Imperial College London

MARIE CURIE ACTIONS

Advanced topics in population and community ecology and conservation

Lecture 4

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Outline

- Applications of SAR
  - estimating number of species in areas of different sizes
  - estimating extinction debt
  - understanding how communities are structured

- Applications of neutral theory
  - predicting how populations and communities will be affected by area and connectivity

- Applications of phyologenetic approaches

- Detecting changes before they happen

Species extinction

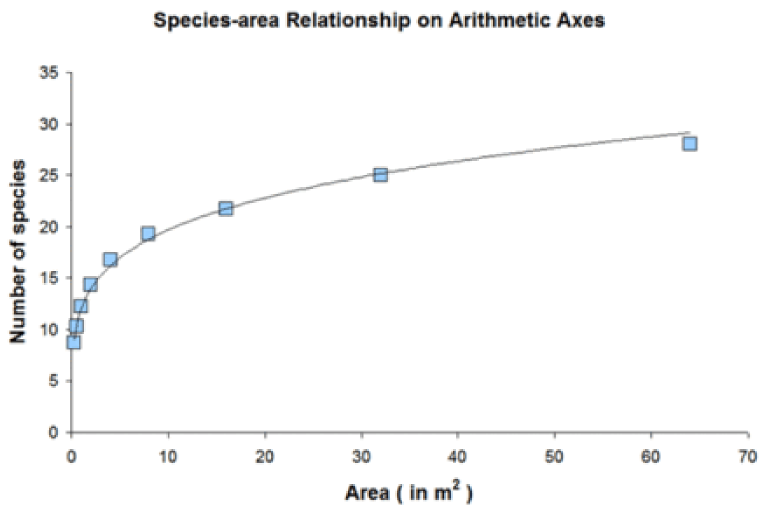
- Every decade **10 million** species are led to extinction due to habitat loss, degradation and fragmentation

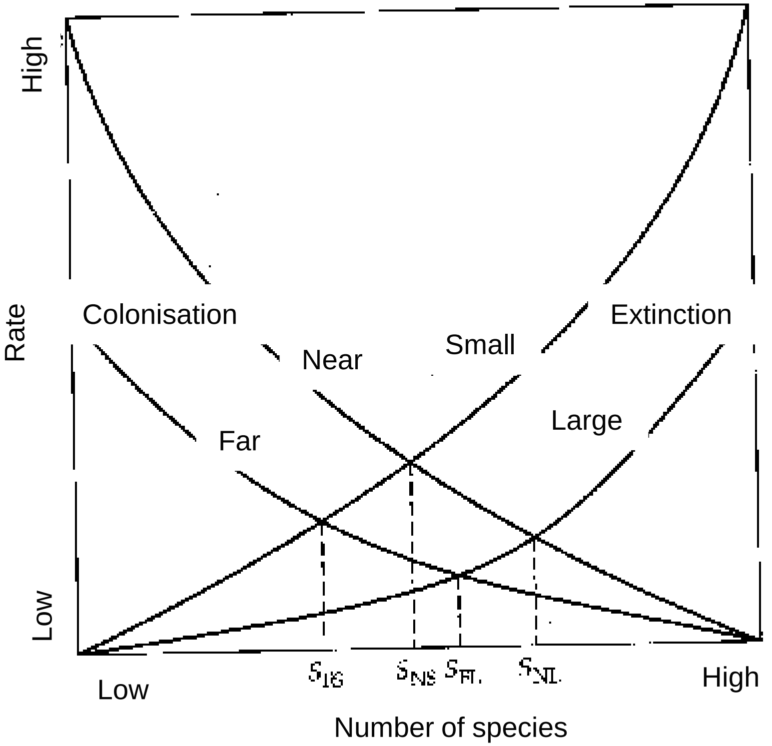
- Species-area relationship

Species-area curve and Island Biogeography

SLOSS – Single Large or Several Small

Landscape Ecology





Extinction debts and relaxation times

Before isolation

After isolation

After relaxation

A_{total}

S_{total}

$A_{fragment}$

$S_{original}$

$A_{fragment}$

S_{now}

$A_{fragment}$

$S_{fragment}$

Relaxation time

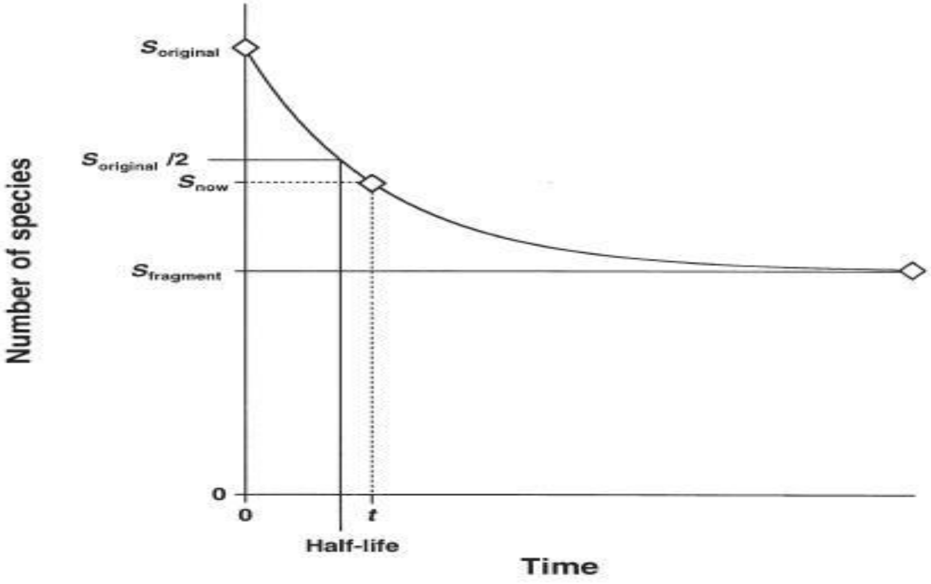
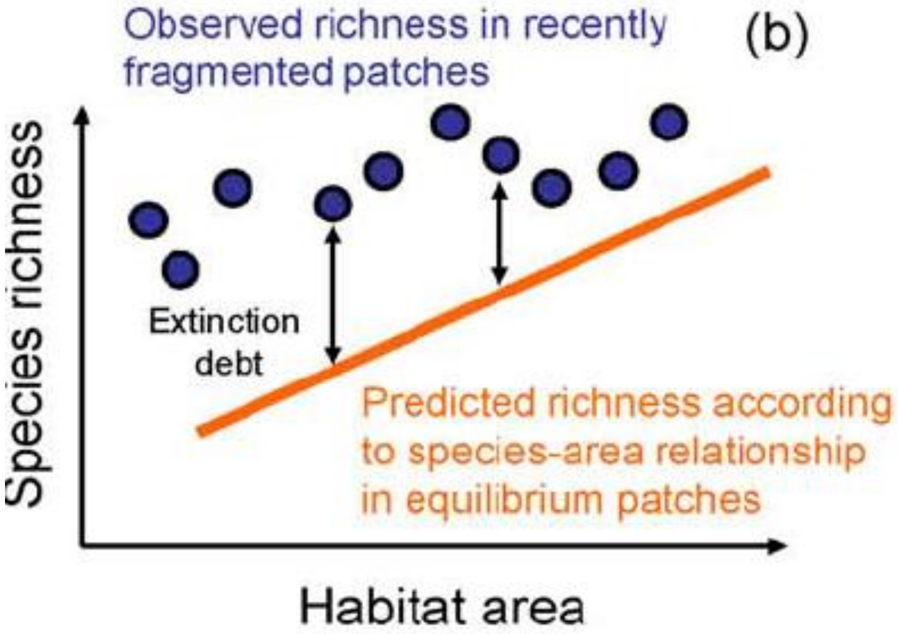
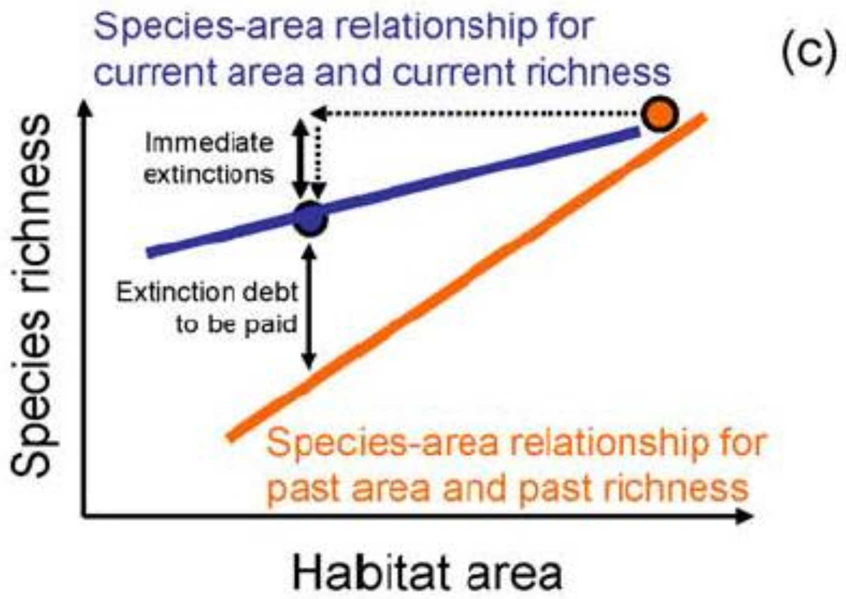


Figure 2. Exponential loss of species from fragmented forest. The number of species in an area of once-continuous forest ($S_{original}$) declines through the number (S_{now}) at the time (t) when a survey was conducted to the number that will eventually survive ($S_{fragment}$). We can estimate $S_{original}$ using $S = cA^z$, with $z = 0.15$ and $S_{fragment}$ using $S = cA^z$ with $z = 0.25$. Because the decay is exponential, we can characterize it by a half-life, the time taken to lose 50% of the species.

Brooks et al. 1999

Using SAR to detect extinction debt





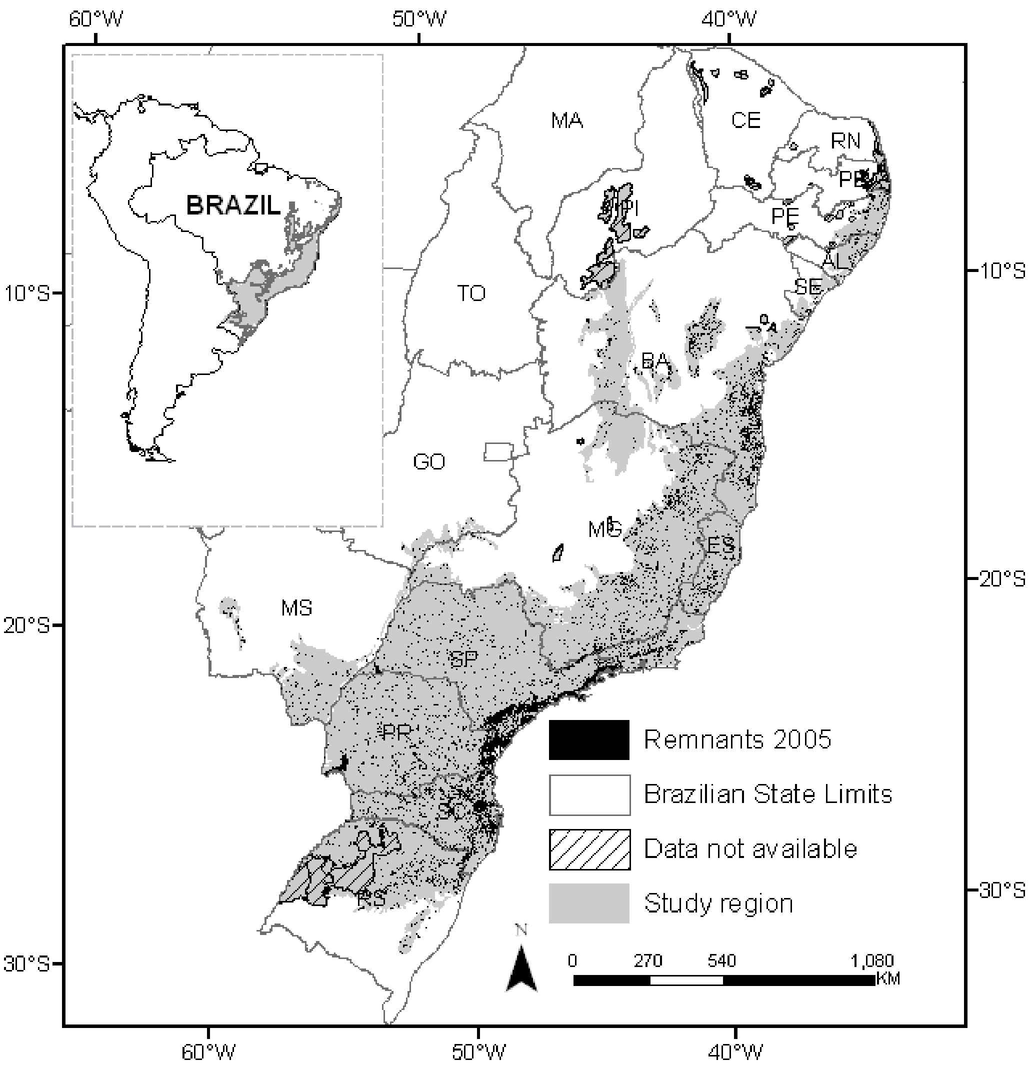
Kuussaari et al. 2009 TREE

LETTER

doi:10.1038/nature09985

Species–area relationships always overestimate extinction rates from habitat loss

Fangliang He[1,2] & Stephen P. Hubbell[3,4]



The Atlantic Forest of Brazil

Ribeiro et al. (2009)

LETTER

doi:10.1038/nature09985

Species–area relationships always overestimate extinction rates from habitat loss

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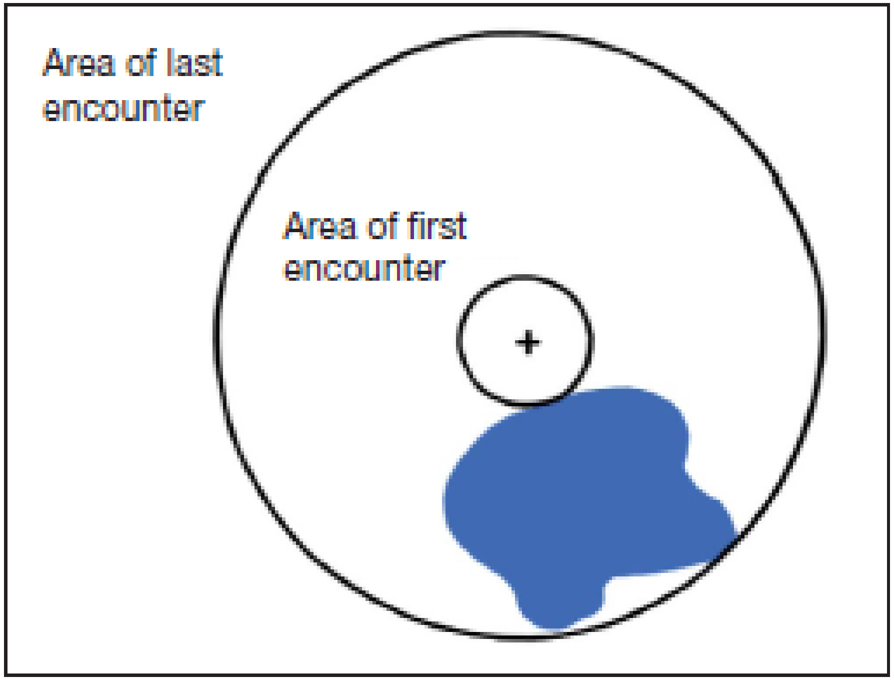


SAR entire area

$$S_A = cA^z$$

SAR portion of area

$$S_a = ca^z$$

SAR species loss in *A*-*a*

$$S_{A-a} = c(A-a)^z$$

Number of species endemic to <u>*a*</u>

$$S_{loss} = S_A - S_{A-a} = cA^z - c(A-a)^z$$

SAR versus EAR method of estimating extinction rate

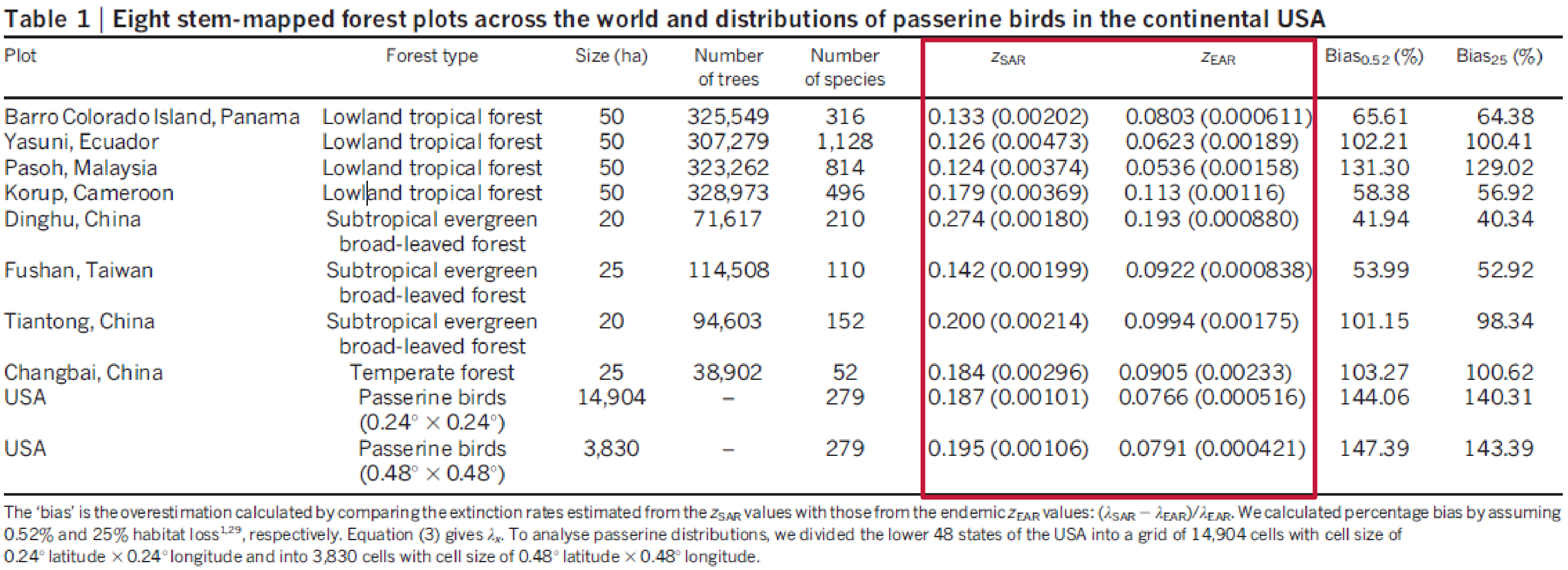
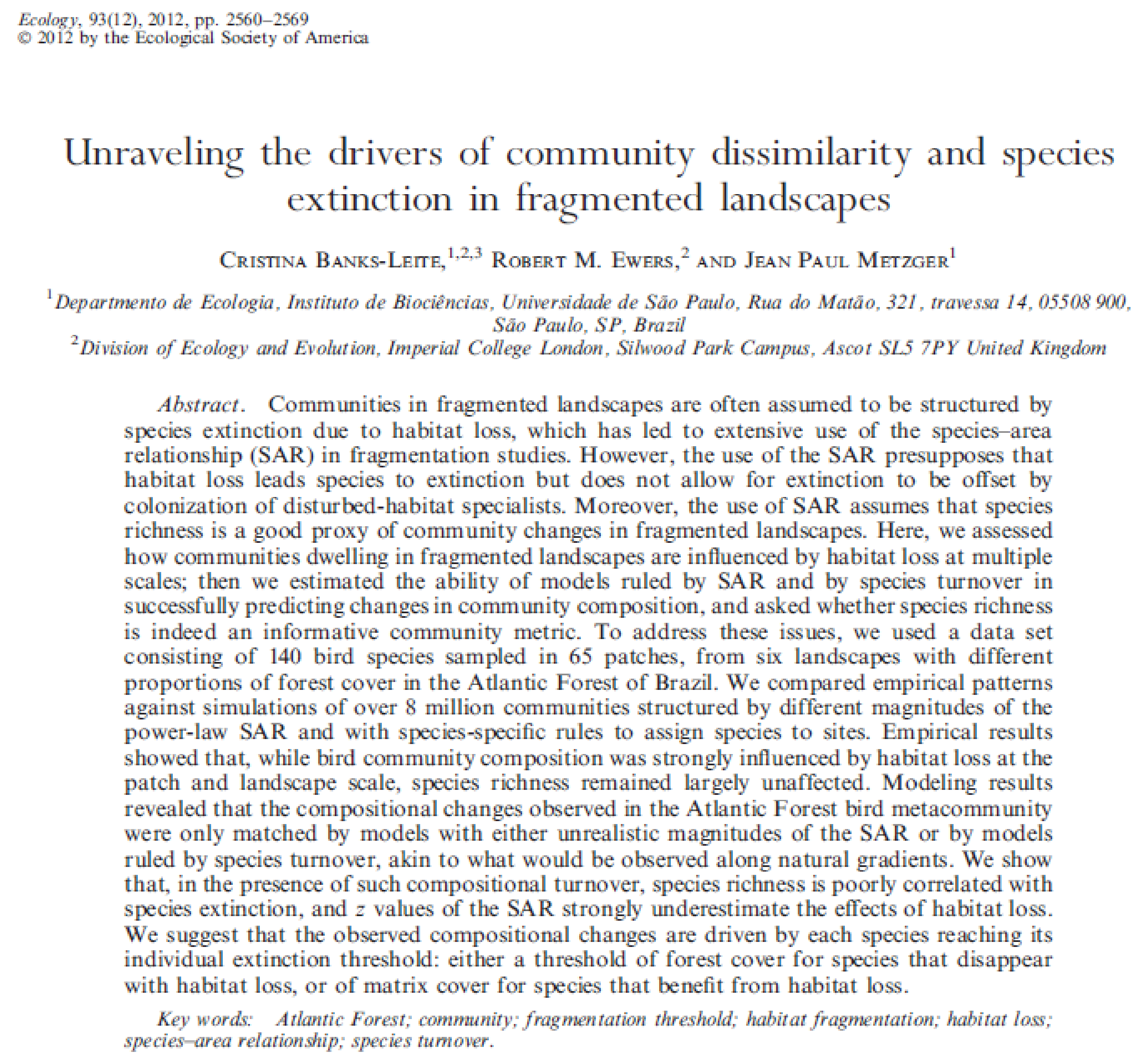


Table 1 | Eight stem-mapped forest plots across the world and distributions of passerine birds in the continental USA

Plot	Forest type	Size (ha)	Number of trees	Number of species	z_{SAR}	z_{EAR}	$Bias_{0.52}$ (%)	$Bias_{25}$ (%)
Barro Colorado Island, Panama	Lowland tropical forest	50	325,549	316	0.133 (0.00202)	0.0803 (0.000611)	65.61	64.38
Yasuni, Ecuador	Lowland tropical forest	50	307,279	1,128	0.126 (0.00473)	0.0623 (0.00189)	102.21	100.41
Pasoh, Malaysia	Lowland tropical forest	50	323,262	814	0.124 (0.00374)	0.0536 (0.00158)	131.30	129.02
Korup, Cameroon	Lowland tropical forest	50	328,973	496	0.179 (0.00369)	0.113 (0.00116)	58.38	56.92
Dinghu, China	Subtropical evergreen broad-leaved forest	20	71,617	210	0.274 (0.00180)	0.193 (0.000880)	41.94	40.34
Fushan, Taiwan	Subtropical evergreen broad-leaved forest	25	114,508	110	0.142 (0.00199)	0.0922 (0.000838)	53.99	52.92
Tiantong, China	Subtropical evergreen broad-leaved forest	20	94,603	152	0.200 (0.00214)	0.0994 (0.00175)	101.15	98.34
Changbai, China	Temperate forest	25	38,902	52	0.184 (0.00296)	0.0905 (0.00233)	103.27	100.62
USA	Passerine birds (0.24° × 0.24°)	14,904	–	279	0.187 (0.00101)	0.0766 (0.000516)	144.06	140.31
USA	Passerine birds (0.48° × 0.48°)	3,830	–	279	0.195 (0.00106)	0.0791 (0.000421)	147.39	143.39

The 'bias' is the overestimation calculated by comparing the extinction rates estimated from the z_{SAR} values with those from the endemic z_{EAR} values: $(\lambda_{SAR} - \lambda_{EAR})/\lambda_{EAR}$. We calculated percentage bias by assuming 0.52% and 25% habitat loss[1,29], respectively. Equation (3) gives λ_x. To analyse passerine distributions, we divided the lower 48 states of the USA into a grid of 14,904 cells with cell size of 0.24° latitude × 0.24° longitude and into 3,830 cells with cell size of 0.48° latitude × 0.48° longitude.

He and Hubbell 2011 Nature



Ecology, 93(12), 2012, pp. 2560–2569

Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes

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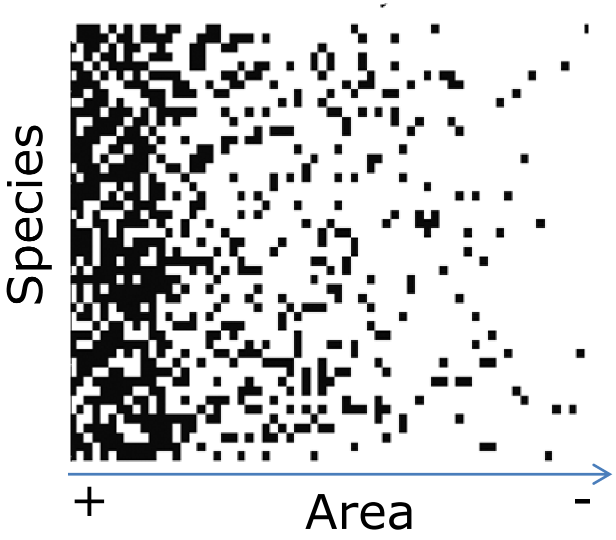
Abstract. Communities in fragmented landscapes are often assumed to be structured by species extinction due to habitat loss, which has led to extensive use of the species–area relationship (SAR) in fragmentation studies. However, the use of the SAR presupposes that habitat loss leads species to extinction but does not allow for extinction to be offset by colonization of disturbed-habitat specialists. Moreover, the use of SAR assumes that species richness is a good proxy of community changes in fragmented landscapes. Here, we assessed how communities dwelling in fragmented landscapes are influenced by habitat loss at multiple scales; then we estimated the ability of models ruled by SAR and by species turnover in successfully predicting changes in community composition, and asked whether species richness is indeed an informative community metric. To address these issues, we used a data set consisting of 140 bird species sampled in 65 patches, from six landscapes with different proportions of forest cover in the Atlantic Forest of Brazil. We compared empirical patterns against simulations of over 8 million communities structured by different magnitudes of the power-law SAR and with species-specific rules to assign species to sites. Empirical results showed that, while bird community composition was strongly influenced by habitat loss at the patch and landscape scale, species richness remained largely unaffected. Modeling results revealed that the compositional changes observed in the Atlantic Forest bird metacommunity were only matched by models with either unrealistic magnitudes of the SAR or by models ruled by species turnover, akin to what would be observed along natural gradients. We show that, in the presence of such compositional turnover, species richness is poorly correlated with species extinction, and z values of the SAR strongly underestimate the effects of habitat loss. We suggest that the observed compositional changes are driven by each species reaching its individual extinction threshold: either a threshold of forest cover for species that disappear with habitat loss, or of matrix cover for species that benefit from habitat loss.

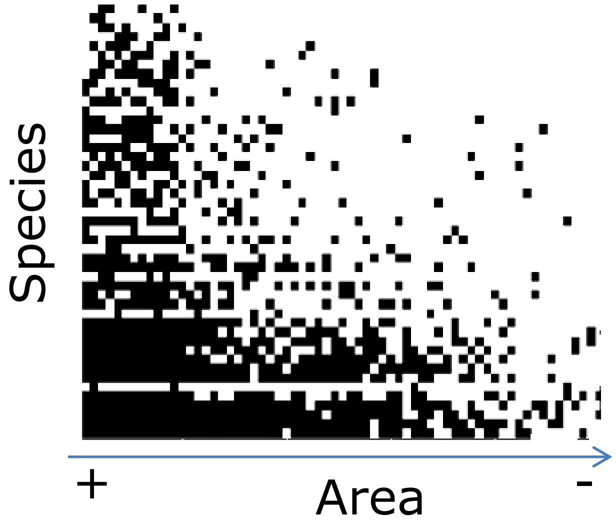
Key words: Atlantic Forest; community; fragmentation threshold; habitat fragmentation; habitat loss; species–area relationship; species turnover.

SAR assumptions: species loss is random and directional

Island biogeography



Terrestrial systems: nestedness



Species loss and species gain

Species-area relationship: assumptions

Species richness is not an informative community metric

Species richness =

Species indentity ≠

Community changes or "community dissimilarity"

- Community composition
  - Species richness
  - Species abundance
  - Species identity

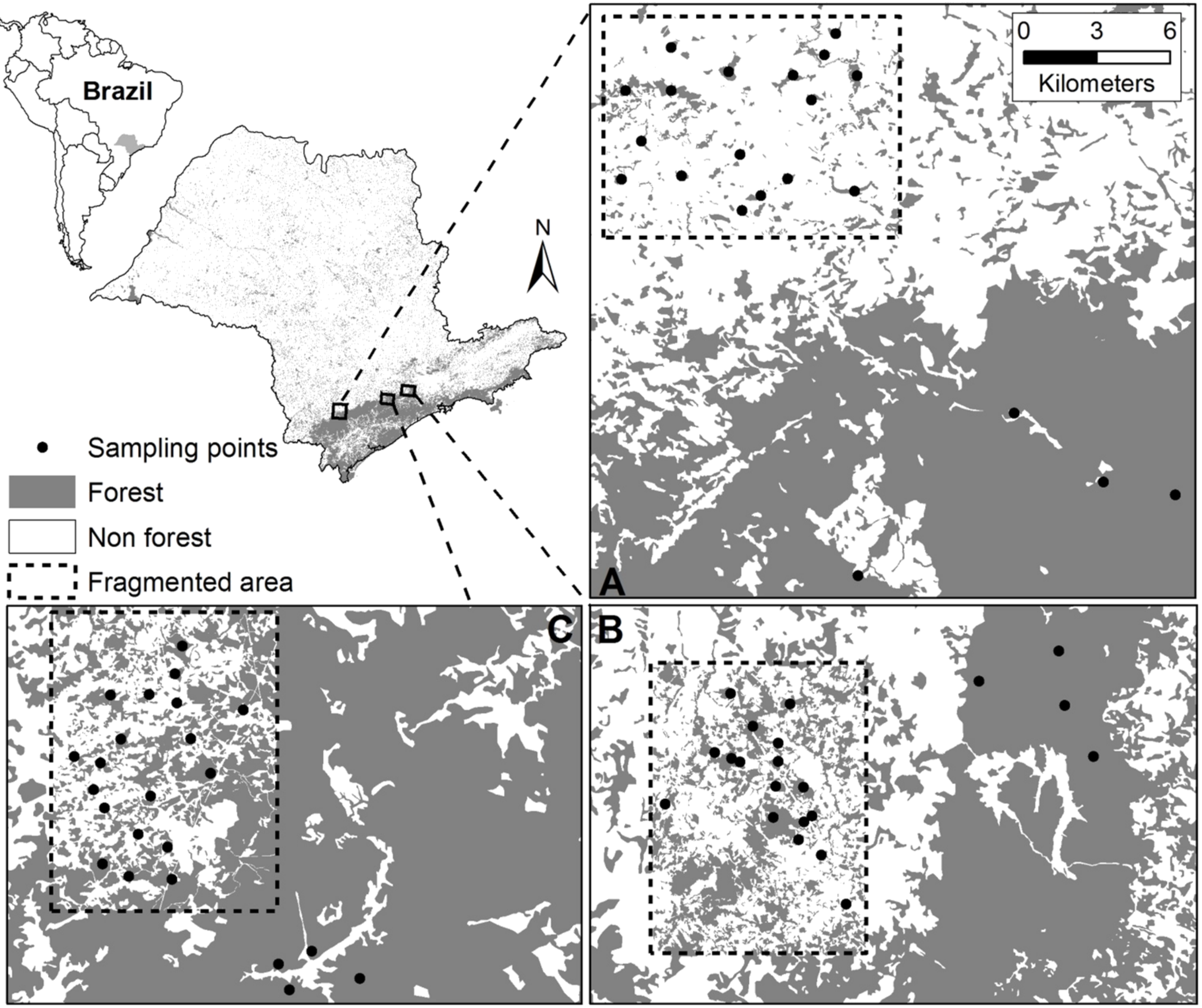
1. Build a similarity matrix (e.g. Euclidean Distance, Bray-Curtis)
2. Build an ordination
3. Obtain the main ordination axes

Research questions

1- Is which species richness an appropriate proxy for species loss?

2- Is the species-area relationship structuring communities in fragmented landscapes?

Study areas



3 fragmented landscapes

10, 30 and 50% forest Cover

53 forest patches

Patch sizes:
2 to 8 ha – small
10 to 40 ha – medium
50 to 150 ha – large

3 continuous landscapes

12 sites

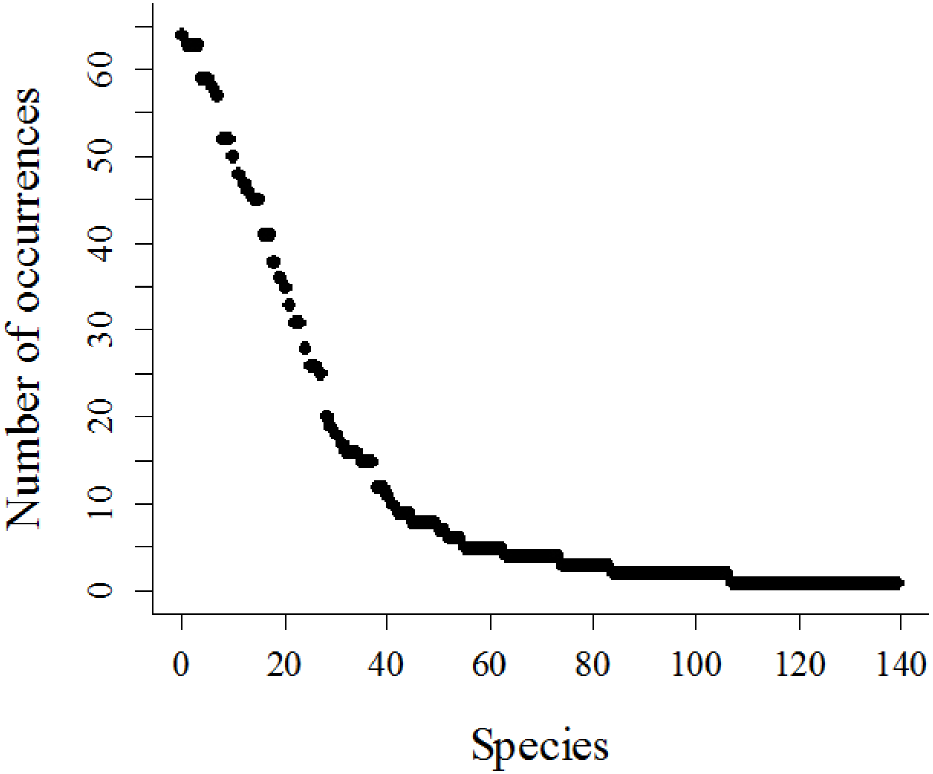
Total = 65 sites sampled

Sampling method

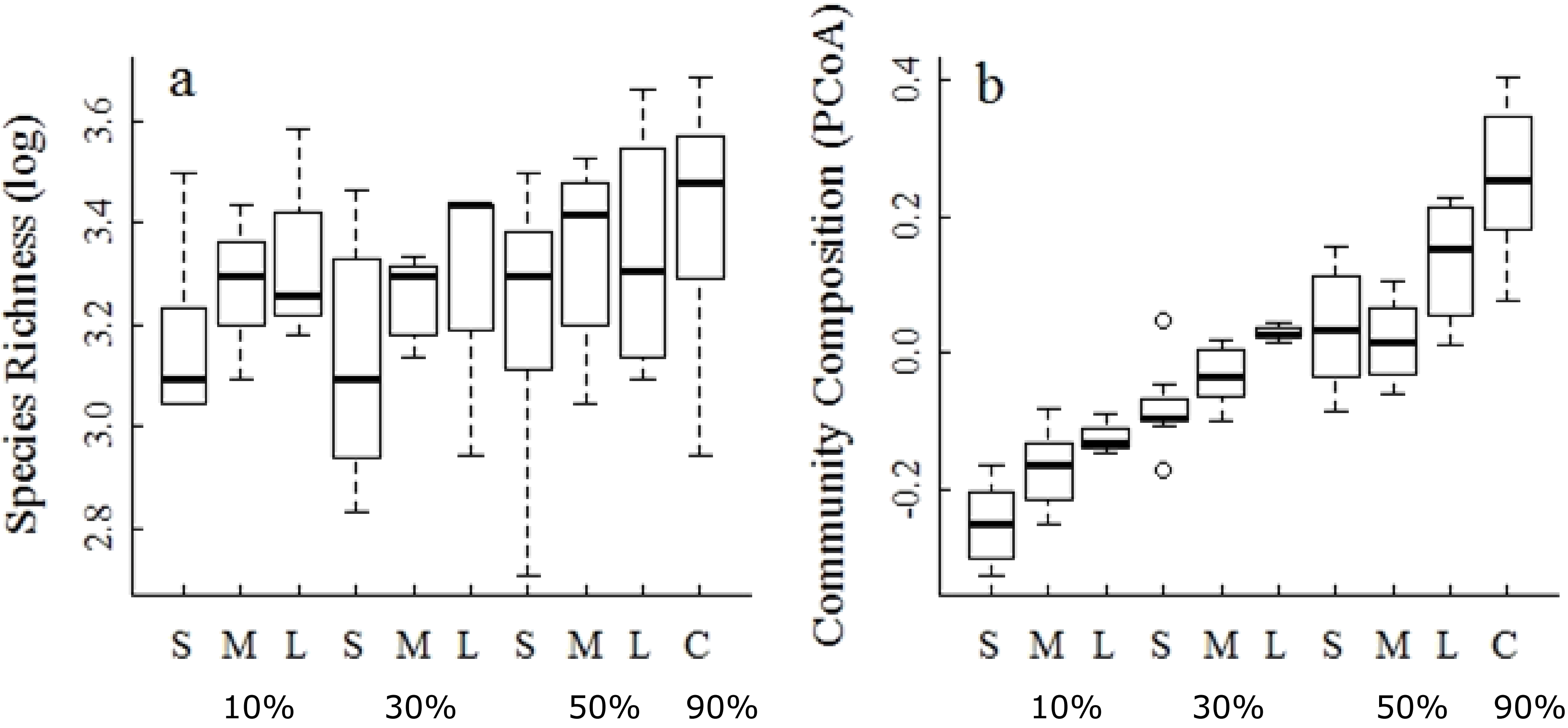
- 10 mist nets (12 m length, 31 mm mesh) at each sampling point
- 540 to 720 net-hours at each sampling point (summer/winter)
- Sunrise to sunset

Empirical dataset: birds from the Atlantic Forest of Brazil

2001 – 2007: 140 species captured from 65 sites (2 to 10,000 ha)



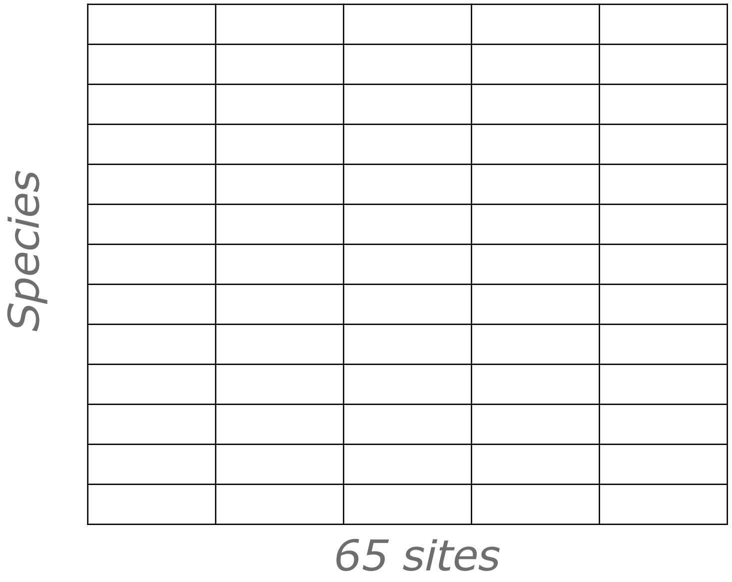
Biodiversity responses to habitat loss at several spatial scales



Simulated dataset: matrices of species by sites

Maximum patch size: 10,000 ha
Maximum observed species richness: 31 species/site

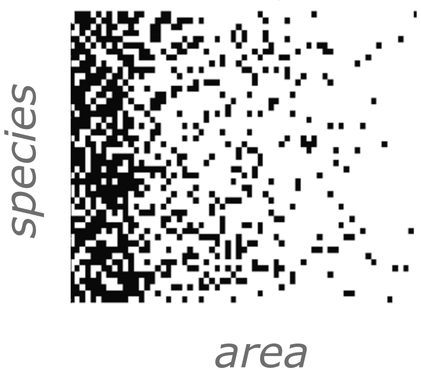
$$S = c*A^z$$



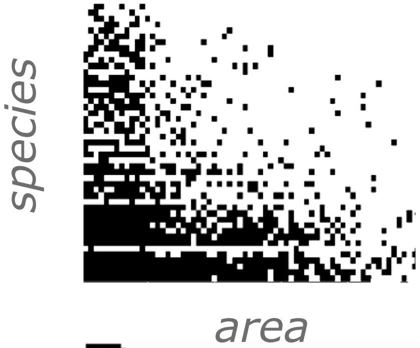
Z-values: varied from 0 to 1 (increments every 0.025)
> 8 million simulated matrices

Simulating communities

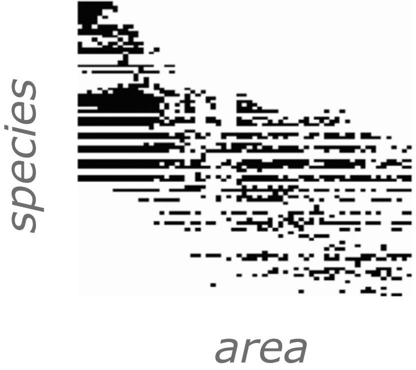
Random community (RAND): species loss is independent of species indentity



Nested community (NEST): rare species are lost first and only common species are found in small areas



Specialised community (SPEC): species are specialised in parts of gradienbt from large to small patches



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Is species richness an appropriate proxy for species loss?

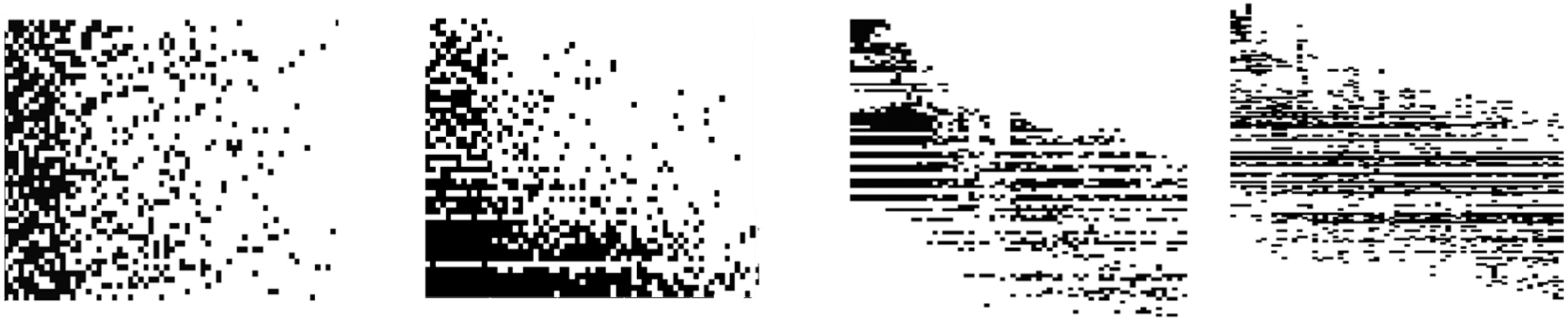
- *Species richness and number of forest species*

	RAND model	NEST model	SPEC model	Bird community
Correlation	1.0 (0.00)	0.99 (0.02)	0.72 (0.2)	0.73
Underestimation	0	0	9.5 (0.5)	9.3

Is the SAR responsible for observed changes in community composition observed in fragmented landscapes?

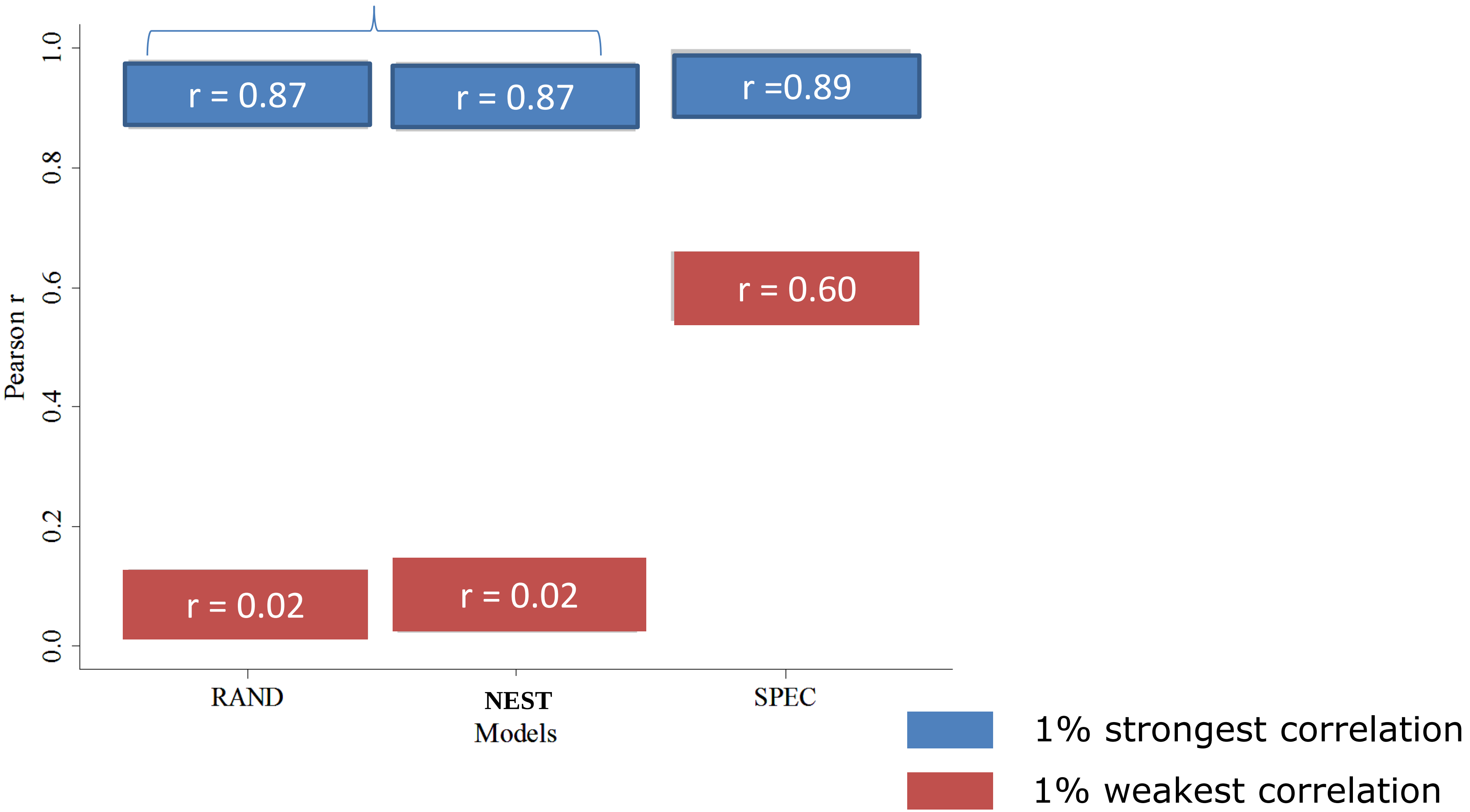
Correlation of ordination scores obtained from simulated matrices and bird community (PCoA – Sørensen Index)

	RAND model	NEST models	SPEC model
Total	0.59 (0.21)	0.63 (0.17)	0.81 (0.05)

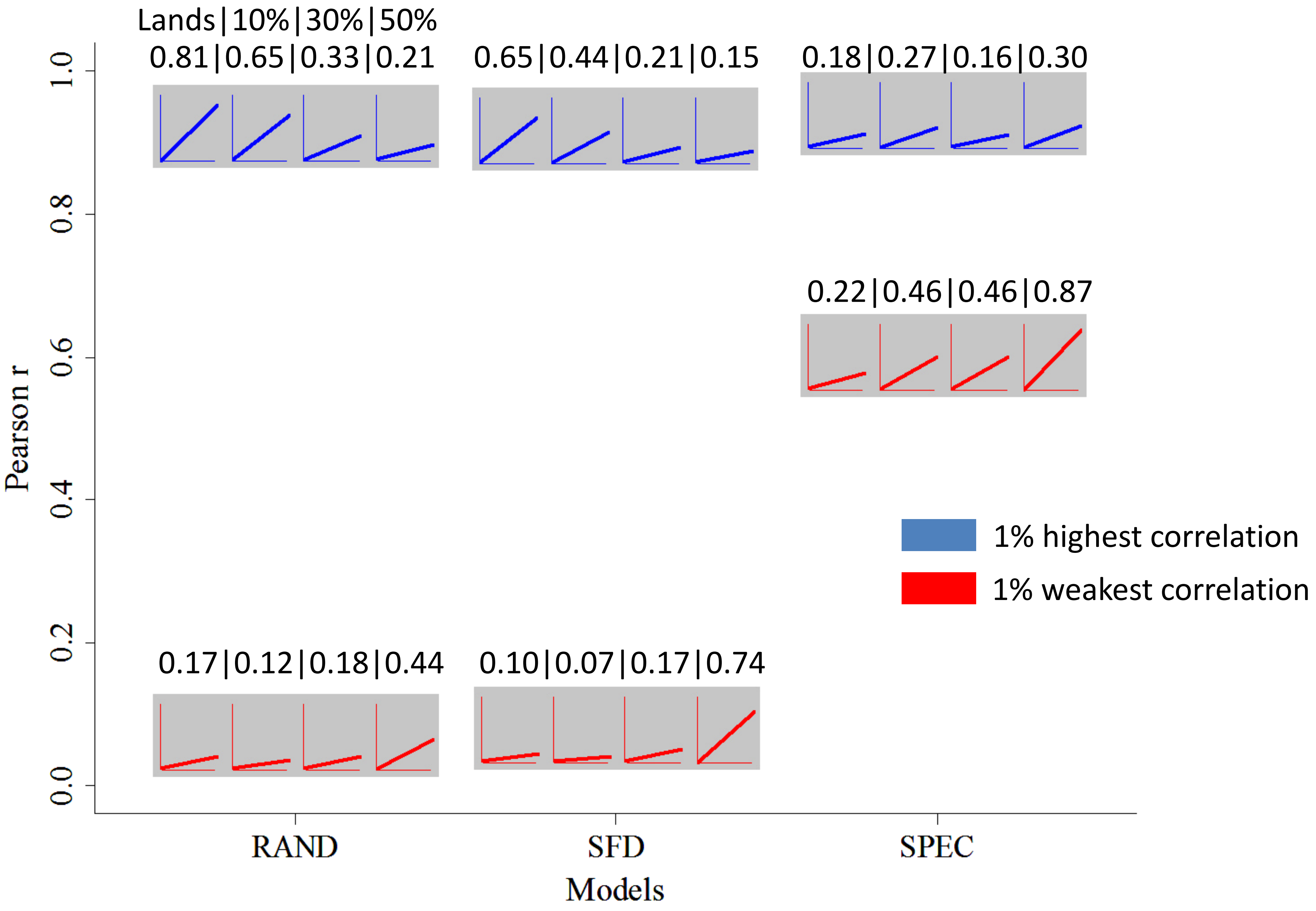


Is the SAR responsible for observed changes in community composition observed in fragmented landscapes?

Unrealistic z-values



Results


Lands|10%|30%|50%
0.81|0.65|0.33|0.21
0.65|0.44|0.21|0.15
0.18|0.27|0.16|0.30
0.22|0.46|0.46|0.87
0.17|0.12|0.18|0.44
0.10|0.07|0.17|0.74
🟦 1% highest correlation
🟥 1% weakest correlation
Pearson r
1.0
0.8
0.6
0.4
0.2
0.0
RAND
SFD
SPEC
Models

Take home messages

1- Is species richness an appropriate proxy for species loss?

- Depends on the community structure
- It can be weakly correlated to species loss and strongly underestimate specie loss

2- Is the SAR responsible for observed changes in community composition and for structuring communities in fragmented landscapes?

- Strong species turnover across the gradient of habitat loss
- No strong evidence of species-area relationship
- Species reach their individual extinction threshold rather than global effect of habitat area determining the maximum number of species coexisting in a community

Lessons from neutral theory to landscape ecology and biodiversity conservation

Neutral theory uses just three parameters:

- Fundamental biodiversity number (θ)
- **Immigration rate (*m*)**
- **Local community size (J)**

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The role of patch size at the population level

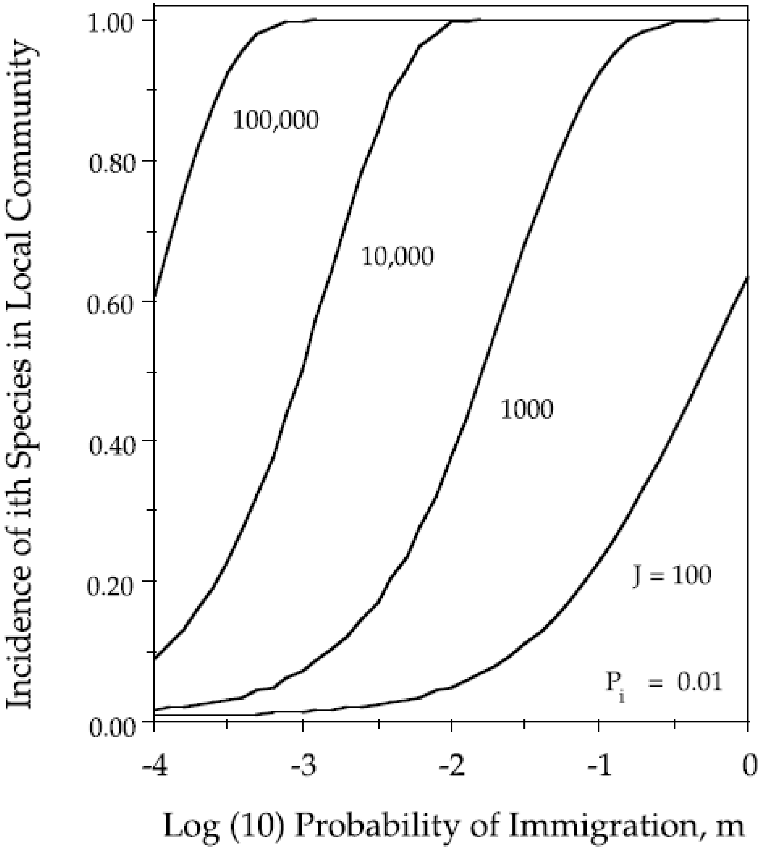


FIG. 7.2. Equilibrium incidence functions for the *i*th species in an ergodic community undergoing zero-sum drift, as a function of probability of immigration *m*, and a metacommunity relative abundance $P_i = 0.01$, for four orders of magnitude variation in local community of size.

Small patches/islands or communities: more likely that species *i* will be absent and more variable the species composition of the community.

The role of immigration at the population level

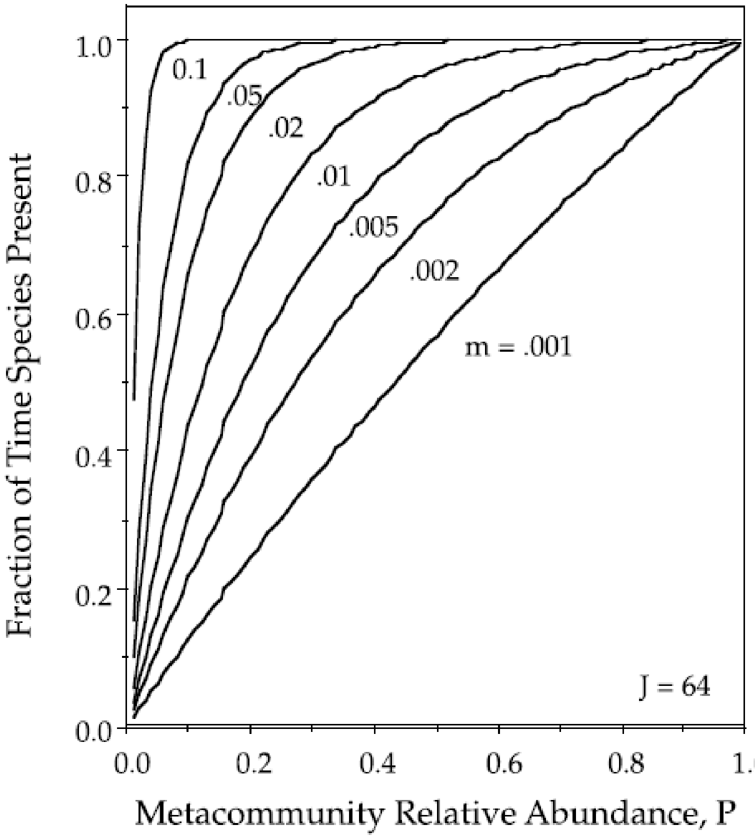
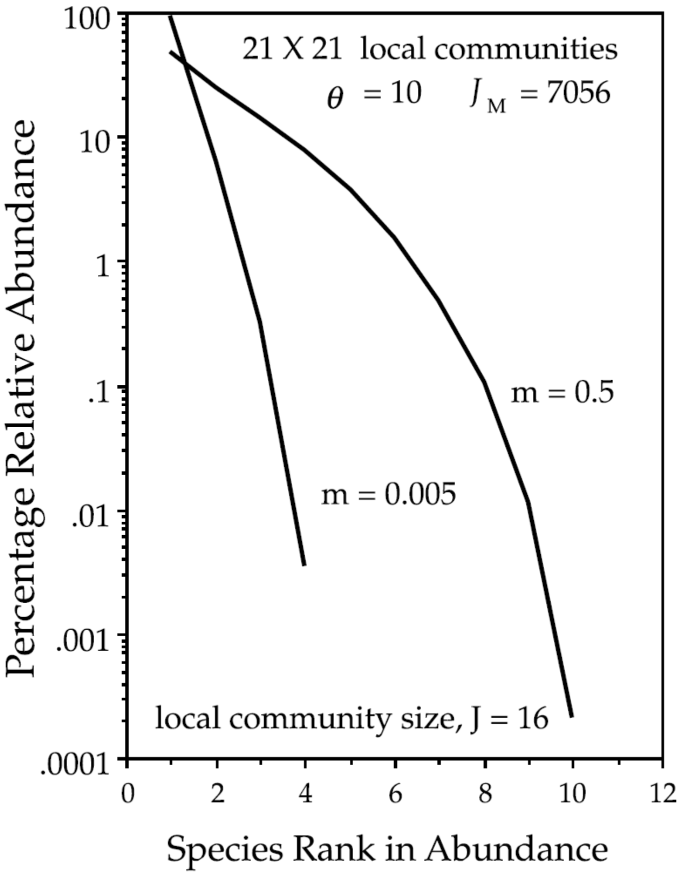


FIG. 7.1. Equilibrium incidence functions for the *i*th species in an ergodic community undergoing zero-sum drift, as a function of probability of immigration m, and metacommunity relative abundance P_i for a local community of size $J = 64$.

The role of immigration on relative species abundance



Low *m*: tendency of dominance by one or more species

High *m*: more diverse communities (higher evennness)

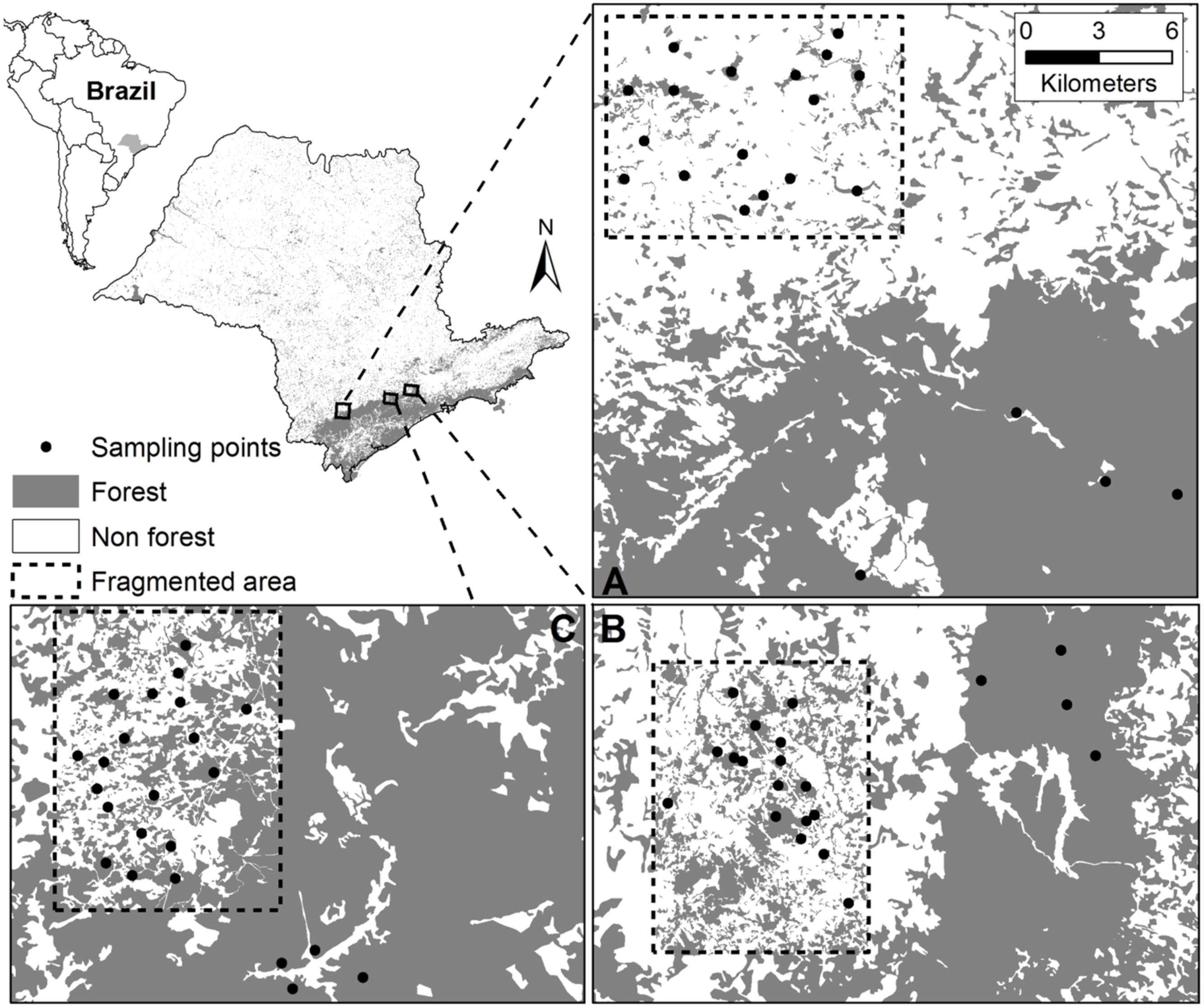
Implications of neutral theory to biodiversity conservation in fragmented landscapes

- By lowering immigration rates, fragmentation can promote persistence of rare local endemics.

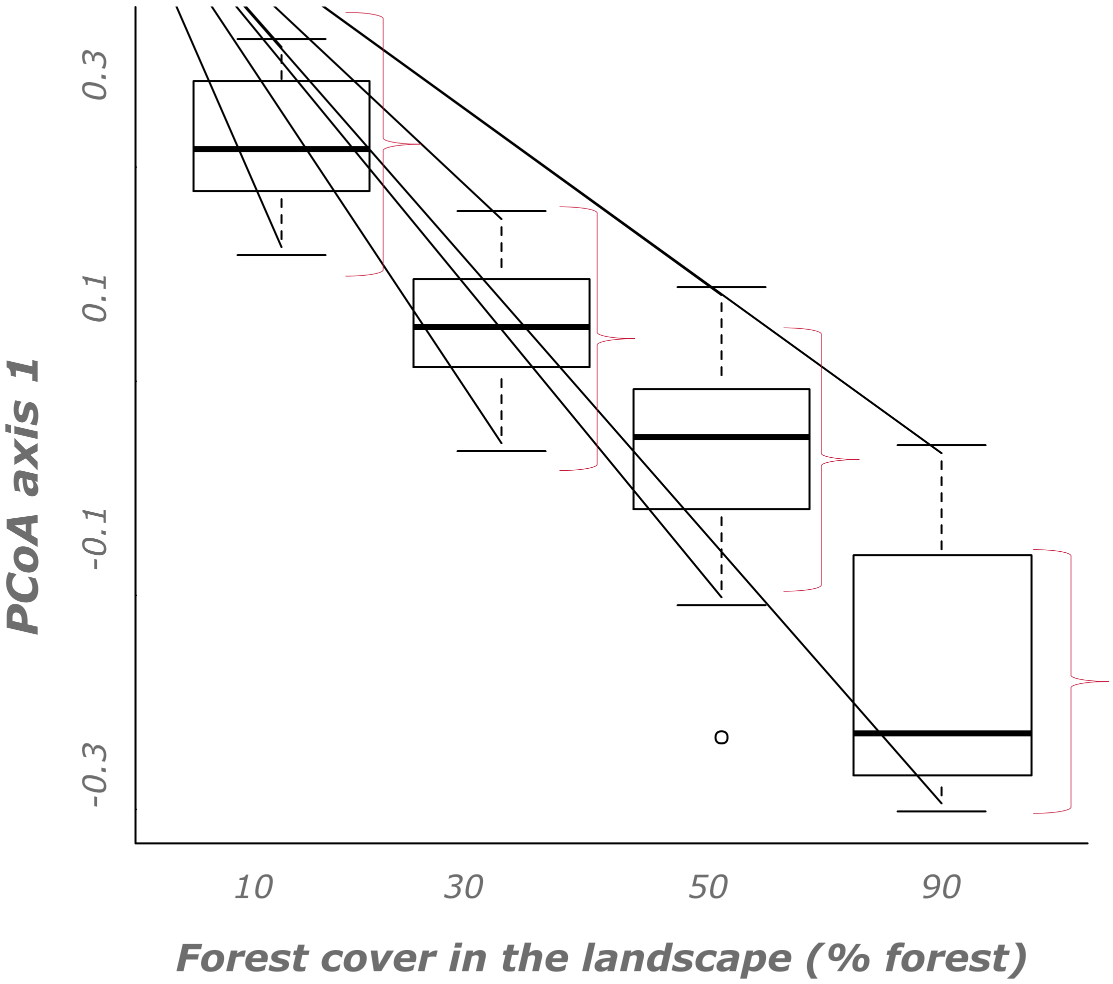
- Common and widespread species prior to fragmentation are more likely to persist in habitat fragments.

- Fragmented landscapes should present higher beta-diversity among patches than continuous landscapes, where *m* is high.

Fragmented landscapes should present higher beta-diversity among patches than continuous landscapes, where *m* is high.



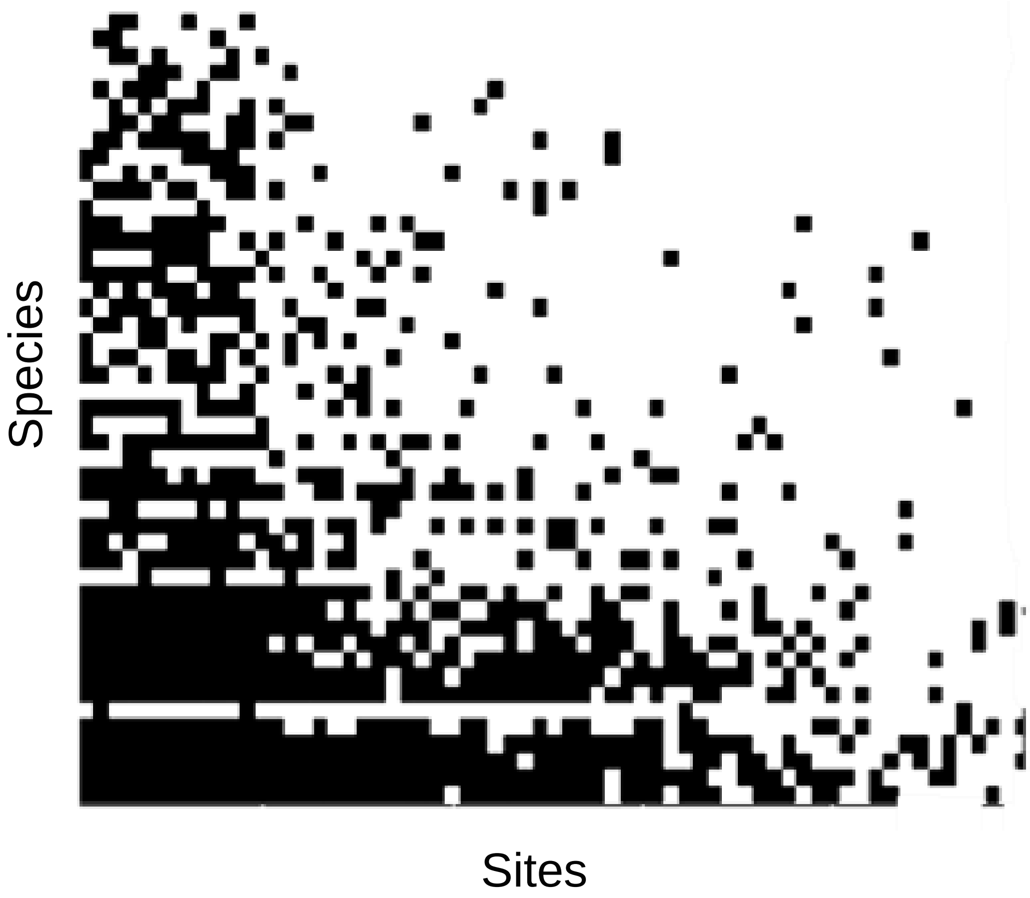
Fragmented landscapes should present higher beta-diversity among patches than continuous landscapes, where *m* is high.



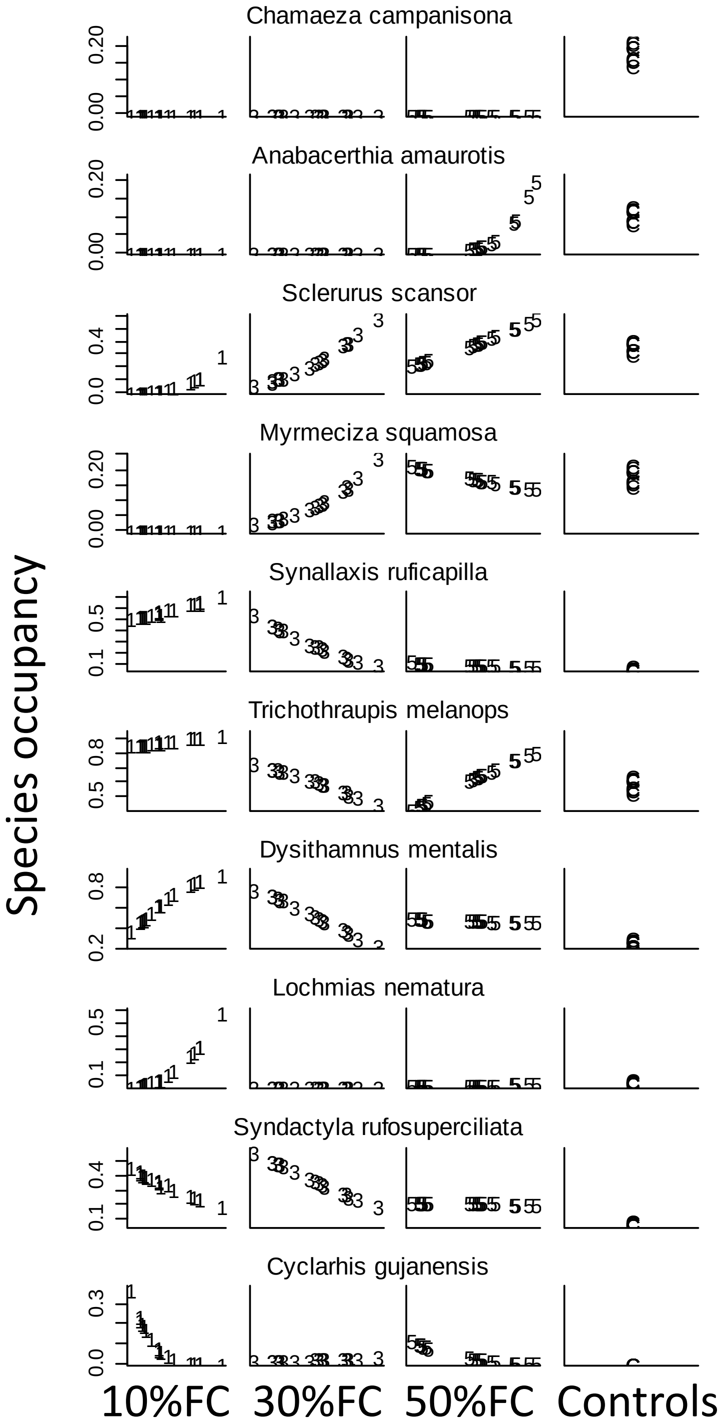
PCoA: Principal Coordinate Analysis performed on Bray-Curtis dissimilarity index

Degree of variation in PCoA scores represents beta-diversity

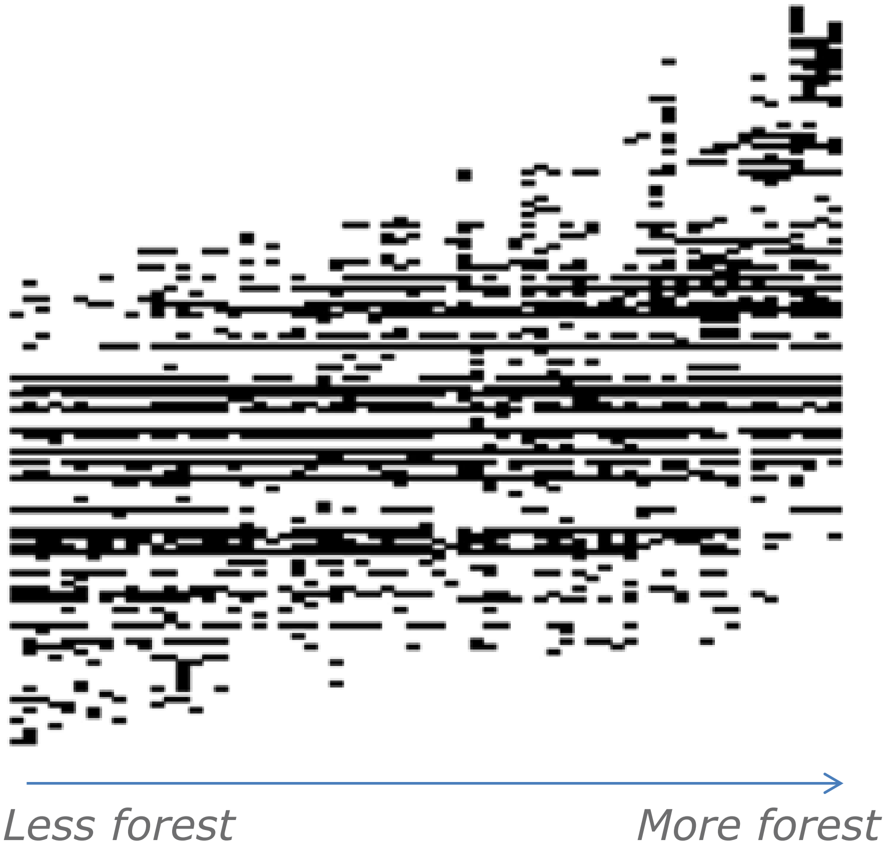
Common and widespread species prior to fragmentation are more likely to persist in habitat fragments



Common and widespread species prior to fragmentation are more likely to persist in habitat fragments



Atlantic Forest bird community



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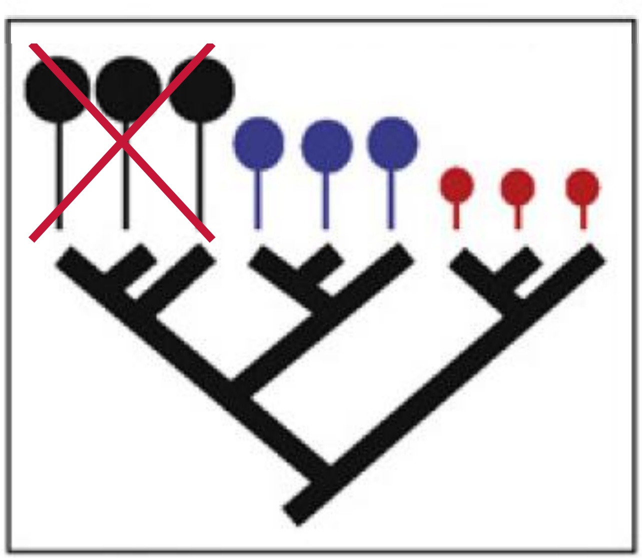
Phylogenies as tools to understanding species sensitivity to environmental change



Morphological and ecological traits as predictors of species sensitivity to change

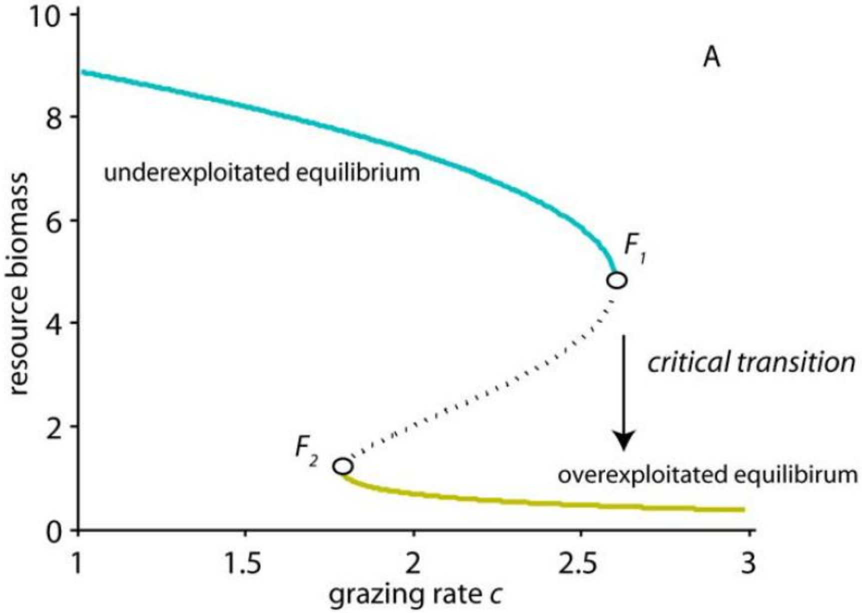
Newbold et al. 2012 ProcB:

Birds:

- Life span
- Body size
- Migratory behaviour
- Feeding guild specialisation

Detecting changes before they hapen

- Gradual change leads the system to a bifurcation point, a tipping point, causing loss in resilience and promoting a shift to alternative state



Dakos et al. 2012 Plos One

Detecting changes before they hapen

- Gradual change leads the system to a bifurcation point, a tipping point, causing loss in resilience and promoting a shift to alternative state

- Critical thresholds are difficult to detect and acquire

- Early warning signals, mathematical indicators, can help detect the proximity of a system to a tipping point

Metric and model-based methods

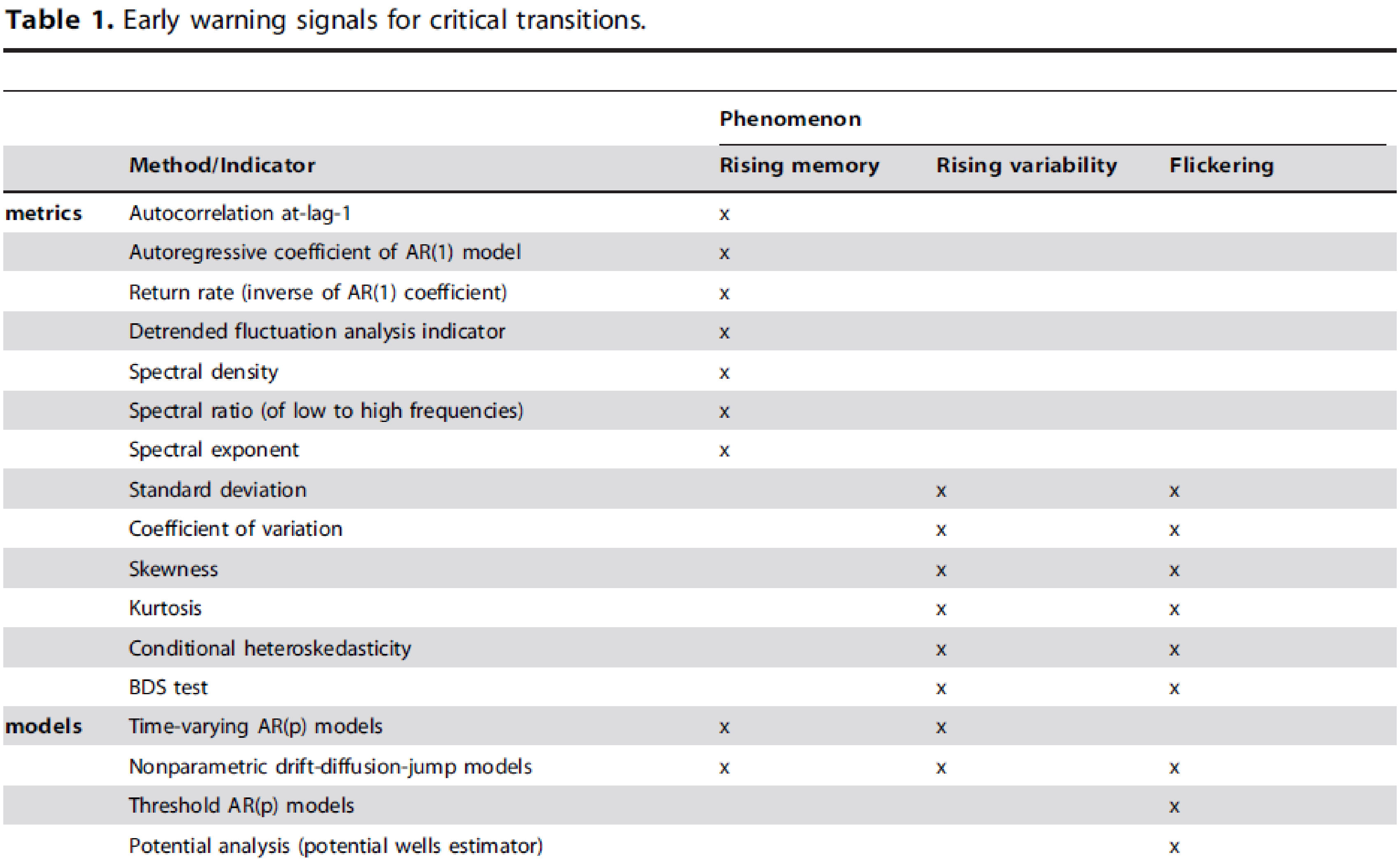


Table 1. Early warning signals for critical transitions.

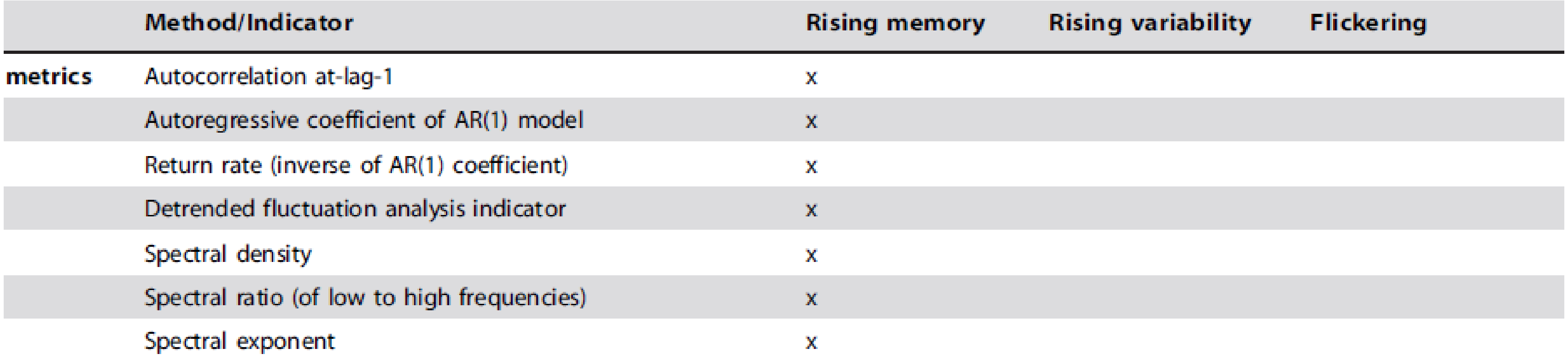
		Phenomenon		
	Method/Indicator	**Rising memory**	**Rising variability**	**Flickering**
metrics	Autocorrelation at-lag-1	x		
	Autoregressive coefficient of AR(1) model	x		
	Return rate (inverse of AR(1) coefficient)	x		
	Detrended fluctuation analysis indicator	x		
	Spectral density	x		
	Spectral ratio (of low to high frequencies)	x		
	Spectral exponent	x		
	Standard deviation		x	x
	Coefficient of variation		x	x
	Skewness		x	x
	Kurtosis		x	x
	Conditional heteroskedasticity		x	x
	BDS test		x	x
models	Time-varying AR(p) models	x	x	
	Nonparametric drift-diffusion-jump models	x	x	x
	Threshold AR(p) models			x
	Potential analysis (potential wells estimator)			x

Dakos et al. 2012 Plos One

Rising memory

- <u>Critical slowing down</u>: rate of return to equilibrium following a perturbation slows down as the systems approach a tipping point, detected by changes in the correlation structure of the time series.

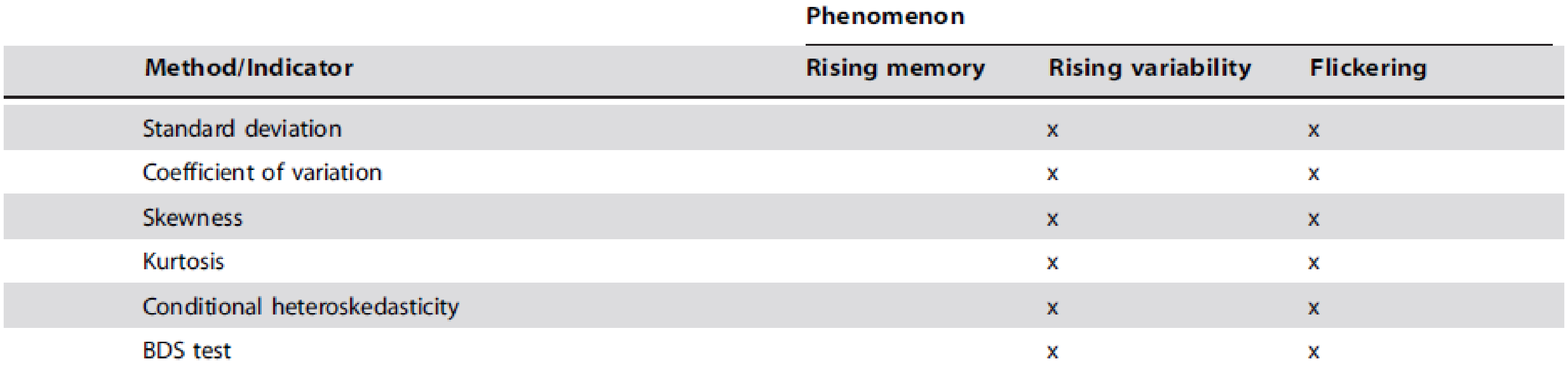
- Critical slowing down causes an increase in short-term memory (correlation at low lags) of a system prior to transition.



	Method/Indicator	Rising memory	Rising variability	Flickering
metrics	Autocorrelation at-lag-1	x		
	Autoregressive coefficient of AR(1) model	x		
	Return rate (inverse of AR(1) coefficient)	x		
	Detrended fluctuation analysis indicator	x		
	Spectral density	x		
	Spectral ratio (of low to high frequencies)	x		
	Spectral exponent	x		

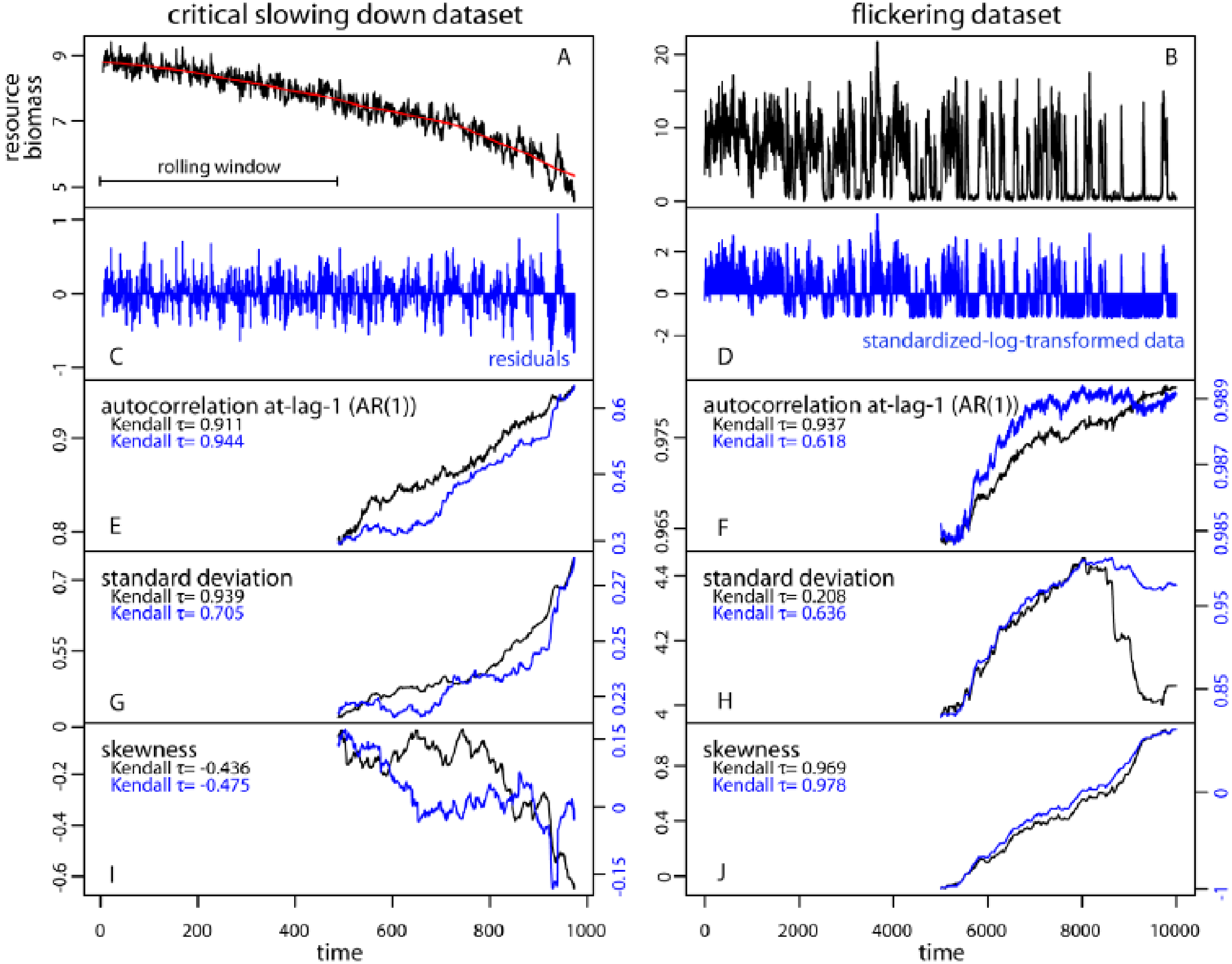
Rising variability

- Drift: slow return rates back to a stable state close to a transition can make the system drift widely around a stable state
- Flickering: strong disturbances can push the system across boundaries of alternative states
- Skewness: slow dynamics near the boundary of either stable state lead to rise in the skewness of a time-series, the distribution of values series will be asymmetric.



	Phenomenon		
Method/Indicator	**Rising memory**	**Rising variability**	**Flickering**
Standard deviation		x	x
Coefficient of variation		x	x
Skewness		x	x
Kurtosis		x	x
Conditional heteroskedasticity		x	x
BDS test		x	x

Early warning signals



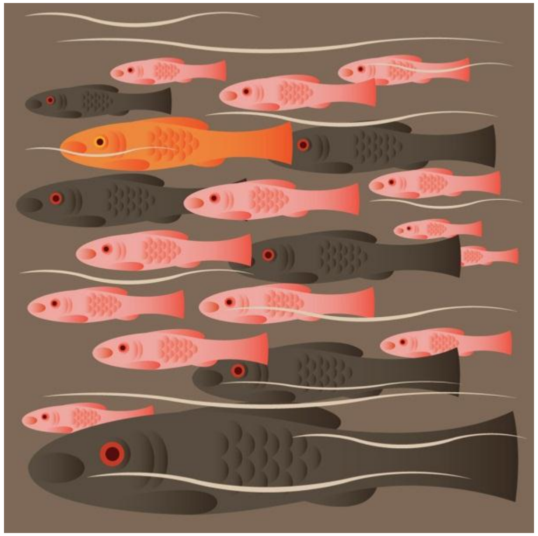
Early warning signals

Dakos *et al*. 2012 Plos One

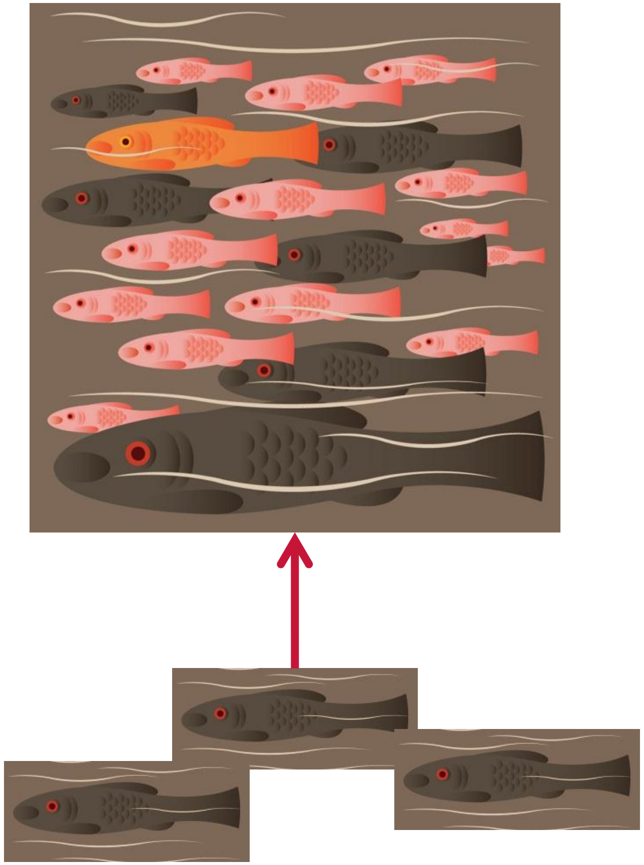
- No single best approach to identifying early warning signals
- Al methods required specific data-treatment to yield sensible results
- Combination of methods is the best way

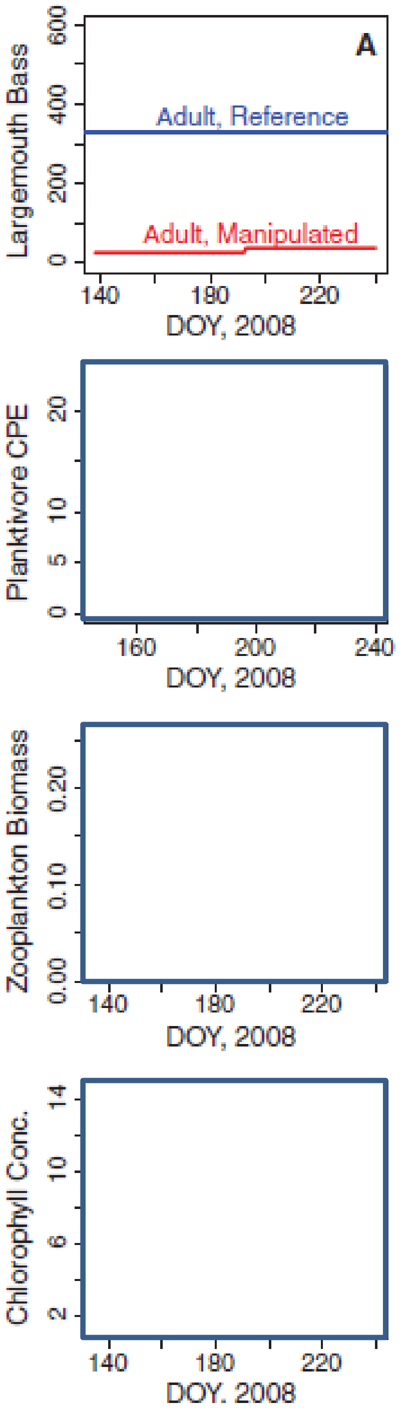
Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment
S. R. Carpenter *et al.*
Science **332**, 1079 (2011);

Reference



Manipulation




A
Largemouth Bass
600
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200
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Adult, Reference
Adult, Manipulated
140
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220
DOY, 2008
Planktivore CPE
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160
200
240
DOY, 2008
Zooplankton Biomass
0.20
0.10
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140
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DOY, 2008
Chlorophyll Conc.
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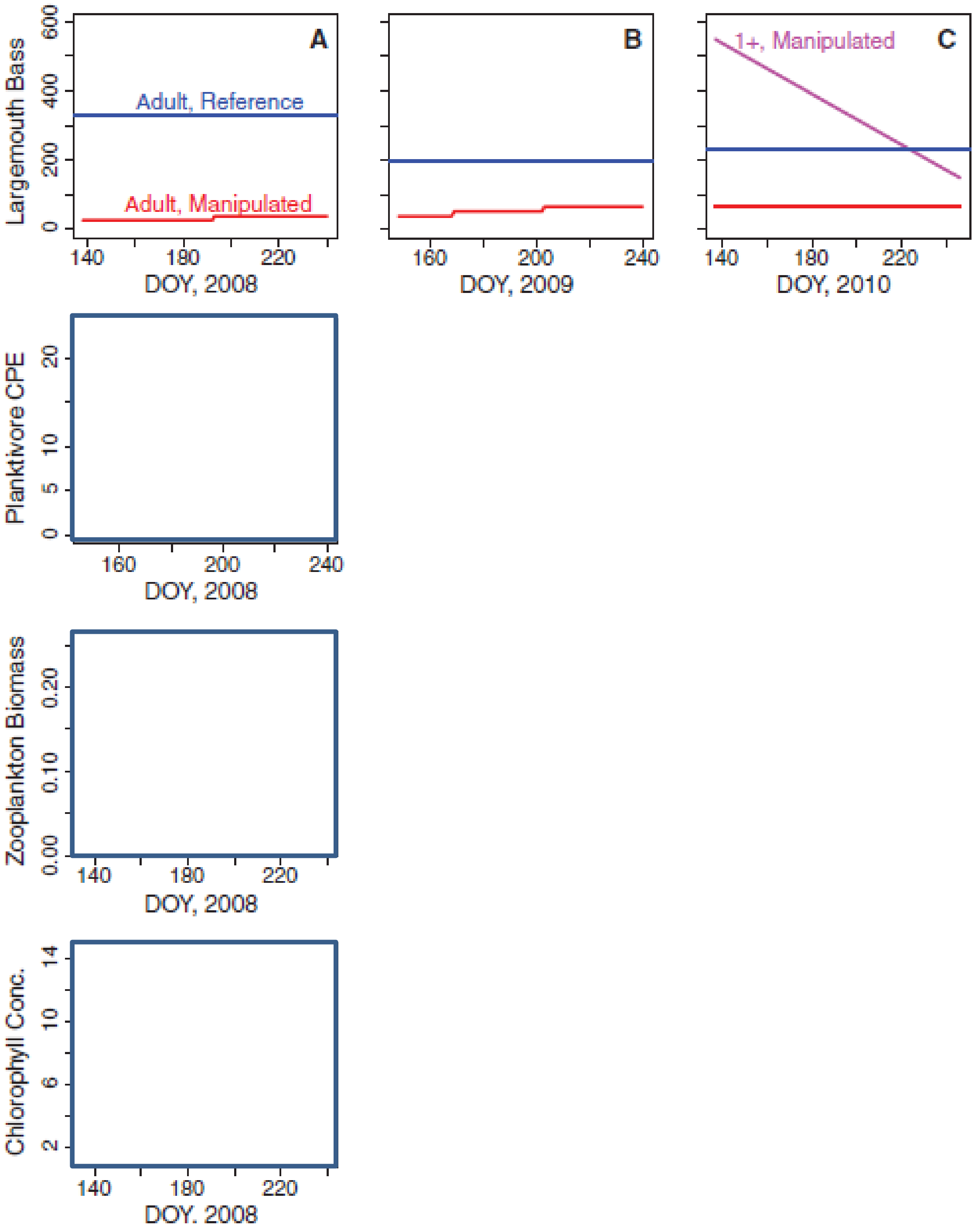
DOY. 2008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Adult, Reference
Adult, Manipulated
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DOY, 2008
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DOY, 2009
C
1+, Manipulated
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180
220
DOY, 2010
Planktivore CPE
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DOY, 2008
Zooplankton Biomass
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DOY, 2008
Chlorophyll Conc.
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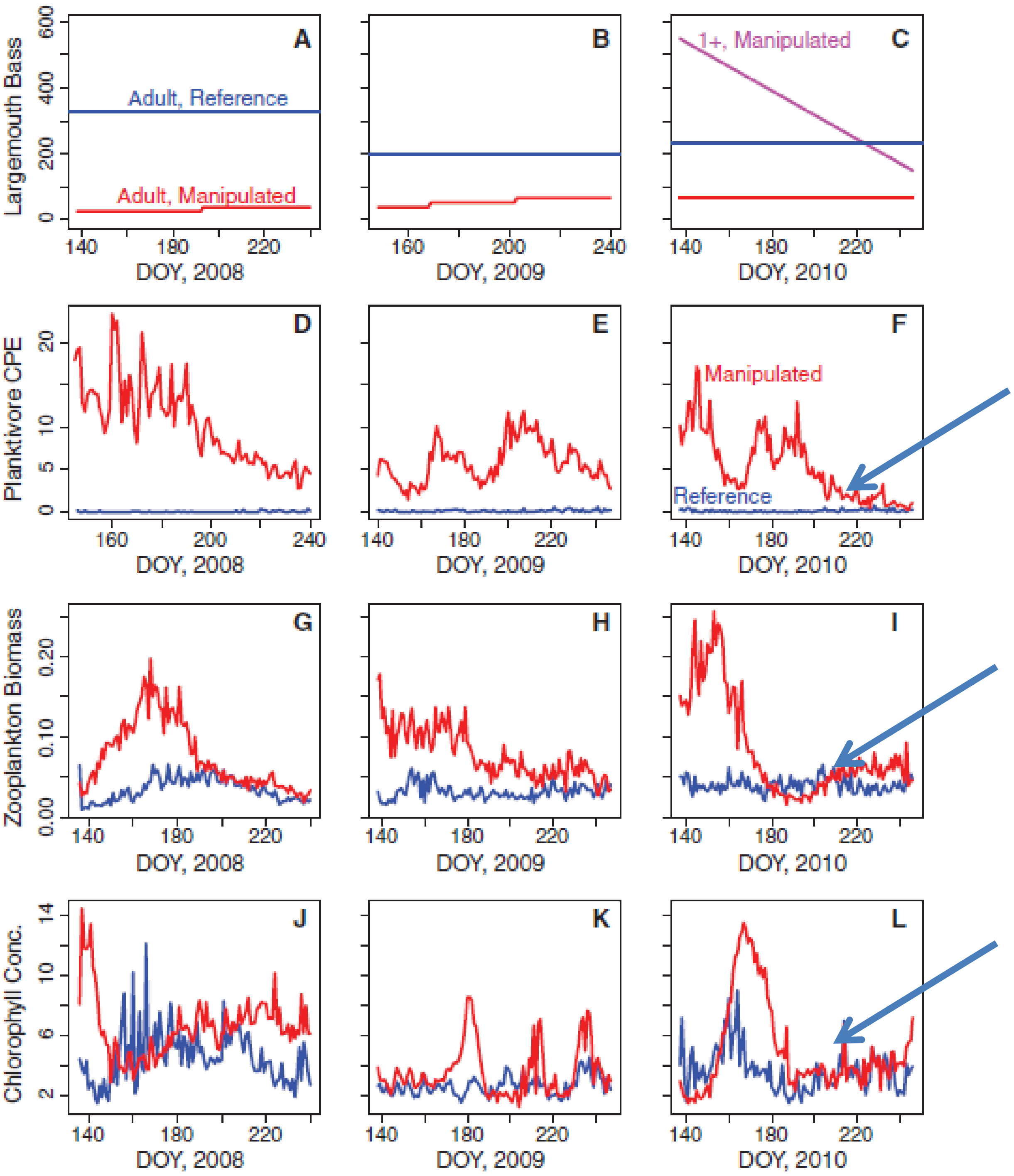
DOY. 2008



Largemouth Bass
Planktivore CPE
Zooplankton Biomass
Chlorophyll Conc.
A
B
C
Adult, Reference
Adult, Manipulated
1+, Manipulated
D
E
F
Manipulated
Reference
G
H
I
J
K
L
DOY, 2008
DOY, 2009
DOY, 2010
0
200
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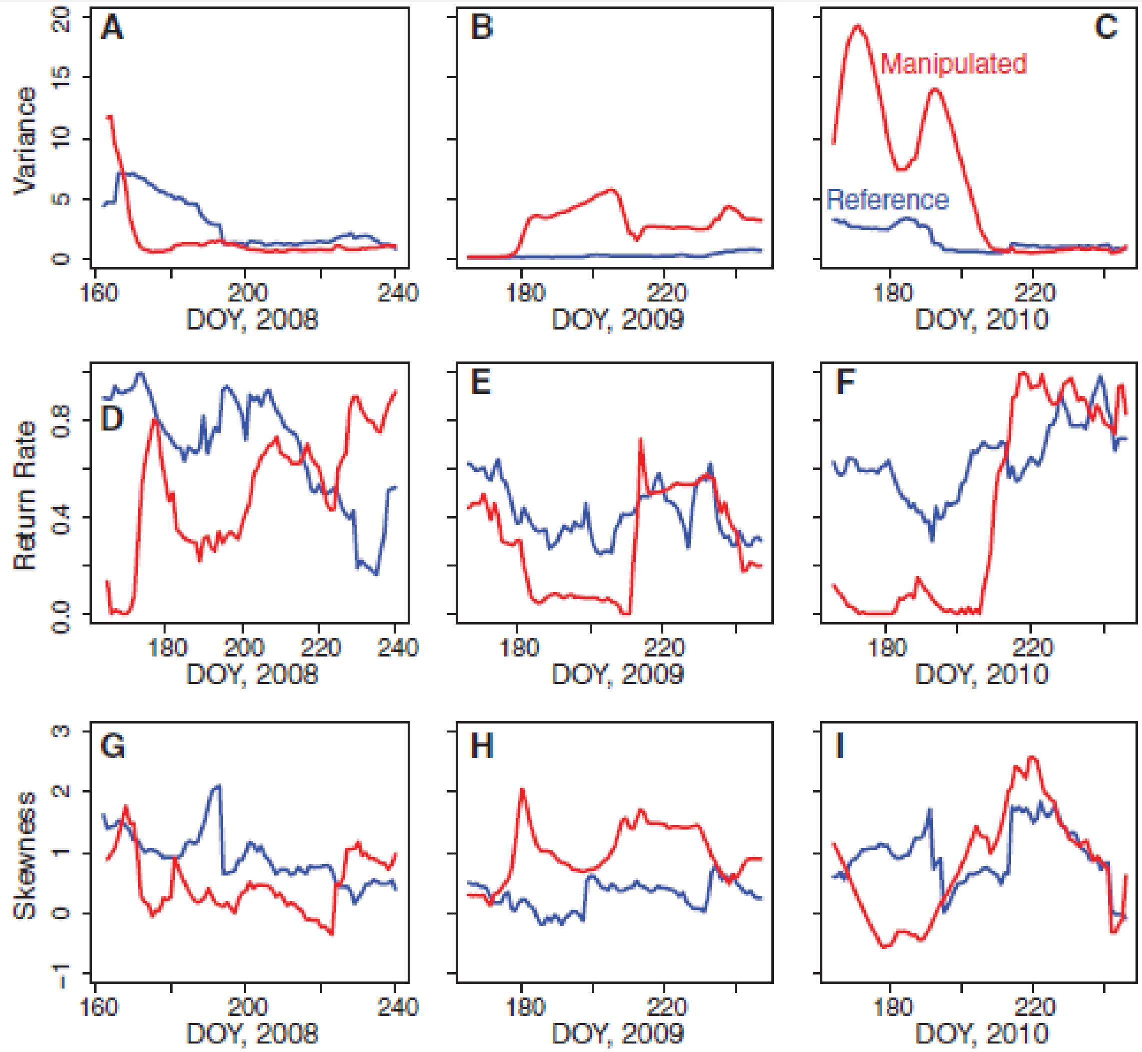

Return rate =0, indicates autocorrelation near 1

Dramatic changes in skewness are associated with shifts between alternate states

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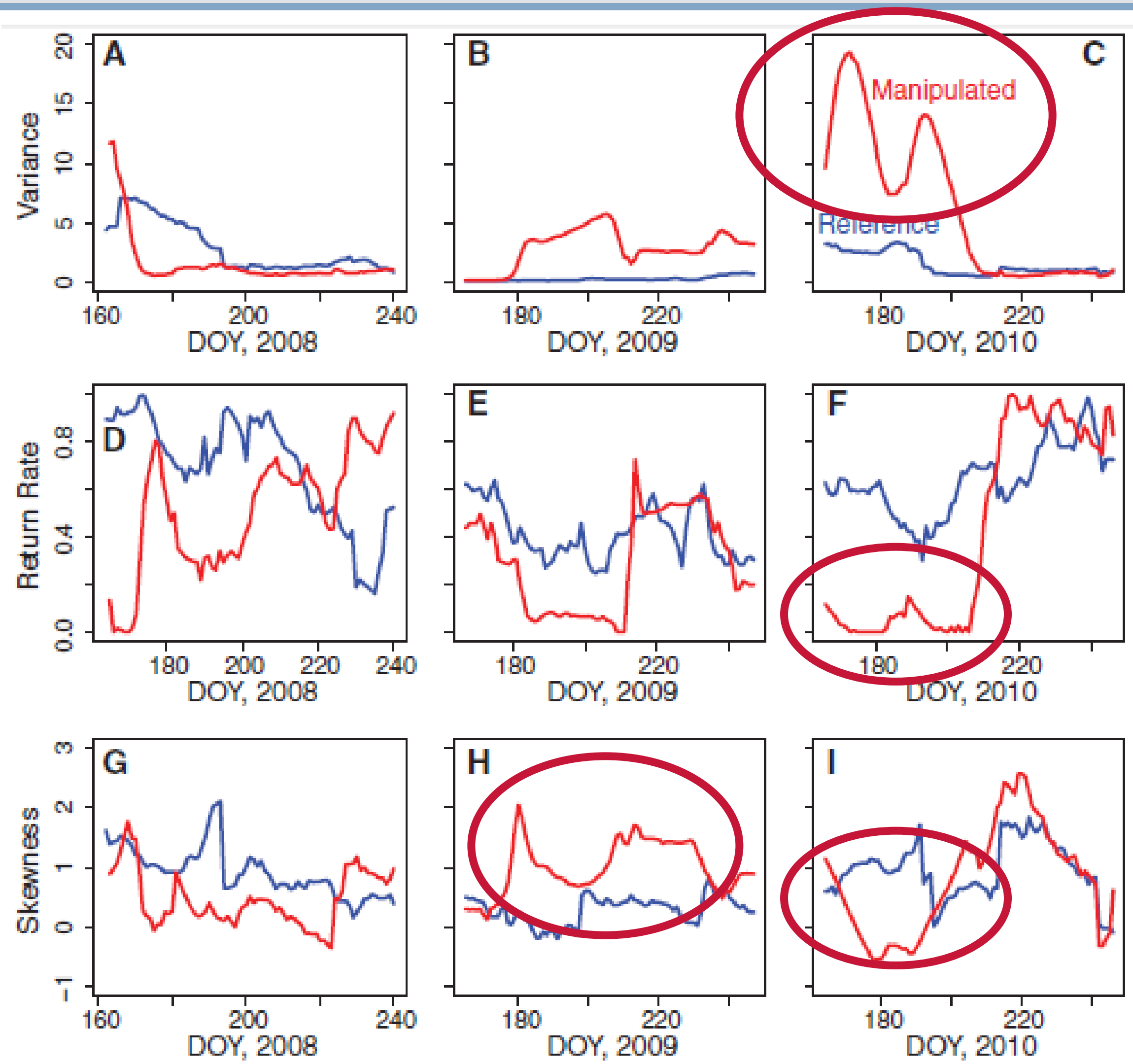

Return rate =0, indicates autocorrelation near 1

Dramatic changes in skewness are associated with shifts between alternate states

Summary

- Current theory can give us guidelines but none allow us to predict how communities will change, or which species are most sensitive to environmental change.

- Species-area relationship is a well-established pattern in unmodified habitats but does not have high predictive power under habitat loss.

- Neutral theory generates several predictions, many of which are still to be tested.

- Evolutionary approach can help us upscale predictions.

- Early warning signals is data hungry but should be the focus of future research.