Title: How can statistical mechanics help ecology?

Speakers: Ricardo Garcia

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Abstract: Statistical mechanics is the branch of physics that explains how macroscopic properties of matter emerge from the behavior of its microscopic constituents. Population ecology studies how and why populations change over time and space, primarily due to the interaction among individuals and between individuals and the environment where they thrive. Although seemingly very different, both disciplines aim to explain large-scale phenomena based on a description of their underlying drivers, and statistical mechanics tools have been largely used to formalize population ecology. For over 100 years, however, mathematical models in population ecology have relied on very strong and unrealistic assumptions about the way individuals move and get to interact with each other and with the environment. Specifically, they assume that individuals behave like the molecules of an ideal gas: following completely random trajectories through the entire area occupied by the population and only interacting with each other when their trajectories intersect.

In this presentation, I will first discuss why mathematical models are powerful tools to understand ecological processes. Then, I will show how traditional models of population dynamics emerge from ideal gas assumptions for individual movement and briefly touch on our recent efforts to refine those models combining more elaborated tools from statistical physics, random walk theory, and GPS tracking data of natural populations.





How can statistical mechanics help ecology?

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Perimeter Institute, March 2021





How can statistical mechanics help ecology?

and the other way around!!

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Perimeter Institute, March 2021



Physics and ecology?

Ecology developed from natural history



Stephen A. Forbes



Frederic E. Clements





Ecological pattern —— dynamical process



♦/■♦





(pattern images from Fig. 1 in Meron, 2019)





RMG et al. PLOS Comp Biol (2018)



Rossine, RMG et al. PLOS Biol (2020)

Macroscopic patterns are independent of microscopic details



Quantitative relations to predict patterns



Population dynamics is an emergent phenomena



Well-mixed model: "law of mass action"

Assumptions: cells are ideal gas particles.

Ballistic or Reflected Brownian Motion within a "solid" container

 $\dot{\mathbf{z}} = g \, \boldsymbol{\xi}(t)$

Steady-state PDF individual position: UNIFORM

$$f(\boldsymbol{z}, t \to \infty) = \begin{cases} \frac{1}{\pi \mathcal{R}^2} & \text{inside } \mathcal{R} \\ 0 & \text{outside } \mathcal{R} \end{cases}$$



Hutchinson & Wasser 2007 Biological Reviews

♦/■♦

Q: How do complex microscopic features translate to macroscopic dynamics?





♦/□♦

Q: How do complex microscopic features translate to macroscopic dynamics?

Well-mixed



 $\dot{N}(t) = (\beta - \delta)N(t) - \gamma N(t)$

Range residency / territoriality



(video from @BoixRichter)

RMG et al. Journal of Theoretical Biology (2020)

Q: How do complex microscopic features translate to macroscopic dynamics?

Let's be physicists:

- *N* = 2
- Harmonic oscillator



How do **two** individuals encounter with each other if they are not well-mixed?

After that...more complex models and larger population sizes STATISTICAL PHYSICS

Encounter rates link movement with population-level processes









Not so mixed: beyond the "law of mass action" Assumptions: 'animals are trapped in harmonic potentials'.

Ornstein-Uhlenbeck models, no need of boundaries.

$$\dot{\mathbf{z}} = -rac{1}{ au} \left[\mathbf{z} - oldsymbol{\lambda}
ight] + g \, oldsymbol{\xi}(t)$$

Steady-state position PDF: NORMAL

Mean position: $oldsymbol{\mu}=(\lambda_x,\,\lambda_y)$

Covariance matrix:
$$\Sigma = \begin{pmatrix} \frac{g\tau}{2} & 0\\ 0 & \frac{g\tau}{2} \end{pmatrix}$$





OU, due to trapping in the harmonic potential, features a spatial scale for interactions at the individual level, $\rho \propto \sqrt{g\tau}$, that is much smaller than the whole habitat occupied by the population.

How does the existence of such scale influence encounters?



Ornstein-Uhlenbeck

Reflected Brownian motion











Key for the calculation: obtain the distribution for the distance between individuals

The steady-state mean encounter rate

Ornstein–Uhlenbeck

$$\tilde{\mathcal{E}}_{OU}(q) \approx \frac{\gamma}{2\pi\sigma_r^2(\boldsymbol{\rho_1}, \boldsymbol{\rho_2}, \boldsymbol{R_\lambda})} \exp\left(\frac{-\boldsymbol{R_\lambda^2}}{2\sigma_r^2(\boldsymbol{\rho_1}, \boldsymbol{\rho_2}, \boldsymbol{R_\lambda})}\right)$$

Reflected Brownian Motion

$$\tilde{\mathcal{E}}_{RBM}(q) \approx \frac{\gamma}{\pi \mathcal{R}^2}$$



Assuming well-mixing biases A LOT encounter results



Assuming well-mixing biases A LOT encounter results



Refined encounter rates could either be higher or lower relative to mass action.

Context dependence makes it very hard to know even in which direction the predictions of well-mixed models will be wrong.

Realistic movement also changes WHERE encounters occur

Probability that two animals encounter at a location, (x, y):

 $f_E(x,y) \propto f_1(x,y) f_2(x,y)$



And we can learn a lot of ecology from it!





Video credits: Smithsonian Tropical Research Institute (Panama)

Data collection: Grace Davis, Meg Croofot (UC Davis & Smithsonian Tropical Researh Institute, Panama)

And we can learn a lot of ecology from it!



Noonan, RMG et al., (2021). Methods in Ecology and Evolution.

Extensions: effect of landscape heterogeneity

$$\dot{\mathbf{z}} = -\frac{1}{\tau} \left[\mathbf{z} - \boldsymbol{\lambda} \right] + g \boldsymbol{\xi}(t) - \mu \nabla \phi(\mathbf{r}, t)$$





Gabriel Andreguetto

Ronaldo Morato

(Instituto Chico Mendes Conservação da Biodiversidade)

Extensions: other encounter metrics.

- · When and where will two animals encounter for the first time?
- What is the probability that a predator encounters a prey within the next 3 days?
- What is the probability that a female and a male encounter each other within a mating season?

First encounter statistics and survival analysis





Benjamin Garcia de Figueiredo

Pirsa: 21030007

Extensions: long-range (but finite) interactions.

$$egin{aligned} \dot{\mathbf{z}}_p &= -rac{1}{ au_p} \left[\mathbf{z}_p - oldsymbol{\lambda}_p
ight] -
abla V_{pv}(|\mathbf{z}_p - \mathbf{z}_v|) + g_p \, oldsymbol{\xi}_p(t) \ \dot{\mathbf{z}}_v &= -rac{1}{ au_v} \left[\mathbf{z}_v - oldsymbol{\lambda}_v
ight] + g_v \, oldsymbol{\xi}_v(t) \end{aligned}$$

- How does this change the frequency and location of encounters?
- Can we account for behavioral state of the animals?
- What makes the pairwise interaction potential a realistic one?
- Can we account for prey avoidance too?

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