availability



Sileshi et al. (2010), J. Veg. Sci.







Pringle et al. (2010), PLoS Biol

OPEN O ACCESS Freely available online

Spatial Pattern Enhances Ecosystem Functioning in an African Savanna

Robert M. Pringle^{1,2}*, Daniel F. Doak^{2,3}, Alison K. Brody^{2,4}, Rudy Jocqué⁵, Todd M. Palmer^{2,6}

1 Society of Fellows, Harvard University, Cambridge, Massachusetts, United States of America, 2 Mpala Research Centre, Nanyuki, Kenya, 3 Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, United States of America, 4 Department of Biology, University of Vermont, Burlington, Vermont, United States of America, 5 Department of African Zoology, Royal Museum for Central Africa, Tervuren, Belgium, 6 Department of Biology, University of Florida, Gainesville, Florida, United States of America







• 0 . (AR Google earth

Image © 2016 DigitalGlobe





Agriculturalists use termite mounds to plant crops





Pre-Columbian raised fields in a savanna near Sinnamary, coastal French Guiana.





What mechanism could lead to this type of pattern?

Map data: Google, © 2015 CNES/Astrium



How Do Termites Organize Across the Landscape?





Juan Bonachela

100 meters

Tarnita et al, in review









Colony Growth







Colony Growth







Colony Reproduction









Colony Reproduction









Competition







Competition



Modeling Termite Colony Competition: When Do Conflicts Occur?





Modeling Termite Colony Competition: When Do Conflicts Occur?





Modeling Termite Colony Competition: When Do Conflicts Occur?





Modeling Termite Colony Competition: Who Wins Conflict?





Modeling Termite Colony Competition: Who Wins Conflict?





Dynamics





Dynamics





Competition and Conflict Result in Pattern: But Is It Similar To The Natural Pattern?





Spatial Statistics: A Voronoi Diagram Allows Comparison Between Patterns





Spatial Statistics: A Voronoi Diagram Allows Comparison Between Patterns




























The Regular Pattern of Termite Mounds Arises from Competition and Conflict



Tarnita et al, in review



In general, same is true across several continents and different species of social insects



Tarnita et al, in review



Does the termite pattern tell us anything about robustness?

Map data: Google, © 2015 CNES/Astrium



Does the termite pattern tell us anything about robustness?

And what happens if both mechanisms coexist?

Map data: Google, © 2015 CNES/Astrium





$$\frac{\partial P}{\partial t} = c \times g_{\max} \times \frac{W}{W + k_1} \times P - d \times P + D_p \Delta P,$$

$$\frac{\partial W}{\partial t} = \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} - g_{\max} \times \frac{W}{W + k_1}$$

$$\times P - r_w \times W + D_w \Delta W,$$

$$\frac{\partial O}{\partial t} = R - \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} + D_0 \Delta O,$$

 $P + k_2$

Rietkerk et al 2002, Am. Nat.

∂t

- c = Yield coefficient for plants (water use efficiency)
- ✤ g_{max} = Maximum plant growth rate.
- * k_1 = Growth efficiency for plants growing on water as limiting nutrient.
- ✤ d = Plant mortality rate.
- * $r_w = Evaporation/loss$ rate for underground water.
- alpha = Maximum infiltration rate for the soil.
- * k_2 = Infiltration efficiency of the soil.
- \bullet W₀ = With alpha and O, minimum water infiltration in the absence of vegetation
- * D_p = Plant dispersion rate.
- * $D_w = Diffusivity of soil water$
- * $D_o = Diffusivity of surface water$



Termite induced heterogeneity in water use efficiency (increase 0-50%) and infiltration efficiency (increase 0-67%)



Simon Levin



Kelly Caylor

IUm

Distance from termite mound



Juan Bonachela

IUm







- ✤ g_{max} = Maximum plant growth rate.
- * k_1 = Growth efficiency for plants growing on water as limiting nutrient.
- ✤ d = Plant mortality rate.
- $r_w = Evaporation/loss rate for underground water.$
- alpha = Maximum infiltration rate for the soil.
- * k_2 = Infiltration efficiency of the soil.
- W_0 = With alpha and O, minimum water infiltration in the absence of
 - vegetation
- * D_p = Plant dispersion rate.
- * $D_w = Diffusivity of soil water$
- $D_0 = Diffusivity of surface water$
- R = precipitation

$$\frac{\partial P}{\partial t} = c \times g_{\max} \times \frac{W}{W + k_1} \times P - d \times P + D_p \Delta P,$$

$$\frac{\partial W}{\partial t} = \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} - g_{\max} \times \frac{W}{W + k_1}$$

$$\times P - r_w \times W + D_w \Delta W,$$

$$\frac{\partial O}{\partial t} = R - \alpha \times O \frac{P + k_2 \times W_0}{P + k_2} + D_o \Delta O,$$

Rietkerk et al 2002, Am. Nat.

c = Yield coefficient for plants (water use efficiency)

















Bonachela et al (2015), Science









Bonachela et al (2015), Science



Northwestern Tanzania

靈

5

C.

10

E.



Northwestern Tanzania

靈

5

C.

10

E.



Northwestern Tanzania

2







Prediction: we should see smaller scale vegetation patterns in between the mounds. But where were they?



In Between the Termite Mounds Vegetation Is Patterned







Jen Guyton



Model predictions match field observations Fourier Transform analysis and comparison of field images and simulations



Efrat Sheffer



So Is This Ecosystem in Danger of Collapse?

Map data: Google, © 2015 CNES/Astrium





With mounds











Vegetation biomass (gm-2)







Vegetation biomass (gm-2)







Vegetation biomass (gm⁻²)

10¹







Vegetation biomass (gm⁻²)

10¹


























Mounds Increase Drought Resistance





Mounds Increase Drought Resistance





<text>

Grassland guardians Termite mounds help dryland habitats resist climate change

ECOLOGICAL FEEDBACKS

Termite mounds can increase the robustness of dryland ecosystems to climatic change

Juan A. Bonachela,¹* Robert M. Pringle,^{1,2} Efrat Sheffer,¹ Tyler C. Coverdale,¹ Jennifer A. Guyton,¹ Kelly K. Caylor,^{2,3} Simon A. Levin,¹ Corina E. Tarnita^{1,2}†







ARTICLE

Received 23 Mar 2014 | Accepted 11 Sep 2014 | Published 22 Oct 2014

DOI: 10.1038/ncomms6234

Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems

Quan-Xing Liu^{1,2}, Peter M.J. Herman¹, Wolf M. Mooij^{3,4}, Jef Huisman², Marten Scheffer⁴, Han Olff⁵ & Johan van de Koppel^{1,5}



Physics of Life Reviews

Available online 16 July 2016

In Press, Corrected Proof — Note to users



Review

Phase separation driven by density-dependent movement: A novel mechanism for ecological patterns

Quan-Xing Liu^{a, b, h,} 📥 , 🔤 , Max Rietkerk^c, Peter M.J. Herman^b, Theunis Piersma^{d, e}, John M. Fryxell^f, Johan van de Koppel^{b, g,} 📥 [,] 🔤



Conclusions

Patterns are **common** in nature and are created by abiotic and biotic processes.

Patterns **matter**: Understanding patterns can help us explain ecosystem functioning and stability. But also **engineer** solutions.

Mechanisms matter: Similar patterns can arise from different processes and have different effects on the ecosystem.

Multiple mechanisms can coexist and interact, possibly at different scales.



Thank you!

Rob Pringle Juan Bonachela Efrat Sheffer Kelly Caylor Simon Levin Jen Guyton **Tyler Coverdale Ryan Long Jess Castillo-Vardaro**









