Unraveling the tangled web of habitat fragmentation effects

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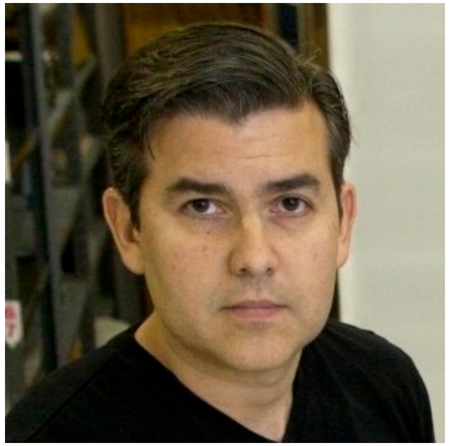
FSU Ecology and Evolution Seminar

September 24th, 2021

Collaborators

Robert (Bob) D. Holt
UF Biology

Robert Fletcher, Jr.
UF Wildlife Ecology and Conservation



Emilio Bruna
UF Wildlife Ecology and Conservation

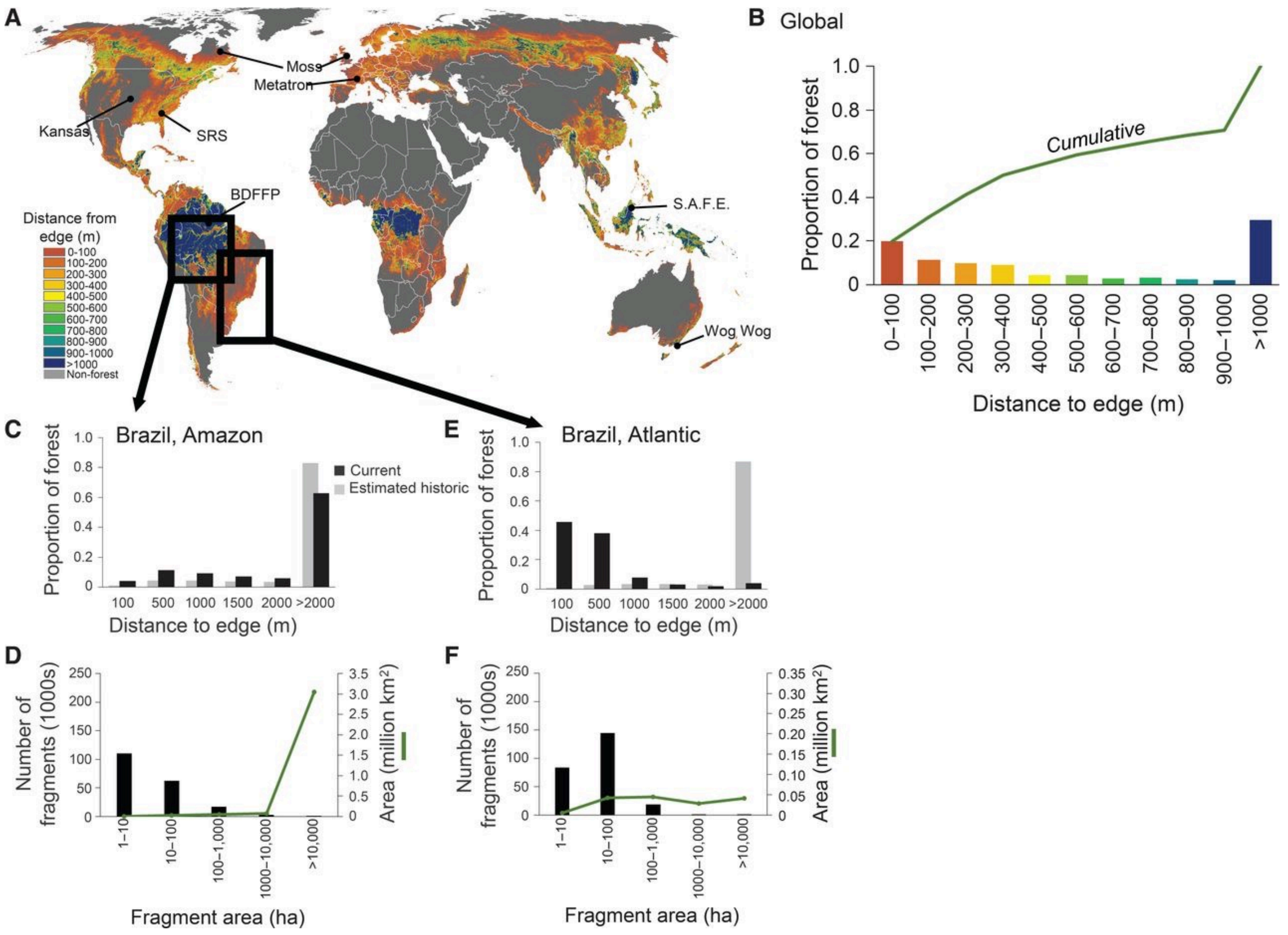
Thomas Smith
UF Wildlife Ecology and Conservation

Habitat Conversion

The major short-term factor affecting biodiversity worldwide

Compared to the past, much of the historical habitat on the planet has been altered in some way.

Huge shift in the distribution of habitat types
Forest dominated -> agriculture dominated



Haddad et al. 2015. Science Advances

Habitat Fragmentation

= Habitat “broken”

Four things happen:

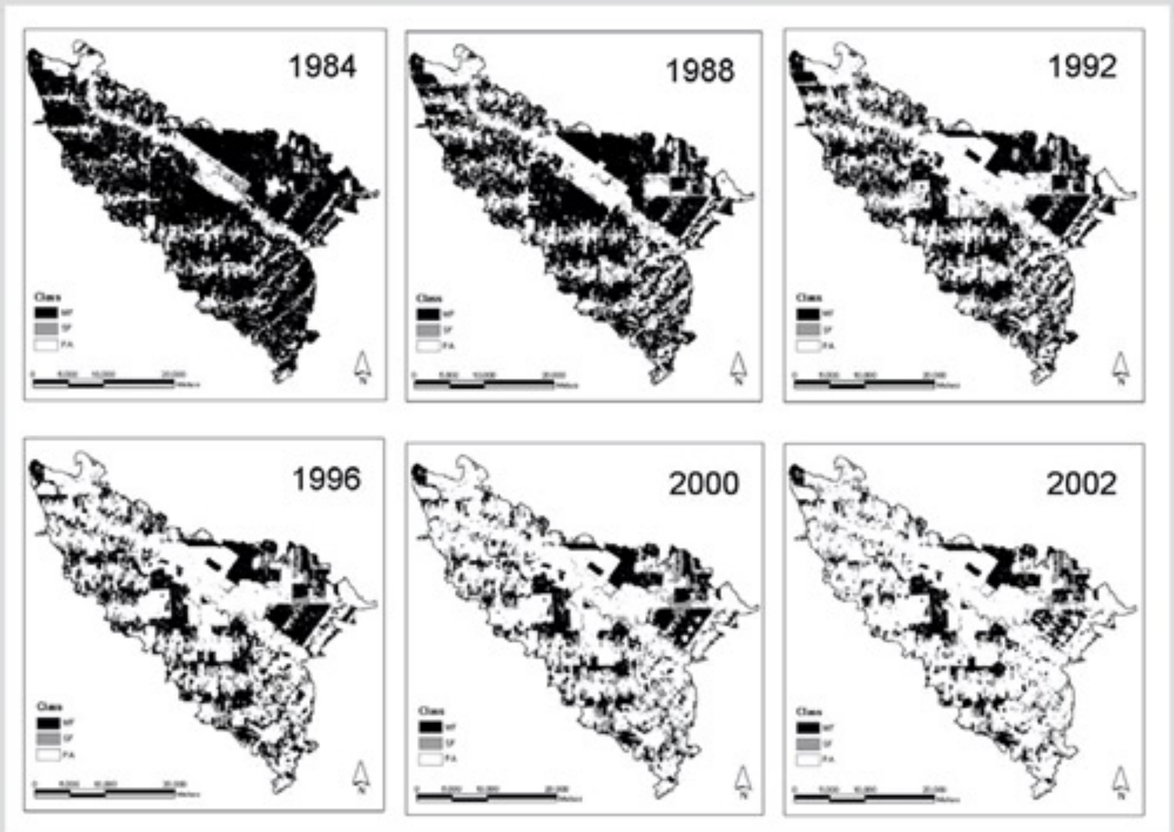
1. Reduction in previously common habitat

2. Habitat “patchy” in nature, when it was not before

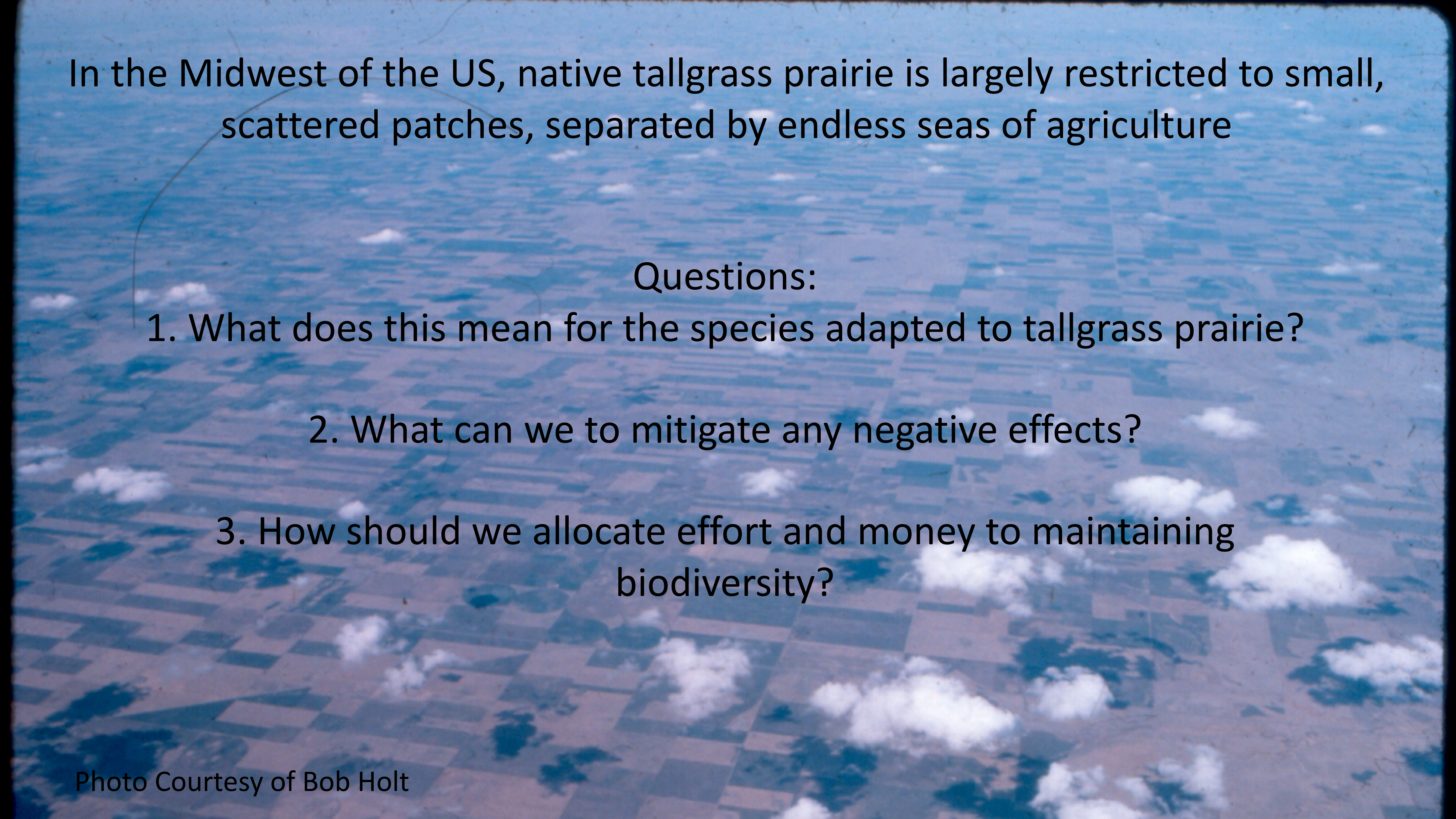
3. Remaining habitat areas are more geographically separated

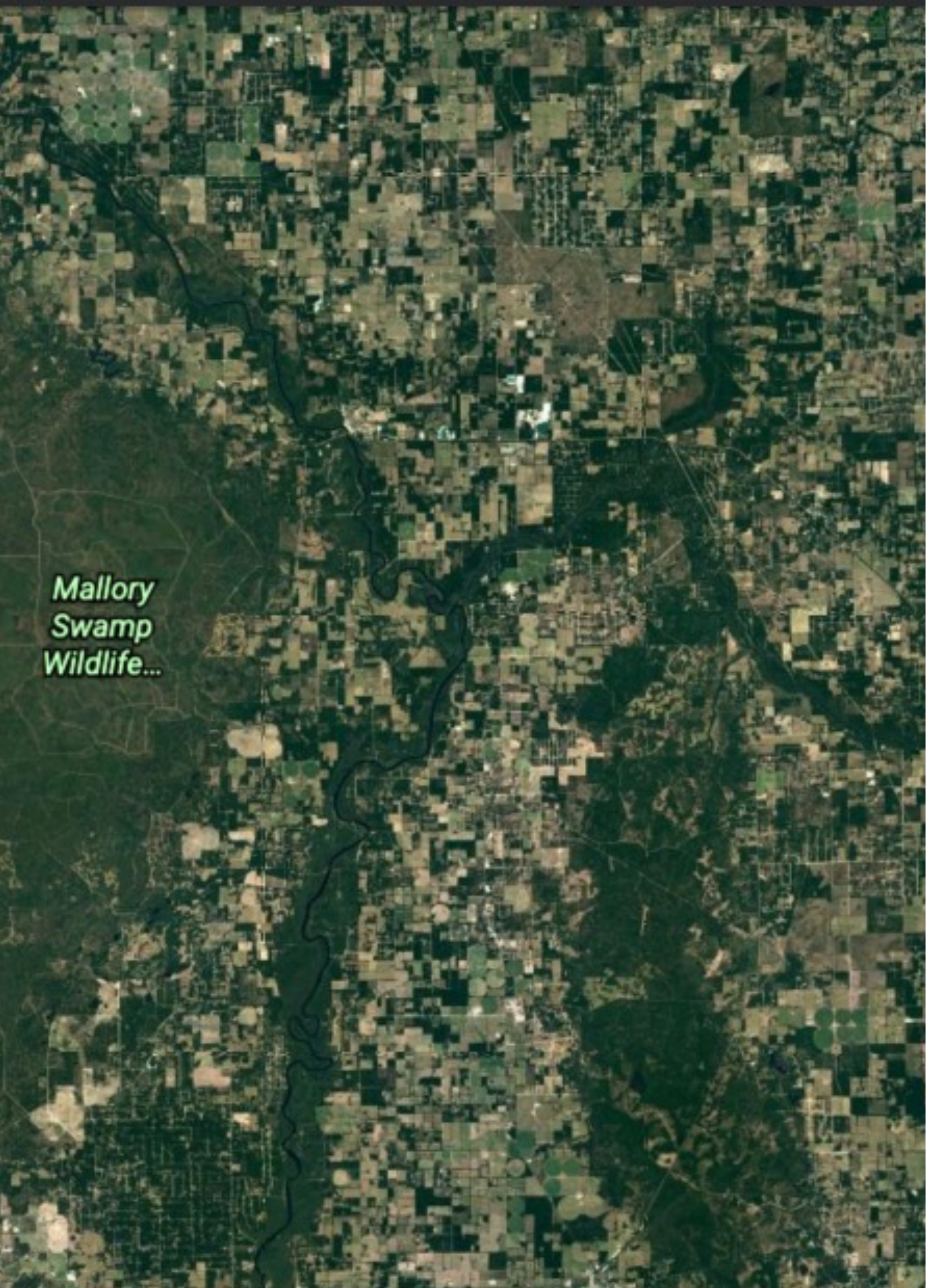
4. Converted habitat (“the matrix”) often less suitable

= mature forest
= secondary forest
= pasture



Time series of Amazonian rain forest
Ferraz et al. 2005. Forest Ecology and Management.


In the Midwest of the US, native tallgrass prairie is largely restricted to small, scattered patches, separated by endless seas of agriculture
Questions:
1. What does this mean for the species adapted to tallgrass prairie?
2. What can we to mitigate any negative effects?
3. How should we allocate effort and money to maintaining biodiversity?
Photo Courtesy of Bob Holt



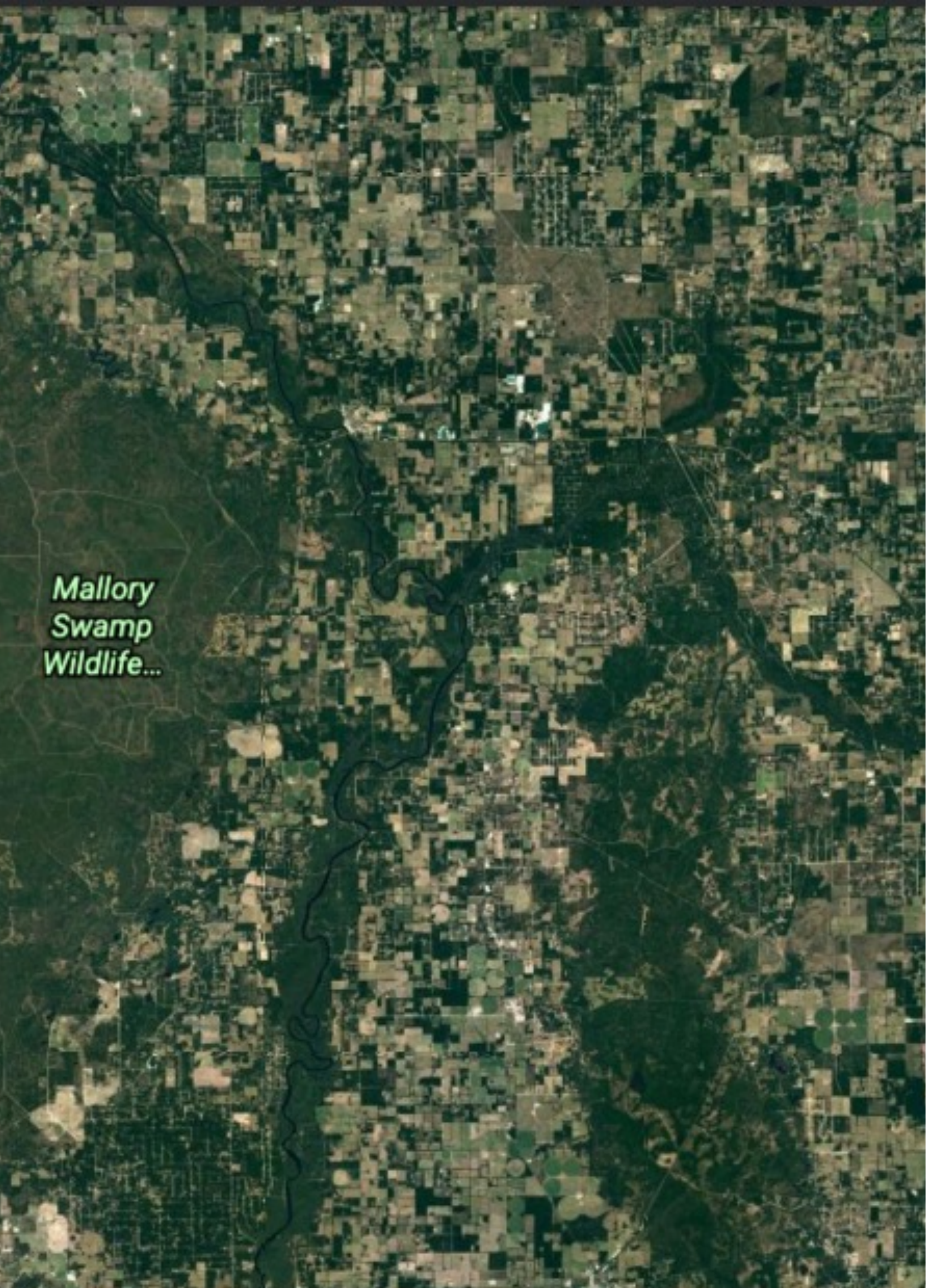
Some preliminaries

- A patch -> a geographical area considered to have the necessary requirements for life of a given species.
  - Species-specific concept

- Fragmentation (lots of metrics)
  - Fundamentally a measure of habitat subdivision

  - Metrics

Average patch size	Number of patches
Average interpatch distance	Patch Aggregation
Patch Edge to Area Ratio	



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Patch Edge to Area Ratio	

We can view these attributes as abstract niche dimensions

The big issues

1. Multicausality

Many factors change following habitat fragmentation. Which is responsible, and in what combination?

2. **Scale**

Example of all the ways factors associated with landscape modification might interact

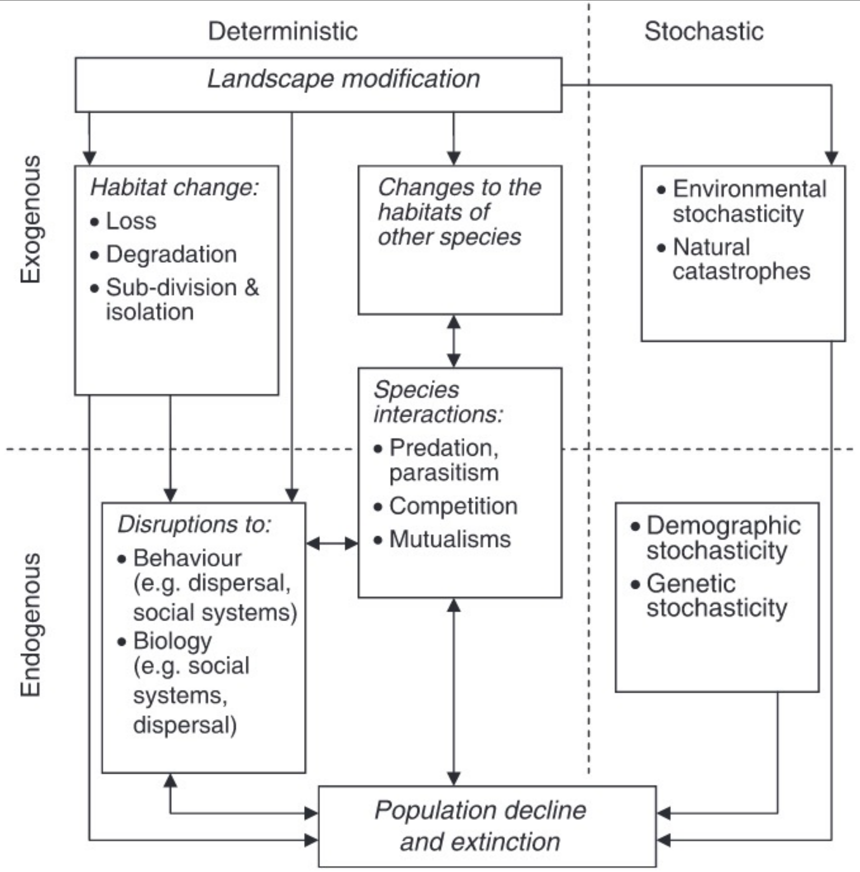

Figure 4 Threatening processes arising from landscape modification as experienced by a declining species. Threatening processes are broadly classified as deterministic versus stochastic, and exogenous versus endogenous. Deterministic threats predictably lead to declines, whereas stochastic threats are driven by chance events. Exogenous threatening processes are external to a species' biology, whereas endogenous threats arise as part of a species' biology (see text for details).

Fischer and Lindenmayer. 2007. Global Ecol. Biogeogr.

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The scale of observation of pattern can sometimes obscure—and sometimes reveal-process.

No guarantee that local-scale phenomena translate directly to pattern at larger scales of observation.

Ecology, 73(6), 1992, pp. 1943–1967

THE PROBLEM OF PATTERN AND SCALE IN ECOLOGY

THE ROBERT H. MACARTHUR AWARD LECTURE
Presented August 1989
Toronto, Ontario, Canada

by

SIMON A. LEVIN
Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003 USA, and Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701 USA

Simon A. Levin
MacArthur Award Recipient

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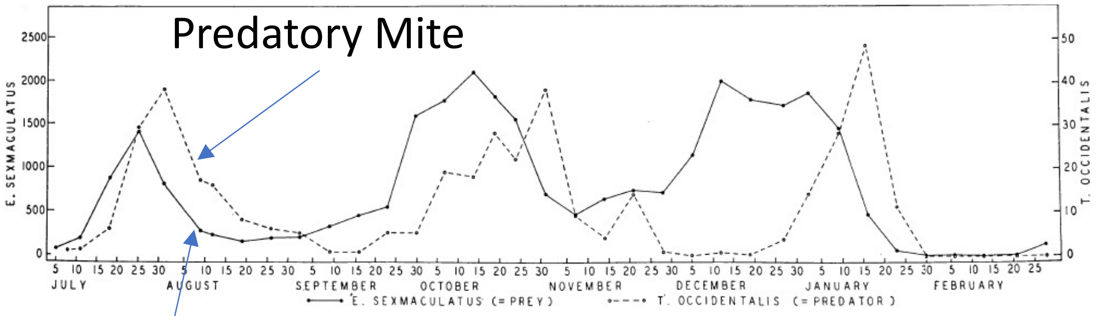
Example: Huffaker's Mites

Predatory Mite



Huffaker. 1958.

Herbivorous mite; Prey

Remind anyone of Hare-Lynx cycles?
Looks like typical predator-prey cycling

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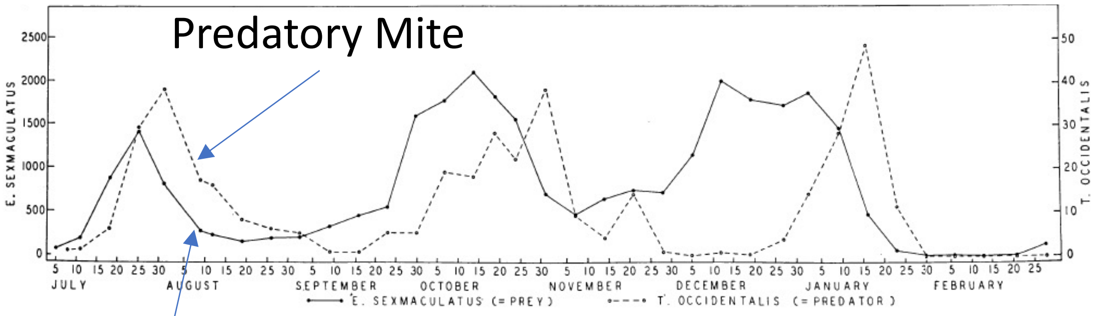

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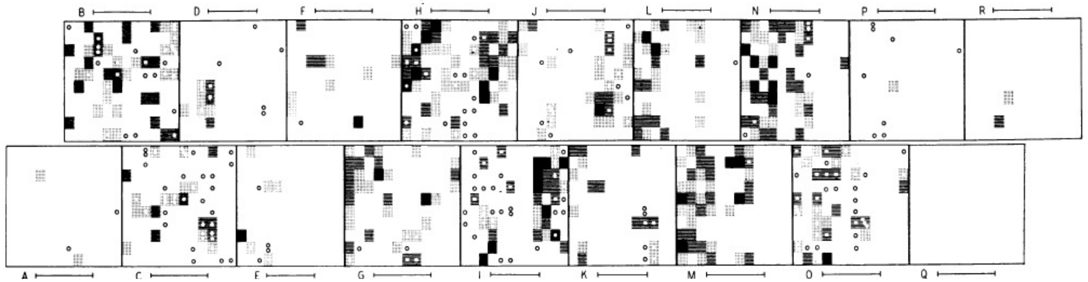

Reality is a complex landscape of resources, refuges, and risk. In any locality (orange), predator and prey do not coexist!

The big issues

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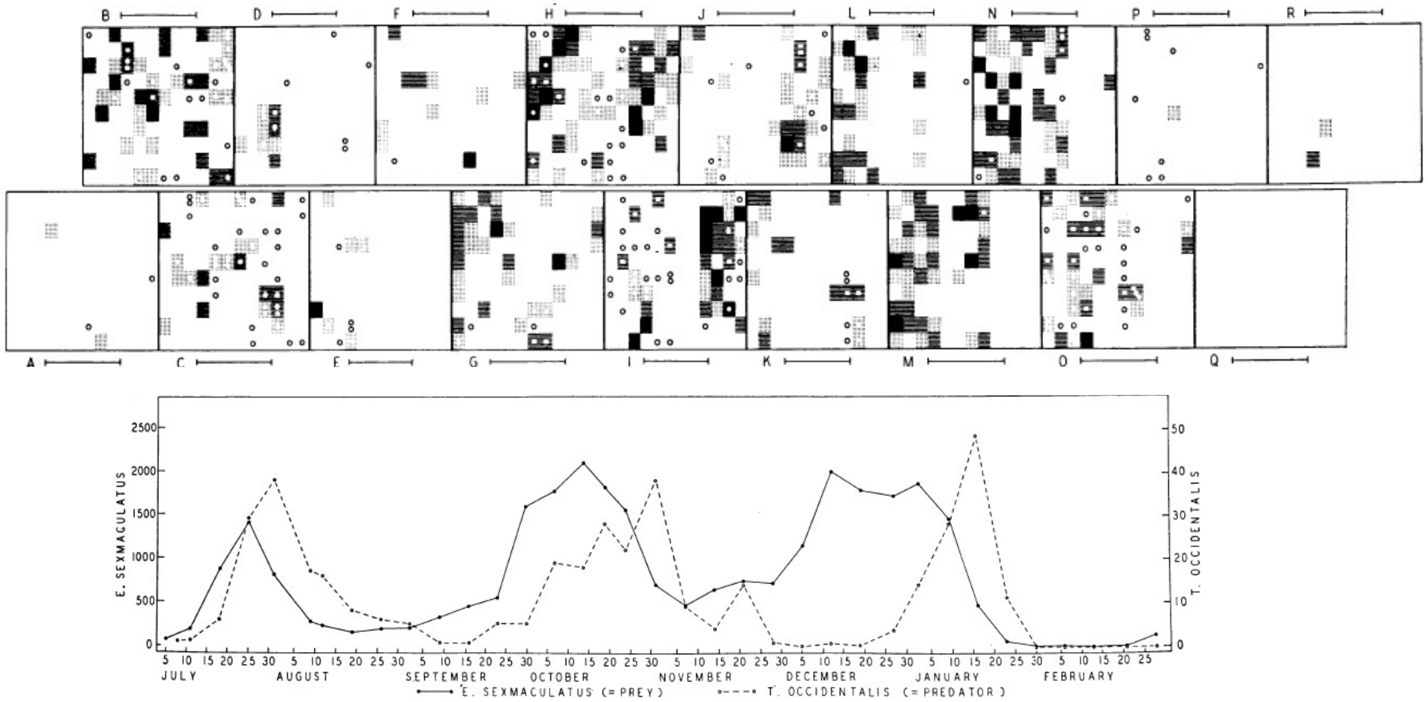
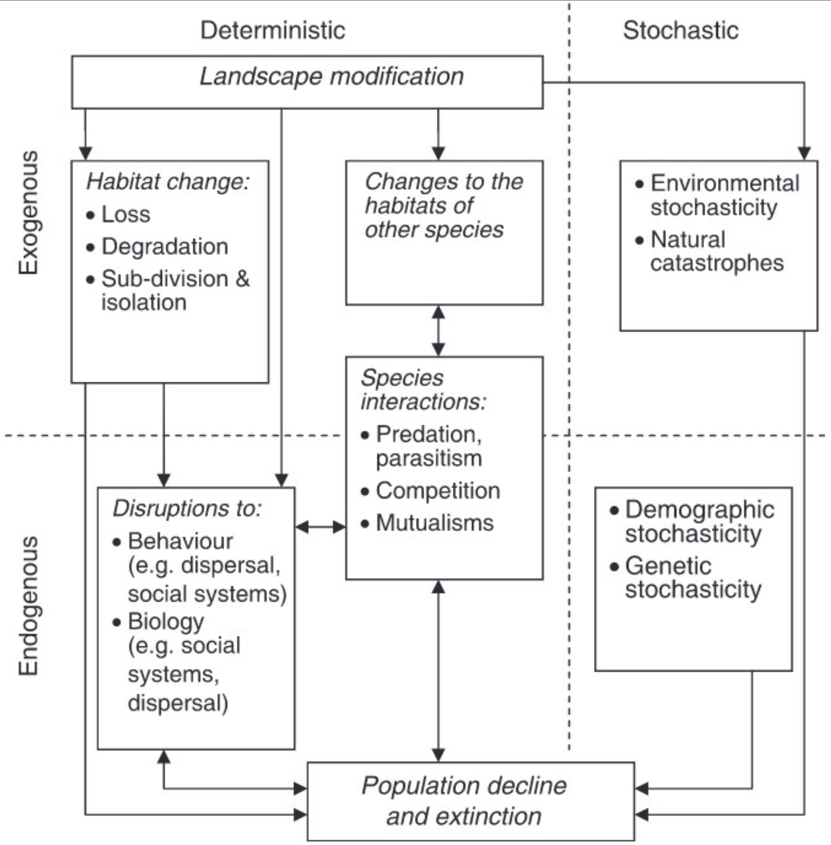


Example of all the ways factors associated with landscape modification might interact



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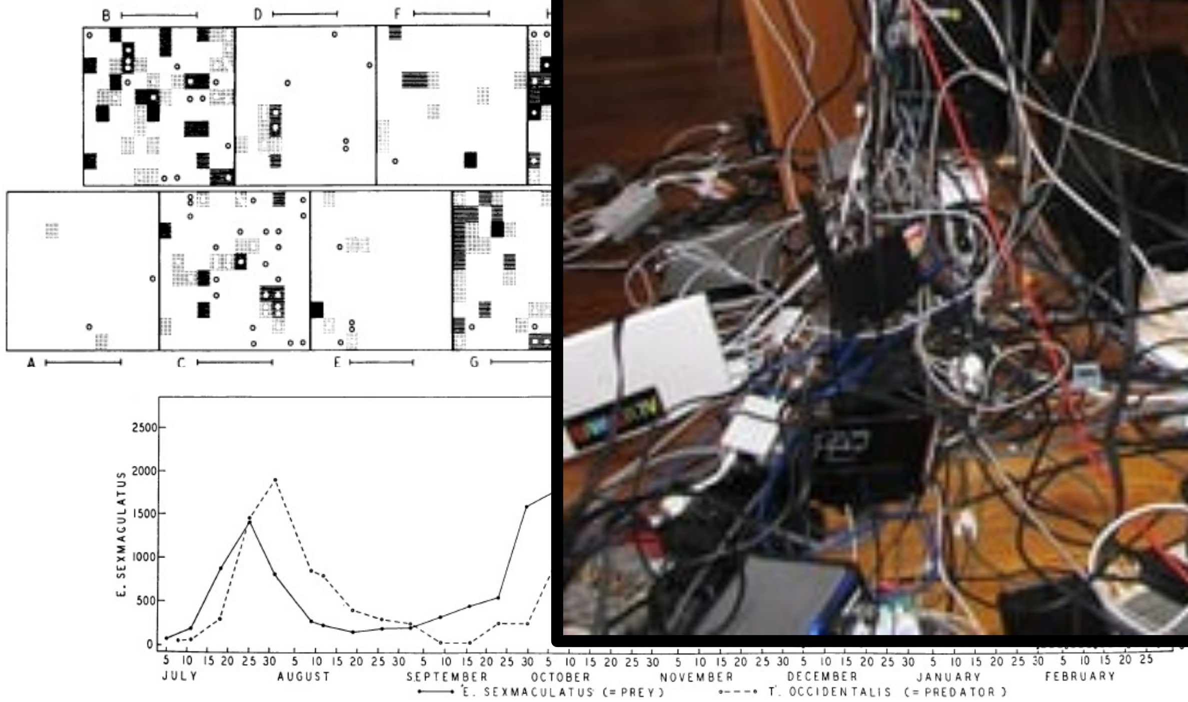

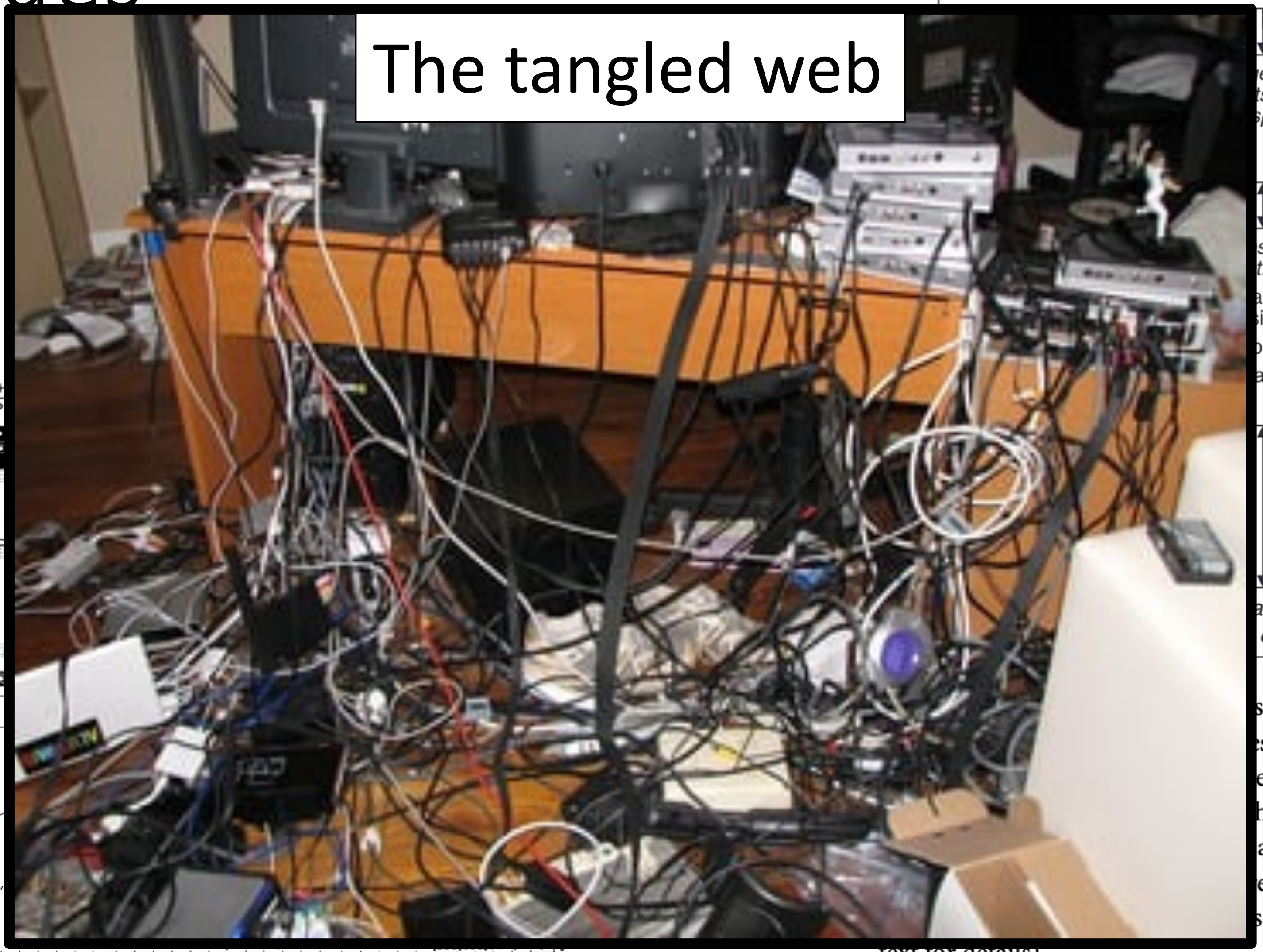

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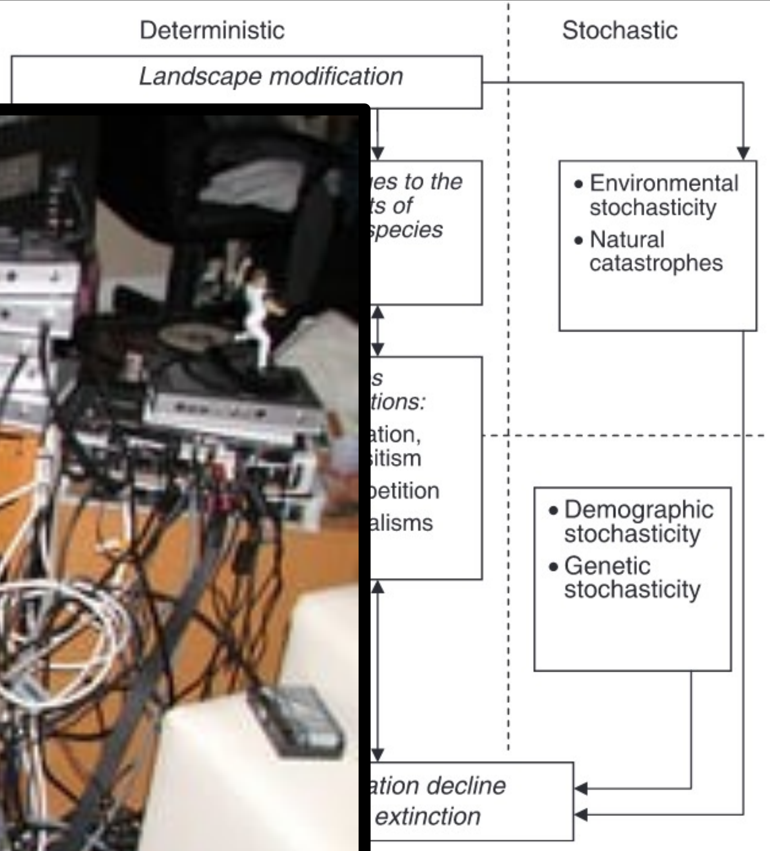

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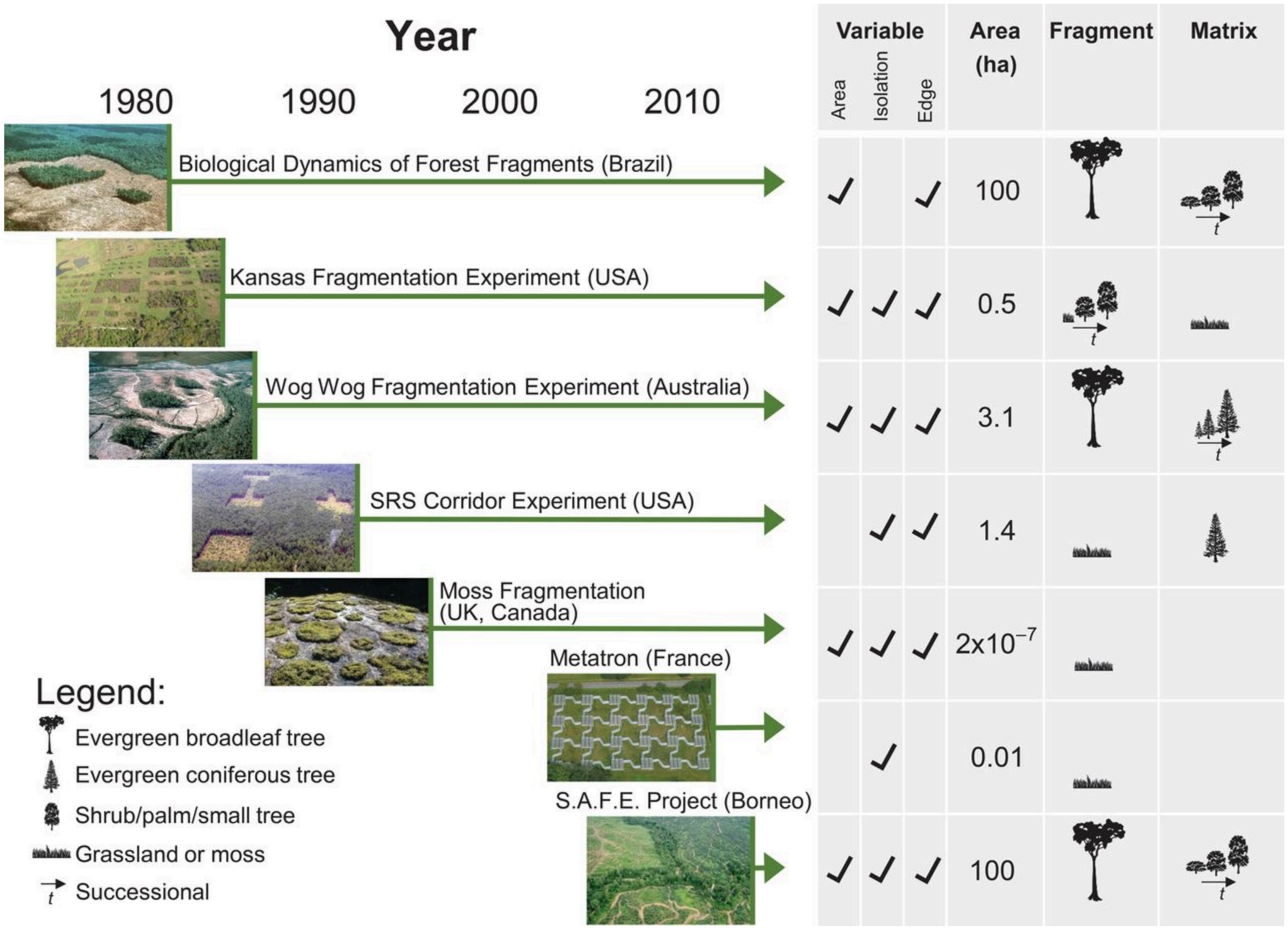
The big issues

How to go about untangling the web?

- Ideally, experiments!
  - But….

Experiments are few and far between, and even these large-scale manipulations are limited



Haddad et al. 2015. Science

Experiments are few and far between, and even these large-scale manipulations are limited

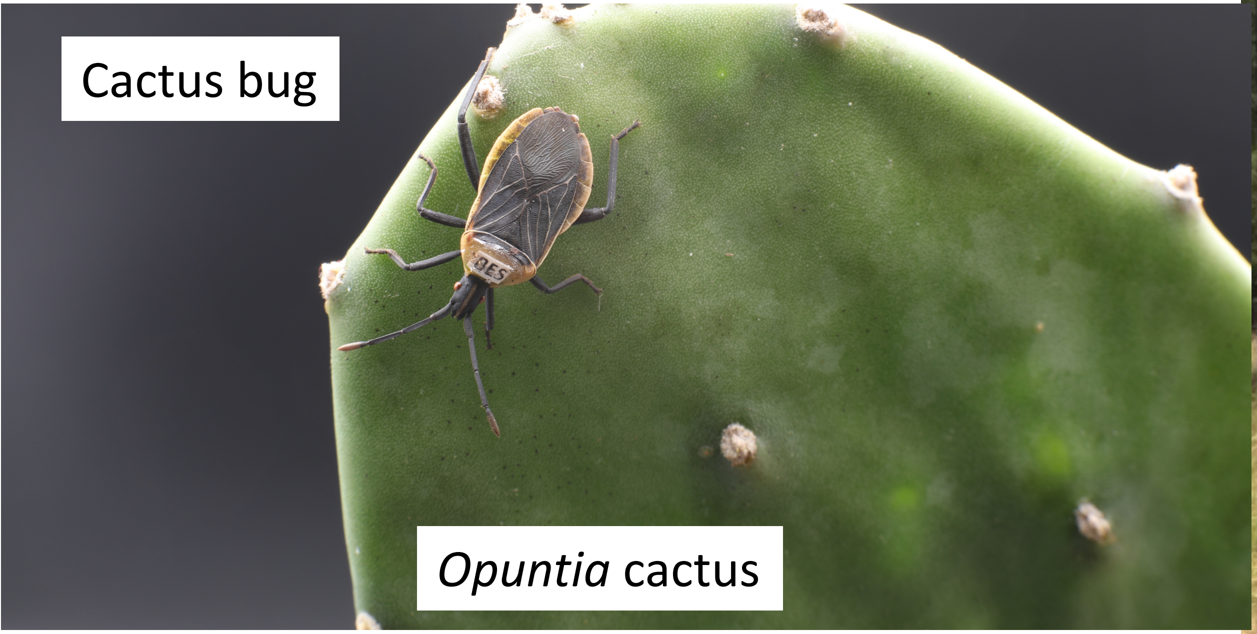
Kansas Fragmentation Experiment

Some argue that the experiment has a sample size of 1

Many patches, many sizes, many distances;
1 landscape with a particular configuration

Photos courtesy of Bob Holt

Add one to the list



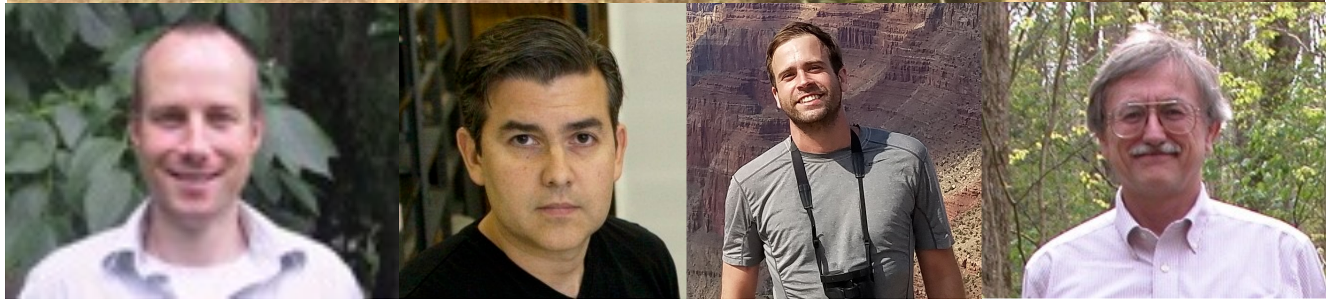
50 m × 50 m Replicate Landscapes

Factorial design of

2 Habitat Loss Treatments

2 Fragmentation Intensity Treatments

2 Matrix Treatments



The effect of lands surrounding fragmented landscapes: theory development and novel experimental tests

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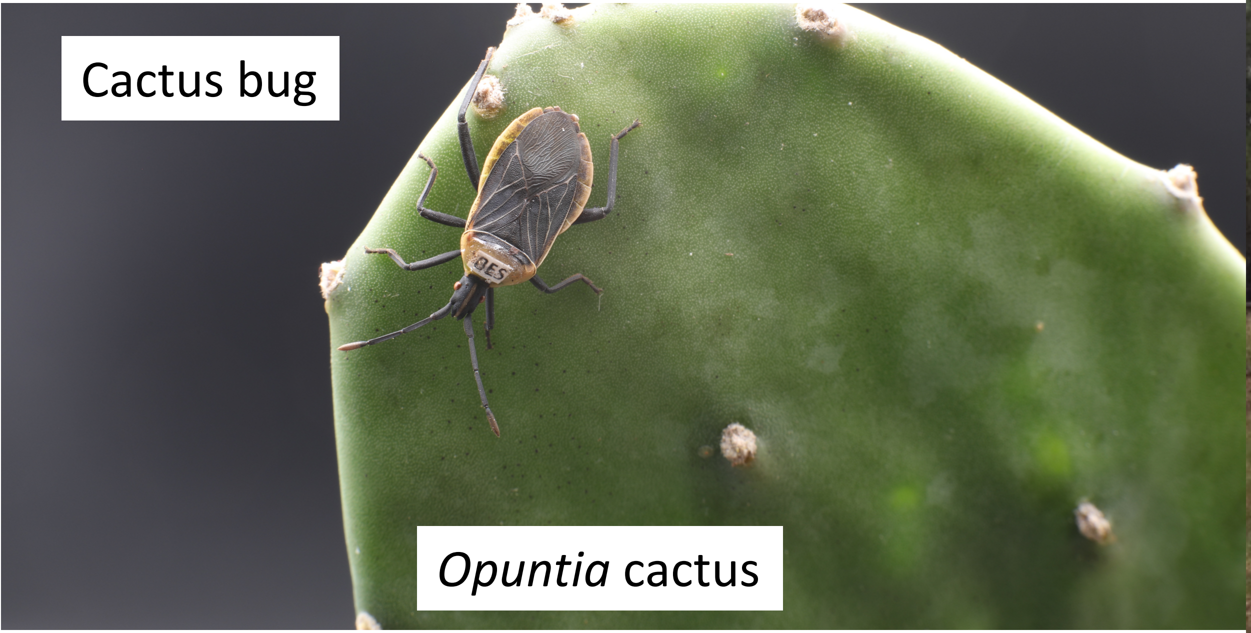

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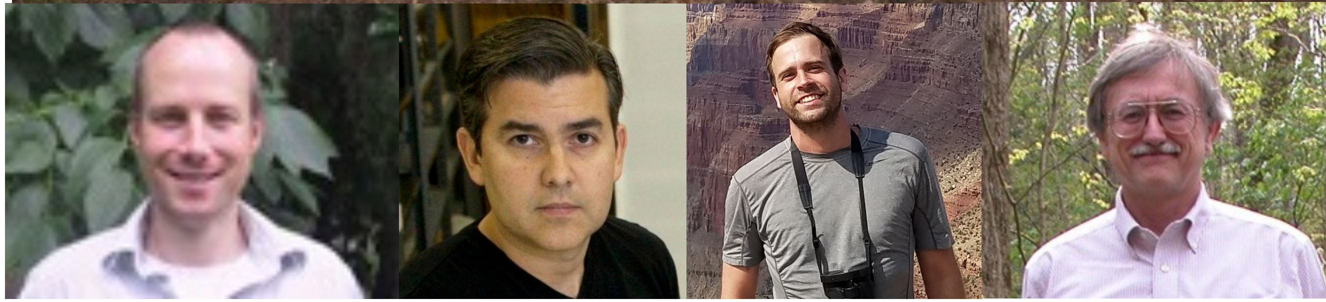

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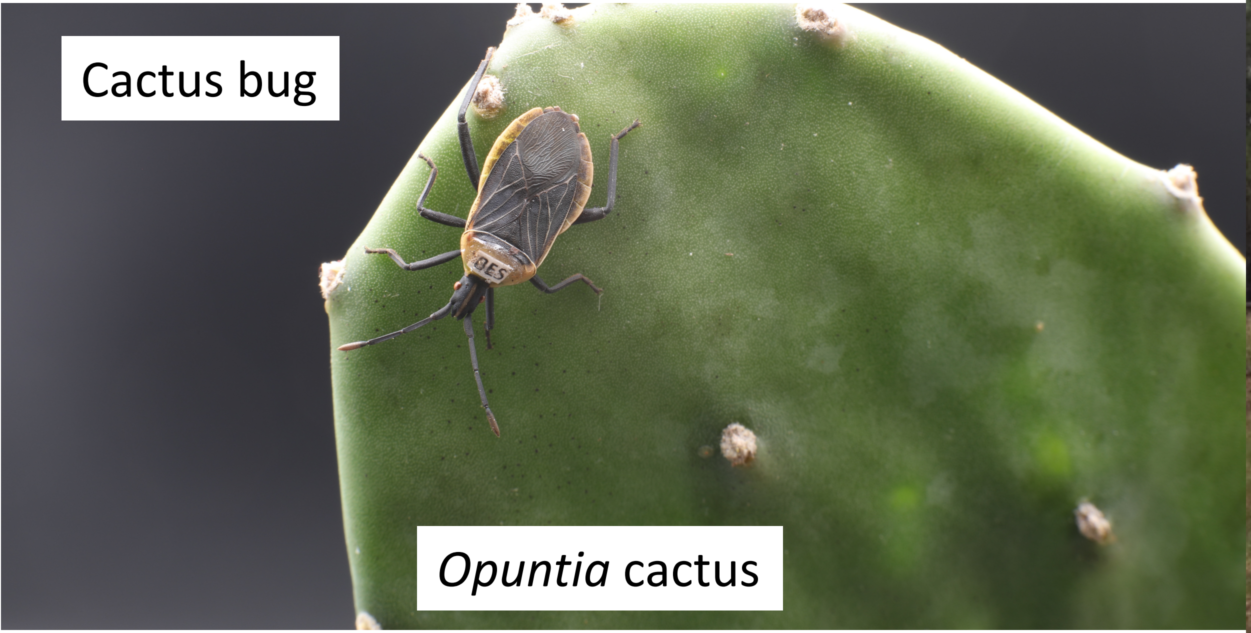

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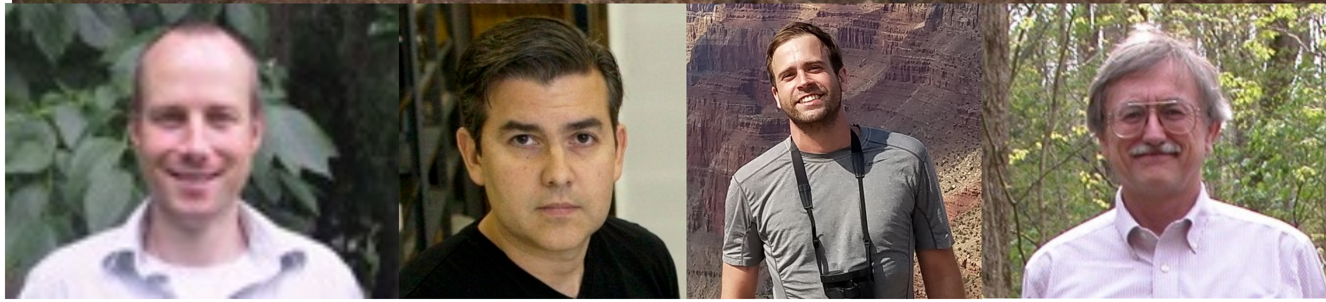


The effect of lands surrounding fragmented landscapes: theory development and novel experimental tests

When we can’t do experiments…*MODELS!*

- We need a way to take local scale information and make large scale inferences.

- We need a way to answer questions like

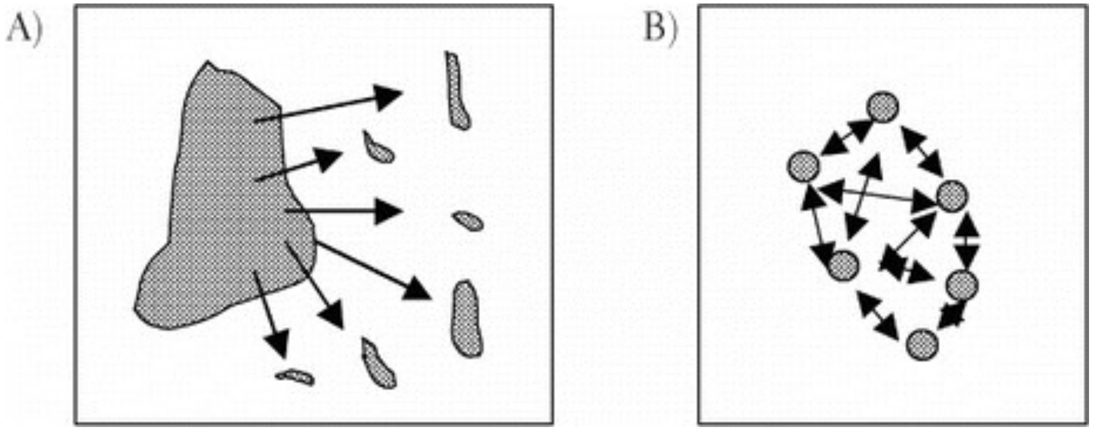
  - What would happen if could manipulate factor X?
  - If things don’t change, what are our long-term expectations for species?
  - Fragmentation occurs, and we observe some effect. Can we infer the cause?
  - Does local effect X matter at larger scales?

- These questions are in the domain of models

Island Biogeography Models

Metapopulation Models

$$\frac{dp}{dt} = cp(1-p) - ep$$



Maschinski and Quintana-Ascencio. 2016.

When we can’t do experiments…*MODELS!*

We have models

They are about extinction risk and establishment success

Their focus is on characteristics of the patch

I argue it’s time we have models that put the focus on individuals

Island Biogeography Models

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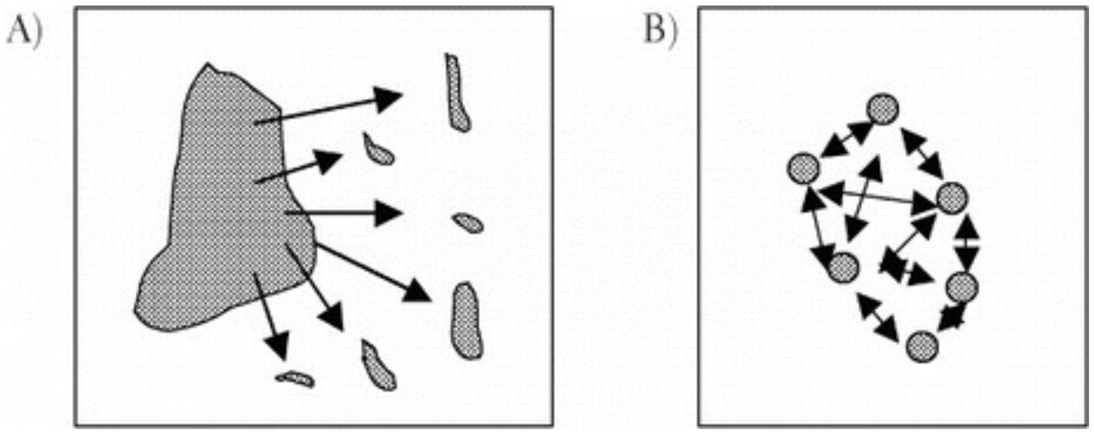
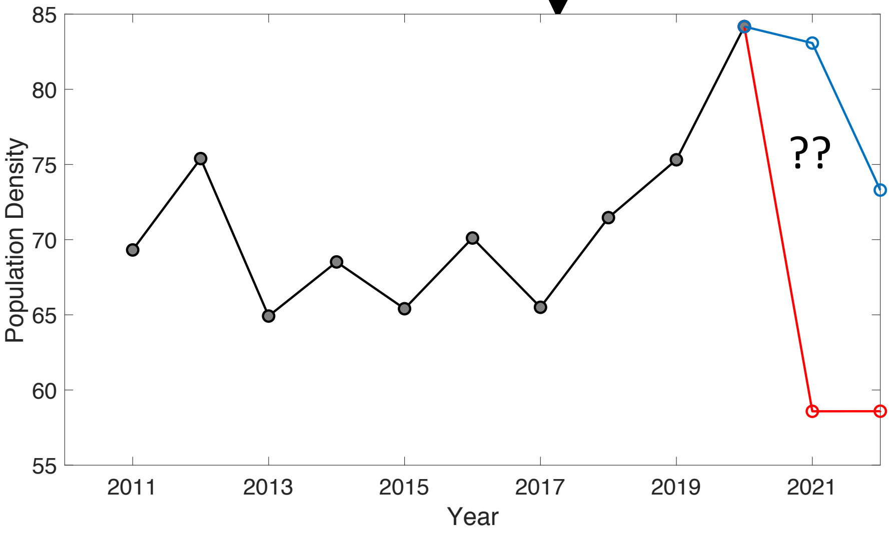


Maschinski and Quintana-Ascencio. 2016.

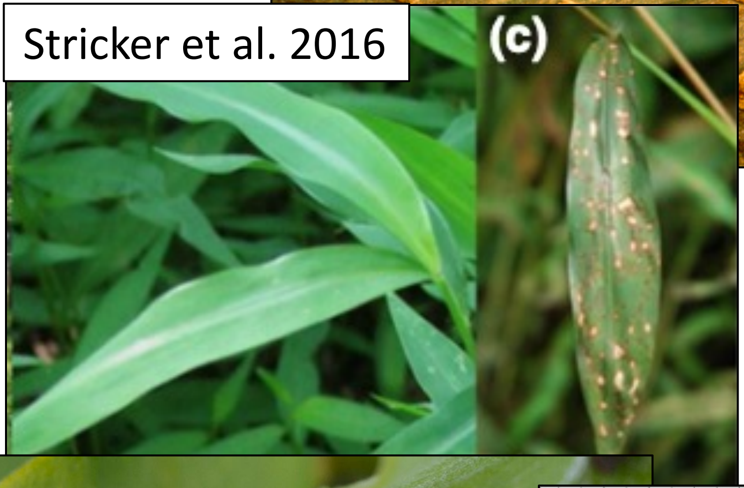
Goal: Develop models and theory that

- 1. Makes projections about population growth and decline
- 2. Can scale up local information to predict and infer processes at larger scales
- 3. Is flexible enough to include many factors
- 4. Is interpretable and provides understanding

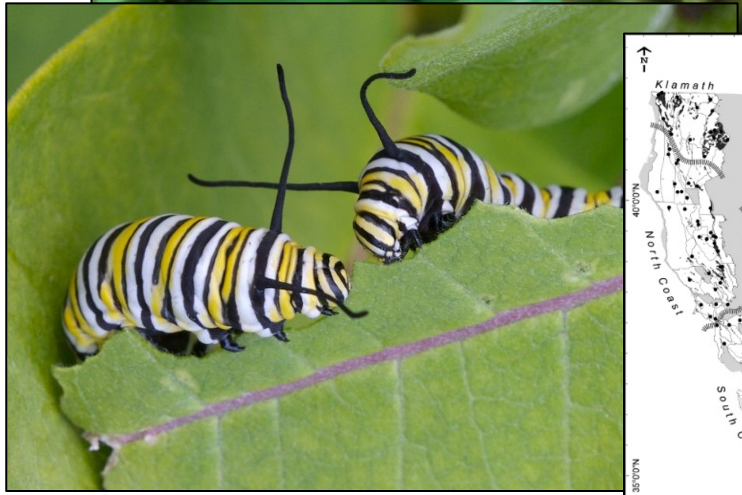


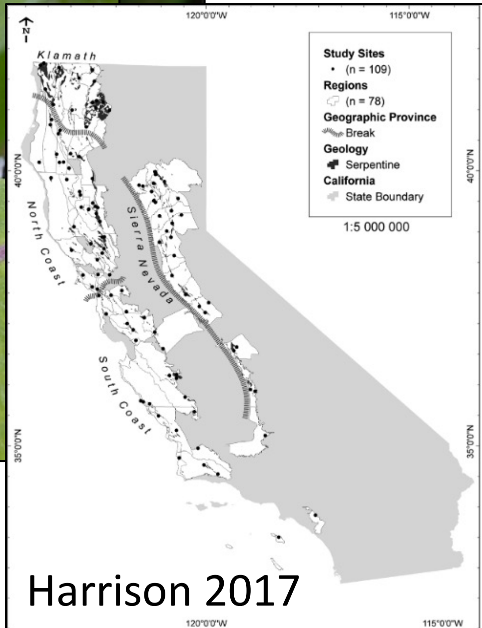
Goal: Develop models and theory that

- Applicable beyond habitat fragmentation
- Plant-pathogen interactions
- Plant-specialist herbivore interactions
- Species adapted to naturally patchy environments



Stricker et al. 2016

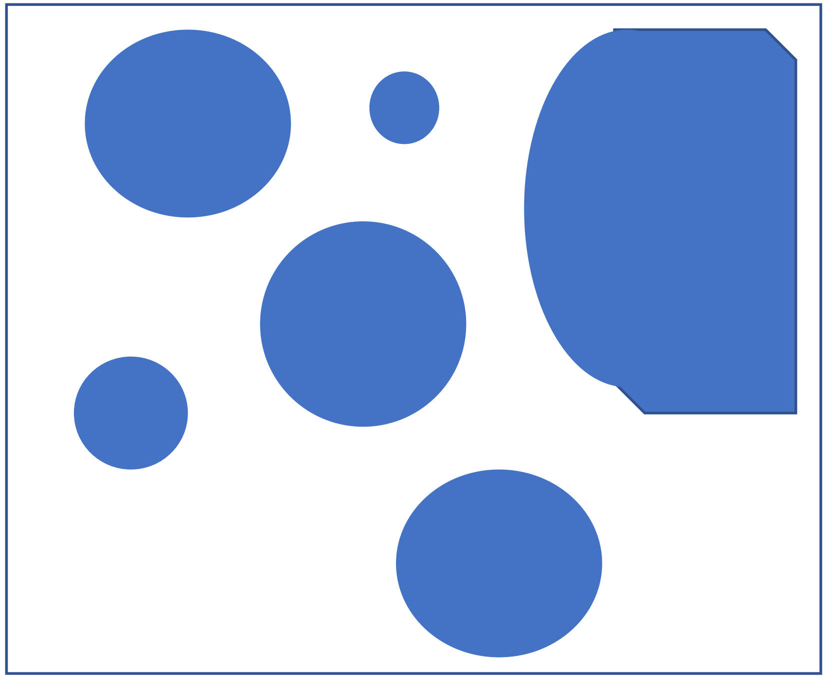




Harrison 2017

Perspectives and Measures

- The dominant perspective (and data collected) is at the level of the patch
- Patches will be our focal unit



n patches

Patches have size S_i

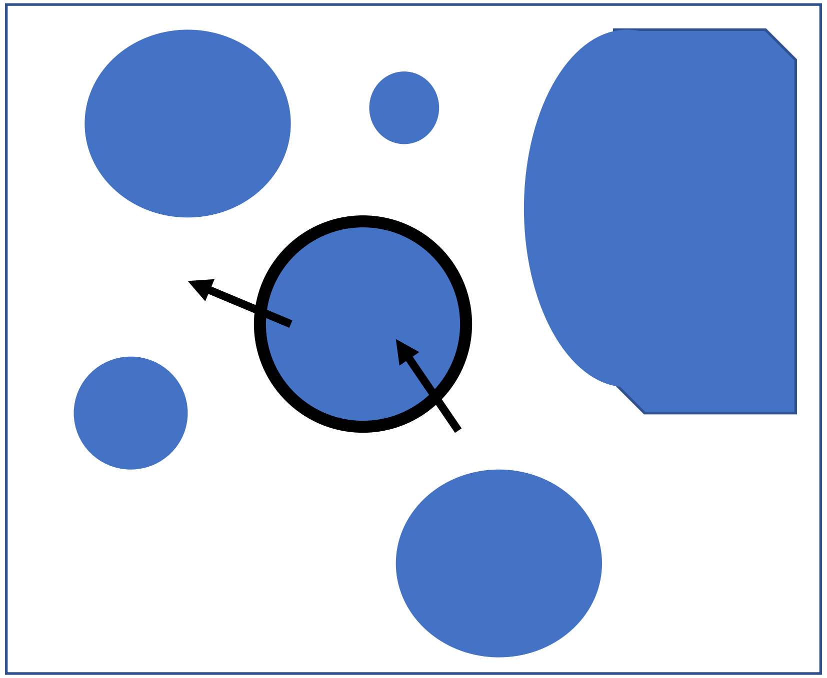
Patches have density N_i

Assume a vector of *factors*, **E**, are important for the biology of a species

Local Dynamics

- The change in numbers of inds. in any patch results from 4 processes:
  - 1. Births
  - 2. Deaths
  - 3. Arrival of new individuals (immigration)
  - 4. Loss because individuals leave (emigration)

$$\frac{dN_i}{dt} = \frac{\#\,\text{births}}{\text{time}} - \frac{\#\,\text{deaths}}{\text{time}} - \frac{\#\,\text{emigrants}}{\text{time}} + \frac{\#\,\text{immigrants}}{\text{time}}$$



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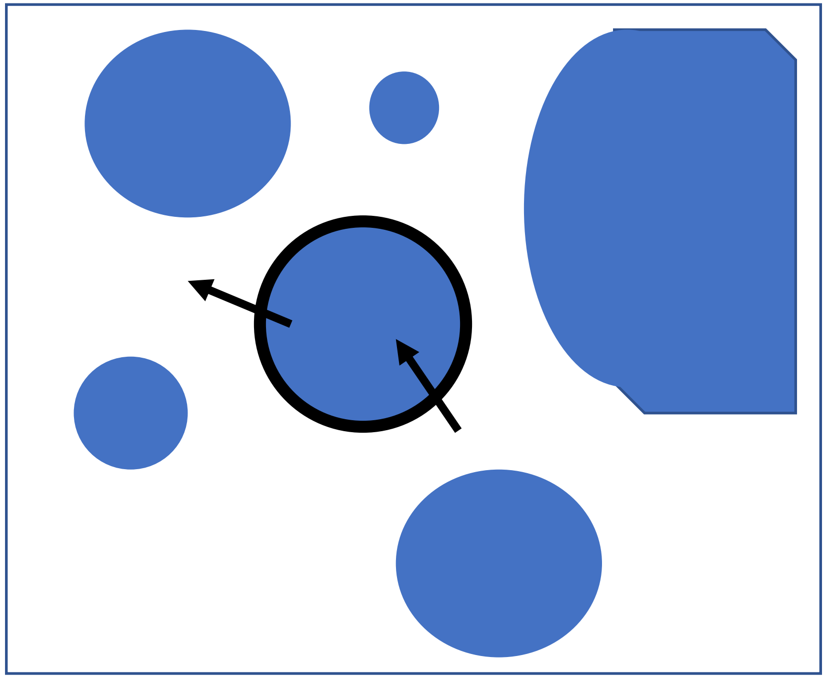

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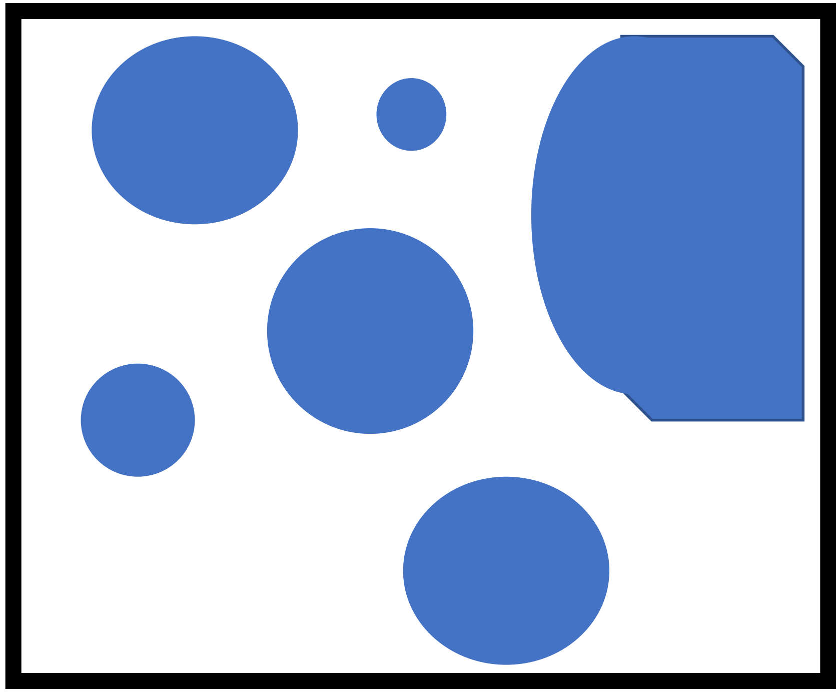
$$\frac{dN_i}{dt} = \left[B_i(\mathbf{E}) - D_i(\mathbf{E}) - M_i(\mathbf{E})\right]N_i + I_i(\mathbf{E})$$

Regional Dynamics

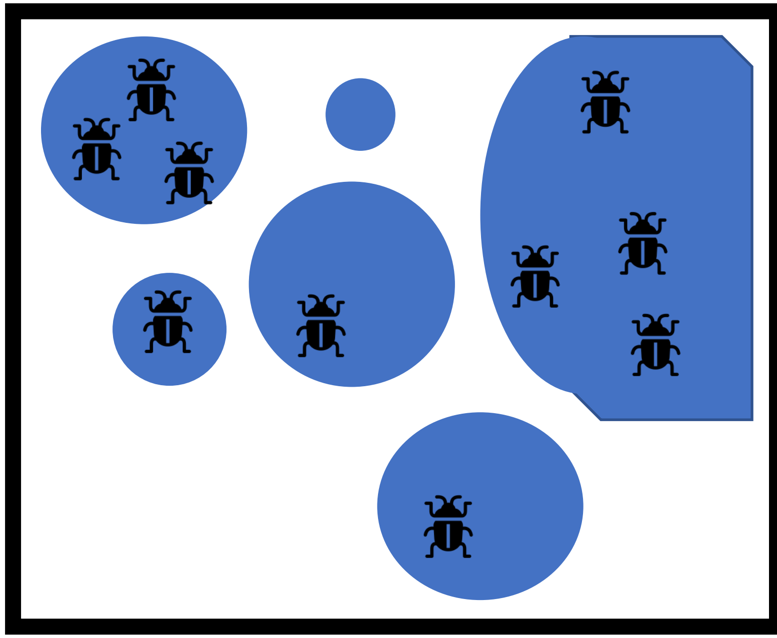
- What is the biology governing population growth when we treat **all local populations as if they were one**, in the aggregate?

$$\frac{d\bar{N}}{dt} = g(\mathbf{E})\bar{N}$$

Population density at the landscape scale

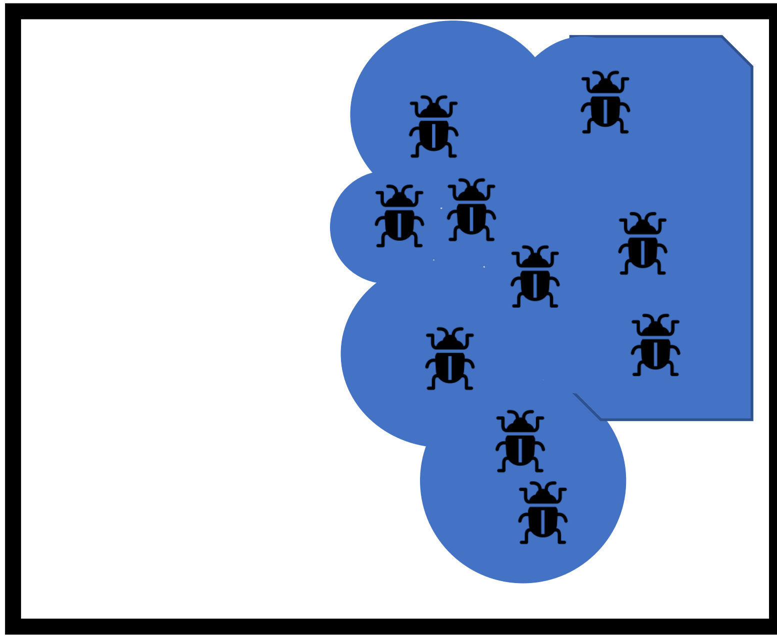


Regional Density



$$\bar{N} = \frac{\text{total individuals on landscape}}{\text{total area in landscape}} = \frac{\sum_{i=1}^{n} S_i N_i}{\sum_{i=1}^{n} S_i}$$

Regional Density



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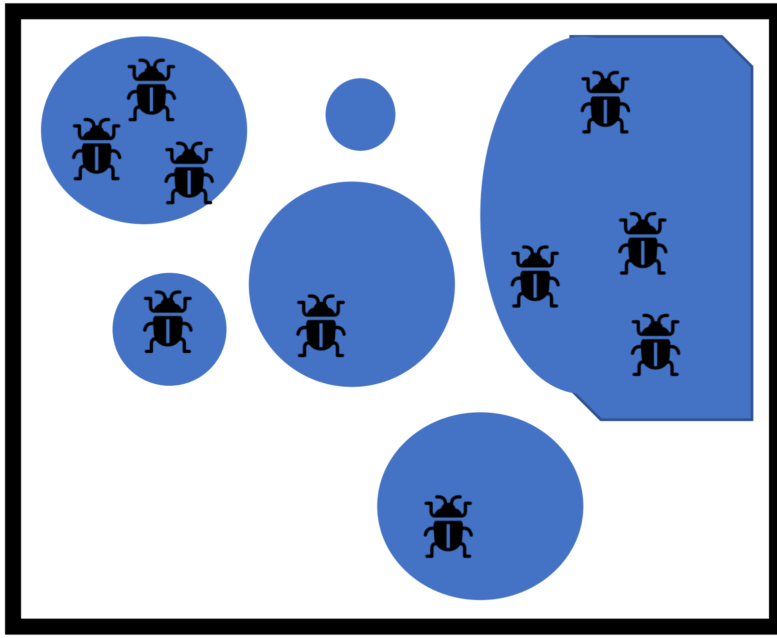


$$\bar{N} = \frac{\text{total individuals on landscape}}{\text{total area in landscape}} = \frac{\sum_{i=1}^{n} S_i N_i}{\sum_{i=1}^{n} S_i}$$

We can rewrite this as a weighted average of the local densities

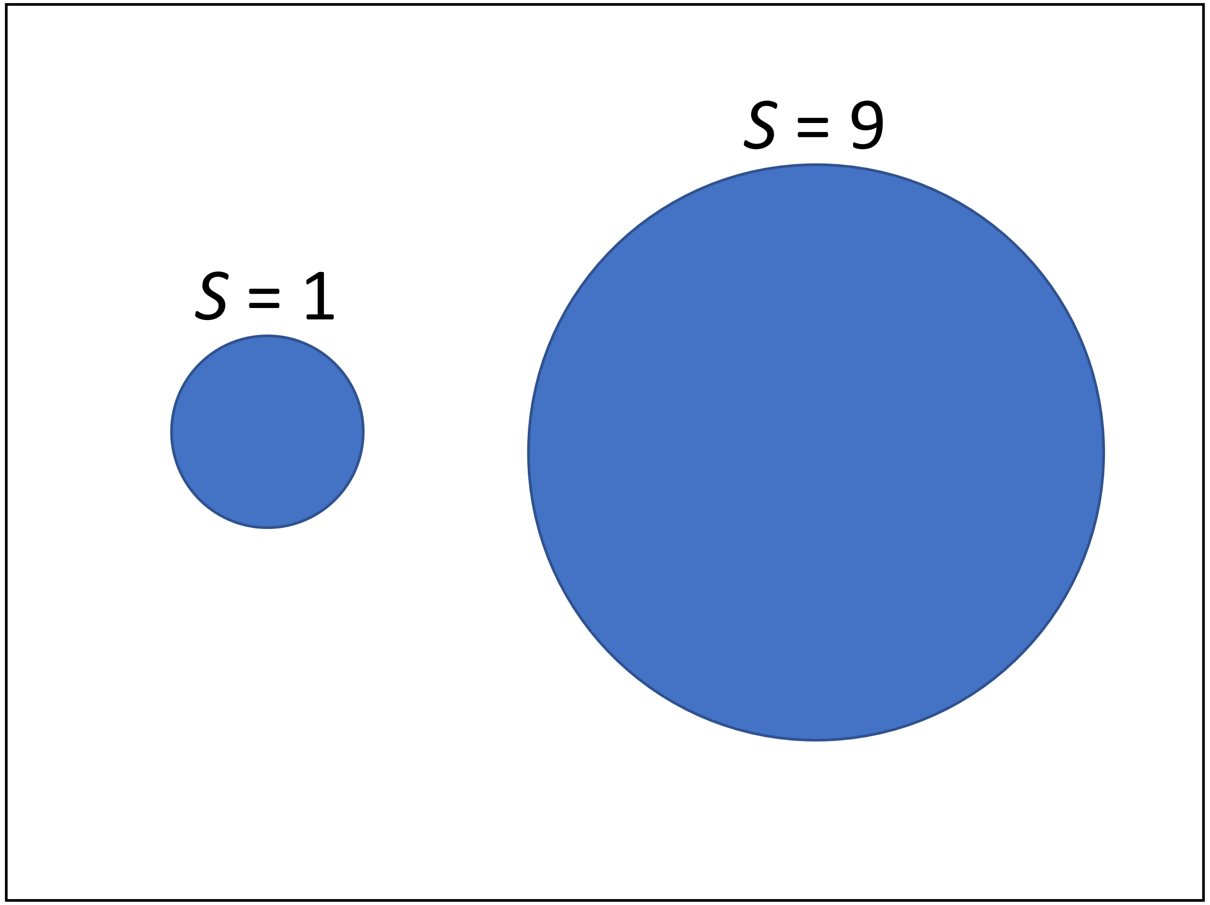
$$\bar{N} = \sum_{i=1}^{n} w_i N_i$$

Weights: proportion of total habitat in patch *i*

$$w_i = \frac{S_i}{\sum_{j=1}^{n} S_j}$$

What's with the weighting factors?

Suppose you want to sample the habitat (blue)

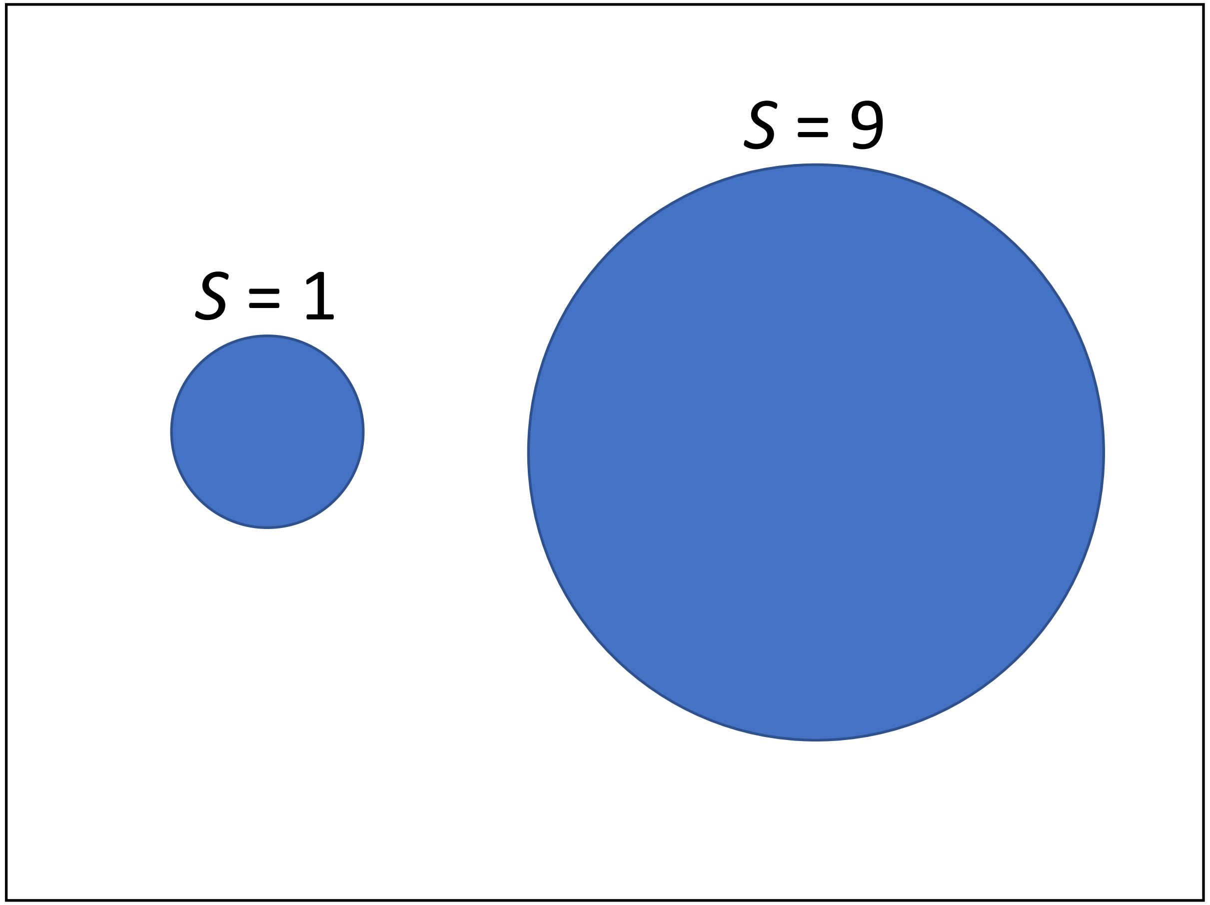


What's with the weighting factors?

Suppose you want to sample the habitat (blue)

Random sampling

Expectation:
9x more sampling points in large patch than small patch



Regional Dynamics

- First lesson:
  - If patches are different sizes
  - Large patches contribute more to dynamics at the larger scale, all else being equal.
  - A patch-based measure is biased at the level of all habitat
  - Need to correct for this bias with

    Weights = proportion of overall habitat in each patch
  - IMPORTANT: All the following averages are weighted this way

Weights

$$w_i = \frac{S_i}{\sum_{i=1}^{n} S_i}$$

$$\bar{X} = \sum_{i=1}^{n} w_i X_i$$

Consequences of weighted average

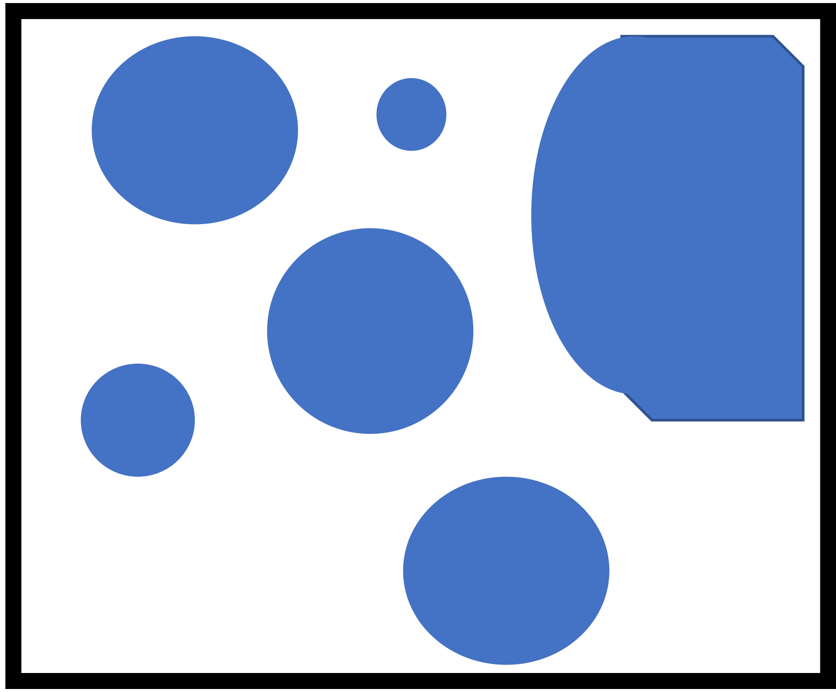
- First prediction: regional population dynamics will be most similar to dynamics in large patches, *ceteris paribus*

Regional Dynamics

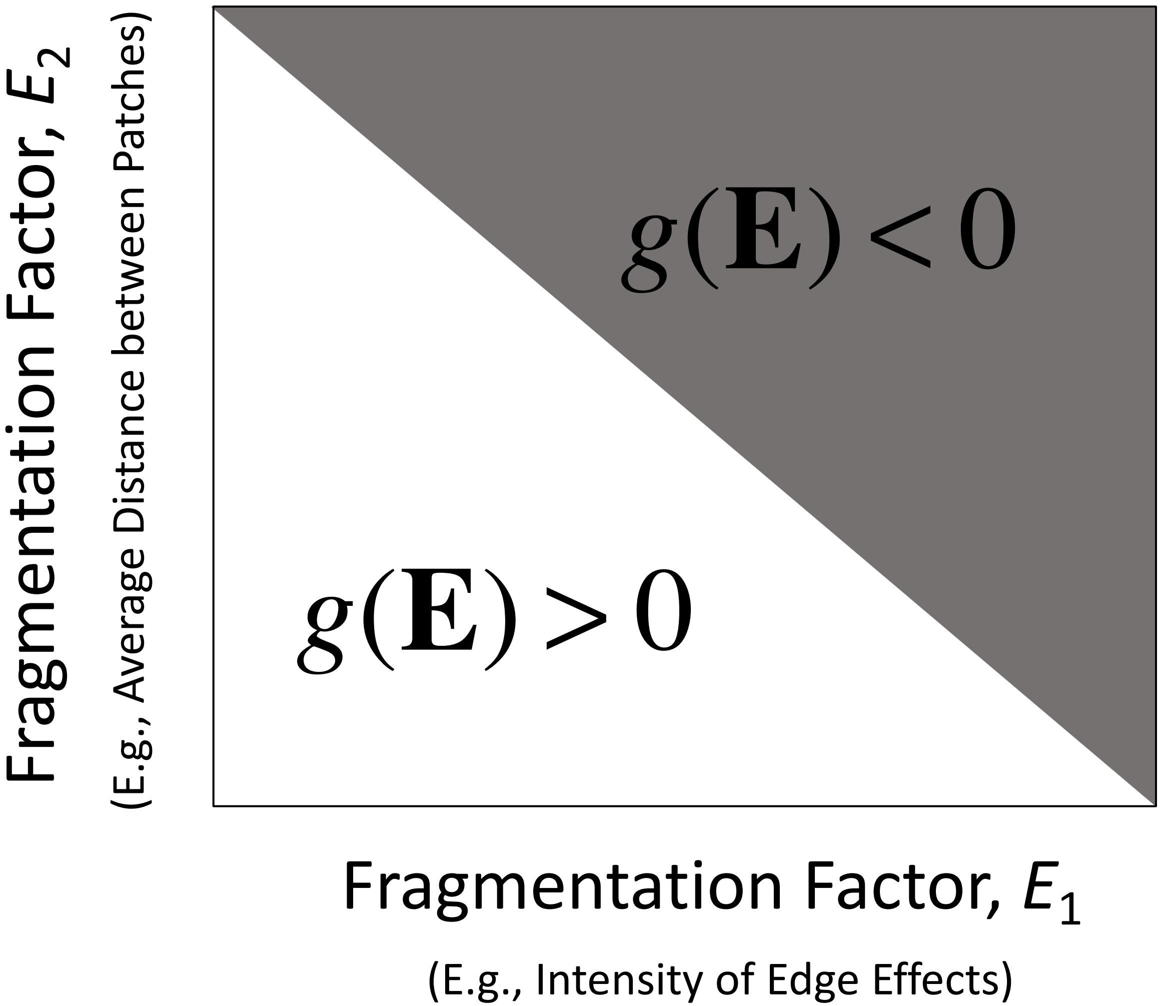
- What is the biology governing population growth when we treat **all local populations as if they were one**, in the aggregate?

$$\frac{d\bar{N}}{dt} = \boxed{g(\mathbf{E})}\bar{N}$$

Per-capita growth rate applied to
the entire population
= the biology



Per-capita Growth Rate at Regional Scale and the Niche



In white area, species persists

In gray area, species goes extinct

Conceptually analogous to Hutchinson's Fundamental Niche

But, we apply it to spatial factors predominate in studies of fragmentation and patchy environments

Regional Dynamics

$$\frac{d\bar{N}}{dt} = \boxed{\left\{ \underbrace{\bar{B} - \bar{D} - \overline{\delta M}}_{\text{Productivity of the average patch}} + \underbrace{\mathrm{Cov}\left(v_i, B_i - D_i - \delta_i M_i\right)}_{\text{Fitness-density covariance}} \right\}} \bar{N}$$

$= g(\mathbf{E})$, the per-capita growth rate at landscape scale

Regional growth rates have two components:

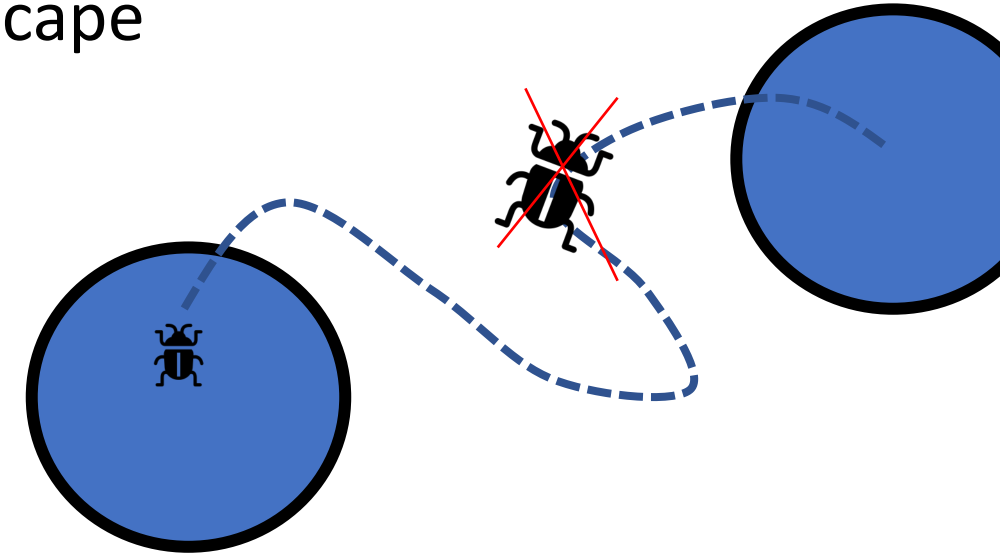
1. Productivity of the average patch
2. Fitness-density covariance

Average Patch Productivity

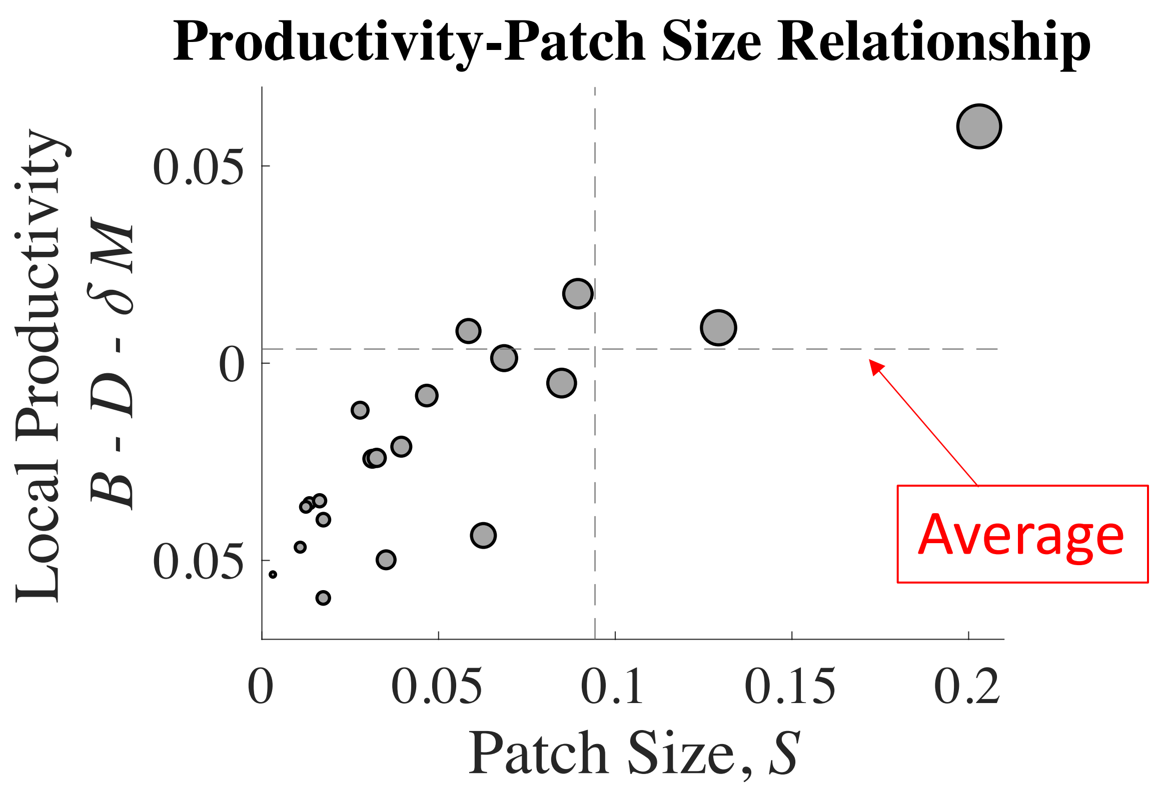
$$\underbrace{\overline{B} - \overline{D} - \overline{\delta M}}_{\text{Productivity of the average patch}}$$

δ = Mortality Fraction During Dispersal

- Measure of the average quality of the landscape
- Patch-average birth rate
- Patch-average death rate
- Rate of dispersal-induced mortality



Average Patch Productivity?



How does one measure it?

Go to each patch, tag individuals, and do demographic analysis.

How many offspring do individuals have?

B

What is their risk of mortality?

D

How frequently do they leave? What is their risk of mortality once leaving?

δM

A note on movement and mortality

$$\overline{\delta M} = \bar{\delta}\bar{M} + \mathrm{Cov}(\delta_i, M_i)$$

Math translation:
Average rate of mortality-induced dispersal =

Average mortality risk during dispersal*Average dispersal rate

+ correlations between mortality risk and dispersal rate

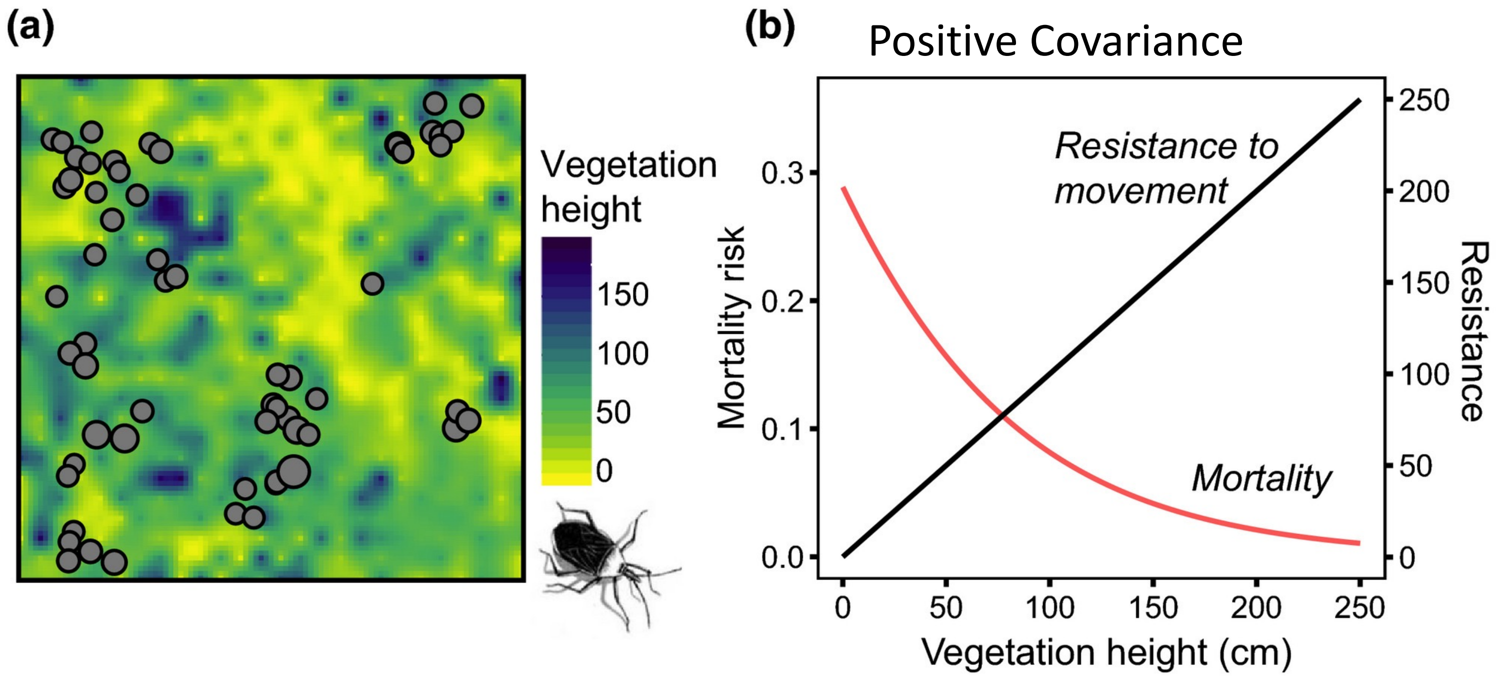
Biologically Speaking

Patches with combination of high emigration rates and high risk of mortality will be low productivity.

These patches are a “drag” on regional population growth.
Low value

A note on movement and mortality

$$\overline{\delta M} = \bar{\delta}\bar{M} + \mathrm{Cov}(\delta_i, M_i)$$



Resistance inverse of *M*

Fletcher et al. 2018. Ecol Letters.

Fitness-Density covariance

$$\frac{d\bar{N}}{dt} = \left\{ \underbrace{\bar{B} - \bar{D} + \overline{\delta M}}_{\text{Productivity of the average patch}} + \boxed{\underbrace{\mathrm{Cov}\left(v_i, B_i - D_i - \delta_i M_i\right)}_{\text{Fitness-density covariance}}} \right\} \bar{N}$$

$$v_i = \frac{N_i}{\bar{N}}$$

Relative density in a patch

> 1 denser than average

< 1 less dense than average

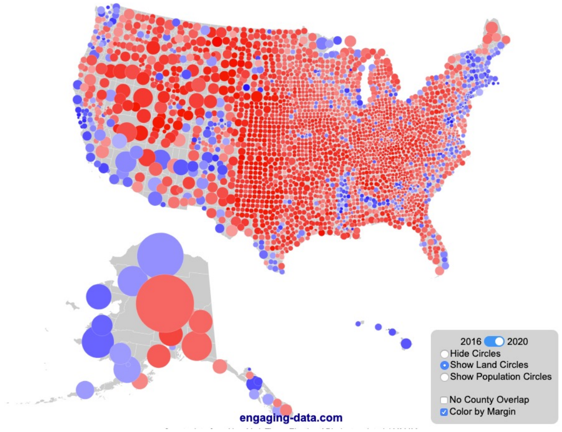
Fitness-Density covariance

$$\underbrace{\mathrm{Cov}\left(\nu_i, B_i - D_i - \delta_i M_i\right)}_{\text{Fitness-density covariance}}$$

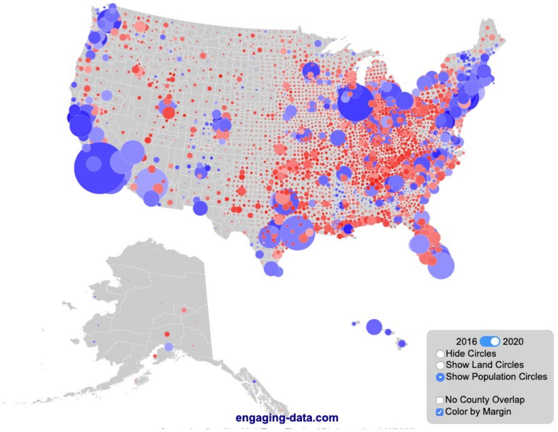
- Quantifies whether individuals are concentrated in high or low productivity patches
- Functionally, it moves us from a patch perspective to an individual perspective
- If no individuals are in a patch, we should discount that patch

Cov(vote diff, vote pop)

Patch Perspective $\longrightarrow$ Individual Perspective



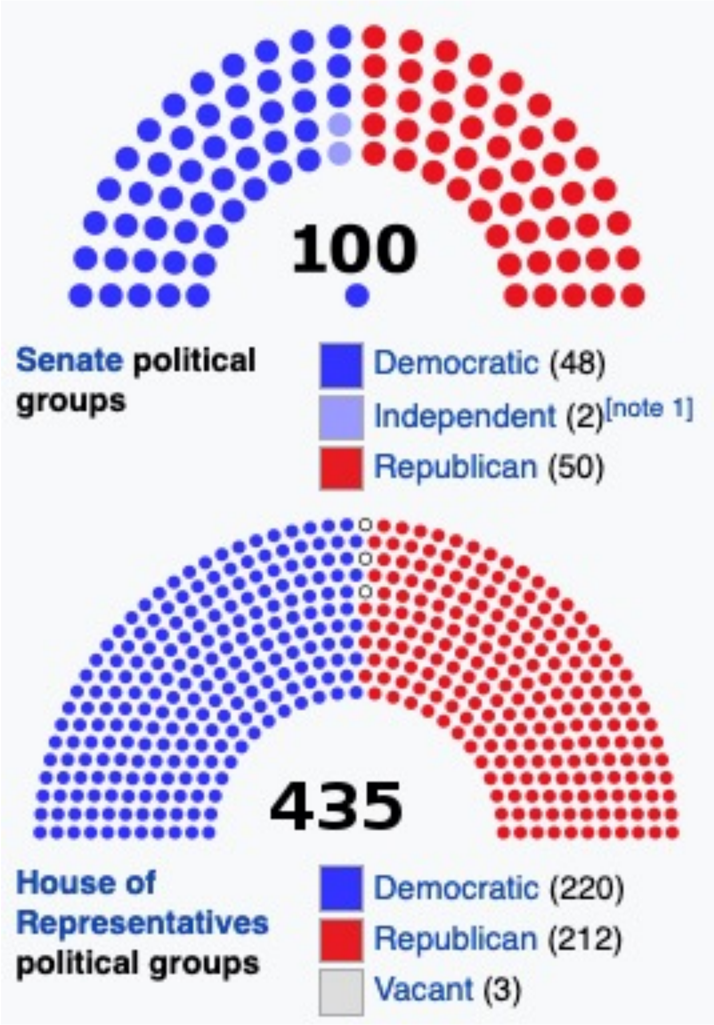
Circles = Area
2020 Election



Circles = Voting Pop
2020 Election

$$\boxed{\begin{aligned}\mathrm{Cov}(X,Y) &= \sum_{i=1}^{n} w_i\left(X_i - \bar{X}\right)\left(Y_i - \bar{Y}\right)\\ &= \mathrm{Corr}(X,Y)SD(X)SD(Y)\end{aligned}}$$

Fitness-Density covariance



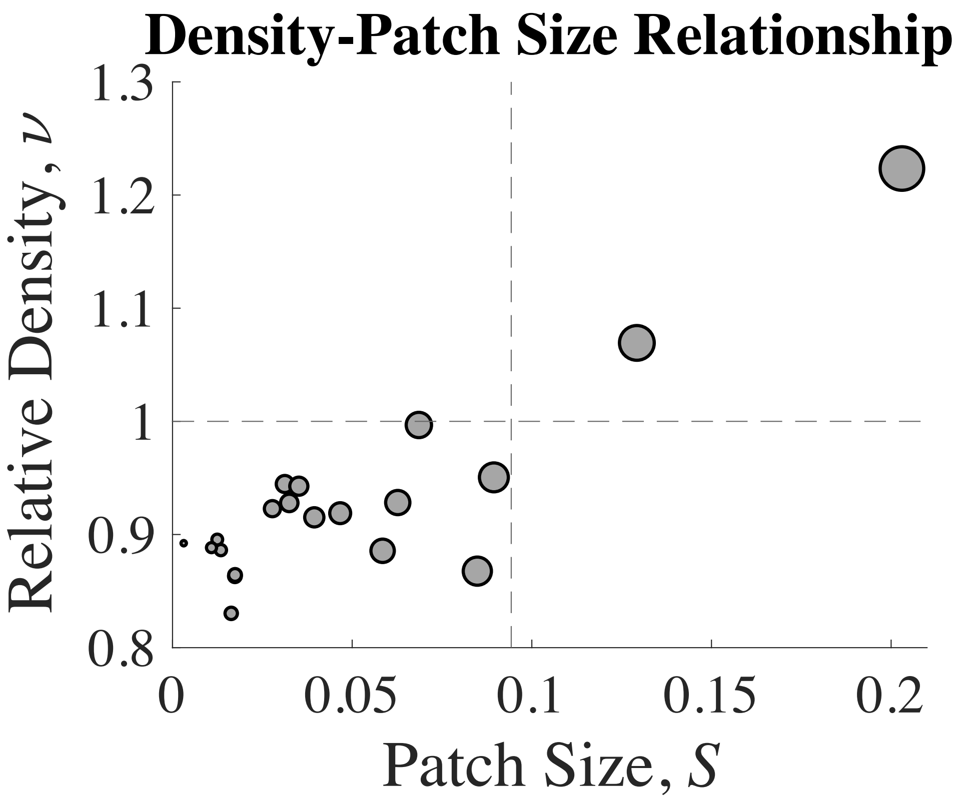
Wikipedia

Patch (state) Perspective

Individual Perspective

- Quantifies whether individuals are concentrated in high or low productivity patches
- Functionally, it moves us from a patch perspective to an individual perspective
- If no individuals are in a patch, we should discount that patch

Quantifying Fitness-Density Covariance

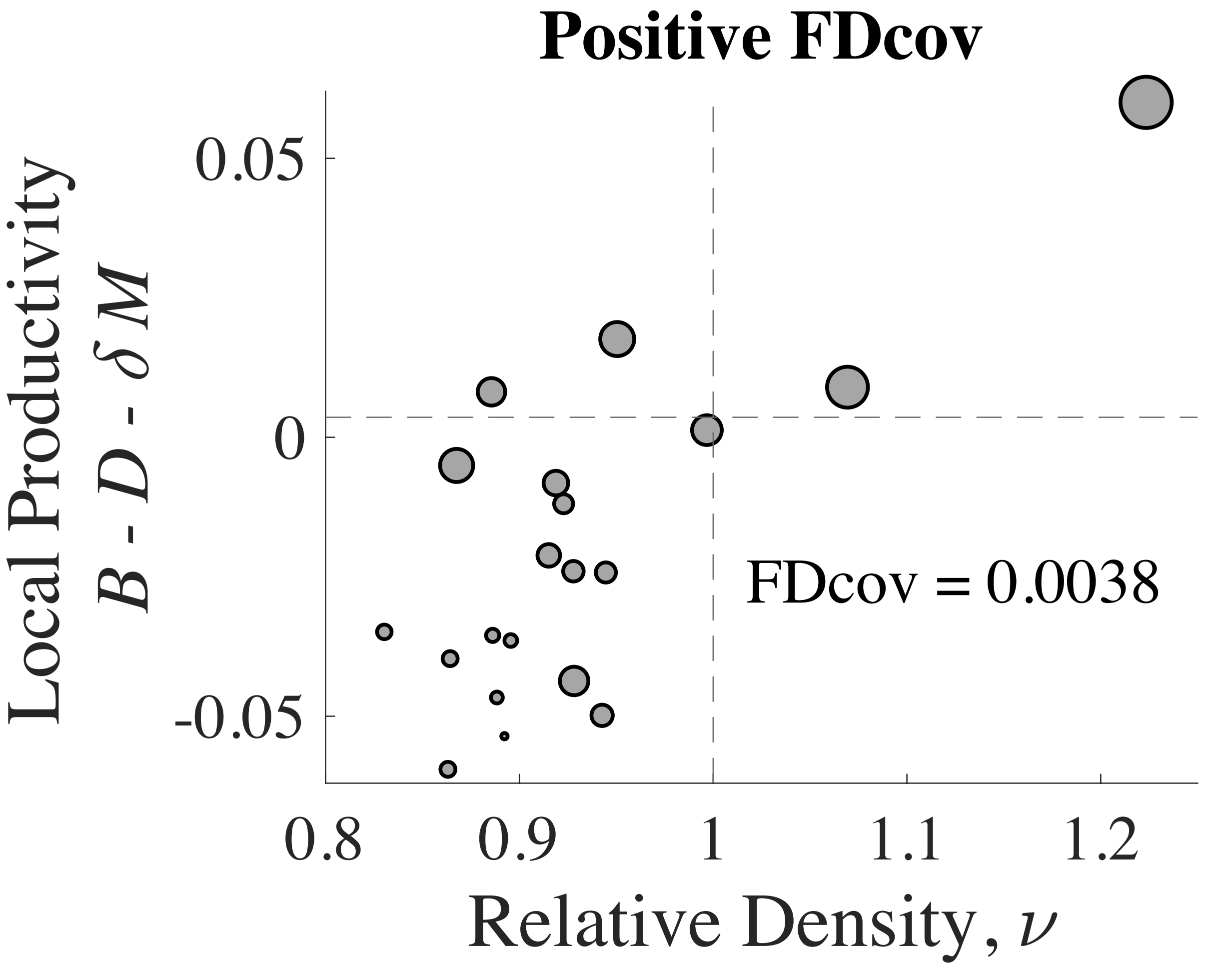


1. Sample density in each patch.

2. Determine relative density in a patch

$$\nu_i = \frac{N_i}{\bar{N}}$$

3. Calculate the covariance



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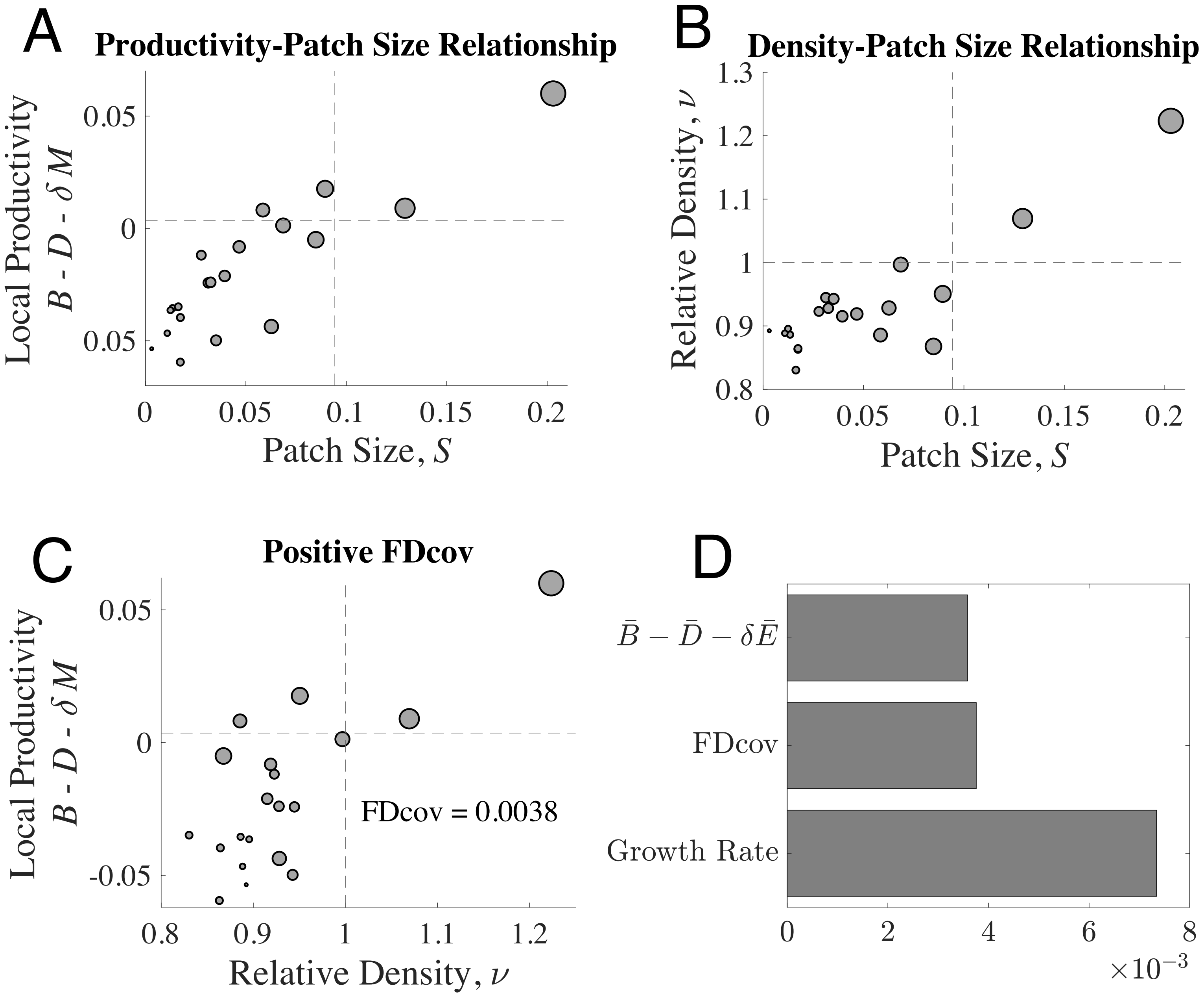
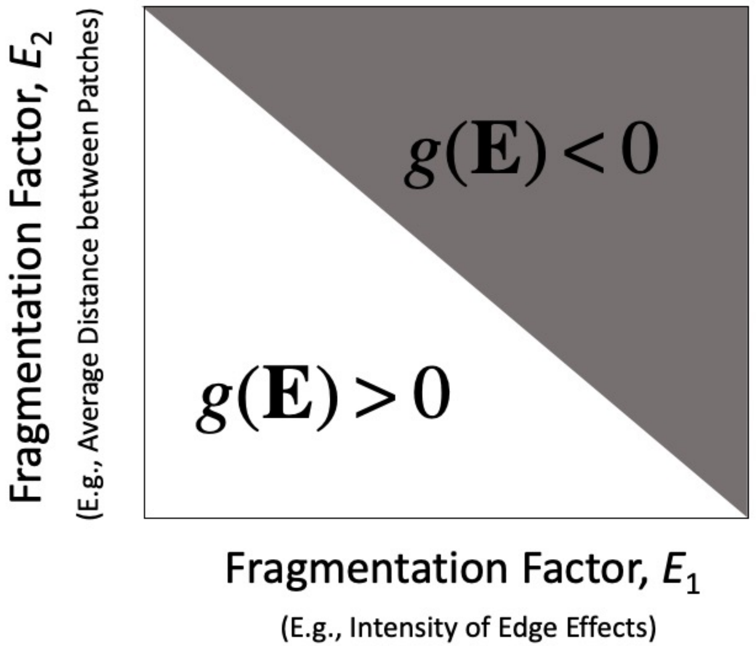
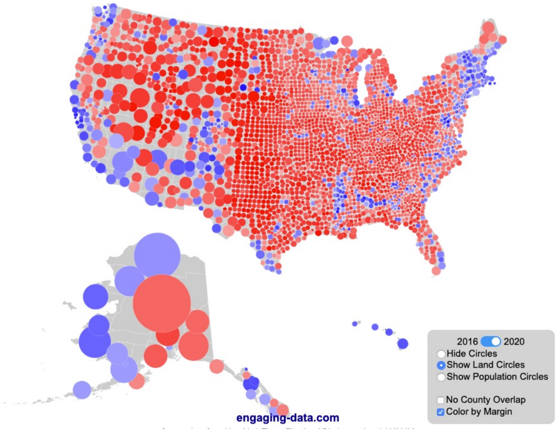


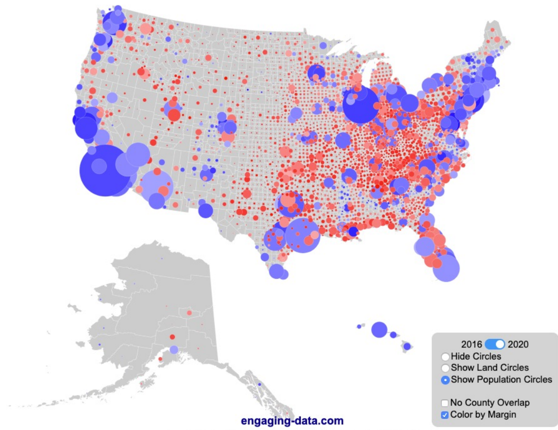
A
Productivity-Patch Size Relationship
Local Productivity
B - D - δM
0.05
0
0.05
0
0.05
0.1
0.15
0.2
Patch Size, S
B
Density-Patch Size Relationship
Relative Density, ν
1.3
1.2
1.1
1
0.9
0.8
0
0.05
0.1
0.15
0.2
Patch Size, S
C
Positive FDcov
Local Productivity
B - D - δM
0.05
0
-0.05
FDcov = 0.0038
0.8
0.9
1
1.1
1.2
Relative Density, ν
D
$\bar{B} - \bar{D} - \delta\bar{E}$
FDcov
Growth Rate
0
2
4
6
8
$\times 10^{-3}$

Conclusions about this section

- A flexible model
- **E** defines the niche factors for species in fragmented landscapes. It will likely be complex (what’s new, it’s ecology!)
- All measures are quantifiable, in principle
- For those that are hard to quantify: assume, predict, evaluate, and repeat.
- Model that moves from place-based measures and individual-based measures



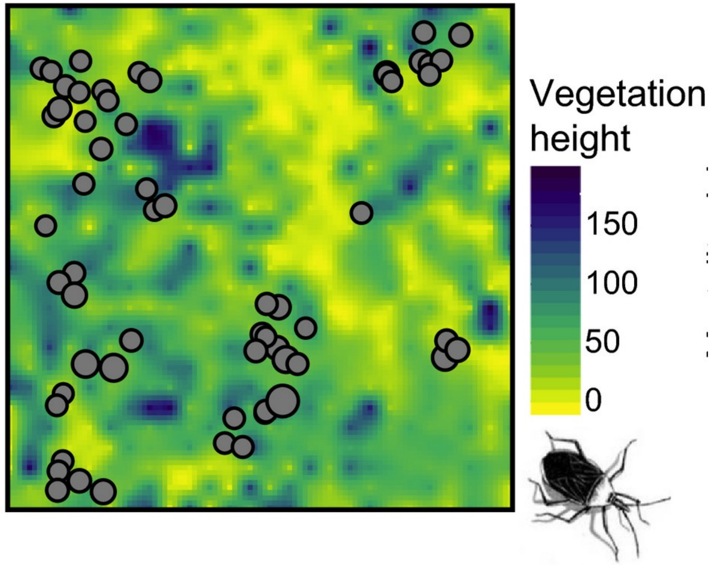




An Example

The matrix.

How does it influence species' responses to fragmentation?



Fletcher et al. 2018. Ecol Letters

The effect of lands surrounding fragmented landscapes: theory development and novel experimental tests

The matrix? Does it matter?

- Around 2000, researchers began asking the question.

BIOLOGICAL CONSERVATION 135 (2007) 212–222

available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/biocon

ELSEVIER

BIOLOGICAL CONSERVATION

Does the matrix matter? A forest primate in a complex agricultural landscape

Julie Anderson[a,b,], J. Marcus Rowcliffe[a], Guy Cowlishaw[a]*

Journal of Biogeography (*J. Biogeogr.*) (2006) **33**, 1791–1792

COMMENTARY

Forest fragmentation and matrix effects: the matrix *does* matter

VOL. 158, NO. 1 THE AMERICAN NATURALIST JULY 2001

The Matrix Matters: Effective Isolation in Fragmented Landscapes

Taylor H. Ricketts*

Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter?

Helen T. Murphy and Jon Lovett-Doust

The relative influence of forest loss and fragmentation on insectivorous bats: does the type of matrix matter?

Annia Rodríguez-San Pedro · Javier A. Simonetti

Biodivers Conserv (2010) 19:1205–1223
DOI 10.1007/s10531-009-9750-z

REVIEW PAPER

Does the type of matrix matter? A quantitative review of the evidence

Jayme Augusto Prevedello · Marcus Vinícius Vieira

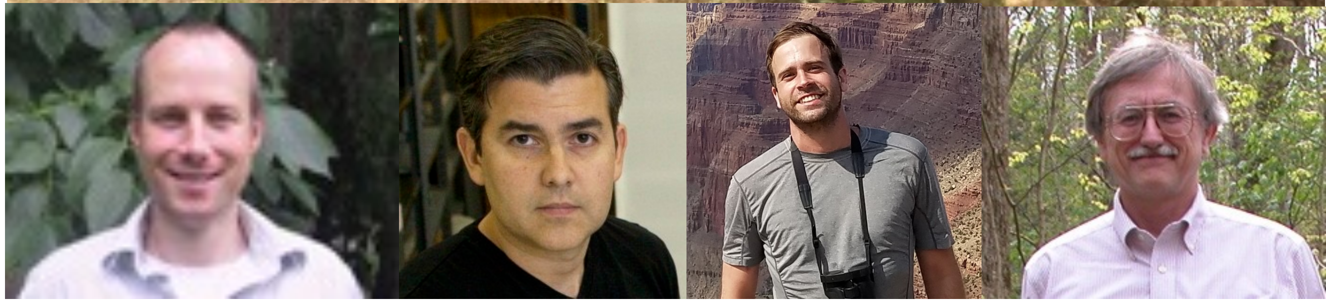
An Example

The matrix.

How does it influence species' responses to fragmentation?

What we know:

Statistical models predicting abundance and richness in patches perform better with matrix features included.



The effect of lands surrounding fragmented landscapes: theory development and novel experimental tests

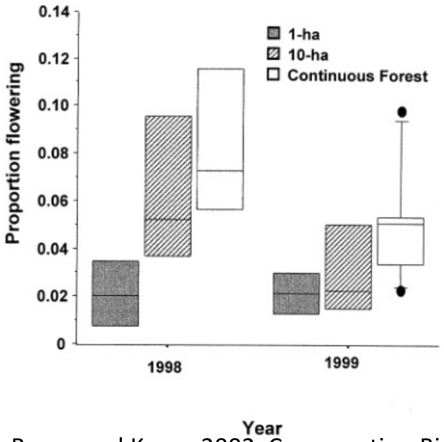
Fletcher et al. 2018. Ecol Letters

Landscape attributes as niche dimensions

- Local matrix effects
  - 1.Habitat degradation within patches

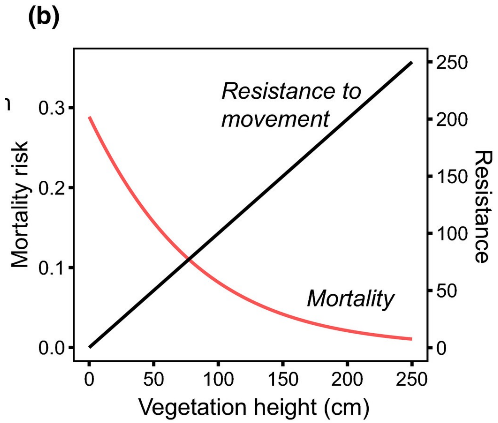
Heliconia acuminata

By Bernard DUPONT from FRANCE - False Bird-of-paradise (Heliconia acuminata), CC BY-SA 2.0, https://commons.wikimedia.org/w/index.php?curid=66109870

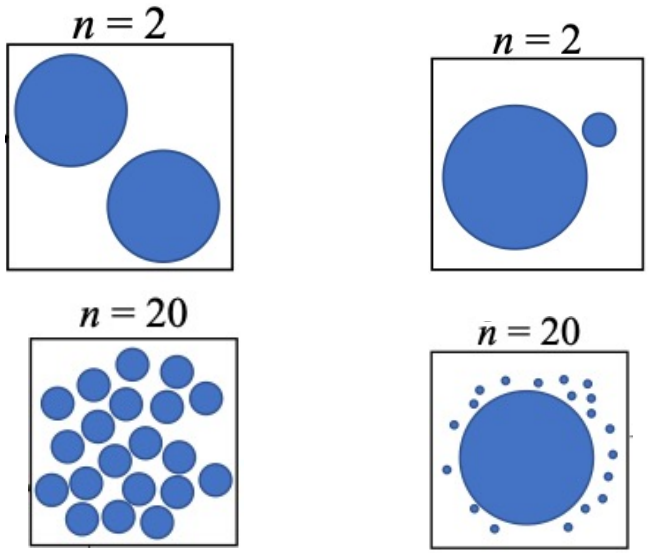


Bruna and Kress. 2002. Conservation Biology

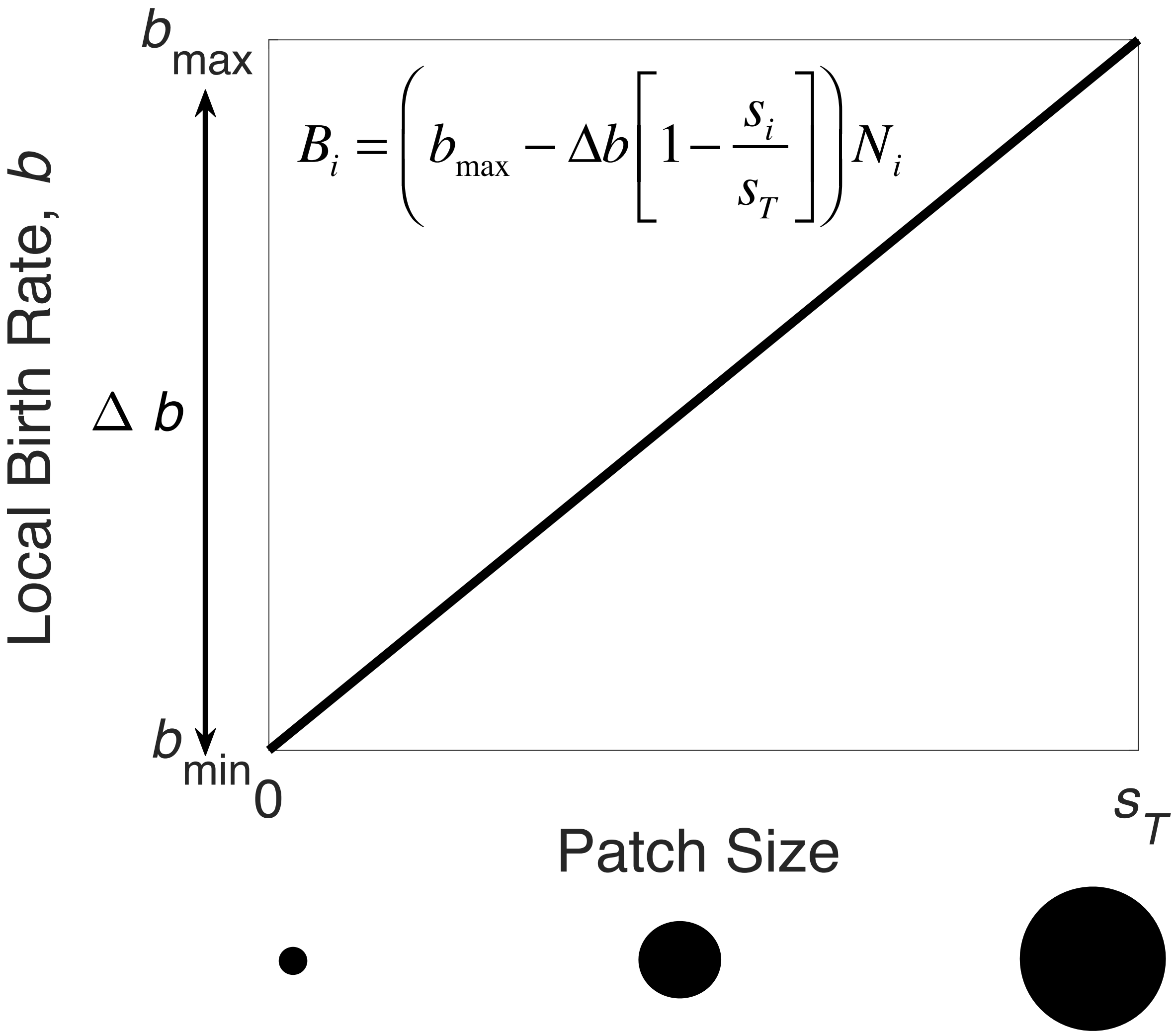
- Regional matrix effects
  - 2.Movement patterns
  - 3.Mortality during dispersal



- Patch distribution attributes
  - 4.Patch number
  - 5.Patch size variation



Local Effects: Habitat Degradation



Assumption: Habitat degradation reduces the per-capita birth rate

$b_{\max}$ is the birth rate in the unaltered habitat

$b_{\min}$ is the birth rate as patch size goes to 0

$\Delta b = b_{\max} - b_{\min}$ is the strength of habitat degradation

Regional Matrix Effects

$$I_i = \underbrace{\sum_{j=1}^{n}(1-\delta)p_{ji}mN_j s_j / s_i}_{\text{Total Surviving Dispersers}}$$

Matrix Quality

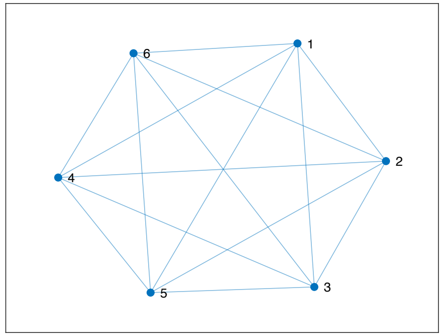
δ, fraction of emigrants dying during dispersal

1–δ is our measure of matrix quality

Movement Networks, p_{ij}

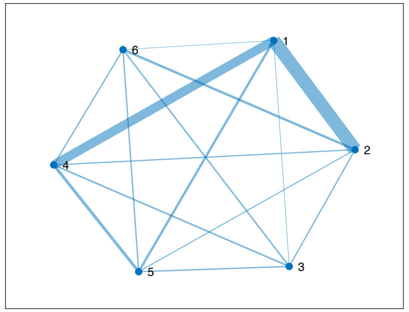
Equally connected, symmetric network

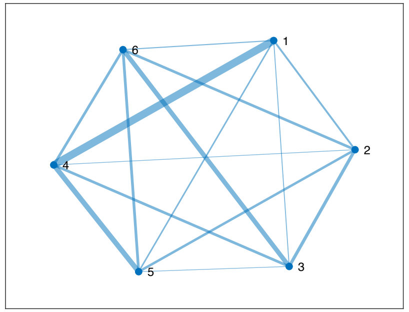
$\sigma^2 = 0$



Unequally connected, asymmetric network

$\sigma^2 = 1$

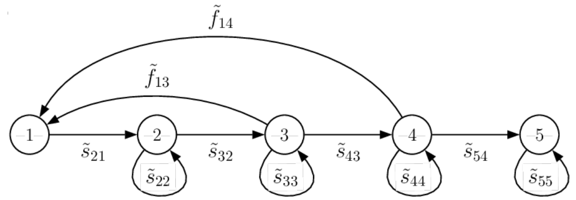




Analysis: Low Density Growth Rate

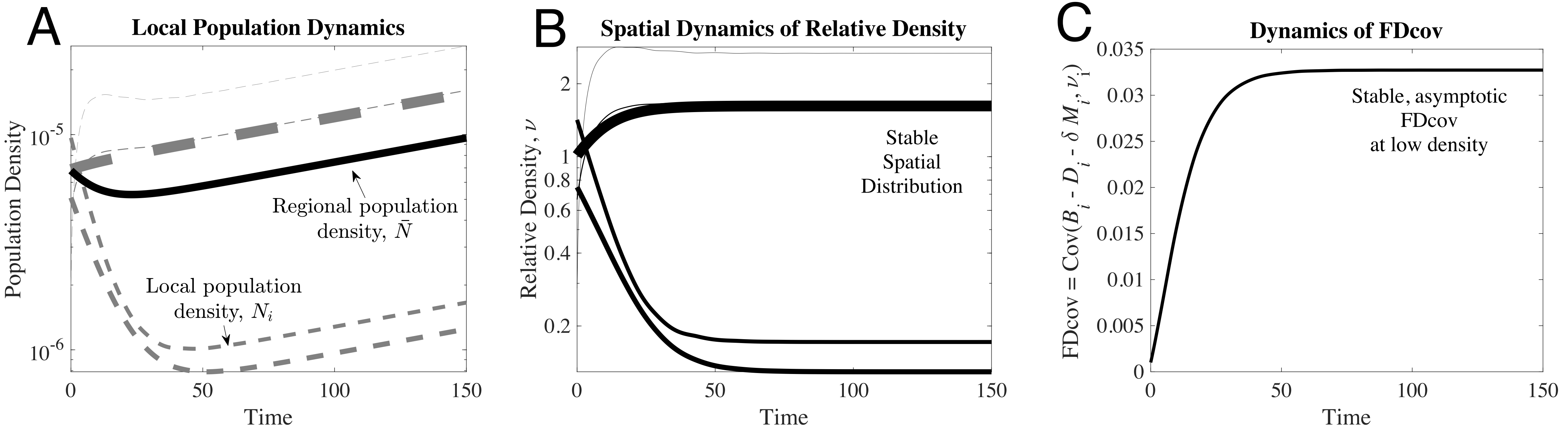
Extinction happens when populations are rare (at low density everywhere)

-> Interested in density-independent growth rate

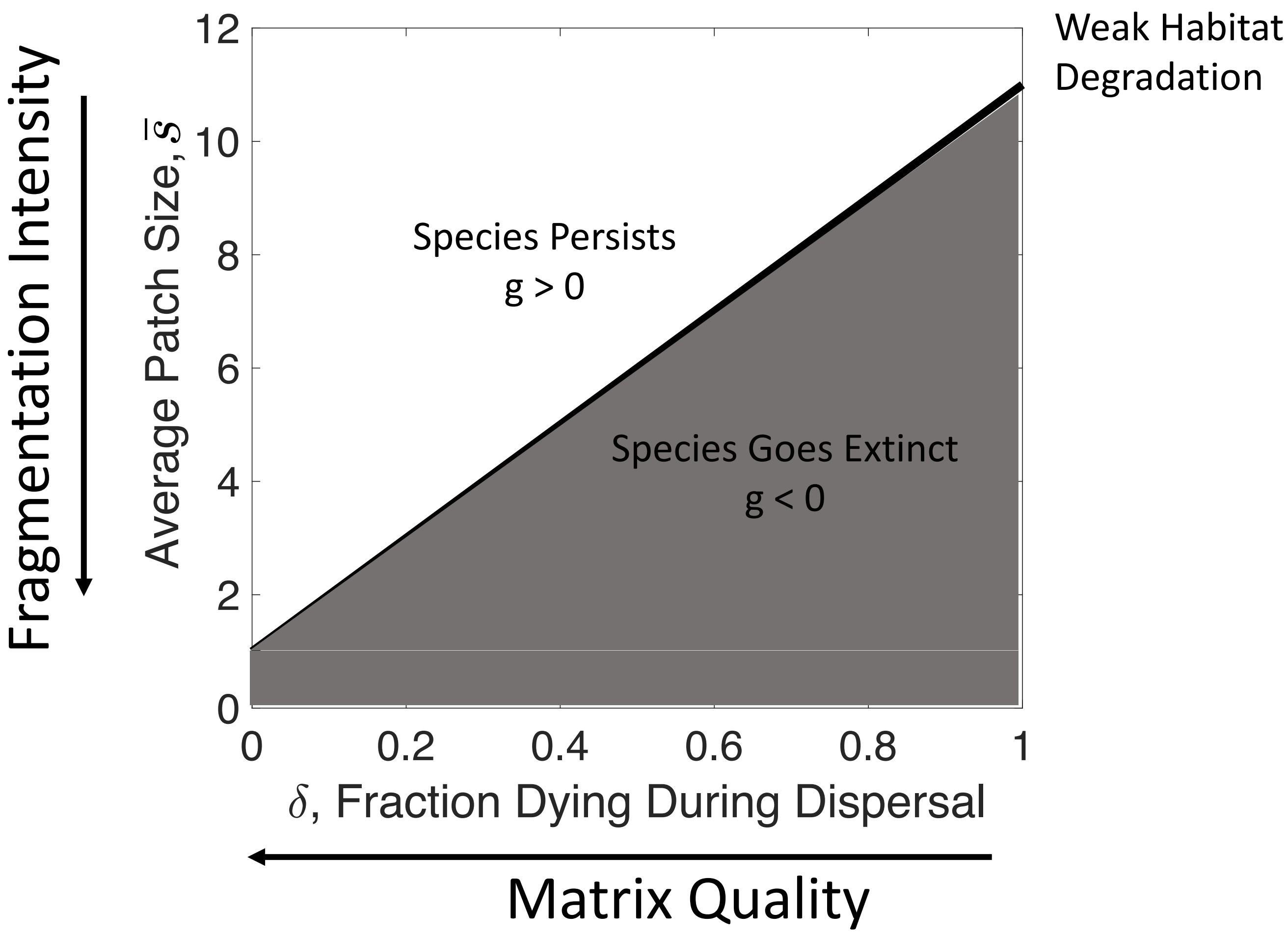


Analogy: Stage-structured matrix population models

“Stable stage distribution”

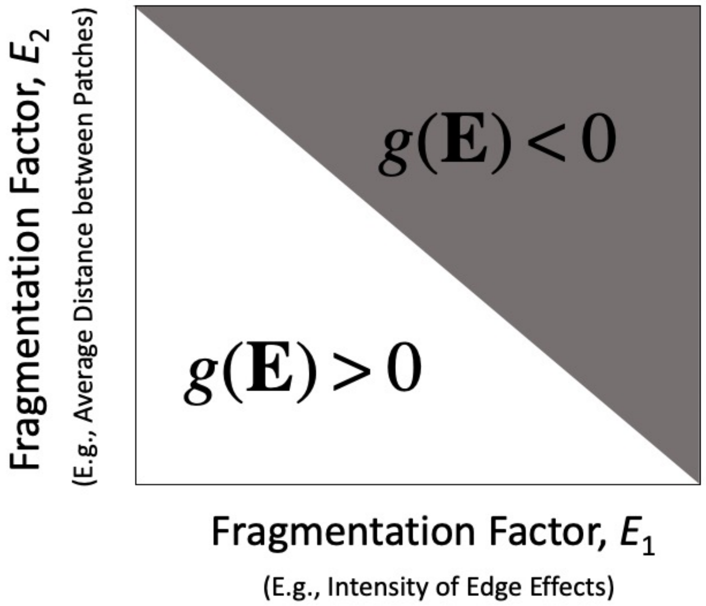


Result 1: Increasing matrix quality makes species more robust to fragmentation

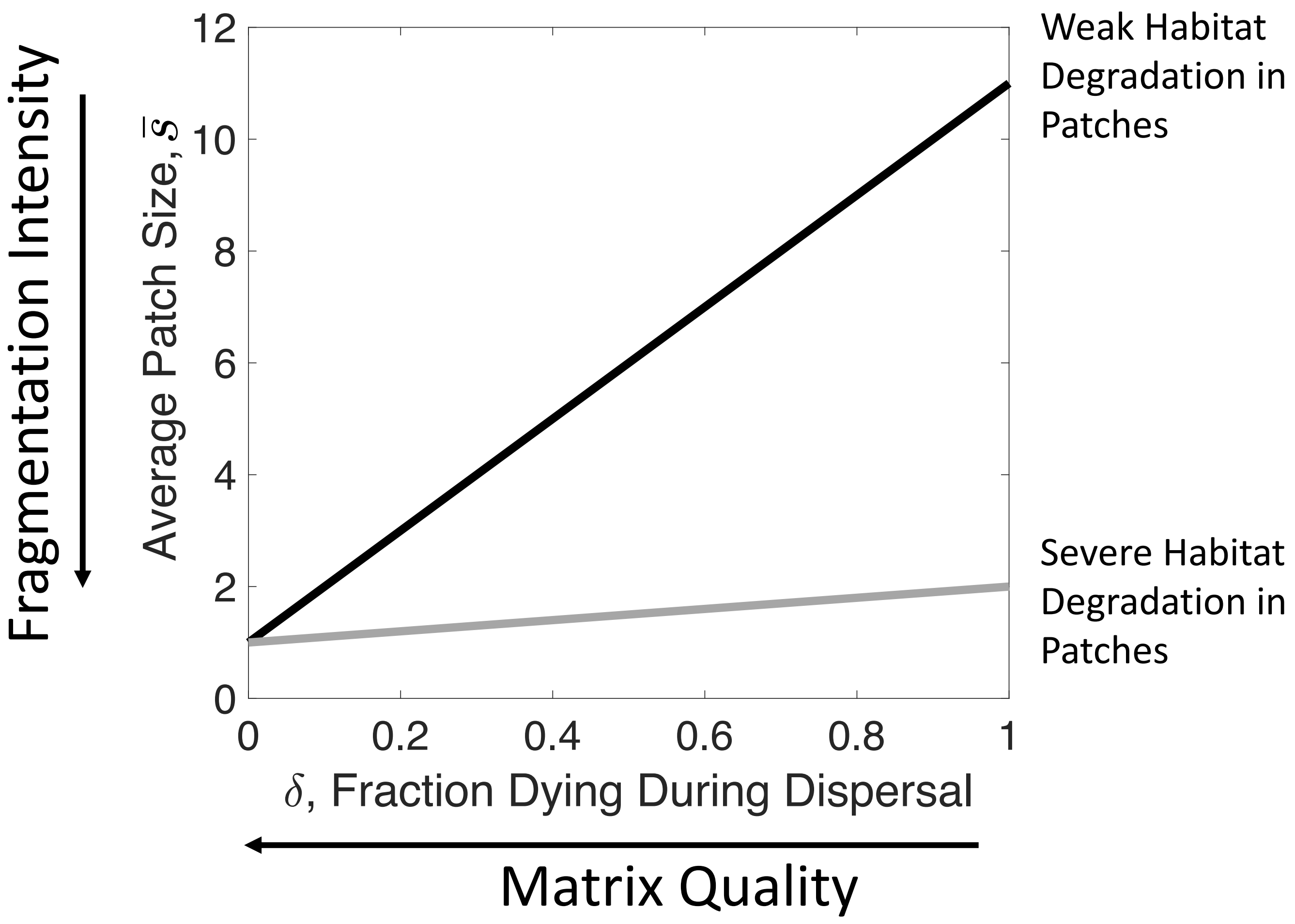


The niche space for a population w.r.t.

- Distribution of patch sizes
- matrix quality



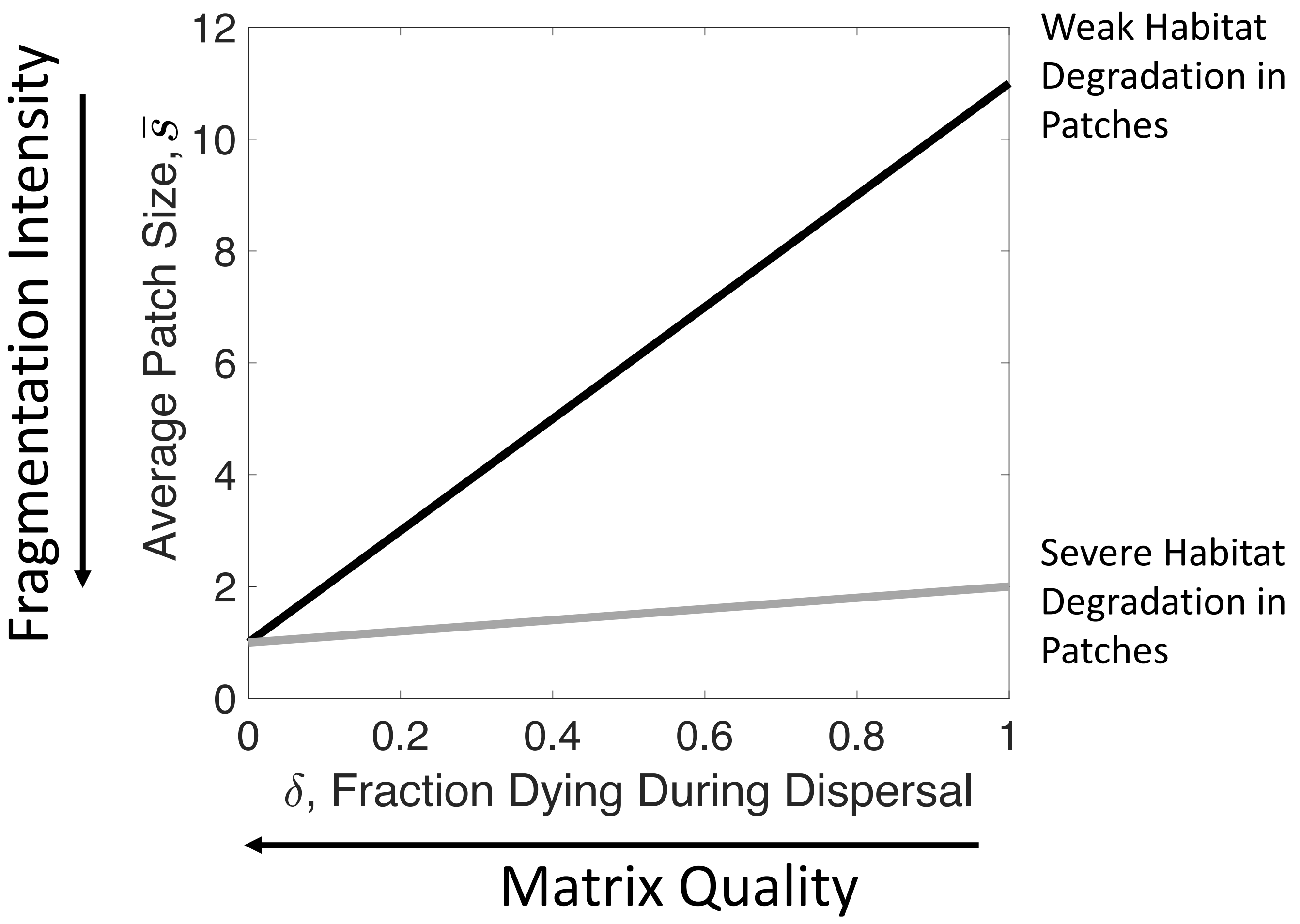
Result 2: Matrix quality effects conditional on severity of habitat degradation in patches



Differential sensitivity to matrix quality.

Matrix quality matters only when habitat degradation weak.

Result 2: Matrix quality effects conditional on severity of habitat degradation in patches

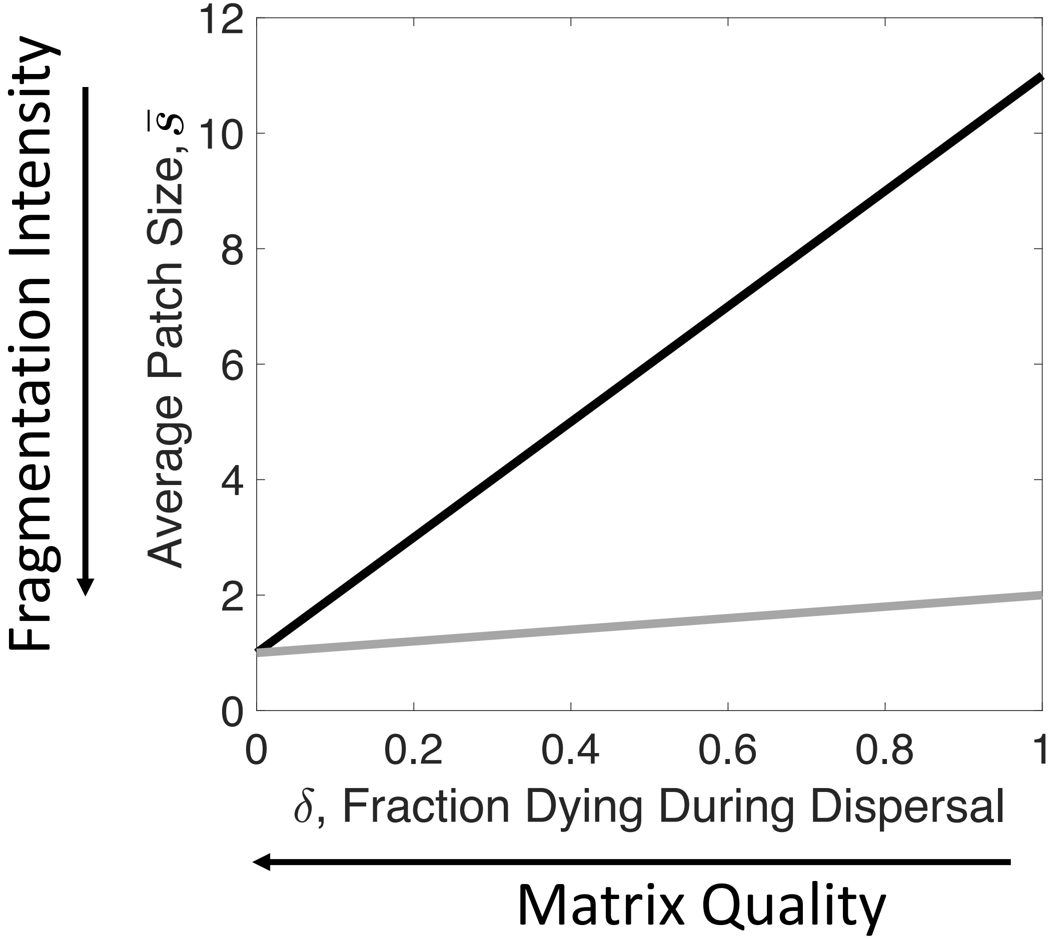


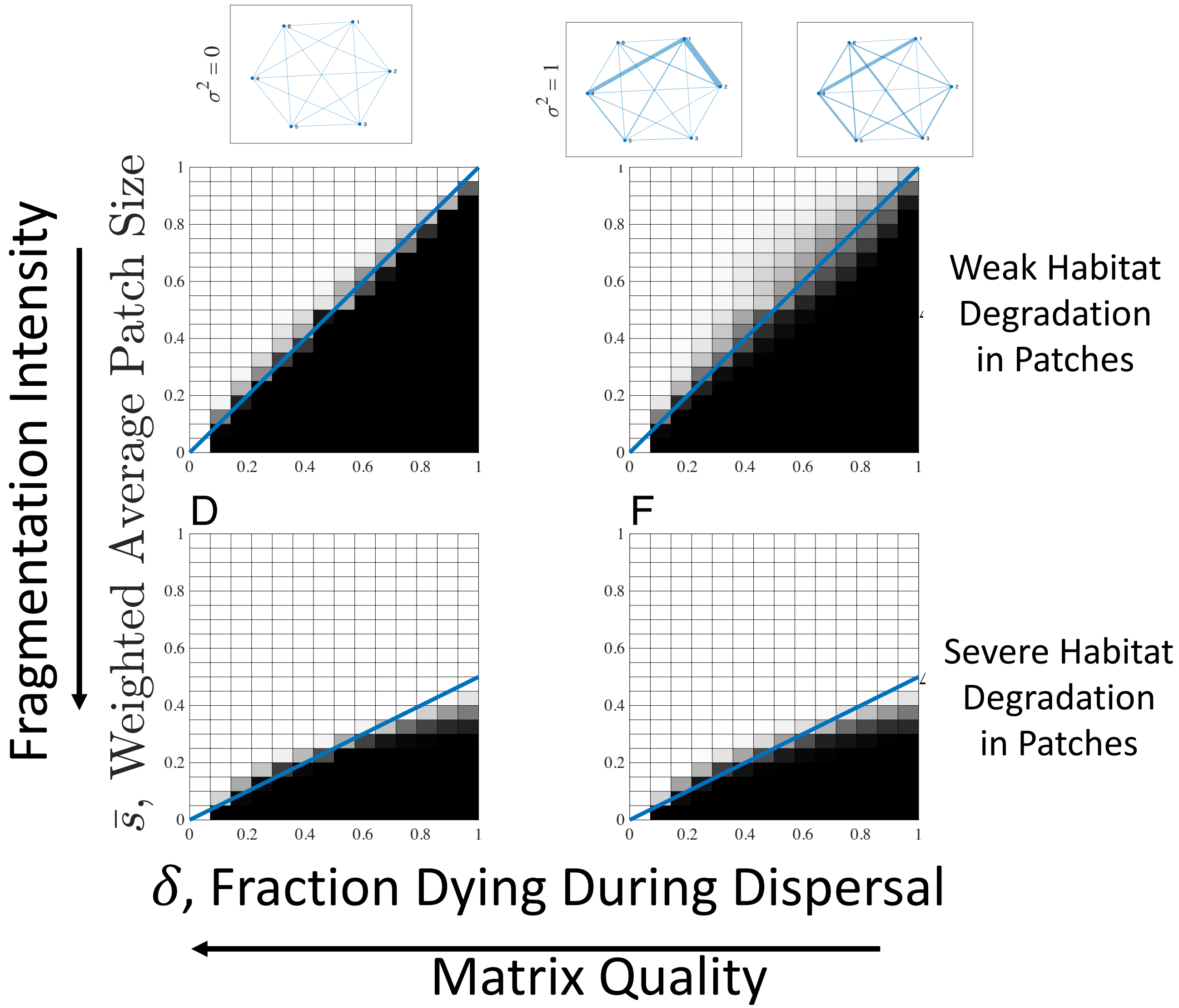
Implication

May not need to account for matrix quality when habitat degradation is severe

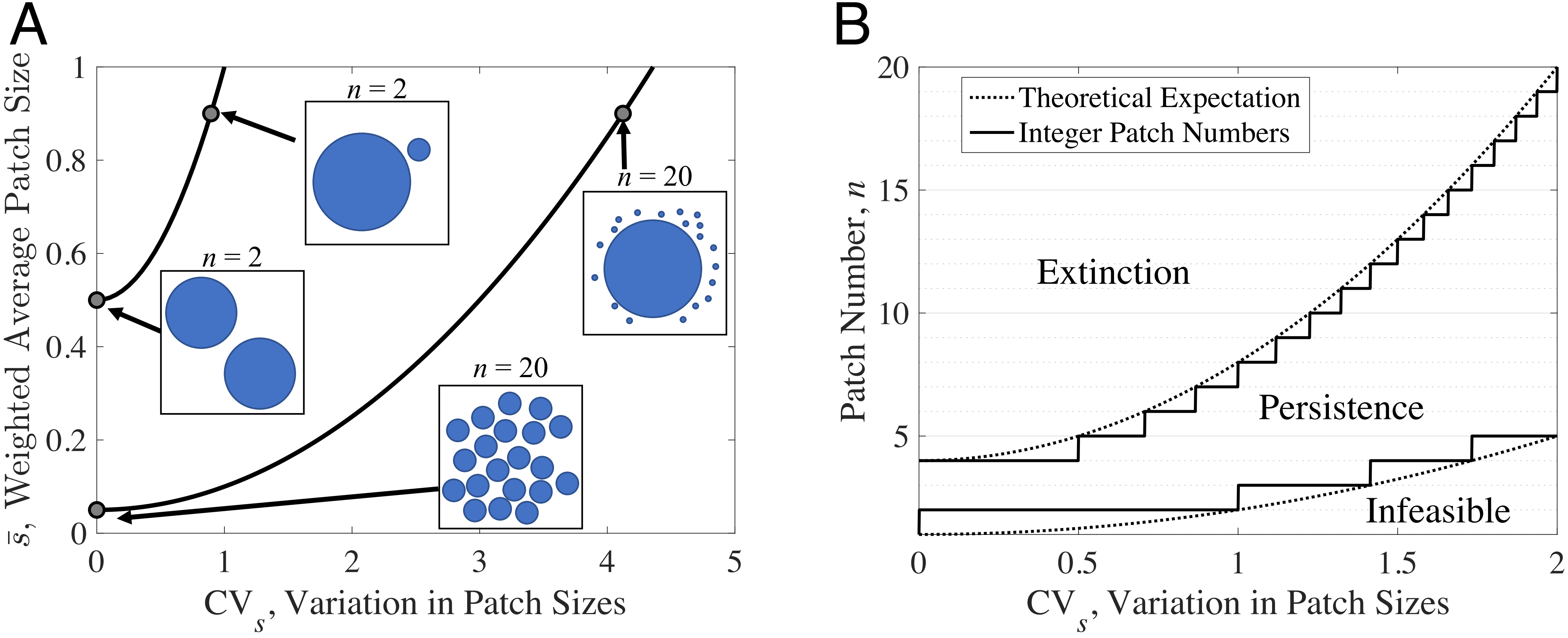
Managing for matrix quality—or connectivity-- will be a losing strategy

Result 3: Connectivity has little effect unless species disperse a LOT!





Result 4: Patch size variability buffers the effects of variation

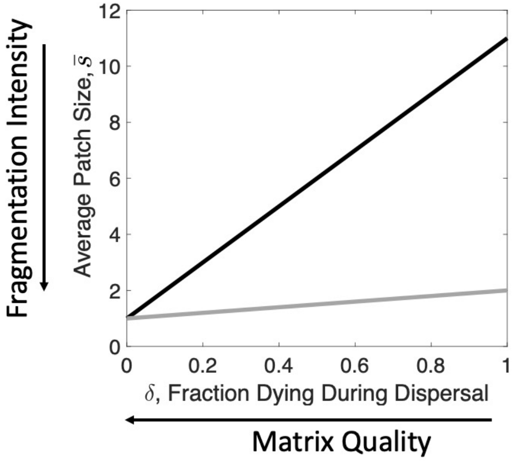


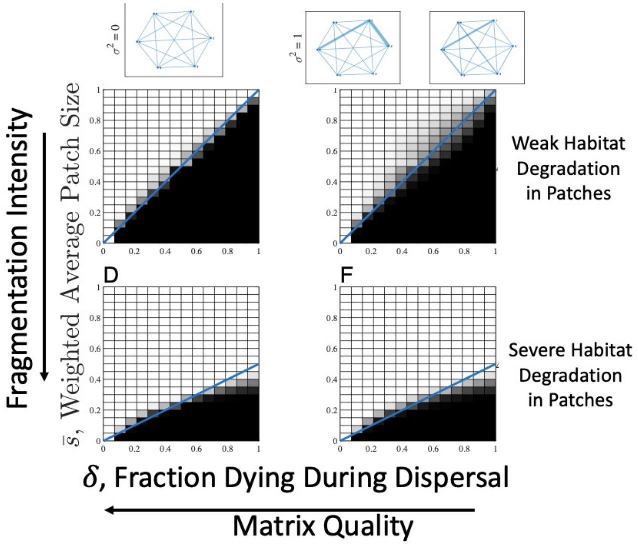
Summary

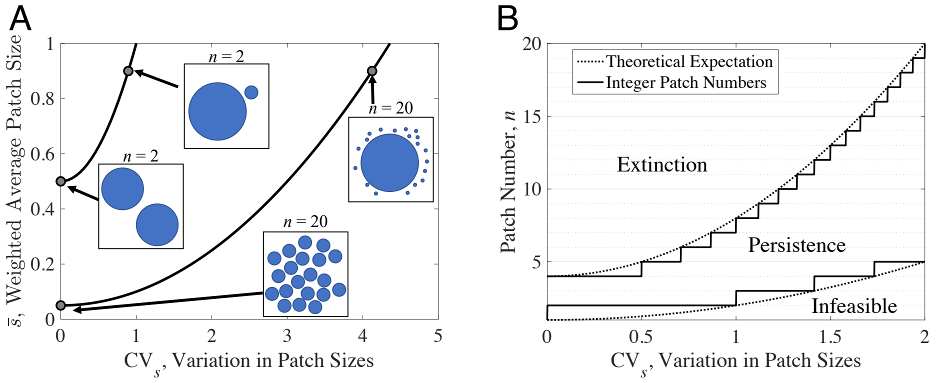
- Local matrix effects
  - 1.Habitat degradation within patches

- Regional matrix effects
  - 2.Movement patterns
  - 3.Mortality during dispersal

- Patch distribution attributes
  - 4.Patch number
  - 5.Patch size variation



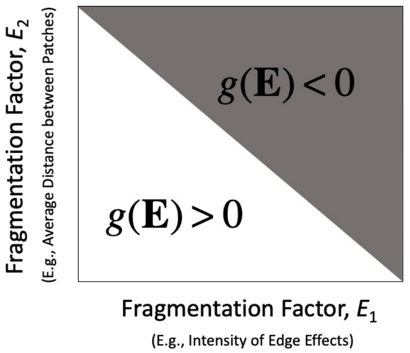


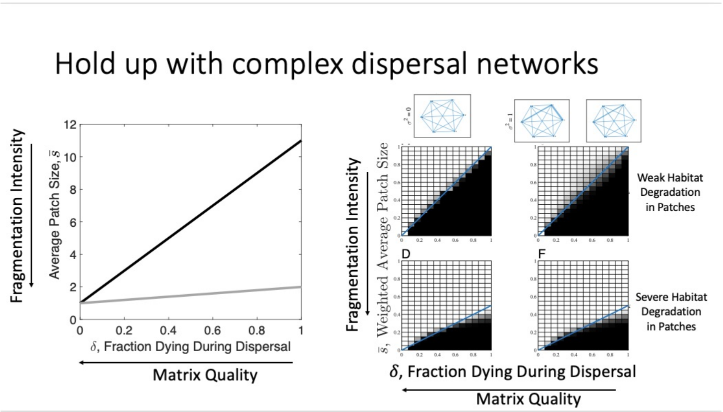


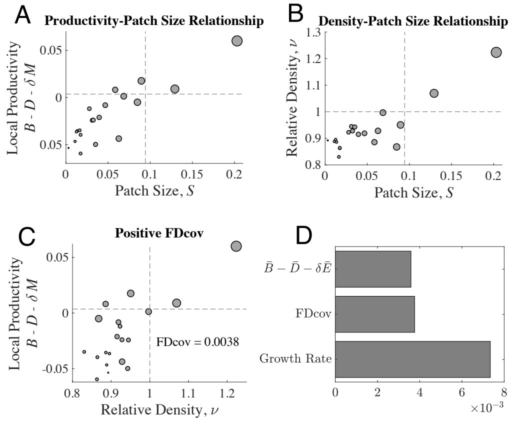
Reflections

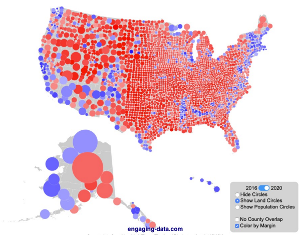
- One can represent spatial attributes of the environment like many other niche factors
- Justification: species may persist in some landscapes--with certain features--but not others
- Use this perspective to understand interactive effects of multiple factors

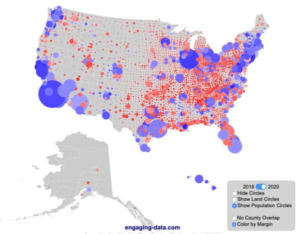
- We can take patch-level attributes and translate to individual-level processes, like growth rate
- Flexible framework to consider effects of fragmentation that cannot be considered practically in the field.





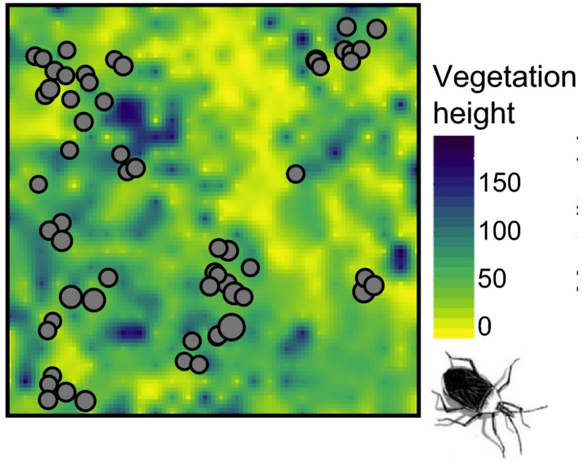


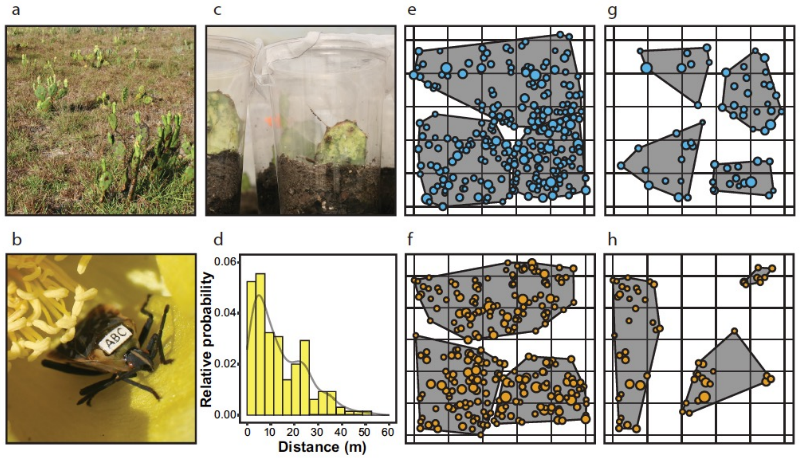




The future

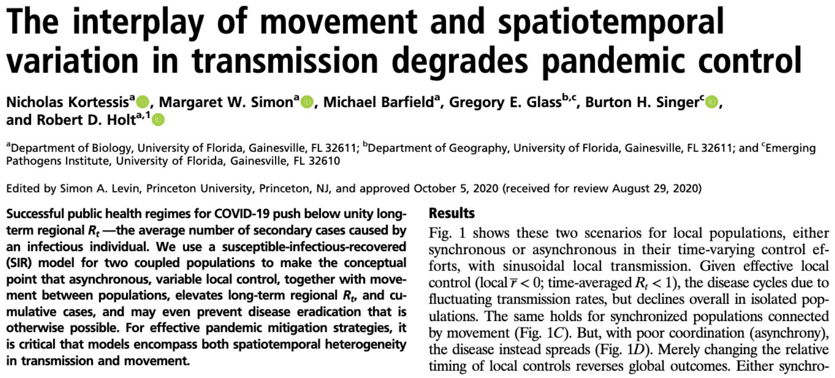
1. Application with data





Fletcher et al. 2018. Ecology

2. Temporal environmental heterogeneity



The interplay of movement and spatiotemporal variation in transmission degrades pandemic control

Nicholas Kortessis[a], Margaret W. Simon[a], Michael Barfield[a], Gregory E. Glass[b,c], Burton H. Singer[c], and Robert D. Holt[a,1]

[a]Department of Biology, University of Florida, Gainesville, FL 32611; [b]Department of Geography, University of Florida, Gainesville, FL 32611; and [c]Emerging Pathogens Institute, University of Florida, Gainesville, FL 32610

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved October 5, 2020 (received for review August 29, 2020)

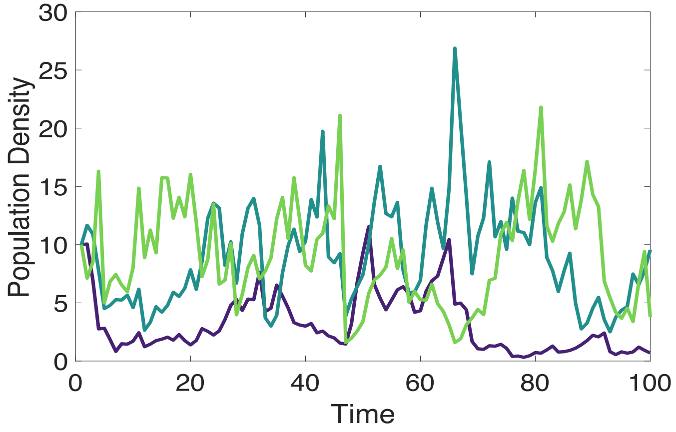
Successful public health regimes for COVID-19 push below unity long-term regional R_t —the average number of secondary cases caused by an infectious individual. We use a susceptible-infectious-recovered (SIR) model for two coupled populations to make the conceptual point that asynchronous, variable local control, together with movement between populations, elevates long-term regional R_t, and cumulative cases, and may even prevent disease eradication that is otherwise possible. For effective pandemic mitigation strategies, it is critical that models encompass both spatiotemporal heterogeneity in transmission and movement.

Results

Fig. 1 shows these two scenarios for local populations, either synchronous or asynchronous in their time-varying control efforts, with sinusoidal local transmission. Given effective local control (local $\bar{r} < 0$; time-averaged $R_t < 1$), the disease cycles due to fluctuating transmission rates, but declines overall in isolated populations. The same holds for synchronized populations connected by movement (Fig. 1*C*). But, with poor coordination (asynchrony), the disease instead spreads (Fig. 1*D*). Merely changing the relative timing of local controls reverses global outcomes. Either synchro-

I can't promise floating skateboards

3. Multiple Species
Predator-prey; competition



Thanks for listening!

Funding sources

NSF-DEB Award 1655555

University of Florida Foundation