Is there only one type of ecosystem? Axioms for community ecology

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Frederic Clements

"...the climax constitutes the major unit of vegetation and as such forms the basis for the natural classification of plant communities."

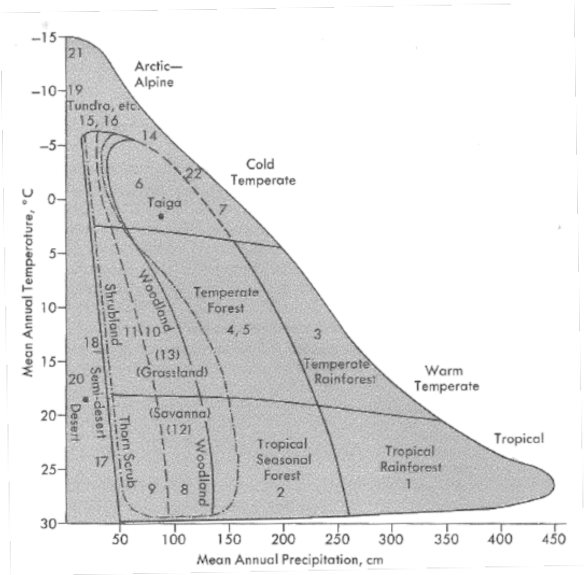
Sources: Photo University of Wyoming, American Heritage Center, Papers, Accession Number 1678, Box 69, Folder 1. Fair use; quotation Clements 1936 J. Ecol. 24:253.

Henry Allan Gleason

“. . . the tendency of the human species is to crystallize and to classify his knowledge; to arrange it in pigeon-holes . . . ”

Sources: Photo NYBG Staff Photographer - The Vertical Files of the LuEsther T. Mertz Library of the New York Botanical Garden, , https://commons.wikimedia.org/w/index.php?curid=73086860; quotation Gleason 1926 Bull. Torrey Bot. Club 53:7.

Types of ecosystem



Whittaker 1975, Communities and Ecosystems, p. 167

Types of ecosystem

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- We really want types of ecosystem that are divided "where the natural joints are."[3]
- Finding non-arbitrary divisions into types is not always easy, *e.g.* x is a human $\iff$ x is a featherless biped?

[3] Plato, Phaedrus 265e

Two humans

Image: David Clifford/The Guardian, https://www.theguardian.com/lifeandstyle/2022/oct/22/the-dog-that-walks-like-a-human-and-other-precocious-pets-duck-cat-parrot

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Euclid's axioms

- A set of five *apparently* self-evident statements about geometry[4].

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- Example: the *parallel axiom* P_1: "for each straight line L and point P outside L, there is exactly one line through P that does not meet L"[5]
- We can get a lot of results from these axioms and not much else, *e.g.* that there are only 5 convex regular polyhedra in $\mathbb{R}^3$.

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The Platonic solids

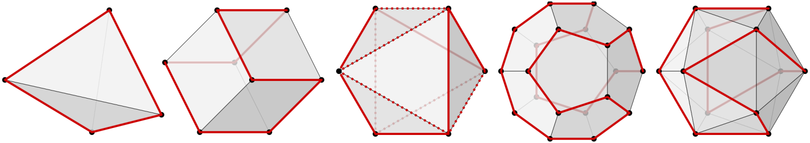

Image cropped from Cmglee - Own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=104005231

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- Replace the parallel axiom by P_2: there are at least two lines through a point P that do not meet line L[6].
- We get a different but internally consistent geometry called *hyperbolic geometry*, which we can think of as geometry on surfaces with negative curvature.

[6] Stillwell, p 361

Hyerbolic geometry

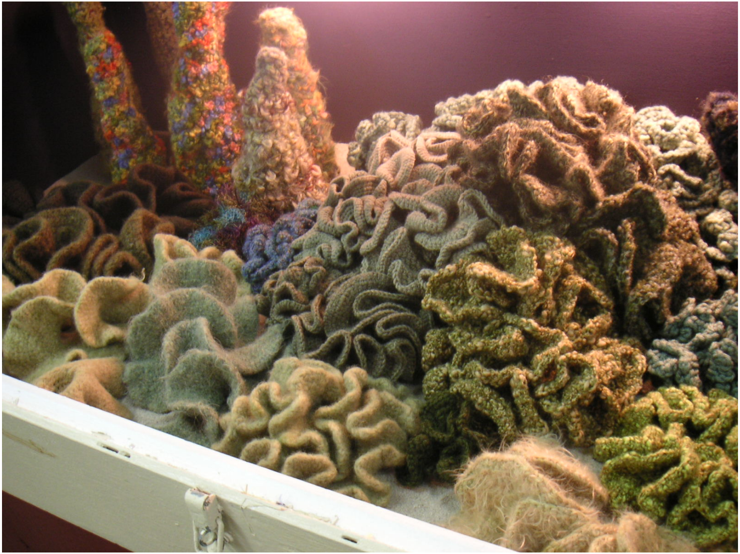

Image by Margaret Wertheim - originally posted to Flickr as crochet hyperbolic kelp, CC BY 2.0, https://commons.wikimedia.org/w/index.php?curid=4352934

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- These axioms alone are not strong enough to give us many results.

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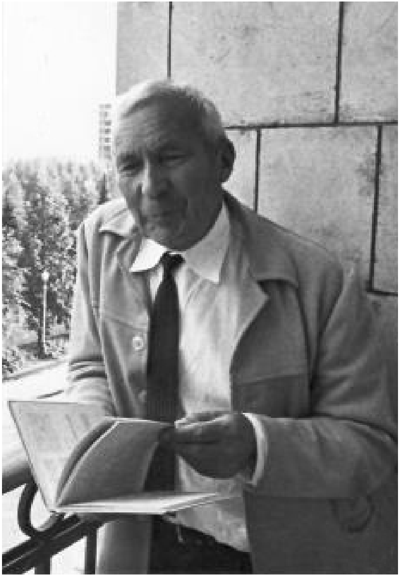
Andrej Kolmogorov



Kolmogorov's axioms

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- Kolmogorov: eight axioms *e.g*: $\frac{\partial K_1}{\partial N_2} \leq 0$, *i.e.* the rate of increase of the prey decreases as the number of predators increases, if the number of prey individuals is constant.

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- Kolmogorov: eight axioms *e.g*: $\dfrac{\partial K_1}{\partial N_2} \leq 0$, *i.e.* the rate of increase of the prey decreases as the number of predators increases, if the number of prey individuals is constant.
- These axioms (plus real analysis) allow only three possible behaviours: approach equilibrium without oscillations or with damped oscillations, or sustained oscillations.

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Recent axiomatic approaches in ecology

- Theory-based ecology[10]: Hutchinson plus inherited individual differences, demographic stochasticity, genetic constraints.
- Clone-consistent ecosystem models[11]: arbitrarily splitting or aggregating populations with the same properties should not change the outcome.

[10] Pásztor et al. 2016

[11] Ansmann and Bollenbach 2021 PLoS Computational Biology 17:e1008635

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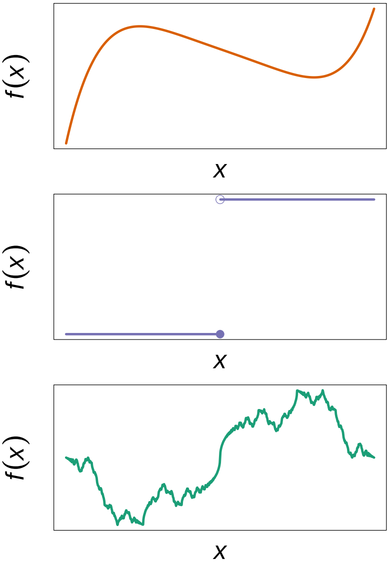
Properties of functions



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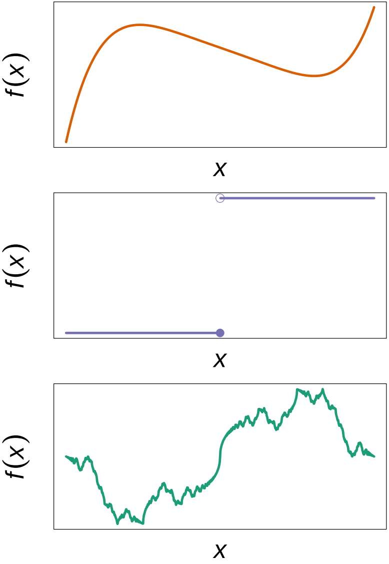

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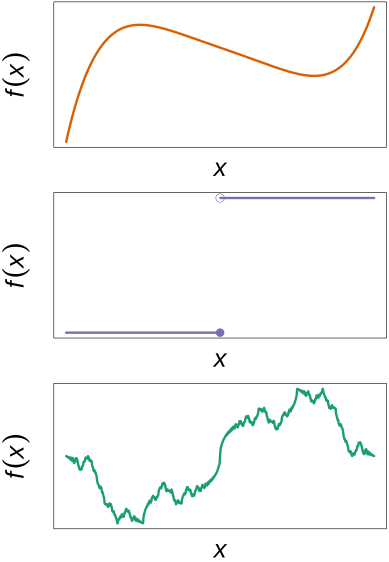
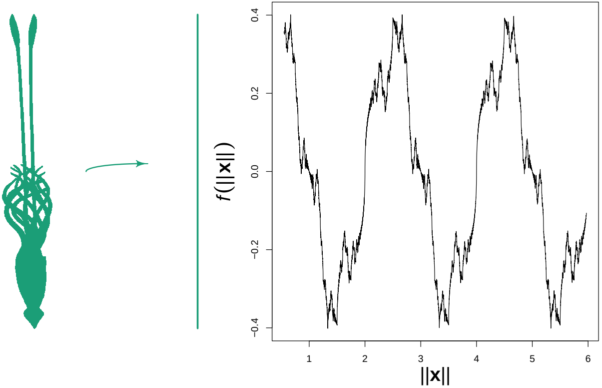


- Real-valued *continuous* functions can be drawn without lifting the pen off the paper.
- *Discontinuous* functions can have sudden jumps.
- Continuous functions can still be "badly-behaved" in some ways, e.g. nowhere differentiable.

The image of a connected space under a continuous function is connected



Squid image redrawn from McClain et al. 2015, `https://peerj.com/articles/715/`

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- Let C be an $|S| \times |S|$ matrix such that $c_{nm} \in C^{\infty}(\mathbb{R}_{+})$: how is consumed m converted into biomass of n?

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  7. (Inefficient Conversion): we get less predator biomass than prey biomass consumed.

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- These are generative axioms: there are corresponding limitative axioms that generate the same set of ecosystems top-down.

Abundances from the axioms

If $e = (S, G, P, C)$ is a G-ecosystem, then abundance $x_{s_n}(t)$ of species s_n at time t is a solution of the Kolmogorov equation

$$\frac{\mathrm{d}x_{s_n}}{\mathrm{d}t} = x_{s_n}\Bigg(g_{s_n,s_n}(x_{s_n}, x_{s_n}) + \sum_{s_m : P(s_n,s_m)=1} c_{s_n,s_m}(g_{s_n,s_m}(x_{s_n}, x_{s_m})x_{s_m}) + \sum_{s_l : P(s_l,s_n)=1} g_{s_l,s_n}(x_{s_n}, x_{s_l}) \Bigg)$$

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- Hence under these axioms, there is only one type of ecosystem.

Sensible measurements on ecosystems are continuous functions

- We aren't allowed to pre-categorize into partitions such as

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- Unlike geometry, the axioms we use in ecology have not often been strong enough to get interesting new results.
- Under our axioms, there is only one type of ecosystem, supporting Gleason rather than Clements.
- There are slightly different sets of axioms that would give us more than one type of ecosystem in relatively uninteresting ways, *e.g.* if we only allow either competition or mutualism but not both, we get two types of ecosystem.

Conclusions

- Axiomatic approaches: internally (relatively) consistent results using a set of principles and nothing else.
- Unlike geometry, the axioms we use in ecology have not often been strong enough to get interesting new results.
- Under our axioms, there is only one type of ecosystem, supporting Gleason rather than Clements.
- There are slightly different sets of axioms that would give us more than one type of ecosystem in relatively uninteresting ways, *e.g.* if we only allow either competition or mutualism but not both, we get two types of ecosystem.
- If we really believe that there is more than one interesting type of ecosystem, what other axioms do we need?

Dynamic assignment function

We say that ψ is a dynamic assignment function if and only if for all $n, m \in \mathbb{N}$:

1. (Prey Consumption and Predator Growth) if $P(n,m) = 1$ then for all $x, y \in \mathbb{R}_+$, $g_{n,m}(x,y) > 0 > g_{m,n}(x,y)$
2. (Producers can Increase when Rare) if $P(m,n) = Prod$ then $n = m$ and there is a $b_n \in \mathbb{R}_+$ such that if $x < b_n$ then $g_{n,n}(x,x) > 0$
3. (Only Predation and Production) if $P(m,n) = 0$ and $n \neq m$ then $g_{m,n}(x,y) = 0$
4. (Non-producers need Prey) if $P(n,n) \neq Prod$ then $g_{n,n}(x,x) < 0$
5. (Producers are Self-Limiting) if $P(n,n) = Prod$ then $g_{n,n}(x,x)$ is strictly decreasing in x
6. (Monotonicity) if $P(n,m) = 1$ then $g_{n,m}(x,y)$ is strictly increasing in y and $g_{m,n}(x,y)$ is strictly decreasing in x.
7. (Inefficient Conversion) If $P(m,n) = 1$ then $0 \leq c_{m,n}(s) < s$, otherwise $c_{m,n} = 0$