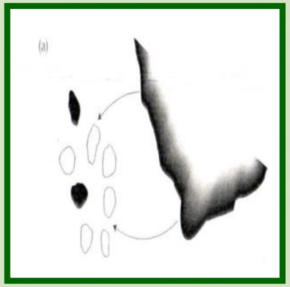
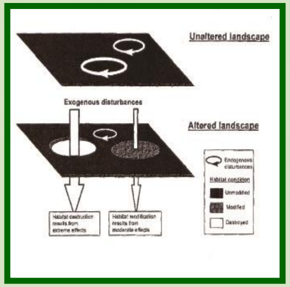
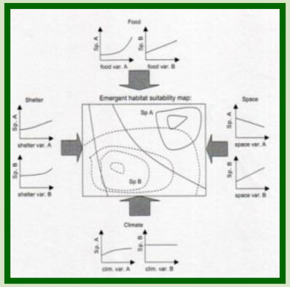
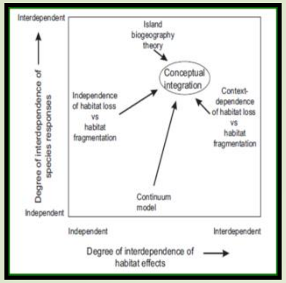
New Developments in Fragmentation Research

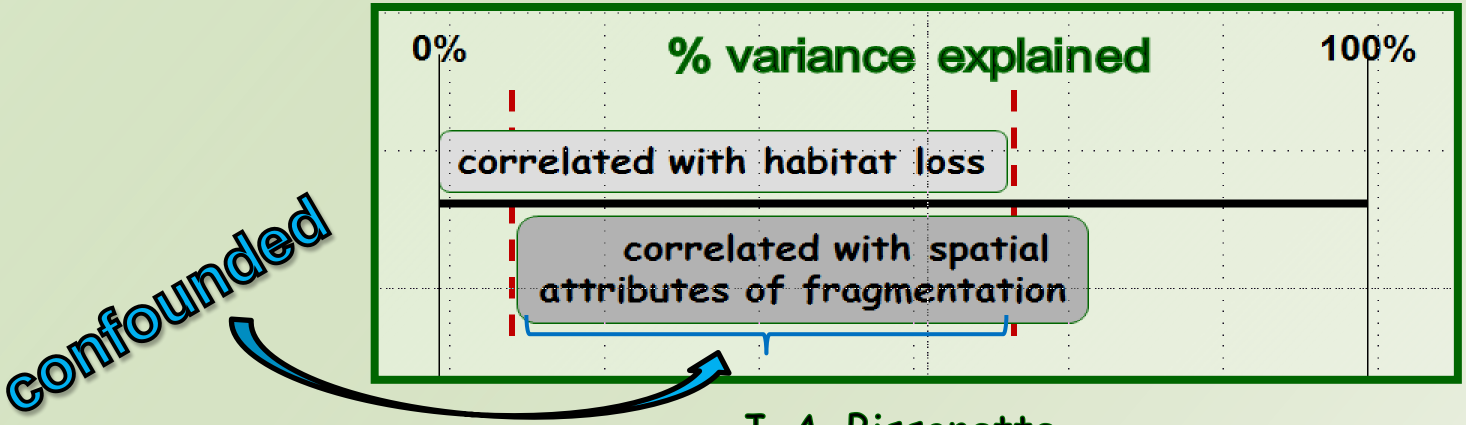
partitioning habitat loss from habitat configuration











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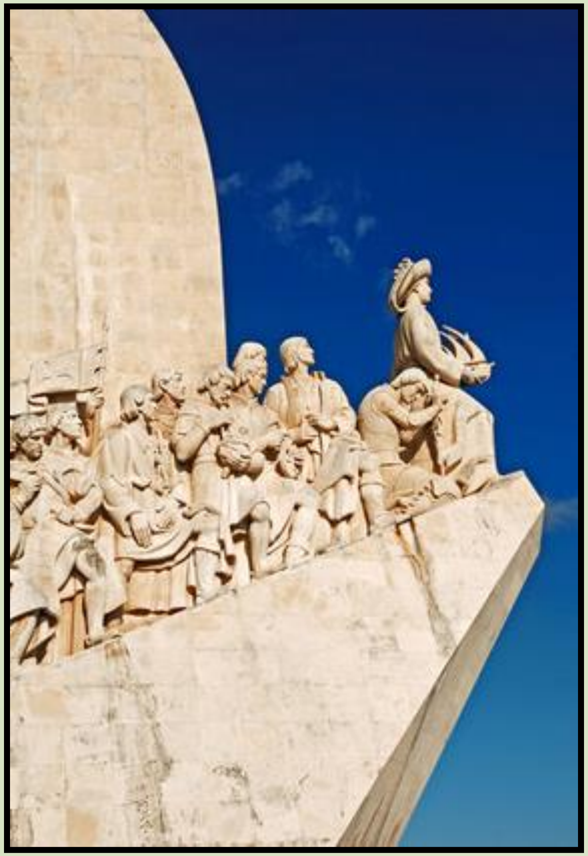


Padrão dos Descobrimentos

The voyage of discovery is not in seeking new landscapes but in having new eyes.

MARCEL PROUST

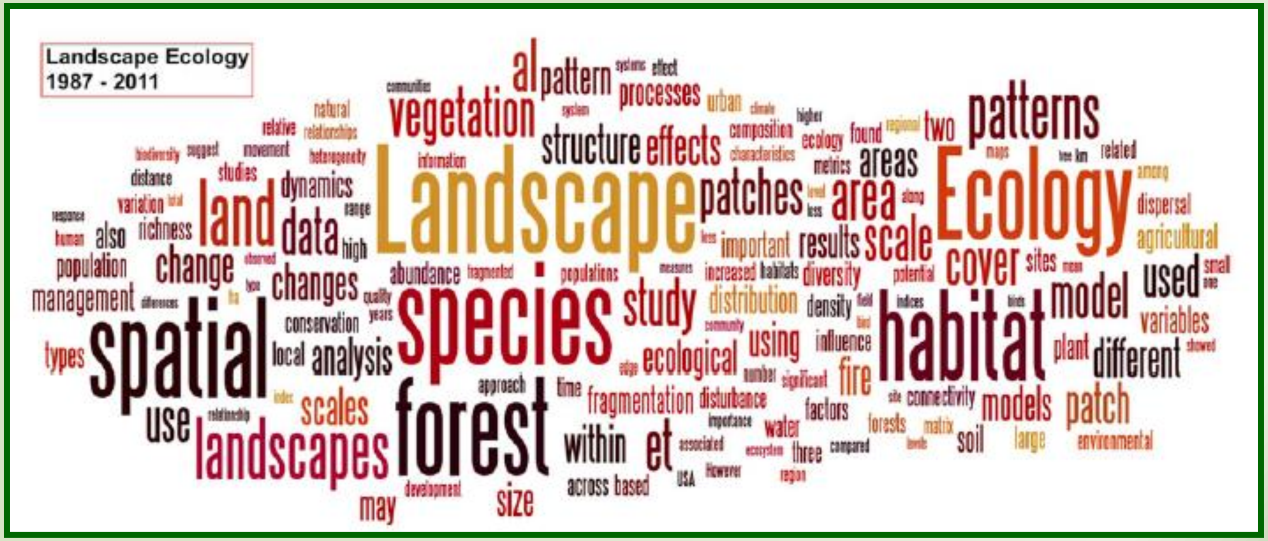
The observer imposes a perceptual bias,
a filter through which the system is viewed.

HOW WE CONCEPTUALIZE (and measure) LANDSCAPE CHANGE MAKES A DIFFERENCE

… . One of the first workshops on landscape ecology in the U.S. in 1983 explicitly emphasized that the paramount emphasis on spatial pattern and heterogeneity is the feature that most distinguishes landscape ecology from other ecological fields… .

Risser et al. 1984 Illinois Nat. History Survey Special Publ. 2
Wu, J. 2013. Landscape Ecology 28:1-11.

A WORD CLOUD FROM LE PAPERS 1987-2011

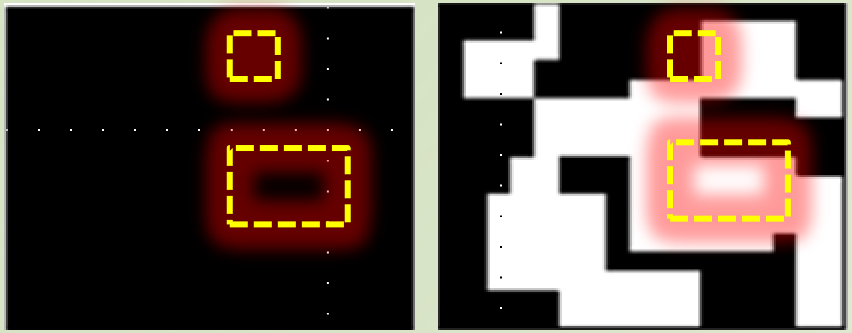


Heterogeneity and Scale

1. Explicit emphasis on spatial heterogeneity necessitates the consideration of pattern, process, and scale.
2. Why is consideration of scale absolutely necessary?

REAL LANDSCAPES ARE HETEROGENEOUS AT ALL SCALE RESOLUTIONS

pixel view



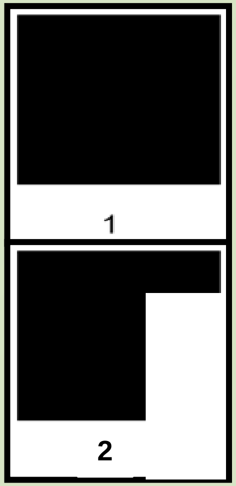
polygon view

If homogeneous, any scale resolution of sampling will give accurate results

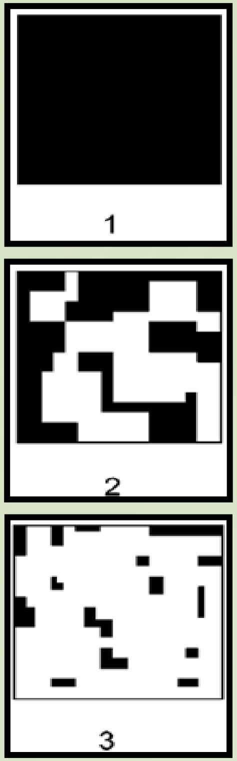
If heterogeneous, different scale resolutions of sampling will give different results = transmutation

If we are interested in wildlife response to heterogeneity… .

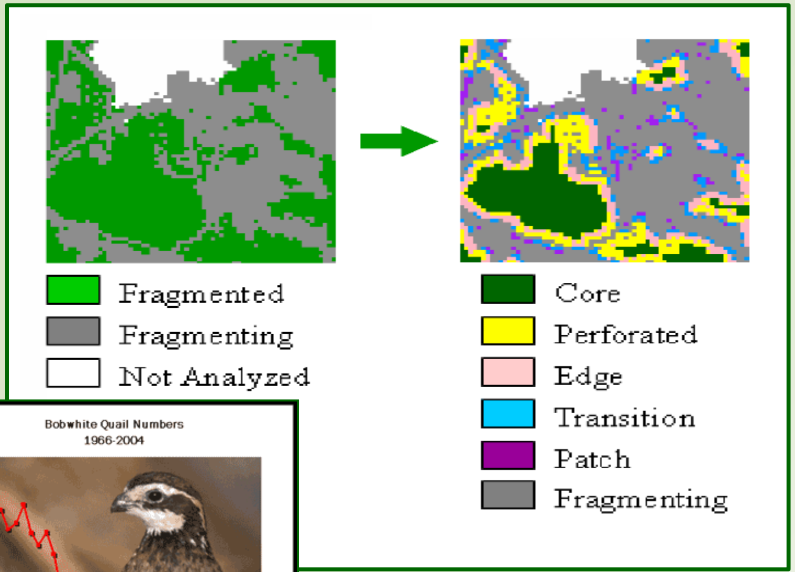
habitat loss

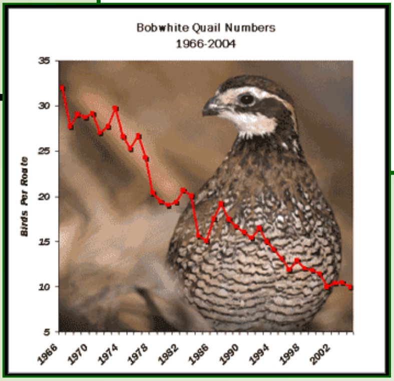


habitat fragmentation and loss



time





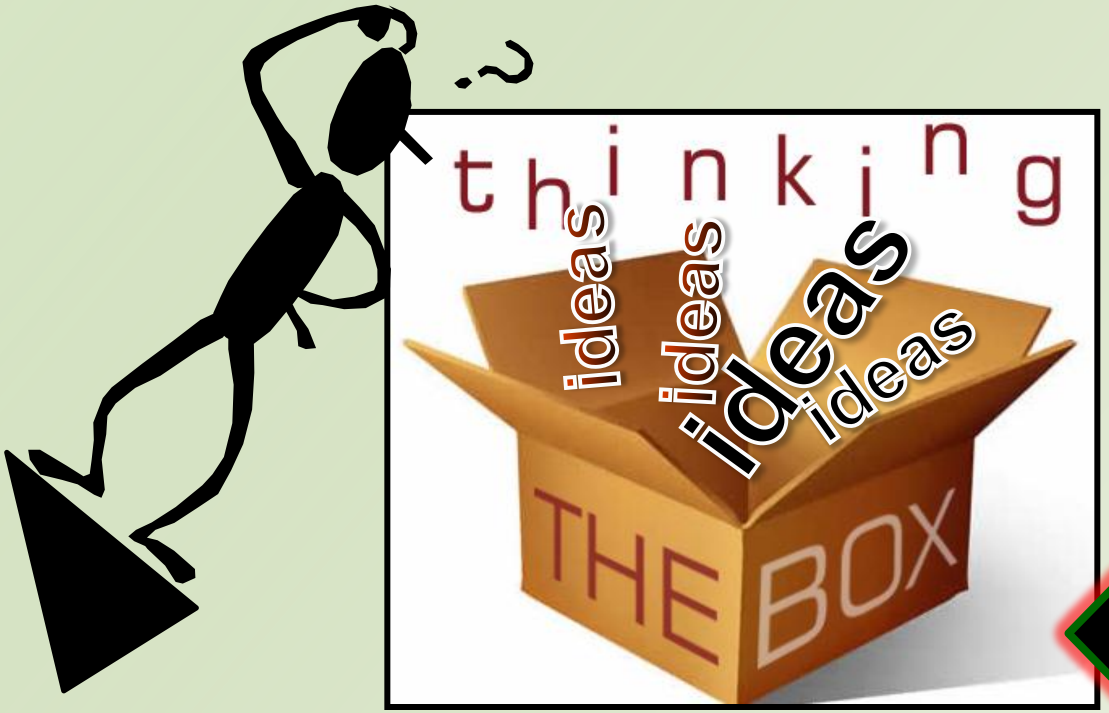
How do we treat the ***components*** of heterogeneity: fragmentation per se (spatial arrangement), & habitat loss?

Our interpretation of science changes based on data

Evolving Paradigms of Landscape Change

"truth lies <u>beyond</u> our perception of the truth"

Koge Yasuda



BUT PERHAPS WE CAN MAKE SOME PROGRESS… .

new data 2012-2103

http://clipbucket.net

A map of this seminar

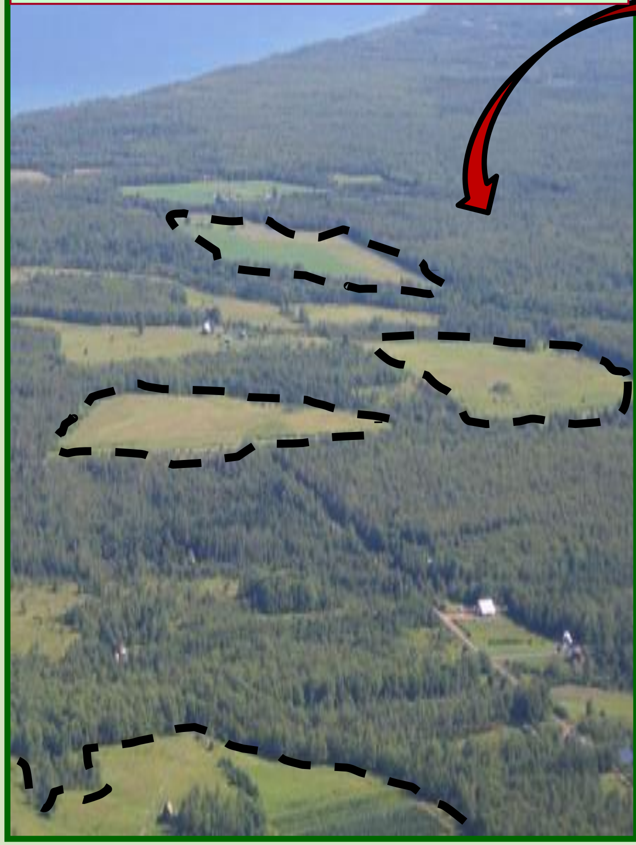
a brief review of landscape models → independent effects? → 2 key questions → so what is new? → fragmentation history in 1 slide → fragmentation problem space → 2 general principles with supporting arguments → dissecting the correlation structure → possible causal models → 2 take home messages

profound thanks to my colleagues around the world for their excellent studies!

Island Biography Theory is a caricature if used in terrestrial systems

a review

TERRESTRIAL HABITAT ISLANDS ARE NOT REAL ISLANDS



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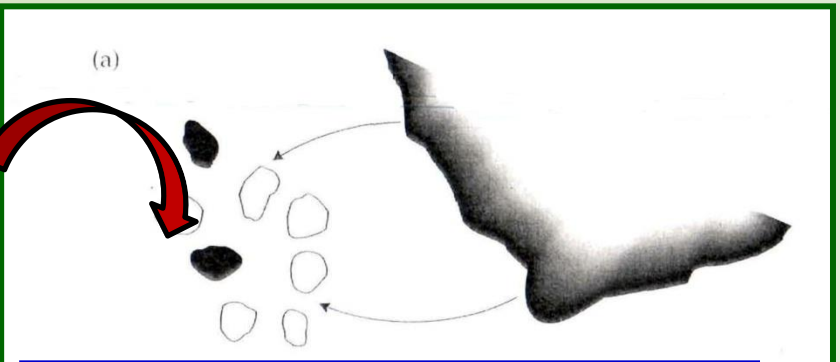


From: Gotelli, N.J. 1995. A Primer of Ecology. SinauerAssociates

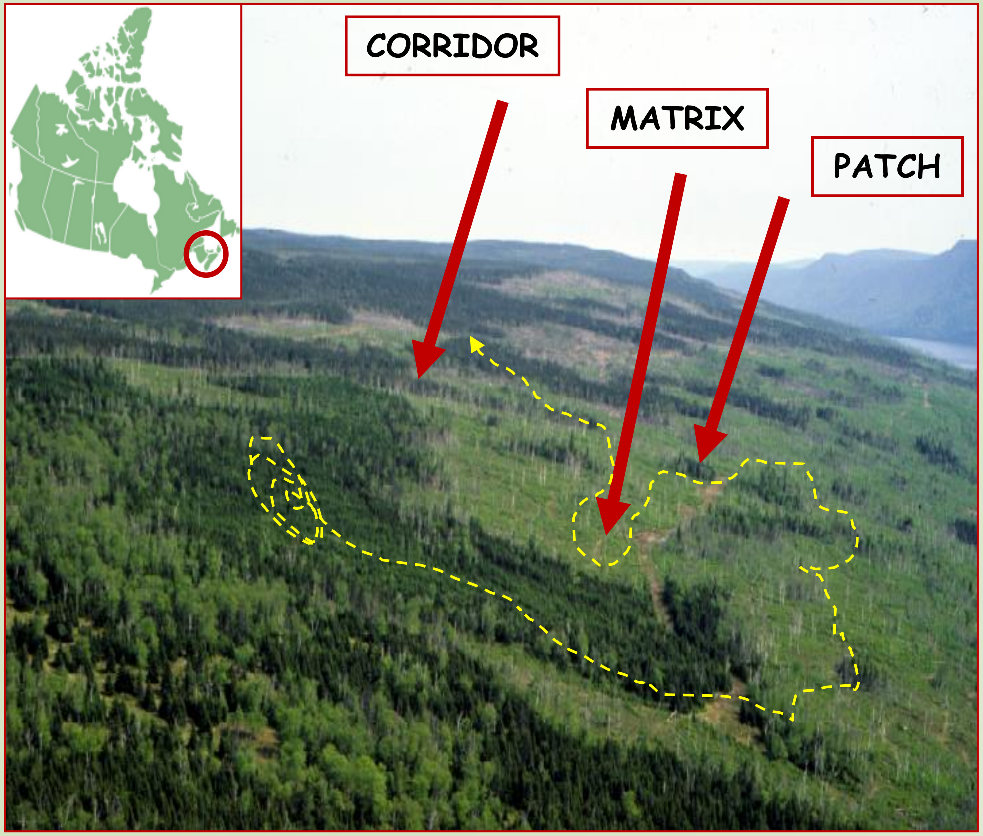
THE ASSUMPTIONS OF ISLAND BIOGEOGRAPHY THEORY USED IN TERRESTRIAL SYSTEMS ARE:

- Fragments are comparable to oceanic islands
- Habitats surrounding fragments are hostile to organisms. (matrix was disturbed)
- Natural pre-fragment conditions were uniform (homogeneous)

A caricature… .

IBT has always been recognized as a caricature (Simberloff and Abele 1976) , but Haila (2002) has argued that "the dominant fragmentation model has been repeatedly conflated with an IBT model"

The 'Islands as Fragments' view has morphed into the patch-corridor-matrix model



the dominant model
useful so persistent

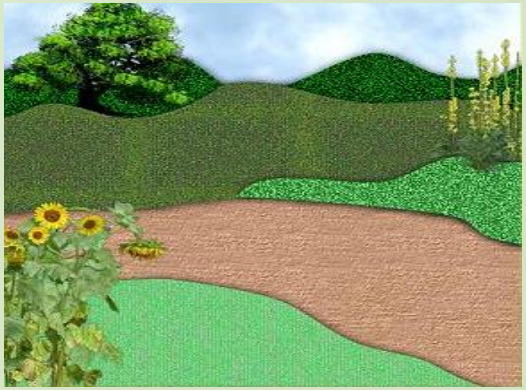
USES:

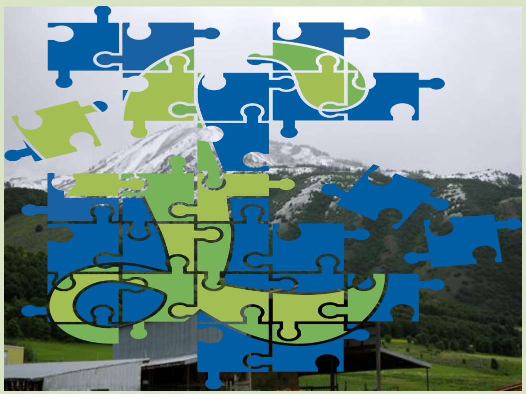
- *Categorical approaches are common in most technical applications*
- *GIS based on categorical classification of the real world*
- *Transition Probability Matrices for landscape change analyses based on discrete landscape types*
- *Graph theory has used discrete identifiable landscape elements*

animal movements may not reflect this model
Structural vs. Functional Connectivity

Limitations of the Patch Corridor Matrix Model

THE DOMINANT FRAGMENTATION MODEL



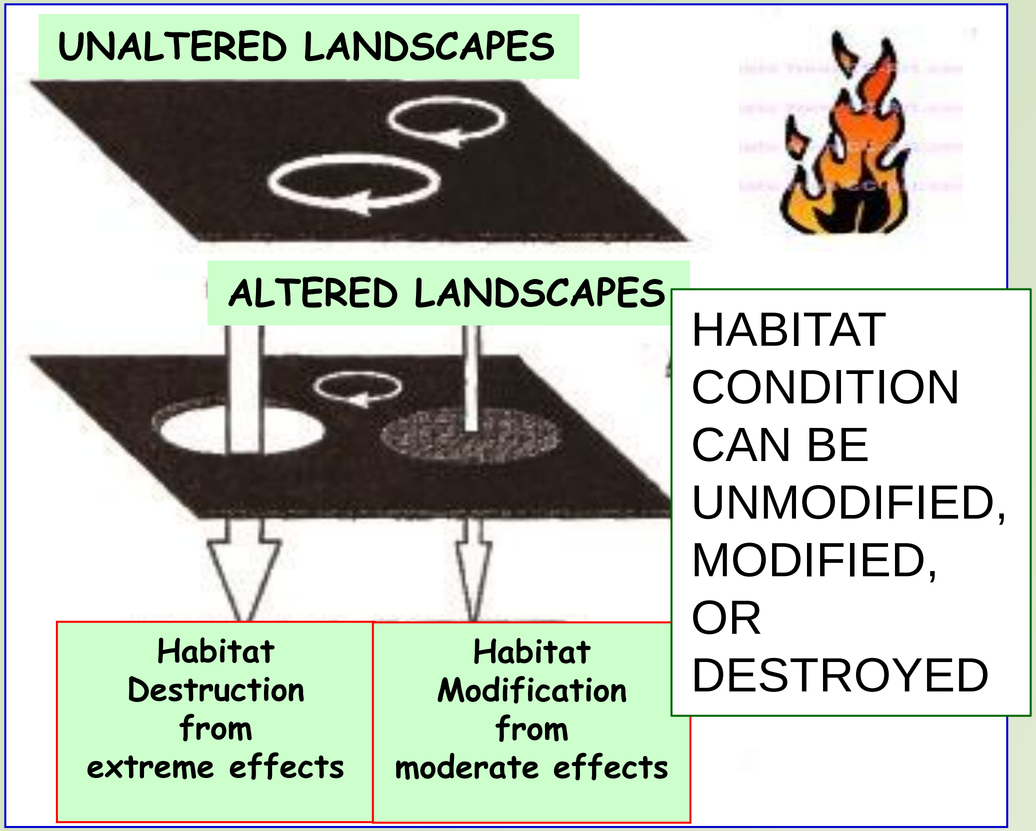


- Landscape elements comparable to pieces of a puzzle presumed to possess sharp, well defined, and unambiguous boundaries
- However near natural and semi-natural landscapes frequently organized as gradients
- Categorical map patterns do not represent such systems appropriately
- Therefore the patch-corridor-matrix model is **overly simplistic** in most cases

Li and Wu, 2004. Ecology 19: 389-99;
McGarigal et al., 2009. Landscape Ecology 24:433-450;
Hoechstetter et al., 2011. Ecological Complexity 8:229-238.

http://www.debisty.com/

Variegated Landscapes were proposed in 1999



McIntyre, and R. Hobbs. 1999. A framework for conceptualizing human effects on Landscapes and its relevance to management and research models. Conservation biology 13(6):1282-1292

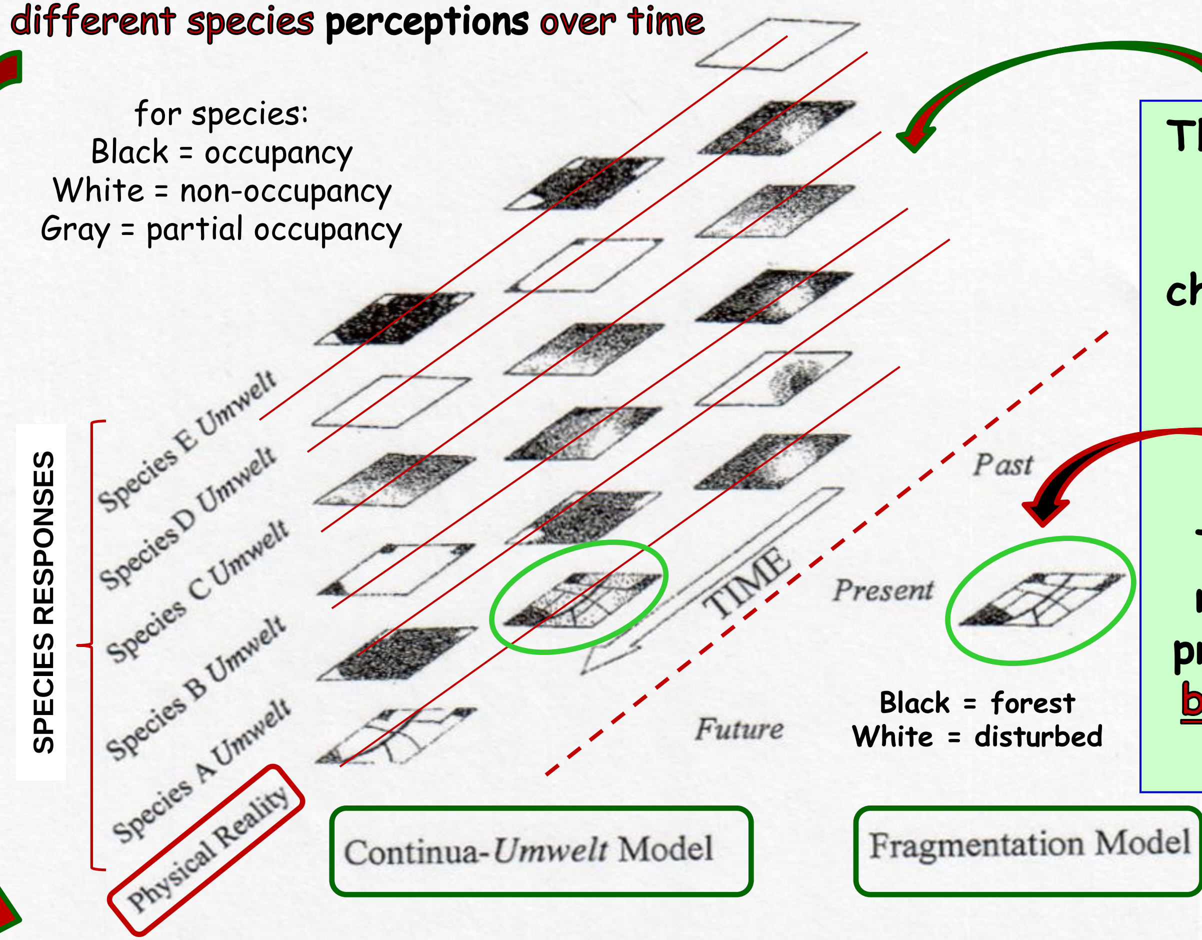
A step forward but:

- Essentially pattern-based, lack a process dimension
- Does not make a distinction between spatial and environmental continua; deals essentially with geographical space
- Lacks a temporal dimension
- Based on independent landscape effects

Umwelt (2004)

different species perceptions over time

for species:
Black = occupancy
White = non-occupancy
Gray = partial occupancy



Black = forest
White = disturbed

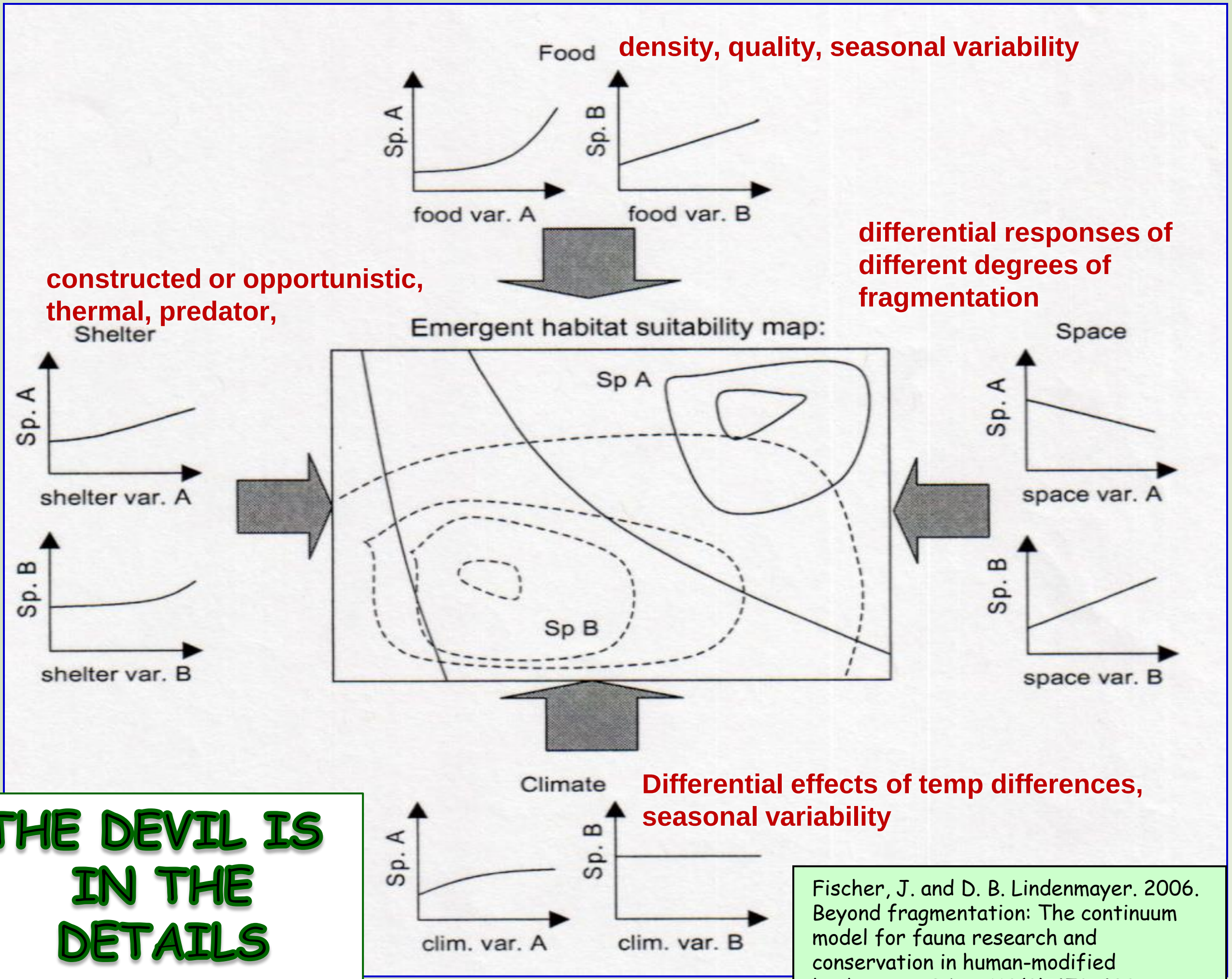
The Continua-Umwelt approach reflects processes and changes through time scaled to animal perception.

The fragmentation model reflects the present and a human based perception of the landscape.

THIS IS SCALE DEPENDENCY!

Manning, A. D., D. B. Lindenmayer and H. A. Nix. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. Oikos 104(3):621-628.

a continuum model (2006)

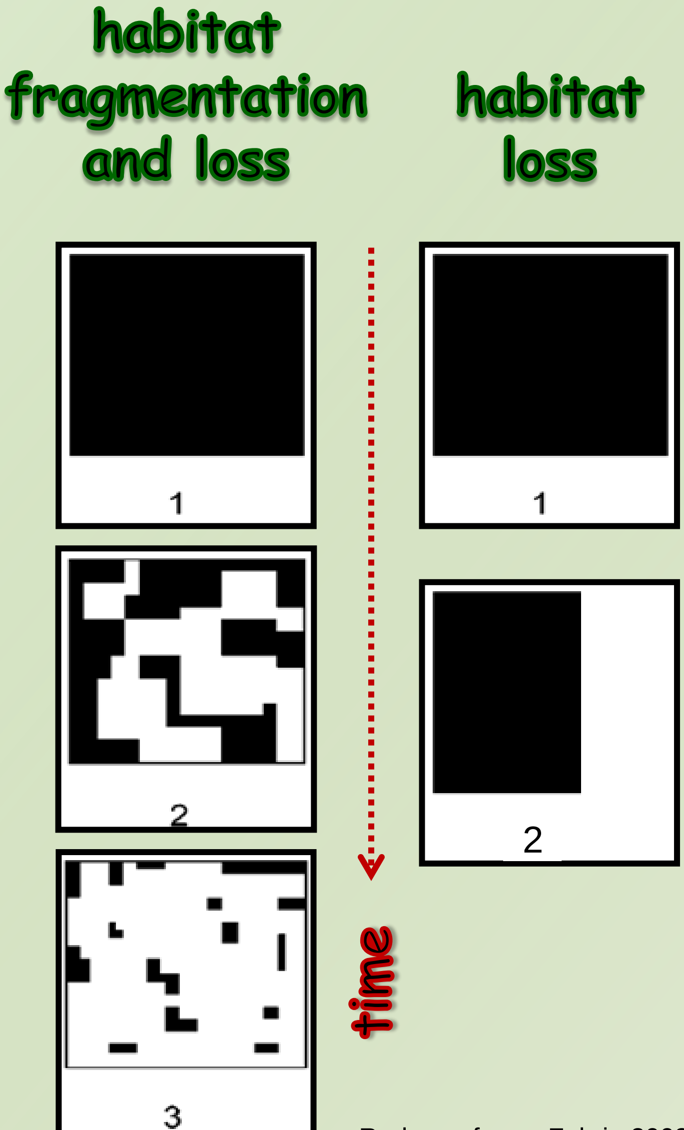


THE DEVIL IS IN THE DETAILS

Fischer, J. and D. B. Lindenmayer. 2006. Beyond fragmentation: The continuum model for fauna research and conservation in human-modified landscapes. Oikos 112(2):473-480

Spatial and Environmental Gradients

Emphasis on linking **ecological processes** related to the important variables (food, shelter, space, climate, other) to individual species distribution patterns



Redrawn from : Fahrig 2003

In large part, research based on earlier models has controlled for habitat loss first and spatial arrangement second (e.g., Fahrig 2003) and has considered species response to be identical (e.g., IBT) or entirely independent (e.g., UMWELT) Manning et al. 2004, Fischer and Lindenmeyer 2007

HABITAT LOSS & SPATIAL ARRANGEMENT WERE TREATED AS INDEPENDENT, AND SPECIES RESPONSES WERE TREATED AS SIMILAR OR ENTIRELY INDIVIDUALISTIC stepping back... .

Two Key Questions

have characterized fragmentation research
(and still do)

emphasis

How do landscape effects
(habitat arrangement & loss)
effect species response?

emphasis

How do species respond to landscape change?

so what's new?

Didham, R.K., V. Kapos, and R.M. Ewers. 2012. Rethinking the conceptual foundation of habitat fragmentation research. *Oikos* 121:161-170

proposed a different way of looking at these models based on a "FRAGMENTATION PROBLEM SPACE" that emphasizes

inter-dependence of landscape effects

THIS IS A CONCEPTUAL **BIG DEAL**!

When we look at a brief history of fragmentation research - 1962-2012

PHASE 1

1962-1993

Ignored inter-correlation between fragmentation and habitat loss (landscape effects)

or

Inappropriate inference from patch data, e.g., scaling problems

PHASE 2

1994-2012

Full landscape perspective

Discrimination between habitat loss and fragmentation based on independent landscape effects

Andren 1994, Fahrig 1997, McIntyre & Hobbs 1999, Manning et al. 2004, Fischer and Lindenmayer 2006

PHASE 3

2012 - ?

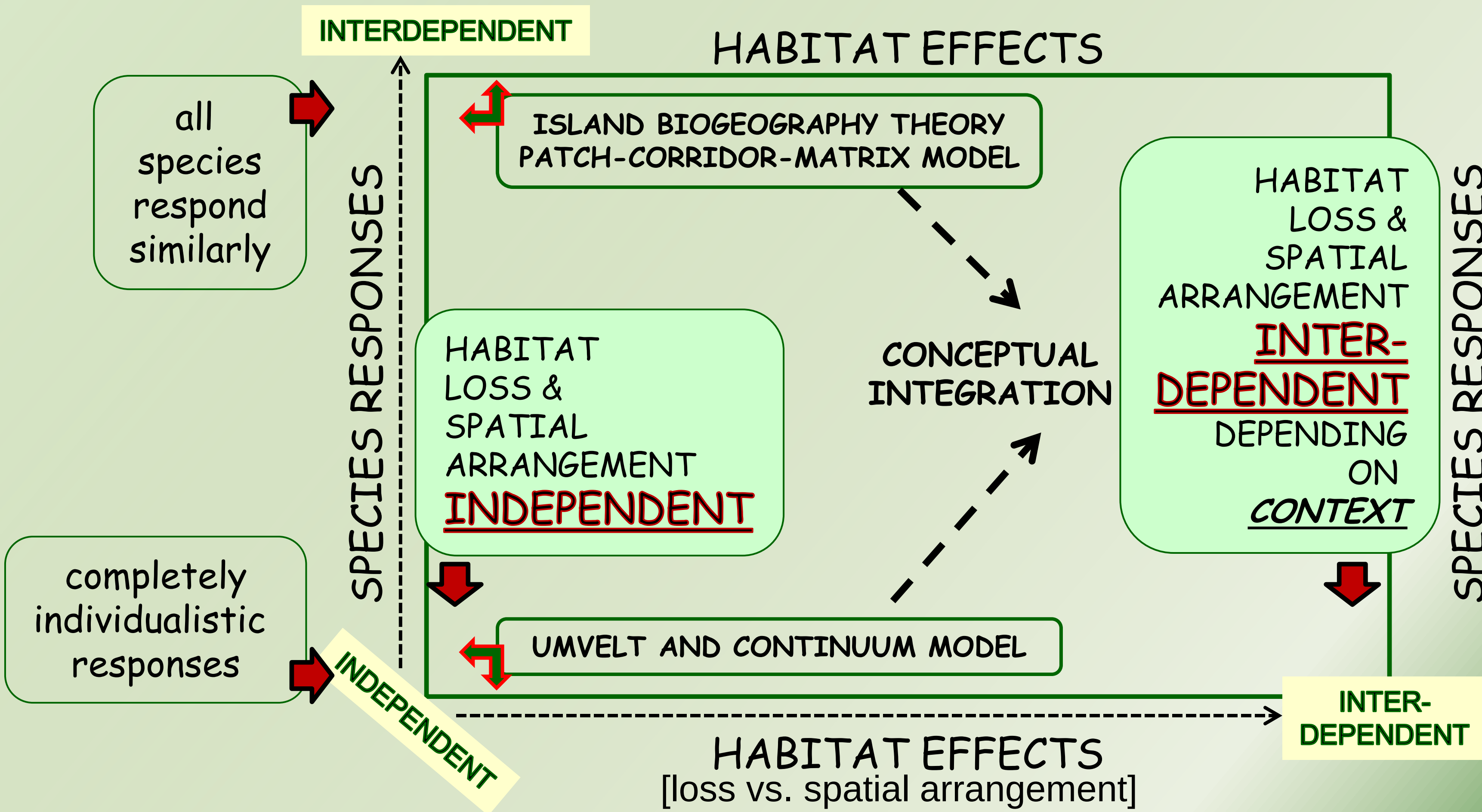
Inter-dependent landscape effects

Didham et al. 2012 Oikos 121:161-170

Lortie et al. 2004 Oikos 107;433-438

a game-changing distinction

CONCEPTUAL FRAGMENTATION
"PROBLEM SPACE"



REDRAWN FROM: Didham, R.K., V. Kapos, and R. M. Ewers. 2012 Oikos 121:161-170

Given the work of Didham et al. 2012, 2 general principles emerge:

Interdependence of landscape effects on species

Can we understand the degree of multiple causal factors affecting species. What is the dependency that characterizes landscape effects?

Interdependence of species responses to landscape change

Can we understand the degree of dependence or independence of species responses to landscape change?
How similar is species response?

How can we separate the landscape effects of

habitat loss vs. habitat arrangement

on species response?

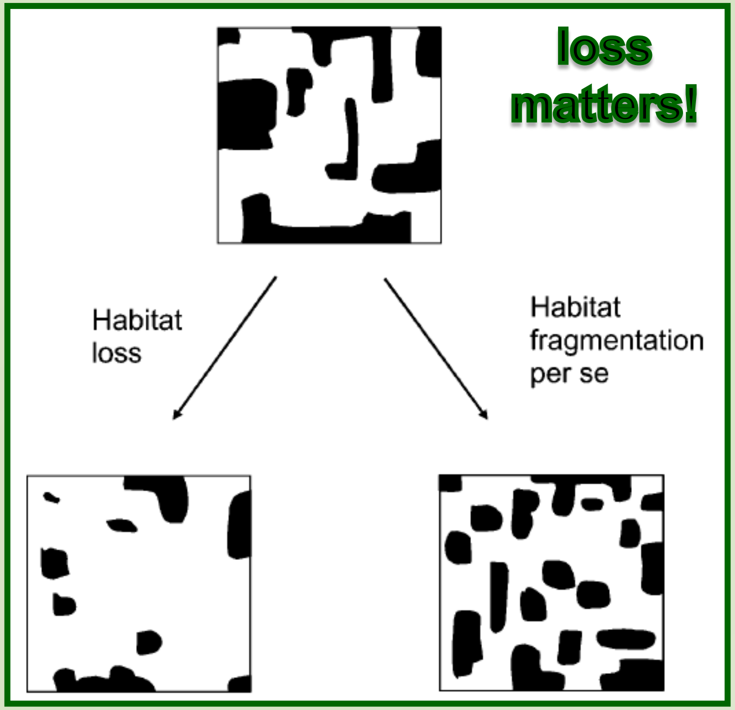
What is the nature of species response to landscape change?

Do species respond identically, independently, or somewhere in between?

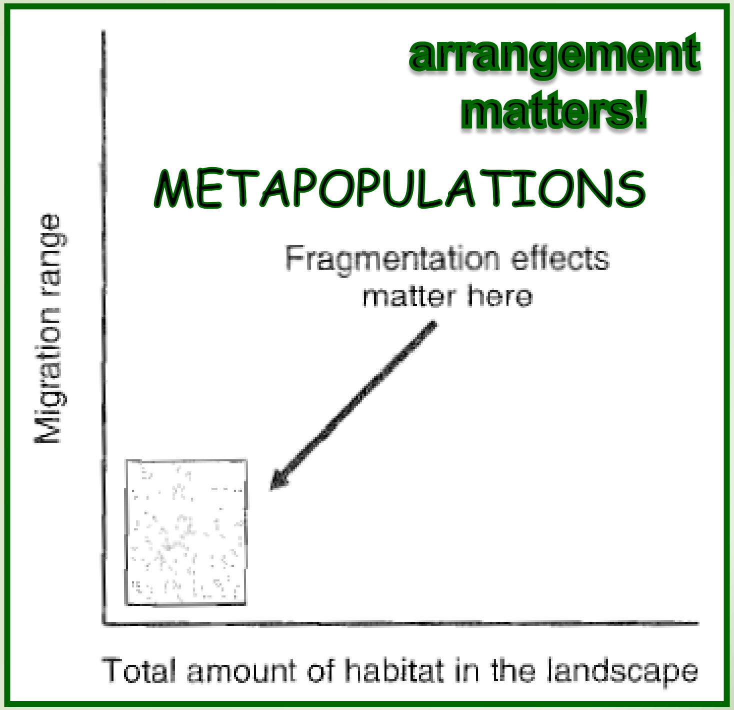
Landscape effects

habitat loss or spatial arrangement?

Fahrig, L. 2003/ Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 2003. 34:487–515



Hanski, I. and O. Gagliotti. 2004. Ecology, genetics, and evolution of metapopulations. Lavoisier.



The Fahrig/Hanski Debate

ASSUMPTION: THE EFFECTS ARE INDEPENDENT

Are species responses totally individualistic ?

if they are… .

"the daunting implication of an assumption of individualistic species responses is that there are as many landscapes as there are organisms"

Manning et. al. 2004, p. 627

perhaps there is a more rational and reasonable way to look at these dichotomies

A parsimonious explanation

based on an interdependence model

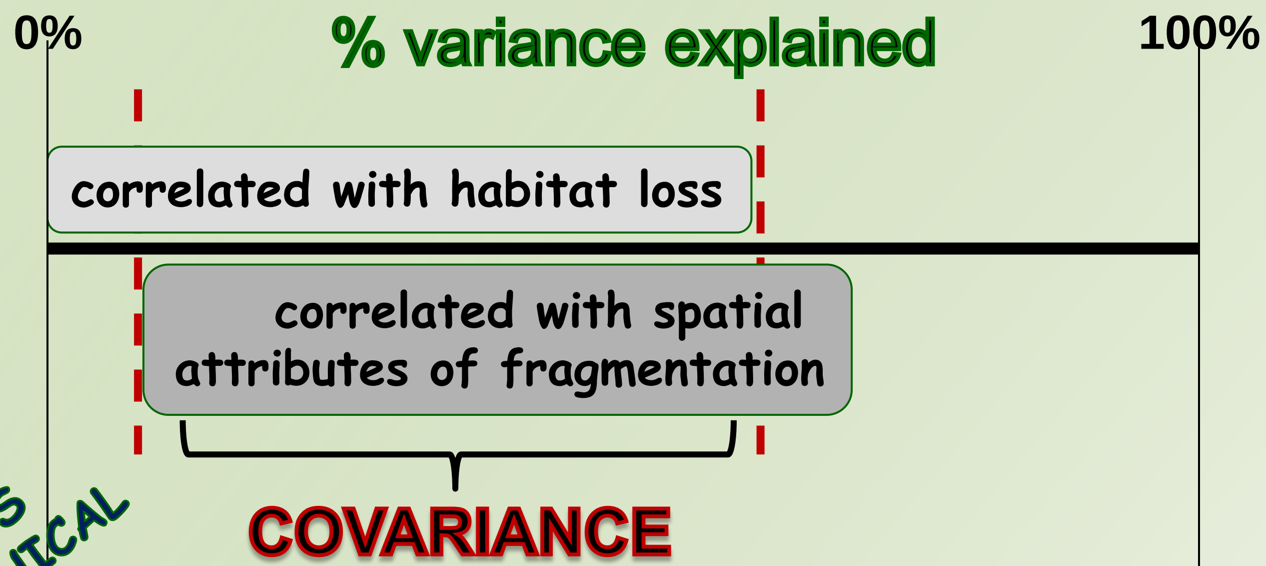
"the effects of habitat loss
are mediated … . by
changing spatial arrangements of habitat… .

habitat loss acts via the
change in habitat arrangement,
not independently of it."

Didham et al. 2012

SO BOTH ARE IMPORTANT

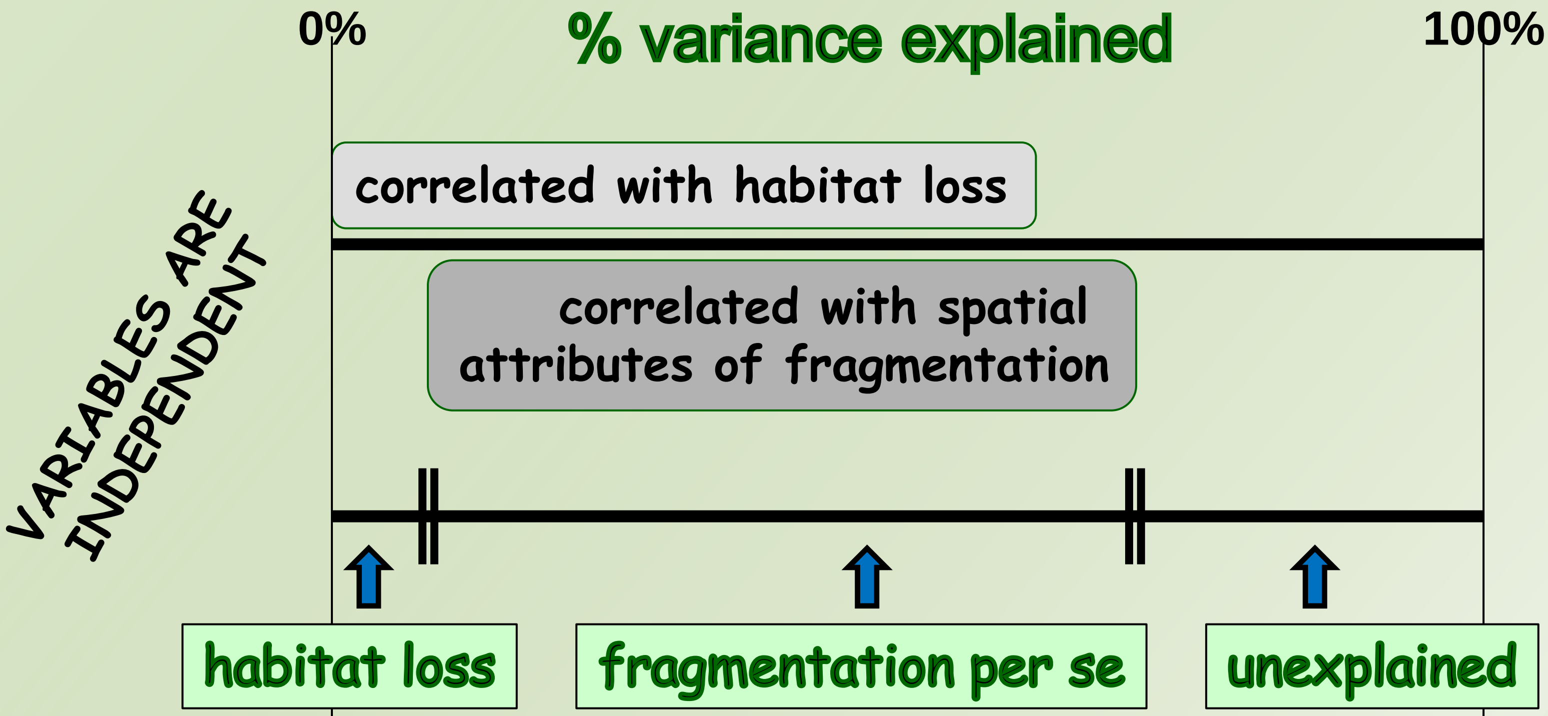
the typical correlation structure of the data



SUGGESTS A HIERARCHICAL APPROACH

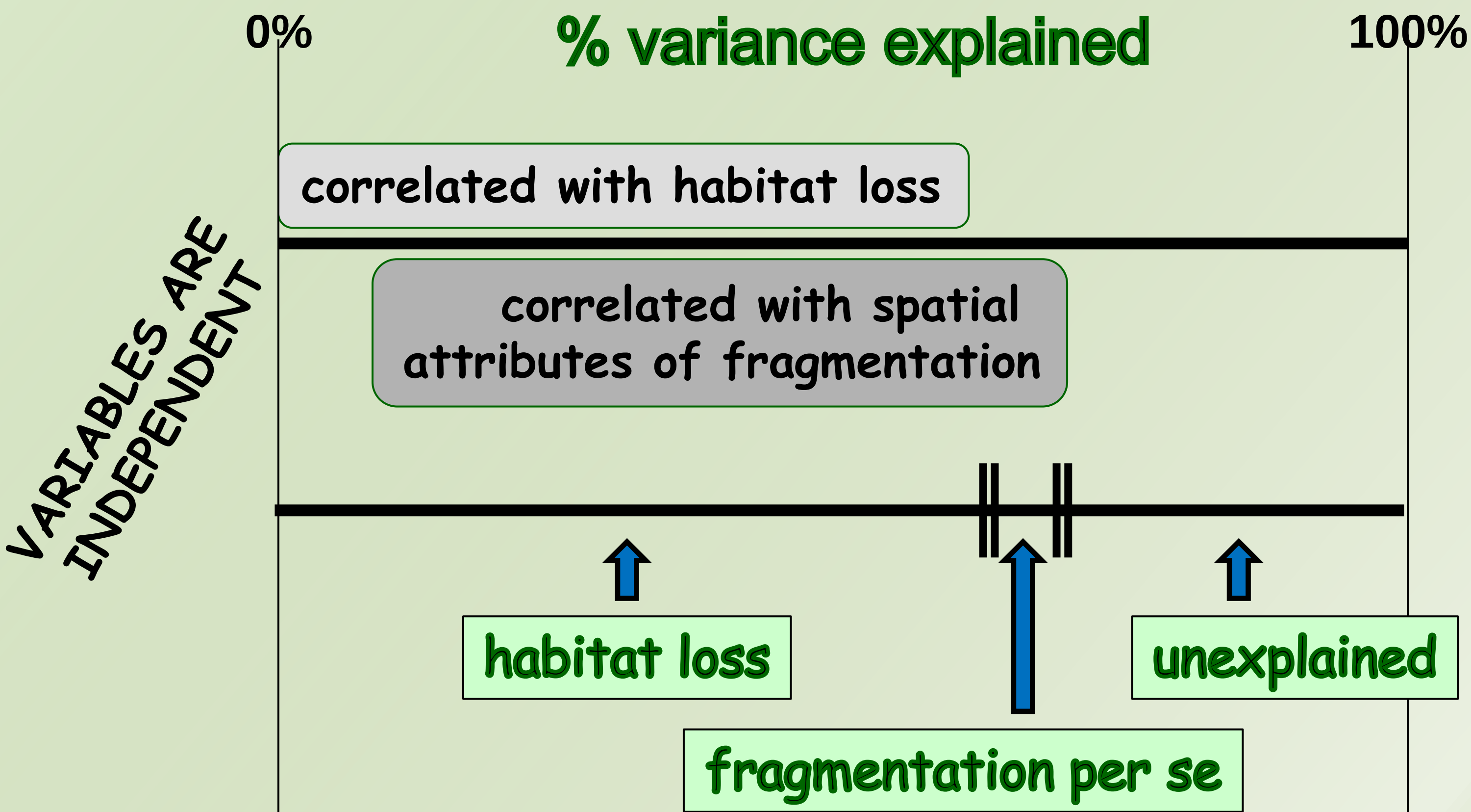
"the effects of habitat loss <u>are mediated</u> … . by changing spatial arrangements of habitat… . "

a patch-biased perspective of how variance is explained



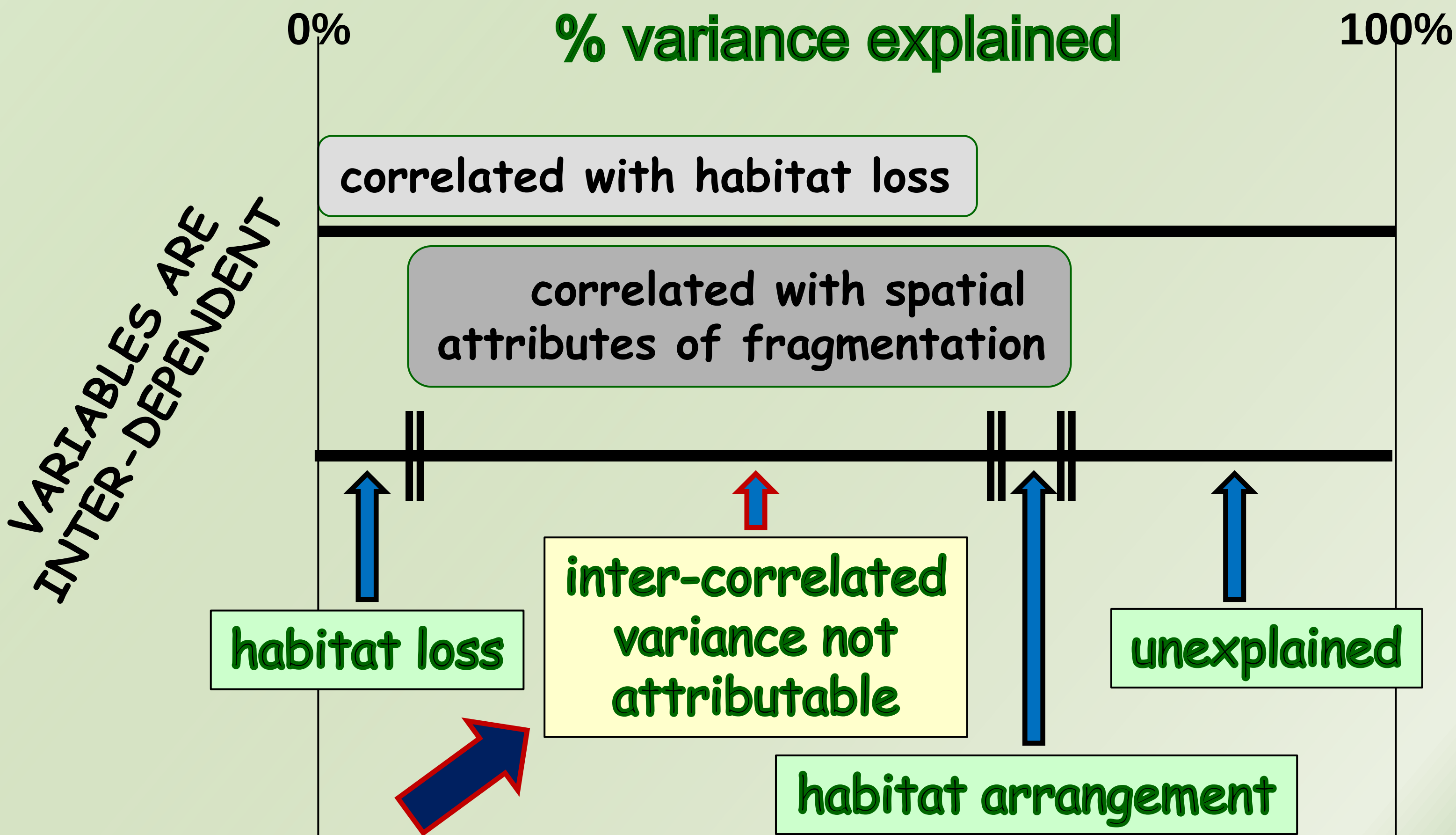
1990s studies: inter-correlation ignored, or inappropriate inference

a landscape-biased perspective of how variance is explained



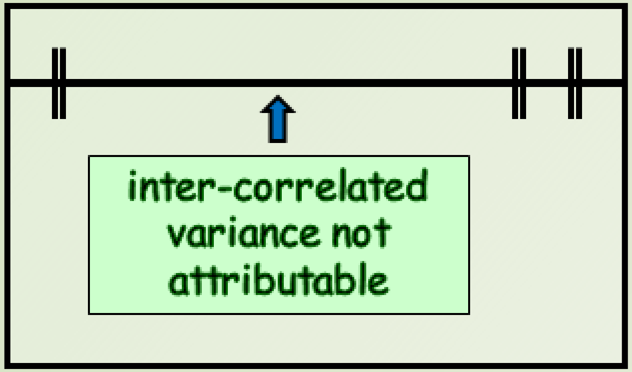
mid-1990s landscape perspective
the de rigeur approach – control for loss, then fragmentation.
“direction of bias just different’

recognition of inter-correlated variance of how variance is explained



partitioning the contributions of habitat loss and fragmentation in the inter-correlated portion is the goal so then,

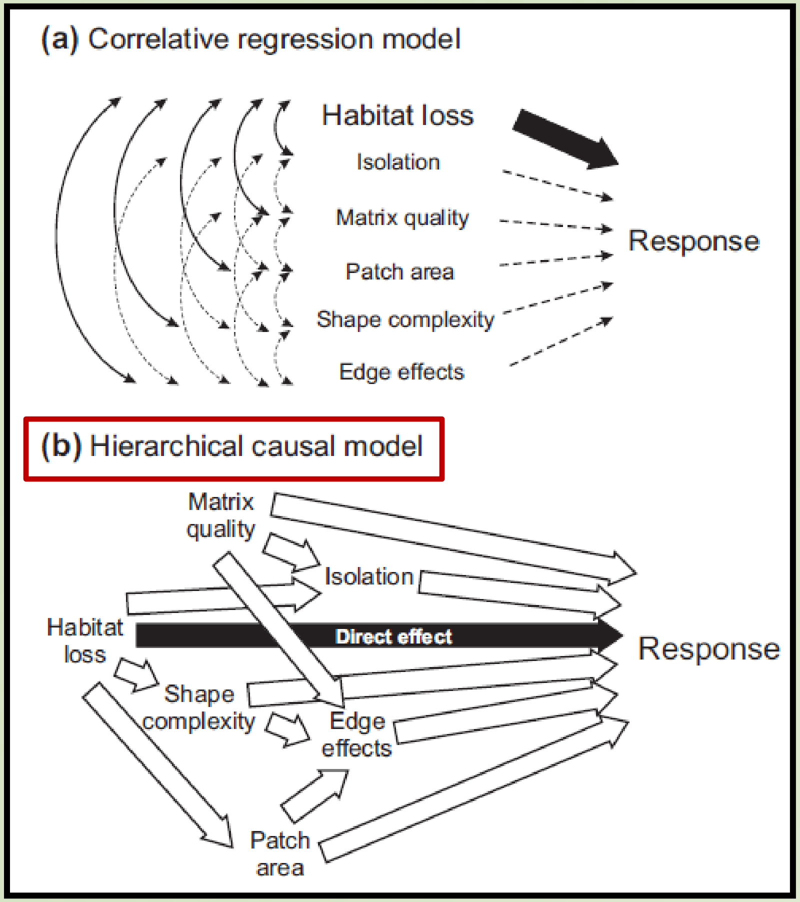
how can we partition the inter-correlated variance?



what might some competing models look like?

they need to be hierarchical

Examples of competing hypothetical models
to investigate the contribution of habitat loss and fragmentation



INDEPENDENT

MULTIPLE REGRESSION MODEL USING A 1990s LANDSCAPE-BIASED APPROACH (**HABITAT LOSS ASSESSED FIRST**)

INTERDEPENDENT

STRUCTURAL EQUATION MODEL. HABITAT LOSS **OPERATES DIRECTLY AND SEPARATELY *AND* INDIRECTLY MEDIATED BY SPATIAL CONFIGURATION**

Wright, Sewall S. (1921). "Correlation and causation". *Journal of Agricultural Research* **20**: 557–85.
Simon, Herbert (1953). "Causal ordering and identifiability". In Hood, W.C.; Koopmans, T.C. *Studies in Econometric Method*. New York: Wiley. pp. 49–74
Bollen, K A, and Long, S J (1993) *Testing Structural Equation Models*. SAGE Focus Edition, vol. 154, ISBN 0-8039-4507-8
Pearl, Judea (2000). *Causality: Models, Reasoning, and Inference*. Cambridge University Press. ISBN 0-521-77362-8.

structural equation modeling

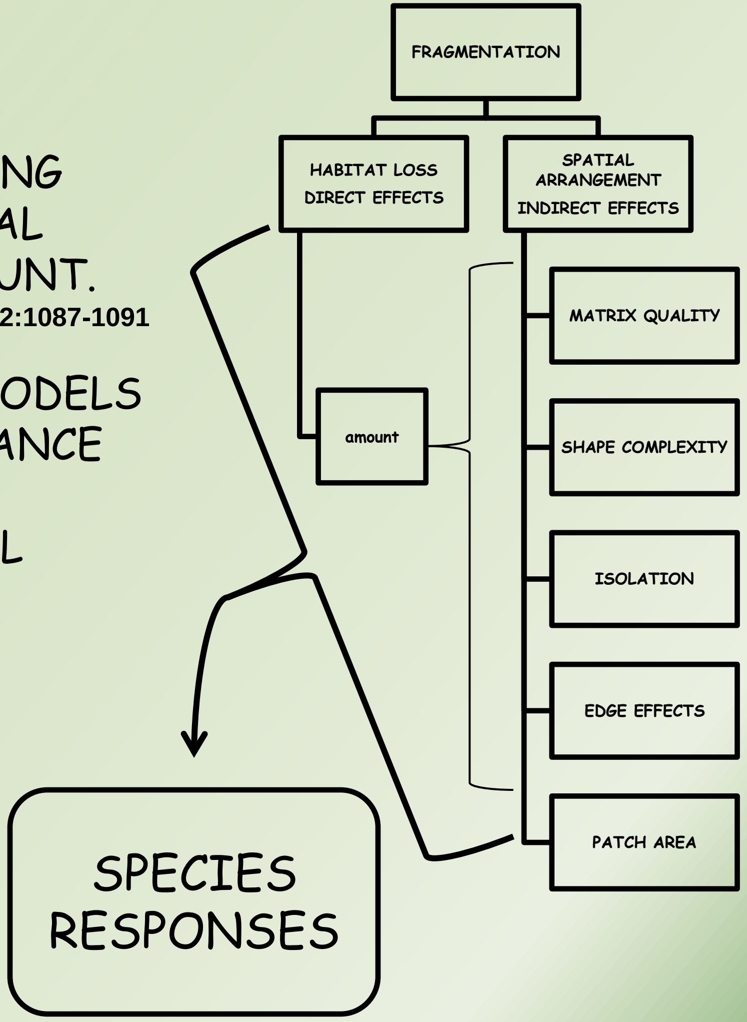
KEY: hierarchical structure

FRAGMENTATION A SINGLE HIERARCHICAL PROCESS RECOGNIZING THE CAUSAL DEPENDENCE OF SPATIAL CONFIGURATION ON HABITAT AMOUNT.

Le Tortorec et al. 2013. J. Animal Ecology 82:1087-1091

REGRESSION TECHNIQUES, MOST MODELS SELECTION PROCEDURES, AND VARIANCE PARTITION DO NOT TAKE INTO CONSIDERATION THE HIERARCHICAL NATURE OF FRAGMENTATION

REQUIRES THINKING UP-FRONT.
EX.: extinction debt (time lag persistence but ultimate failure)
Smaller, more isolated patches, changes to the matrix suggested causes. SEM a way to test the model.



nota bene

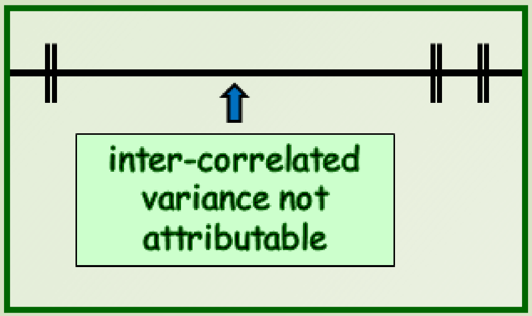
DIRECT AND INDIRECT EFFECTS OF HABITAT LOSS & SPATIAL CONFIGURATION
DO NOT THEMSELVES EXPLAIN ANIMAL RESPONSE

RATHER, THE EFFECTS OPERATE THROUGH INTERVENING, MORE PROXIMATE BIOTIC AND ABIOTIC VARIABLES

One Possible Causal Network

Idea redrawn from:
Didham, R.K., V. Kapos, and R. M. Ewers. 2012 Oikos 121:161-170

INTERVENING VARIABLES



HABITAT

loss	configuration
⇩	⇩
patch area size & shape	matrix quality and contrast
⇩	⇩
edge effects	isolation
⇩	⇩
edge contrast	patch area
⇩	⇩

proximate variables → vegetation structure | resource availability

response variables → VITAL RATES
Birth, Immigration, Death, Emigration

$\underbrace{\text{Birth, Immigration, Death, Emigration}}_{\text{Population Change}}$

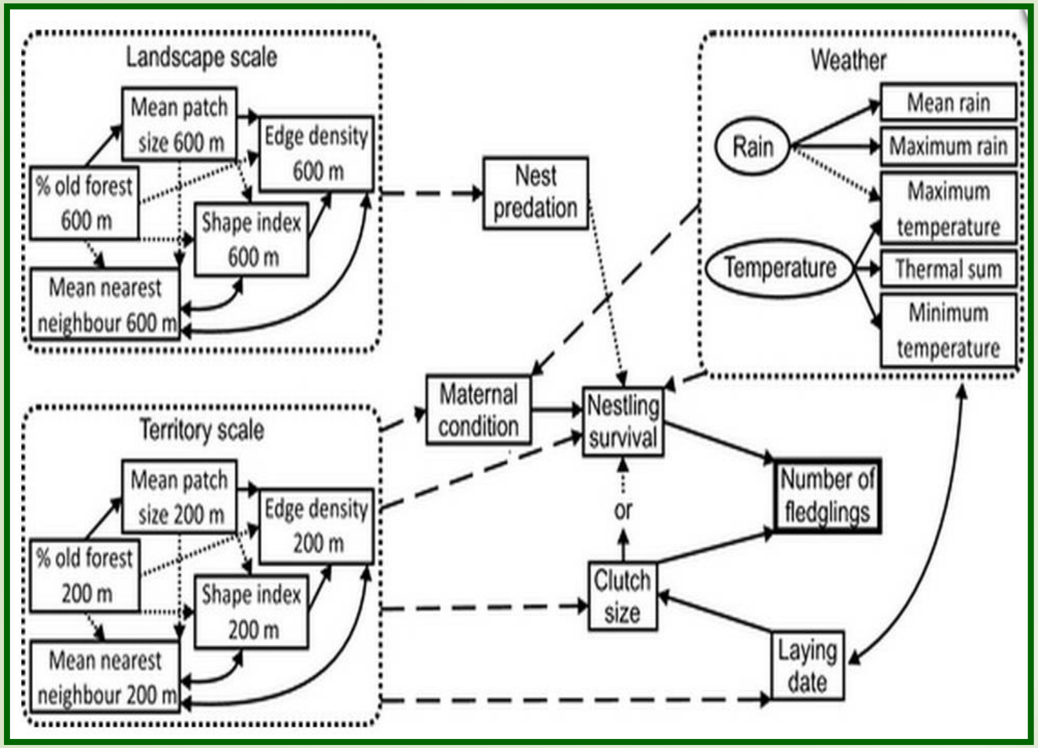
A REAL EXAMPLE USING STRUCTURAL EQUATION MODELLING

HABITAT EXTENT

NEST PREDATION RATES

REPRODUCTIVE SUCCESS

SPATIAL CONFIGURATION OR HABITAT LOSS



investigated how old forest fragmentation was associated with the # of fledged offspring of the area-sensitive Eurasian treecreeper (Certhia familiaris).

Le Tortorec et al. 2013. J. Animal Ecology 82:1087-1097.

SOME POSSIBLE QUESTIONS

an inter-dependent conceptualization allows new and different and seemingly more relevant questions (driven by our knowledge of the system) to be asked:

e.g.:

TO WHAT DEGREE DOES PATCH ISOLATION PLAY A PART IN THE VITAL RATES OF CORE-SENSITIVE SPECIES?

HOW DOES MATRIX TYPE, QUALITY, OR STRUCTURE INTERACT WITH PATCH SIZE AND CORE AREA?

IS MATRIX/PATCH CONTRAST IMPORTANT IF THE SPECIES IS A GENERALIST?

DO HARD VS. SOFT EDGES , e.g., CONTRASTING VEGETATION STRUCTURE MAKE A DIFFERENCE TO ANIMAL MOVEMENT, AND IF SO, WHAT OTHER ELEMENTS OF FRAGMENTATION PER SE ARE INVOLVED?

a take-home message

An inter-dependence approach to parse the landscape effects of habitat loss and habitat fragmentation on species response and to assess species responses to landscape change appears to be a much more fruitful approach to understanding the full effects of changing landscapes

To say that there are 'scale effects' or that 'fragmentation' results in 'species responses' is uninformative. Parsing the effects of habitat loss and spatial arrangement is more likely to be more satisfying.

the last slide (almost)

the models we use impose a perceptual bias, a filter through which the system is viewed and analyzed.

this has fundamental significance, because models that represent the state of nature more closely are likely to give better answers to complex questions

Relevant Papers

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proortions of suitable habitat: a review. *Oikos* 71:355-366.

Bunnell, **F.** 1999. Foreword. Let's kill a panchreston: Giving fragmentation a meaning. Pages vii–viii *in* J. Rochelle, L.A. Lehmann and J. Wisniewski (eds), *Forest Wildlife and Fragmentation: Management Implications*. Leiden, Germany: Brill.

Didham, R.K., V. Kapos, and R. M. Ewers. 2012. Rethinking the conceptual foundation of habitat fragmentation research. *Oikos* 121:161-170

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.

Fischer, J. and D.B. Lindenmayer. 2006. Beyond fragmentation: The continuum model for fauna research and conservation in human-modified landscapes. *Oikos* 112:473–480.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. *Ecological Applications* 12:321–334.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.

Lindenmayer, D.B. and J. Fischer. 2007. Tackling the habitat fragmentation panchreston. *Trends in Ecology and Evolution* 22:127–132.

Lord, J.M. and D.A. Norton. 1990. Scale and the spatial concept of fragmentation. *Conservation Biology* 4:197–202.

Manning, A.D., D.B. Lindenmayer and H.A. Nix. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos* 104:621–628.

McIntyre, S. and G.W. Barrett. 1992. Habitat variegation, an alternative to fragmentation. *Conservation Biology* 6:146–147.

McIntyre, S., G.W. Barrett and H.A. Ford. 1996. Communities and ecosystems. Pages 154–170 *in* I.F. Spellerberg (ed), *Conservation Biology*. Essex, UK: Longman Group.

McIntyre, S. and R.J. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology* 13:1282–1292.

Preston, F.W. 1962. The canonical distribution of commonness and rarity: Part II. *Ecology* 43;410-432.

Ritchie, M.E. 1997. Populations in a landscape context: Sources, sinks, and metapopulations. Pages 160–184 *in* J.A. Bissonette (ed), *Wildlife and Landscape Ecology: Effects of Pattern and Scale*. New York: Springer.

Saunders, D.A., R.J. Hobbs and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18–32.

Villard, M.A. 2002. Habitat fragmentation: Major conservation issue or intellectual attractor? *Ecological Applications* 12:319–320.

Le Tortorec, E., S. Helle, N. Kayhko, P. Suorsa, E. Huhta, and H. Hakkarainen. 2013. Habitat fragmentation and reproductive success: a structural equation modelling approach. *Journal of Animal Ecology* 82:1087-1097.

History of SEM

- Methodology is still developing
- Fundamental concepts are subject to challenge and revision

SEM changes

= ☺ for some & ☹ for others

http://sunburst.usd.edu/~rrraszko/SEMdummies/SEM4dummies.pdf

What is SEM?

SEM is an umbrella of 3 processes:

1. Path Analysis
   - Analysis of structural models of observed variables
2. Confirmatory Factor Analysis
   - Analysis of a priori measurement models where both the number of factors and their correspondence to the indicators are explicitly specified
3. Structural Regression Models
   - The synthesis of (1)path and (2)measurement models

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What is SEM?

SEM is a confirmatory technique

- **DO** use SEM to determine if a model is valid for the data in conjunction with prior research
- **DON'T** use SEM to find a suitable model (it's not an exploratory technique)

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Structural equation modelling (**SEM**) is a statistical technique for testing and estimating causal relations using a combination of statistical data and qualitative causal assumptions. This definition of SEM was articulated by the geneticist Sewall Wright (1921),[1] the economist Trygve Haavelmo (1943) and the cognitive scientist Herbert A. Simon (1953),[2] and formally defined by Judea Pearl (2000) using a calculus of counterfactuals.[3]

Structural equation models (SEM) allow both confirmatory and exploratory modeling, meaning they are suited to both theory testing and theory development. Confirmatory modeling usually starts out with a hypothesis that gets represented in a causal model. The concepts used in the model must then be operationalized to allow testing of the relationships between the concepts in the model. The model is tested against the obtained measurement data to determine how well the model fits the data. The causal assumptions embedded in the model often have falsifiable implications which can be tested against the data.[4]

With an initial theory SEM can be used inductively by specifying a corresponding model and using data to estimate the values of free parameters. Often the initial hypothesis requires adjustment in light of model evidence. When SEM is used purely for exploration, this is usually in the context of exploratory factor analysis as in psychometric design.[*clarification needed*]

Among the strengths of SEM is the ability to construct latent variables: variables that are not measured directly, but are estimated in the model from several measured variables, each of which is predicted to 'tap into' the latent variables. This allows the modeler to explicitly capture the unreliability of measurement in the model, which in theory allows the structural relations between latent variables to be accurately estimated. Factor analysis, path analysis and regression all represent special cases of SEM.

In SEM, the qualitative causal assumptions are represented by the missing variables in each equation, as well as vanishing covariances among some error terms. These assumptions are testable in experimental studies and must be confirmed judgmentally in observational studies.