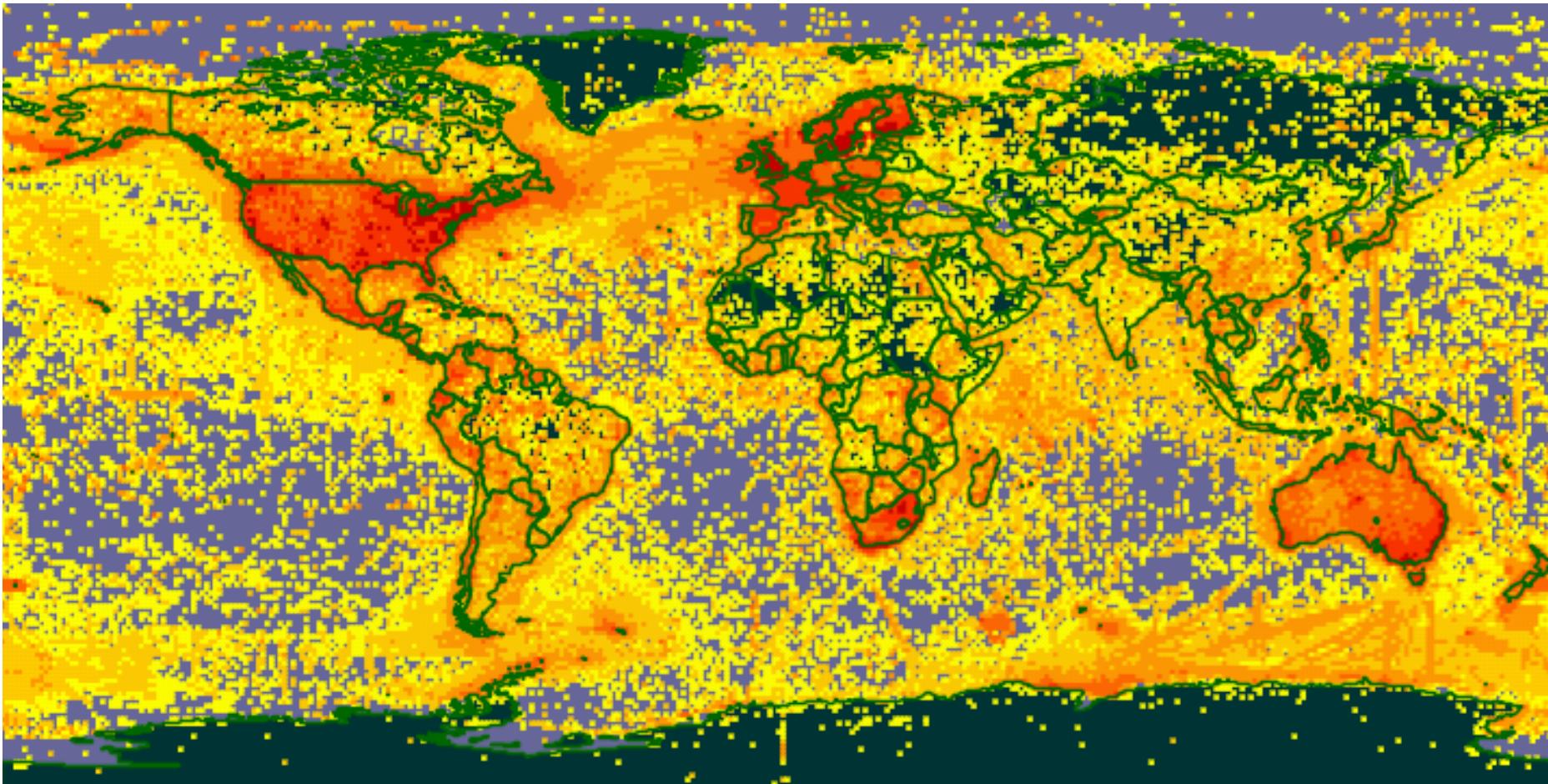


An introduction to ecological modelling

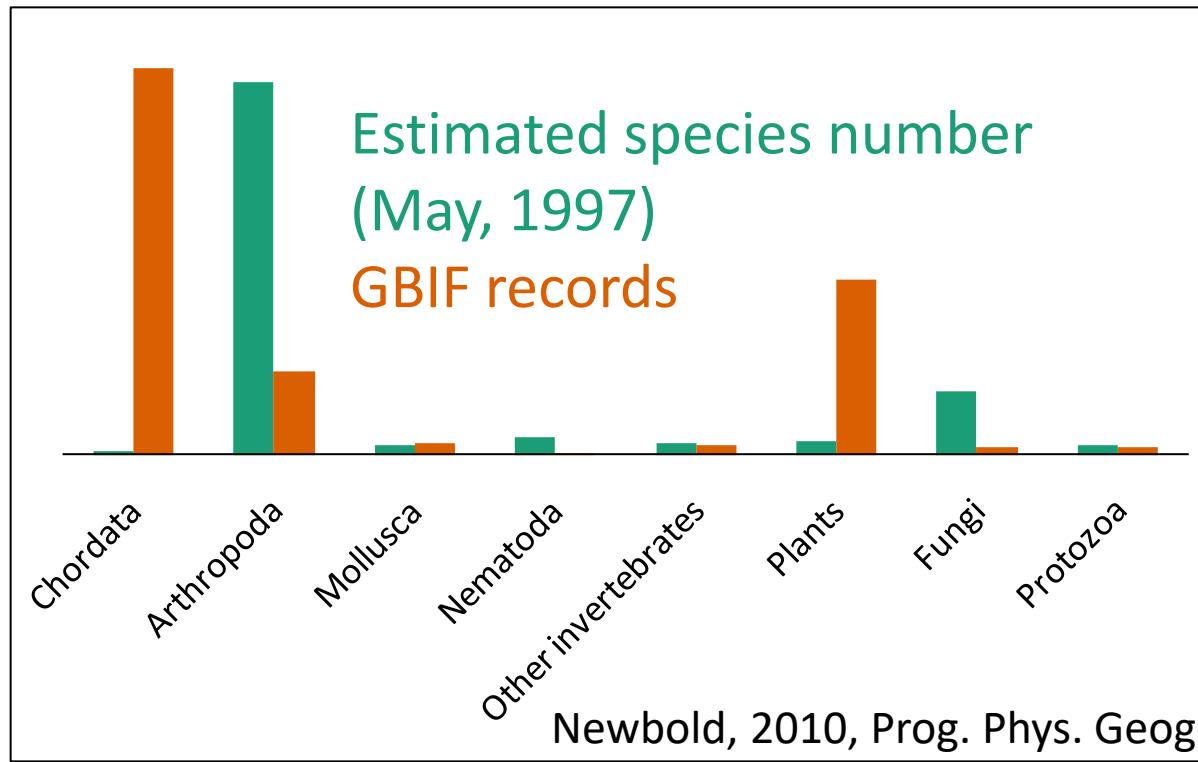
2. Theoretical/Mechanistic Ecological Models

Ecological data are biased, spatially...



Data from the Global Biodiversity Information Facility (GBIF): <http://gbif.org>

...and taxonomically



86% of terrestrial and 91% of ocean species undescribed
(Mora et al., 2011, *PLoS Biology* 9: e1001127.)

Understanding the diversity of ecological communities, and how they respond to human threats



Lecture Outline

Simple theoretical models in ecology

Complex mechanistic ecosystem models

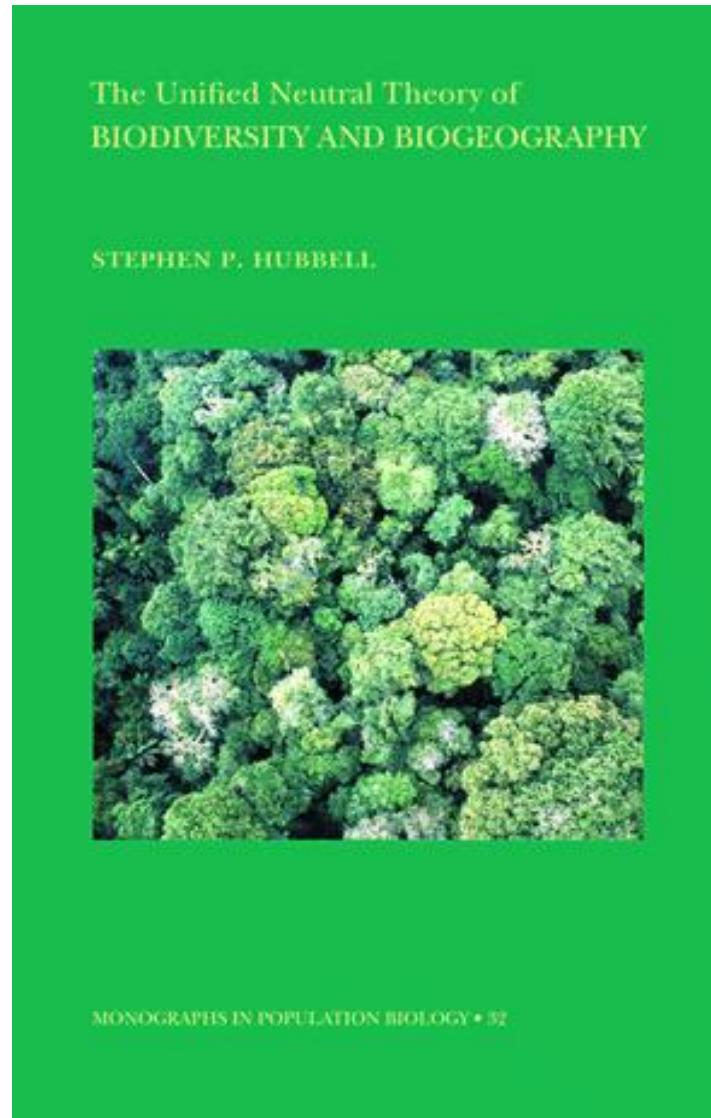
Lecture Outline – Part 1: simple theoretical models

Simple models of the species richness of ecological communities

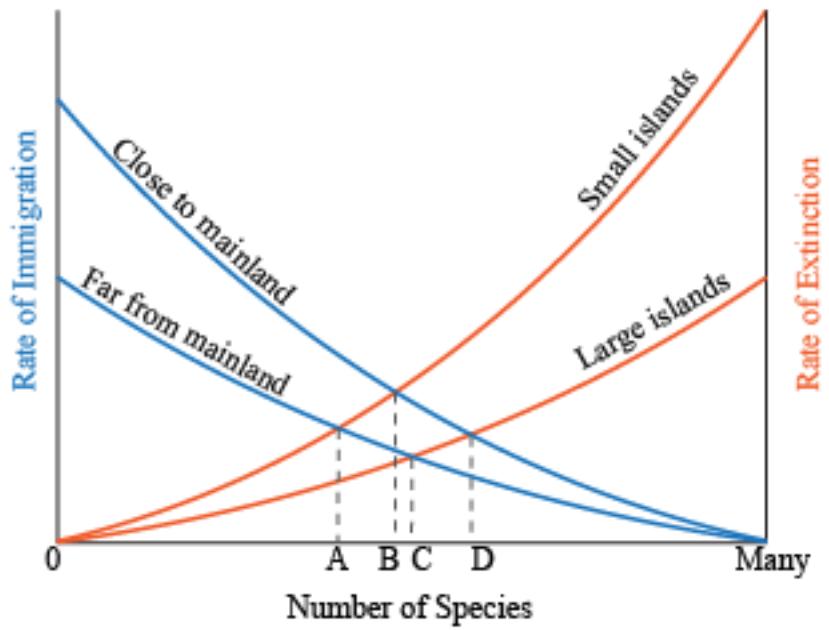
Simple models of individual-level processes

- Competition
- Predation
- Metabolism

A model I don't have time to talk about



The Equilibrium Theory of Island Biogeography

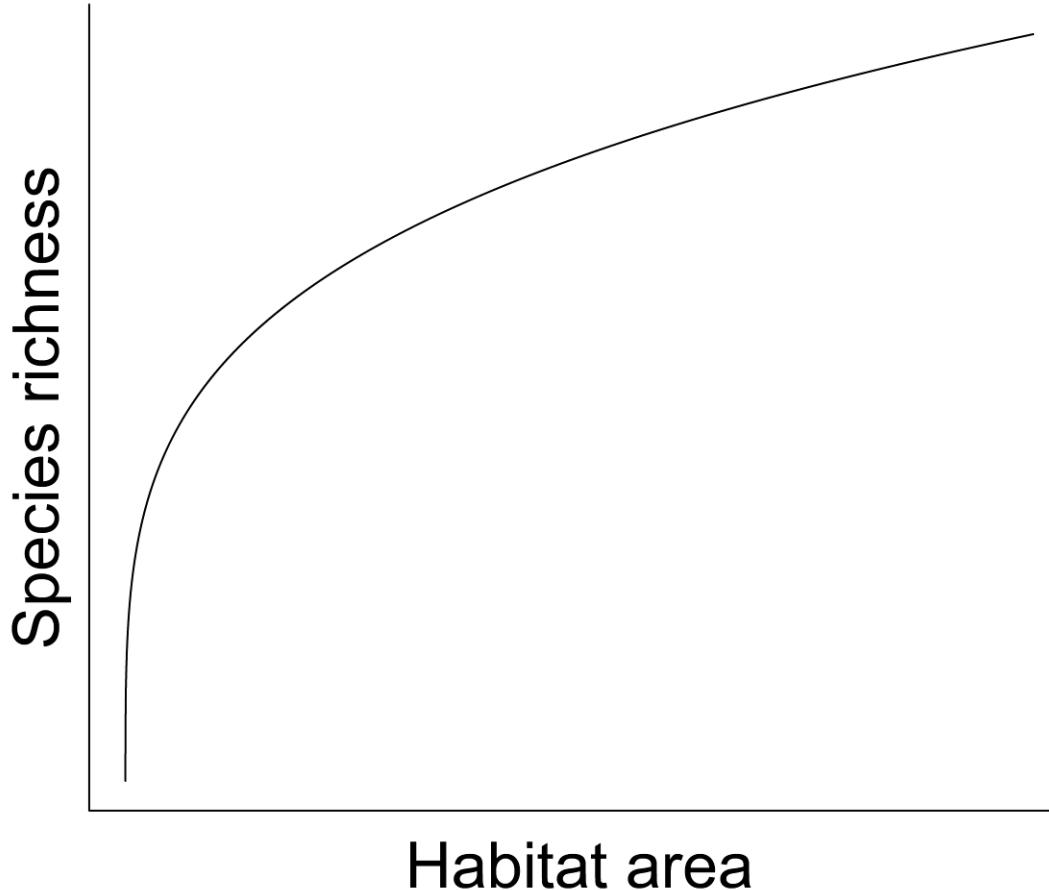


MacArthur & Wilson (1967). *The Theory of Island Biogeography*. Princeton University Press

Species number depends on the balance between immigration and extinction rates

Extinction rates are lower on larger islands; immigration rates are higher on islands nearer the mainland

The species-area relationship



First described by Arrhenius
(1921). *J Ecology* 9: 95-99.

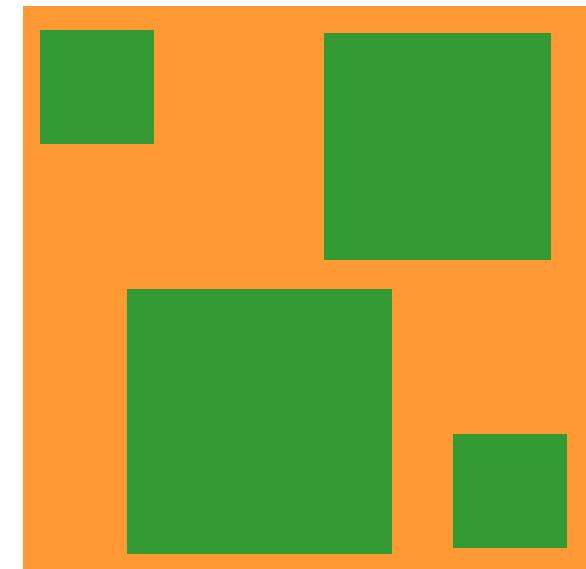
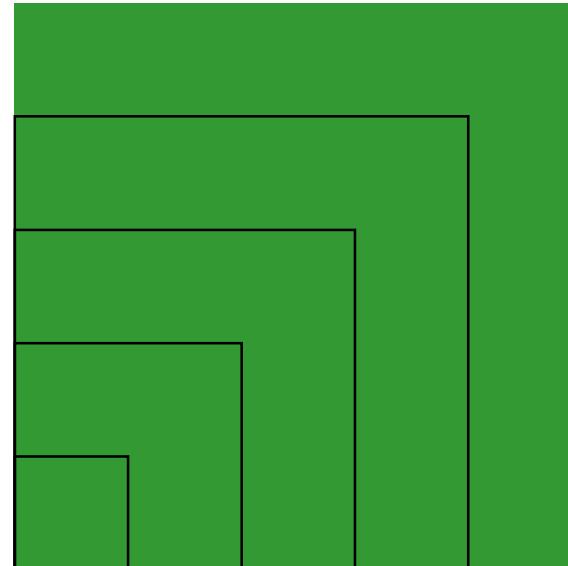
$$S = cA^z$$

Species-area relationships: theoretical considerations

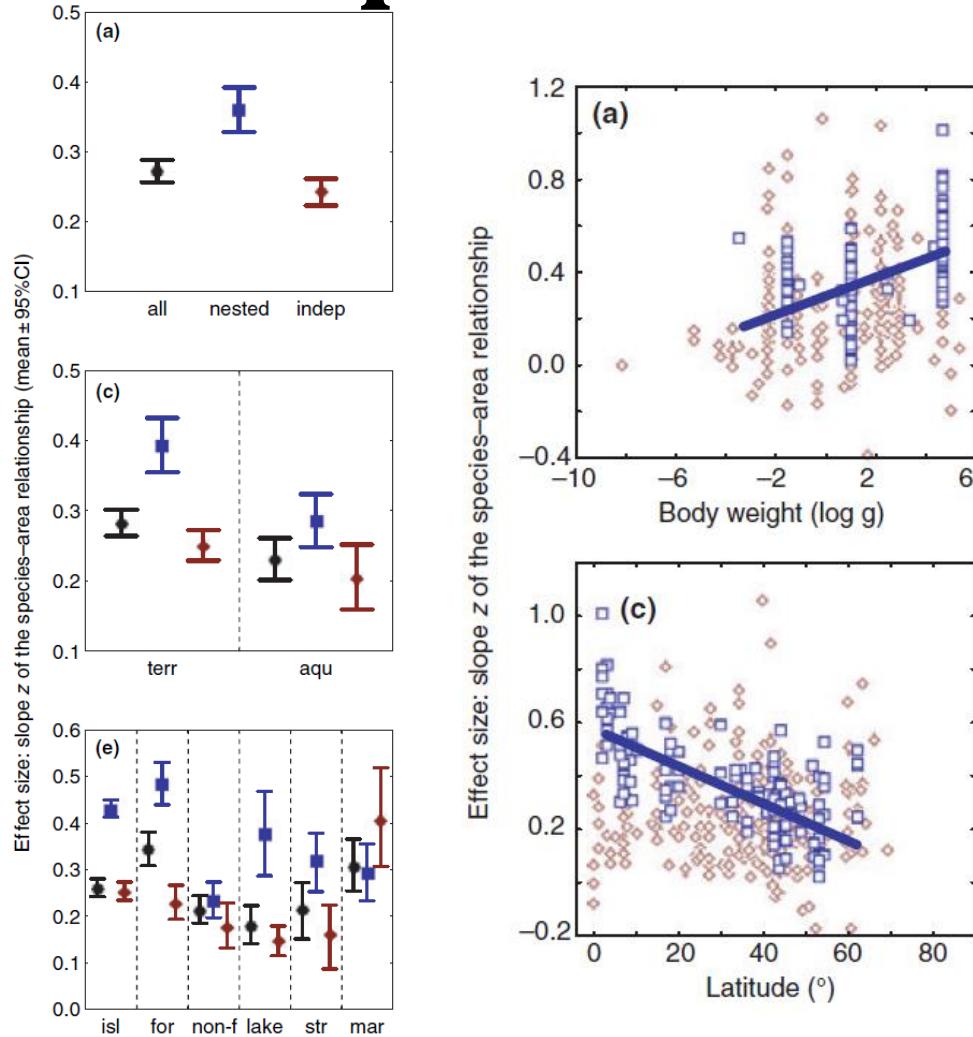
True islands vs. habitat islands



Nested samples vs. isolated samples



Species-area relationship: variation in shape



Average exponent (z) of species-area relationship = 0.27, but ranging from 0 to 1

Higher with nested compared with independent sampling

Higher for terrestrial compared with aquatic systems

Higher in forests and oceans than non-forests and lakes/streams

Increases with body mass and at lower latitudes (increased turnover of community composition)

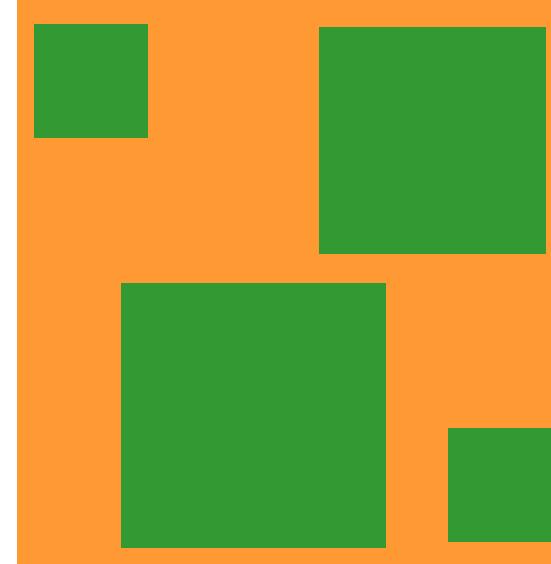
Applications of species-area relationships

Predicting the consequences of habitat loss and fragmentation

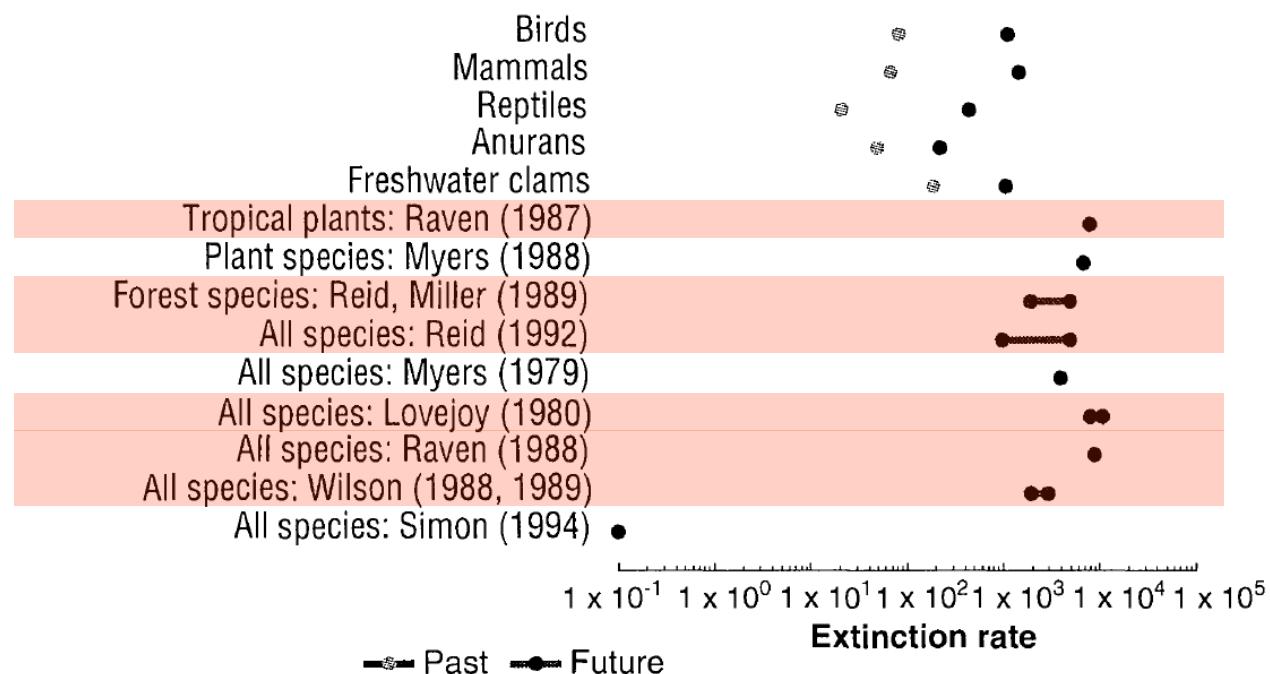
Easily applied to maps of habitat

Makes simple predictions of species loss

$$\frac{S_{new}}{S_{original}} = \left(\frac{A_{new}}{A_{original}} \right)^z$$



Applications of species-area relationships



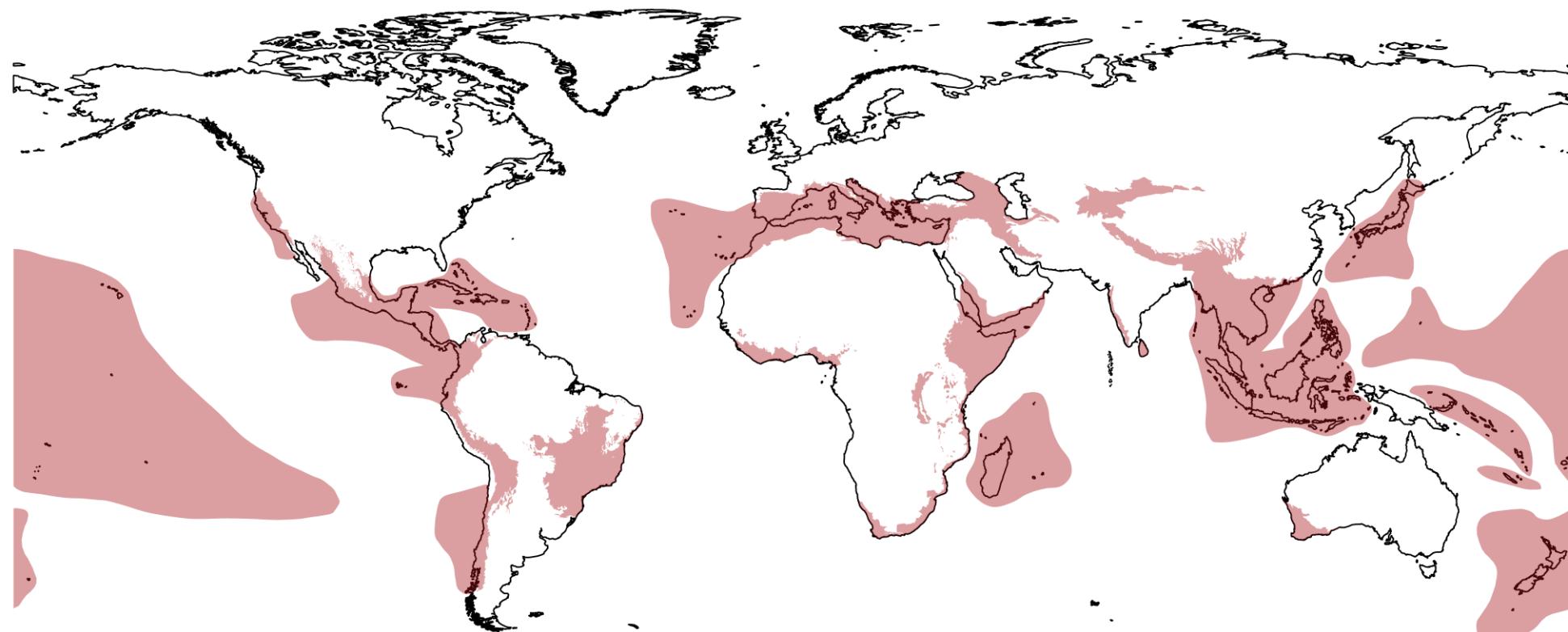
Naturally: 0.1—1 Extinctions per Million Species-Years (E/MSY)

With habitat loss: 1,000—10,000 E/MSY

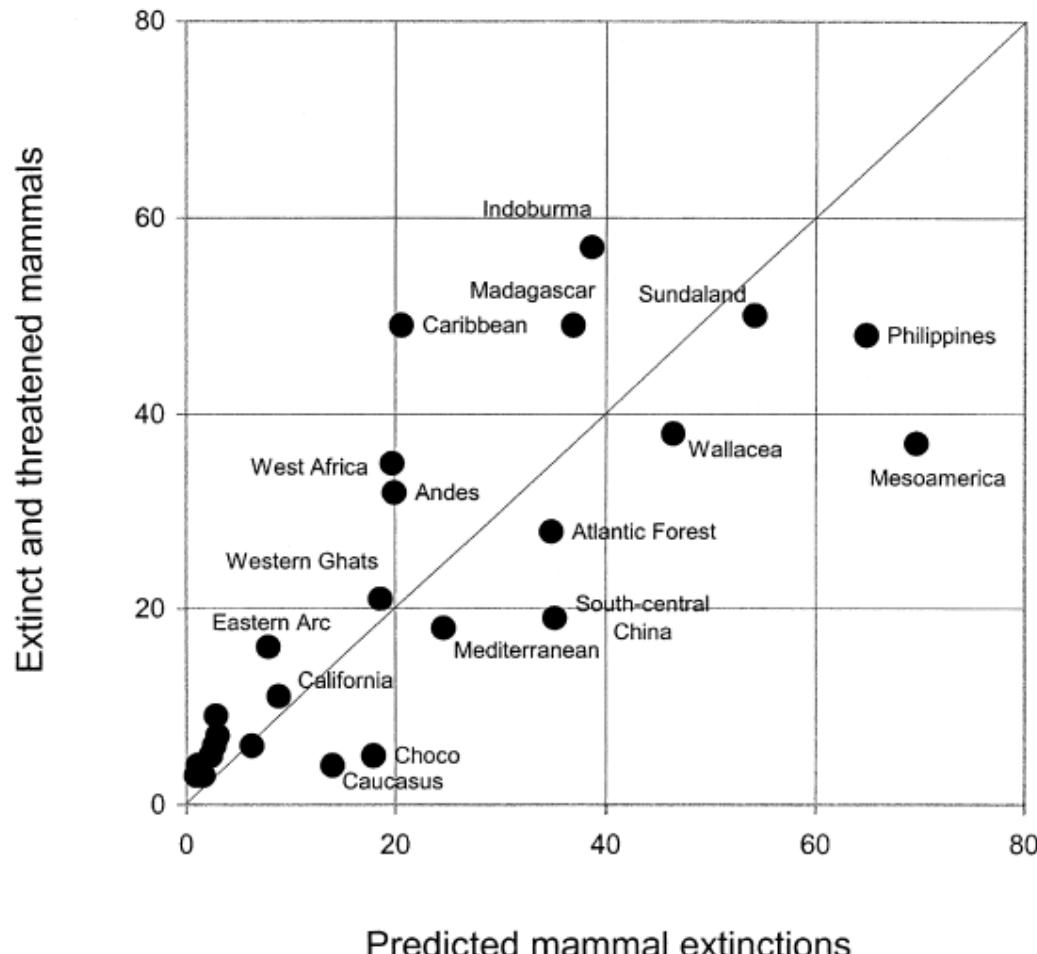
Only appropriate to apply species-area relationships to species endemic to an area

Applications of species-area relationships

The biodiversity hotspots: concentrations of endemic species in areas that have suffered a high degree of habitat loss



Applications of species-area relationships



Application of species-area relationships for vertebrates and plants in the biodiversity hotspots

Predictions based on past habitat loss matched known numbers of known extinctions and threatened species well for mammals and birds

Less good for amphibians, reptiles and plants (probably because of poor data on threatened species)

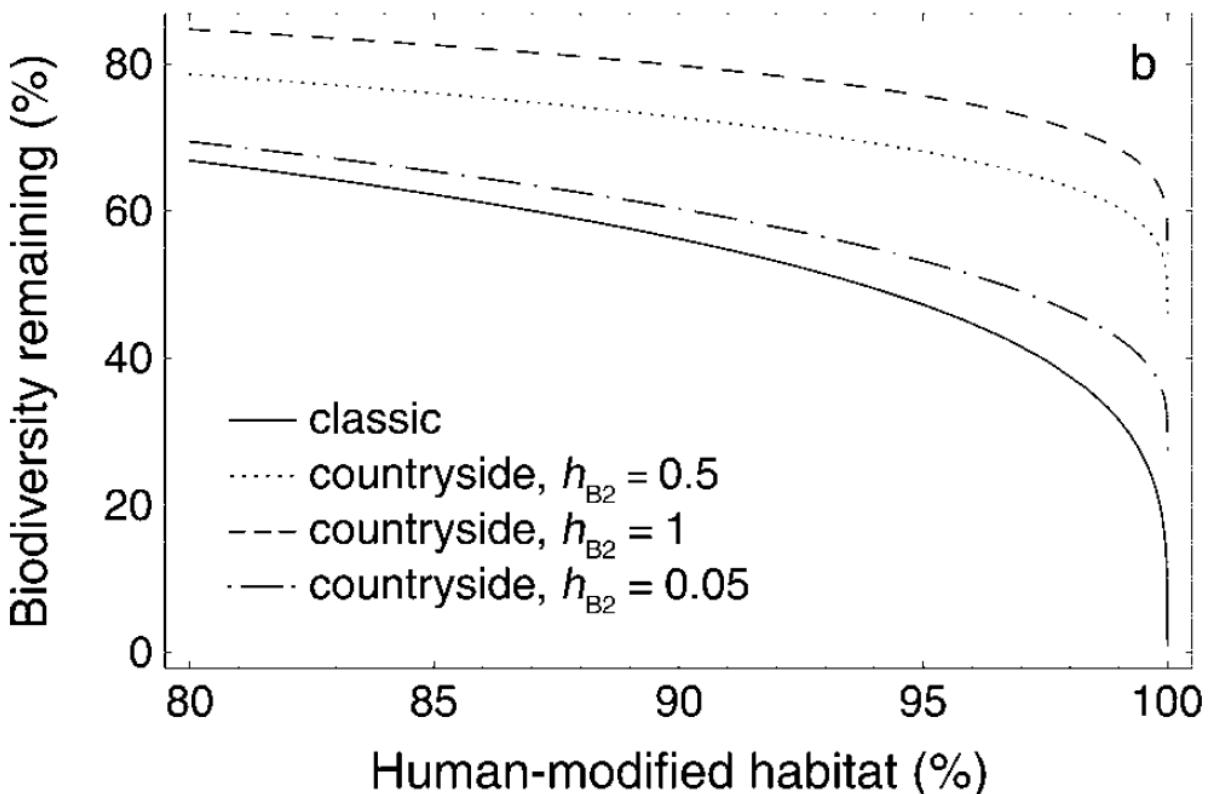
Applications of species-area relationships

Hotspot	Additional Extinctions	
	Plants	Vertebrates
Eastern Arc and Coastal Forests of Tanzania-Kenya	121.4	9.8
New Caledonia	96.5	3.2
Philippines	70.2	6.2
Polynesia-Micronesia	59.1	4
Cape Floristic Province	56.6	0.5
Caribbean	34.4	3.8
Western Ghats-Sri Lanka	23.1	3.8
Madagascar	23.2	1.8
Southwest Australia	18.8	0.4
Sundaland	15.9	0.7
Mediterranean Basin	13.8	0.2
Tropical Andes	11.3	0.9
Brazil's Atlantic Forest	11.4	0.8
Succulent Karoo	11.8	0.3
Indo-Burma	8.3	0.6
Southcentral China	7.3	0.4
Choco-Darien-Western Ecuador	6.3	1.2
Wallacea	4.5	1.6
New Zealand	5.4	0.4
California Floristic Province	4.7	0.2
Caucasus	4.5	0.2
Mesoamerica	3.6	0.8
Central Chile	3.3	0.1
West African Forests	2.5	0.3
Brazil's Cerrado	2.1	0.1

Predictions of species loss with a fixed amount (1,000 km²) of additional habitat loss reveals differing sensitivity

Brooks et al. (2002). *Conservation Biology* 16: 909-923

Species-area relationships: accounting for species in the matrix



The traditional species-area relationship assumes that species are confined to natural habitat

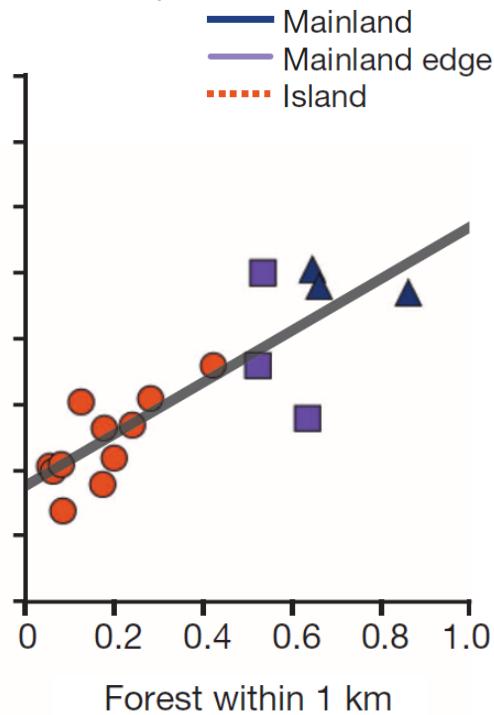
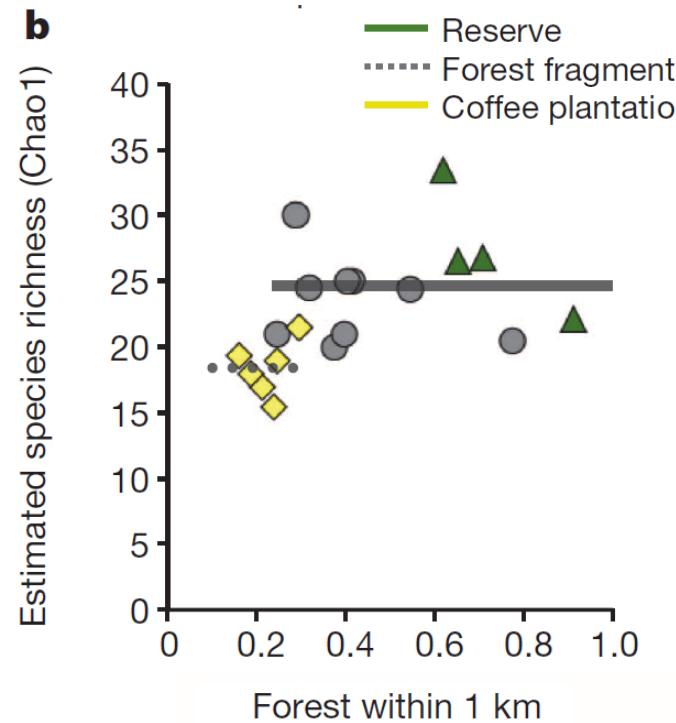
However, other habitats are not completely barren of species

Countryside species-area relationship:

$$S = c \left(\sum_j h_j A_j \right)^z$$

where h_j is the affinity of species for habitat j

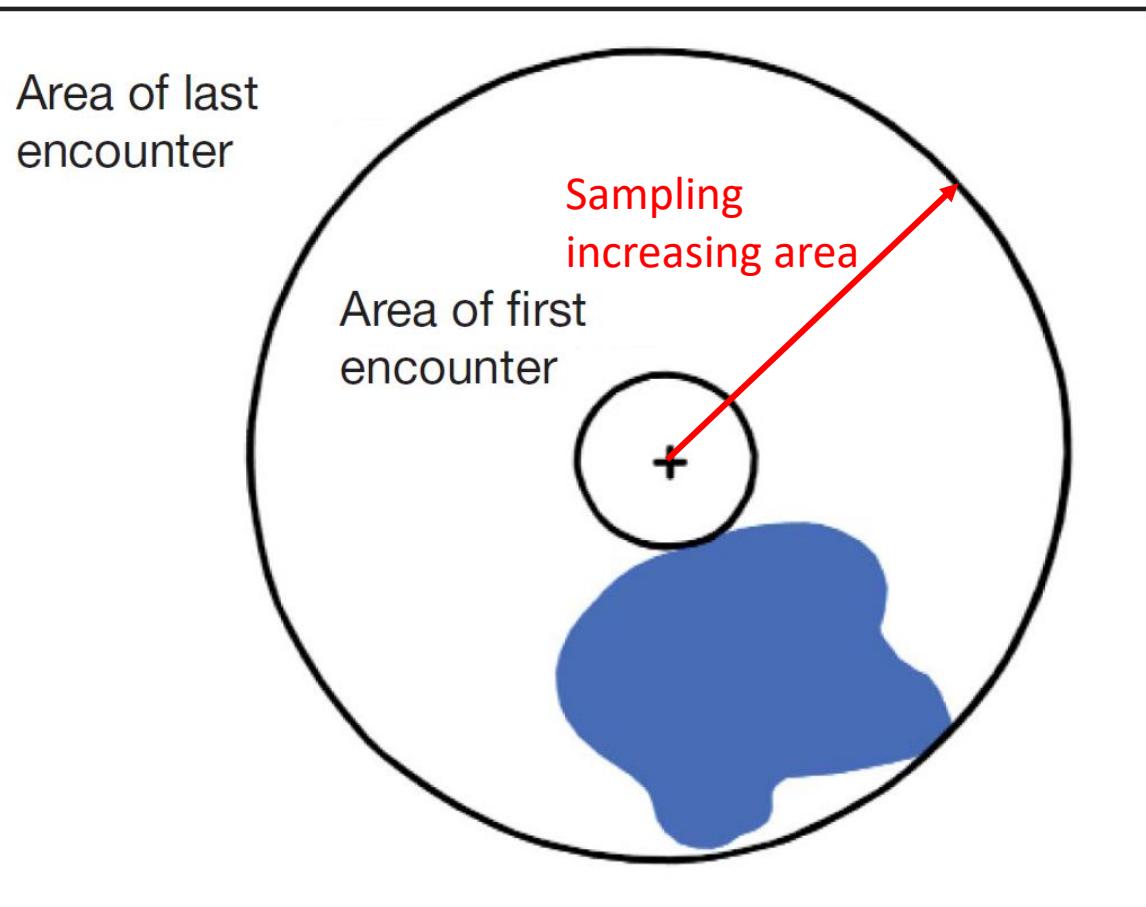
Species-area relationships: accounting for species in the matrix



Data on bat biodiversity conform to species-area relationships for true islands

But no relationship with forest area for habitat islands

Species-area relationships: sampling issues

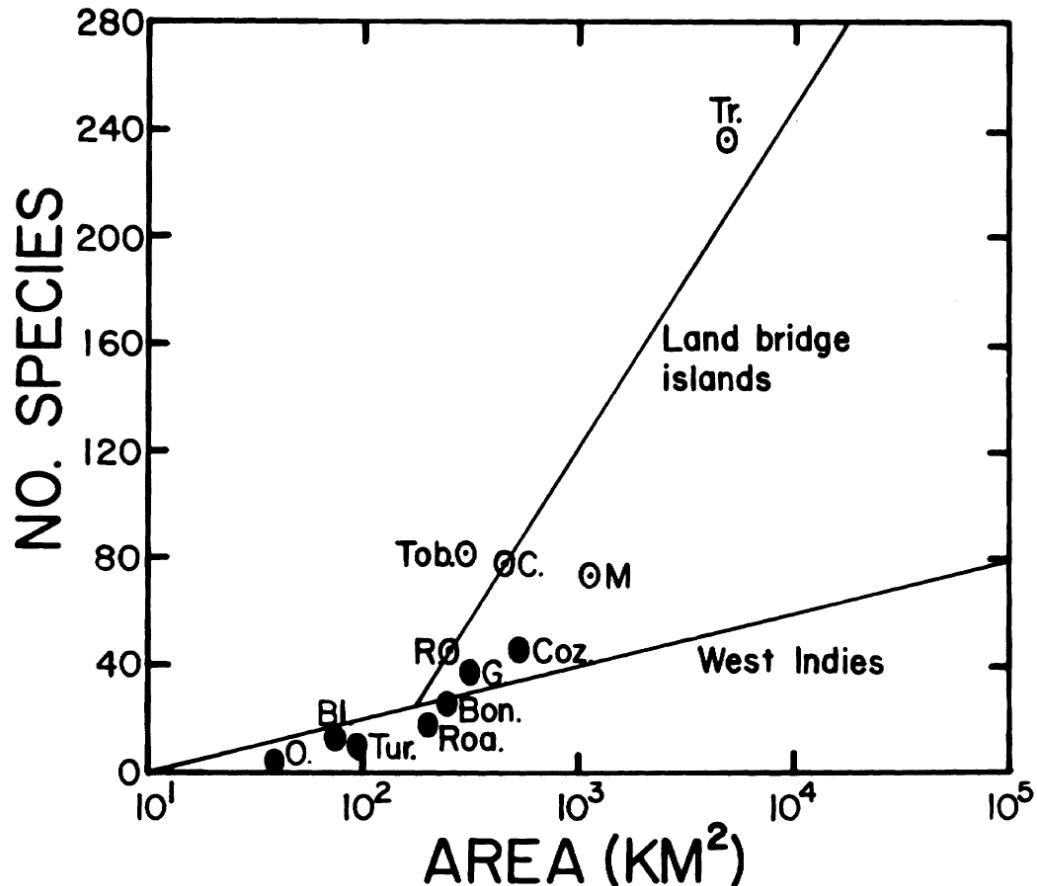


Application of species-area relationships to habitat loss is based on the reverse of the accumulation of species sampled with increasing area

But more area has to be lost for the entire range of a species to be lost, than for first detection

Classic species-area relationships are only useful if species are randomly distributed – in reality distributions are often clumped

Extinction debt

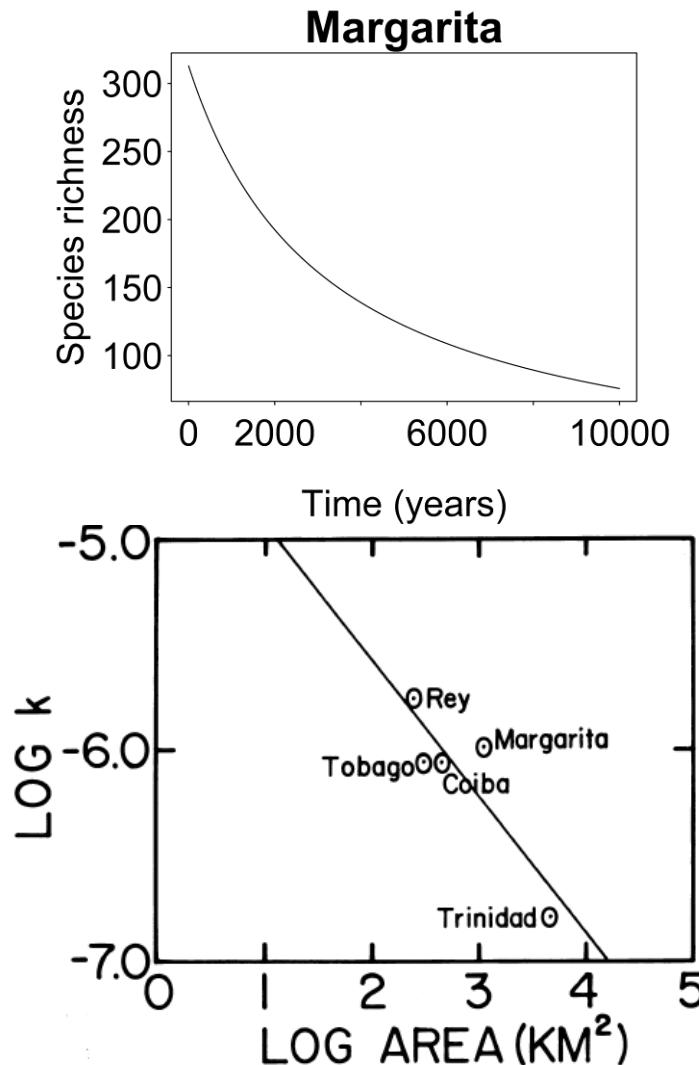


Land-bridge islands (formed relatively recently by sea-level rise) have more species than expected based on their area

May still be undergoing 'relaxation'

In other words, they have an 'extinction debt'

Extinction debt



$$\frac{dS}{dt} = -kS^2$$

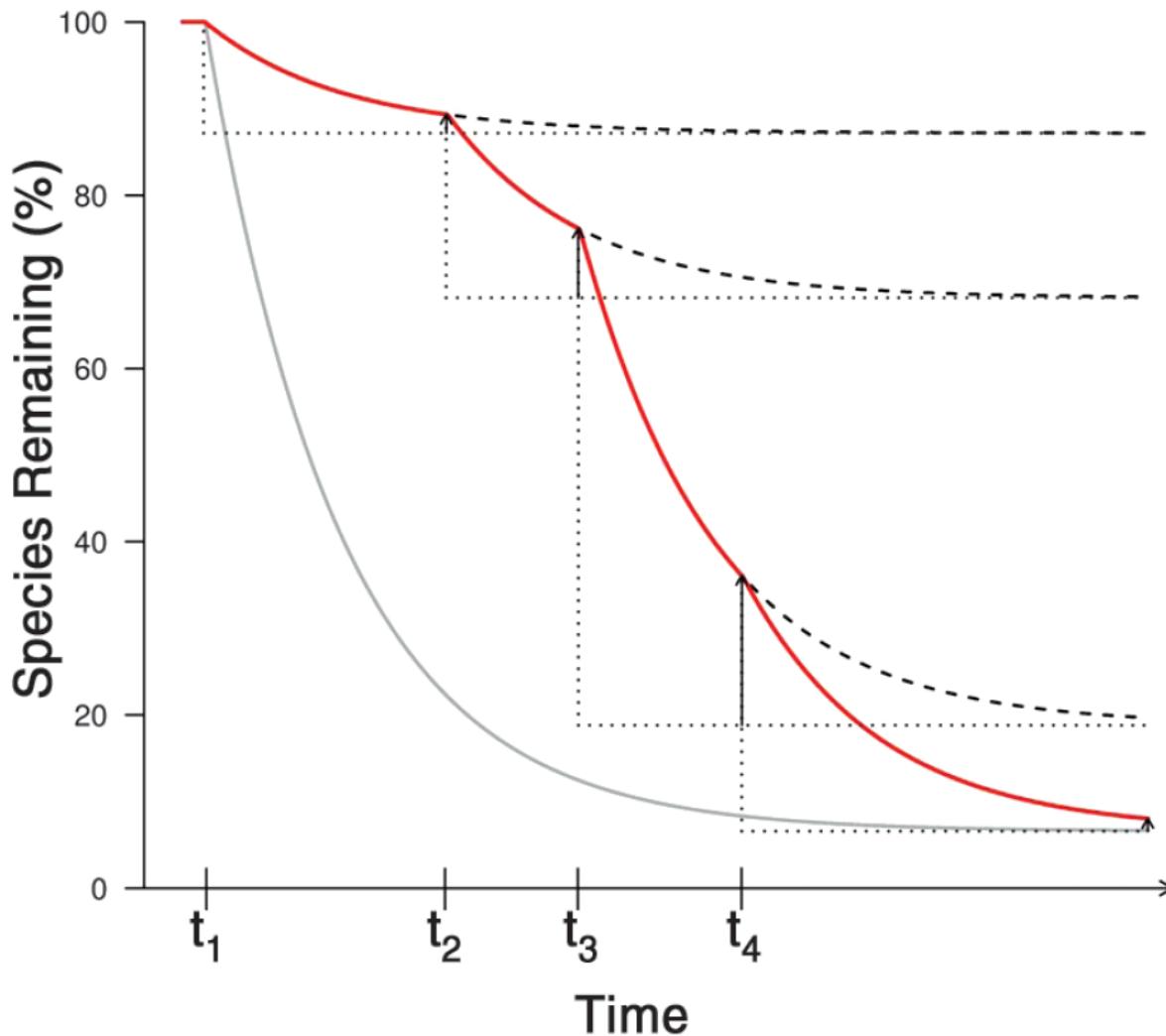
$$k = \frac{\frac{1}{S_p} - \frac{1}{S_o}}{t}$$

S = species richness, k = extinction rate, S_o = original species richness, S_p = present species richness

Fitting to data shows negative relationship between island size and extinction rate

Predicted 17 extinctions on Barro Colorado Island (observed = 13 to 18)

Applications of extinction-debt models



$$\begin{aligned}\frac{dS}{dt} &= -k(S - S_{eq}) \\ &= -k(S - cA^z)\end{aligned}$$

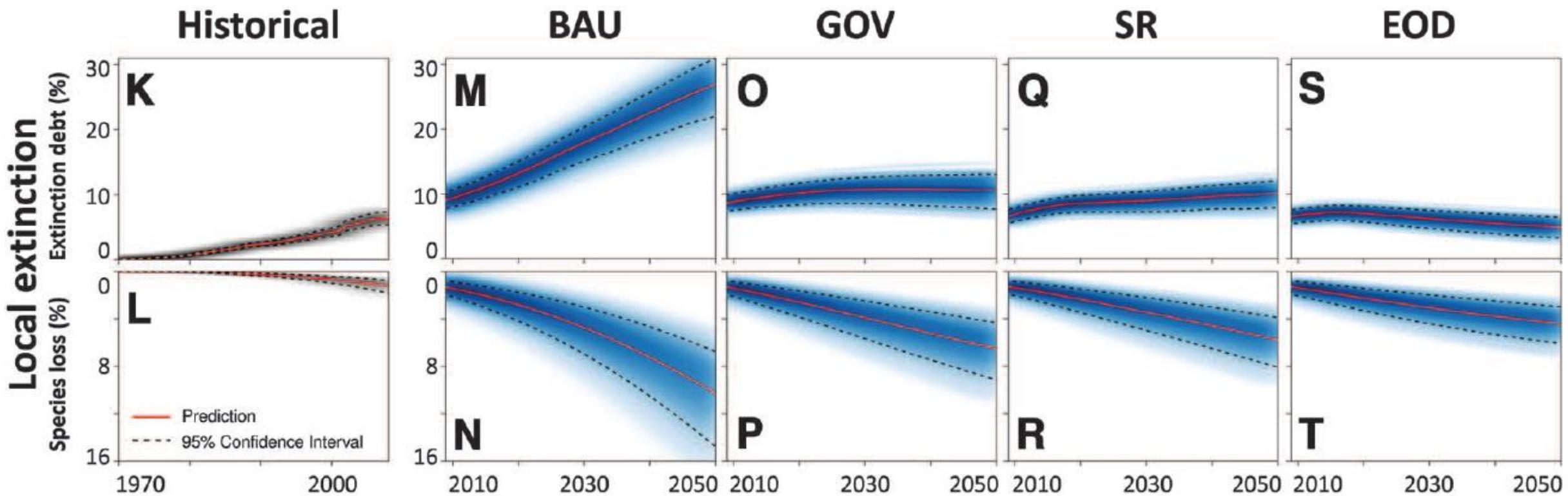
Species-area relationships for forest-dependent amphibians, mammals and birds

Maps of forest cover through time

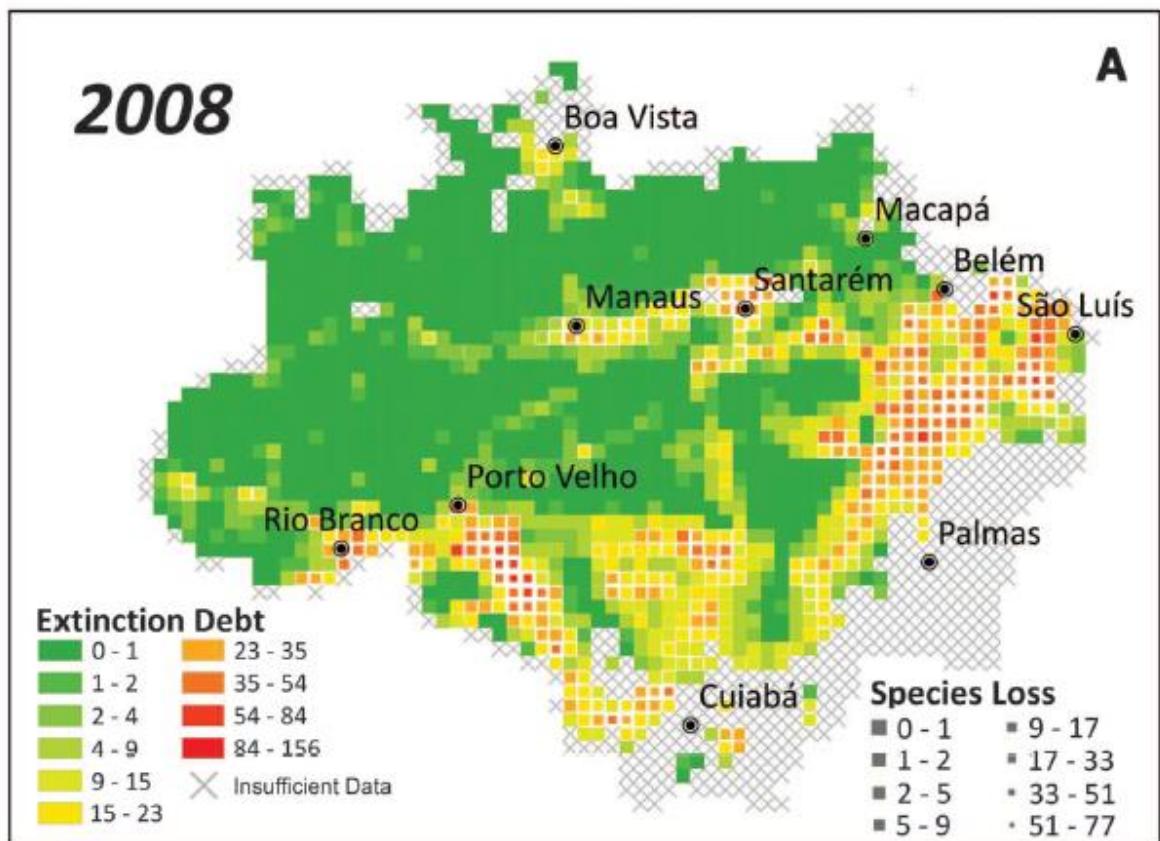
Applications of extinction-debt models

Most extinctions from past habitat loss yet to occur

Predictions of extinction debt correspond well with known threatened species



Applications of extinction-debt models



Spatial patterns of actual species loss and extinction debt

Basic population biology

$$N_{t+1} = N_t + B - D + I - E$$

B = births, D = deaths, I = immigrations, E = emigrations

Basic population biology: life tables

Age (days)	Number surviving (a_x)	Proportion surviving (I_x)	Fecundity (F_x)	Proportional fecundity (m_x)	$I_x m_x$
0-63	996	1.000	0	0.00	0.00
63-124	668	0.671	0	0.00	0.00
124-184	295	0.296	0	0.00	0.00
184-215	190	0.191	0	0.00	0.00
215-264	176	0.177	0	0.00	0.00
264-278	172	0.173	0	0.00	0.00
278-292	167	0.168	0	0.00	0.00
292-306	159	0.160	53.0	0.33	0.05
306-320	154	0.155	485.0	3.13	0.49
320-334	147	0.148	802.7	5.42	0.80
334-348	105	0.105	972.7	9.26	0.97
348-362	22	0.022	94.8	4.31	0.10
362-	0	0.000	0	0.00	0.00
				TOTAL:	$R_0 = 2.41$



Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing. Data from Leverich & Levin (1979). *The American Naturalist* **113**: 881-903.

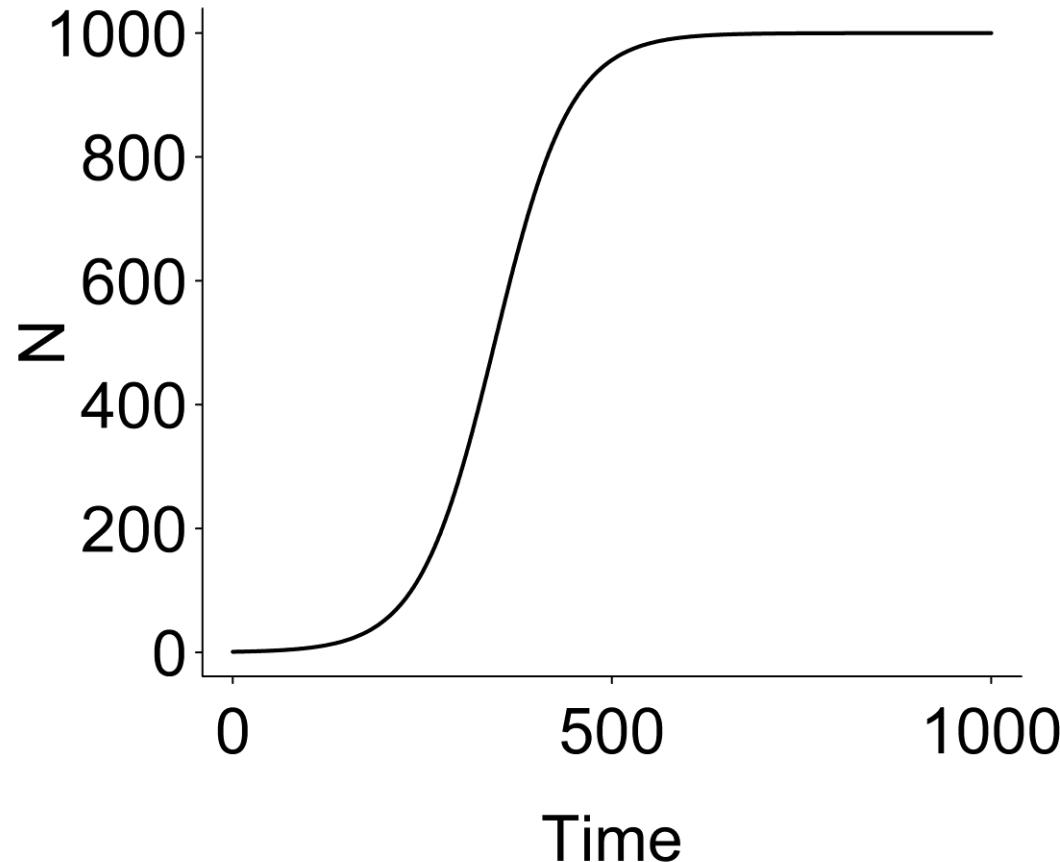
Basic population biology: life tables

Age (years)	Number surviving (a_x)	Proportion surviving (I_x)	Proportional fecundity (m_x)	$I_x m_x$	$x I_x m_x$
0	1,000,000	1.000	0	0	0
1	62	0.0000620	4600	0.285	0.285
2	34	0.0000340	8700	0.296	0.592
3	20	0.0000200	11600	0.232	0.696
4	15.5	0.0000155	12700	0.197	0.788
5	11	0.0000110	12700	0.140	0.700
6	6.5	0.0000065	12700	0.082	0.492
7	2	0.0000020	12700	0.025	0.175
8	2	0.0000020	12700	0.025	0.200
			TOTAL:	$R_0 = 1.282$	3.928

$$r = \frac{\ln R_0}{T_c}; T_c = \frac{\sum x I_x m_x}{R_0} = \frac{3.928}{1.282} = 3.1; r = \frac{\ln 1.282}{3.1} = 0.08014$$



Competition: Lotka-Volterra Model



Based on logistic population growth
(i.e. with density-dependence, e.g.
via intraspecific competition):

$$\frac{dN}{dt} = rN \frac{K - N}{K}$$

r = intrinsic population growth, K =
carrying capacity

Competition: Lotka-Volterra Model

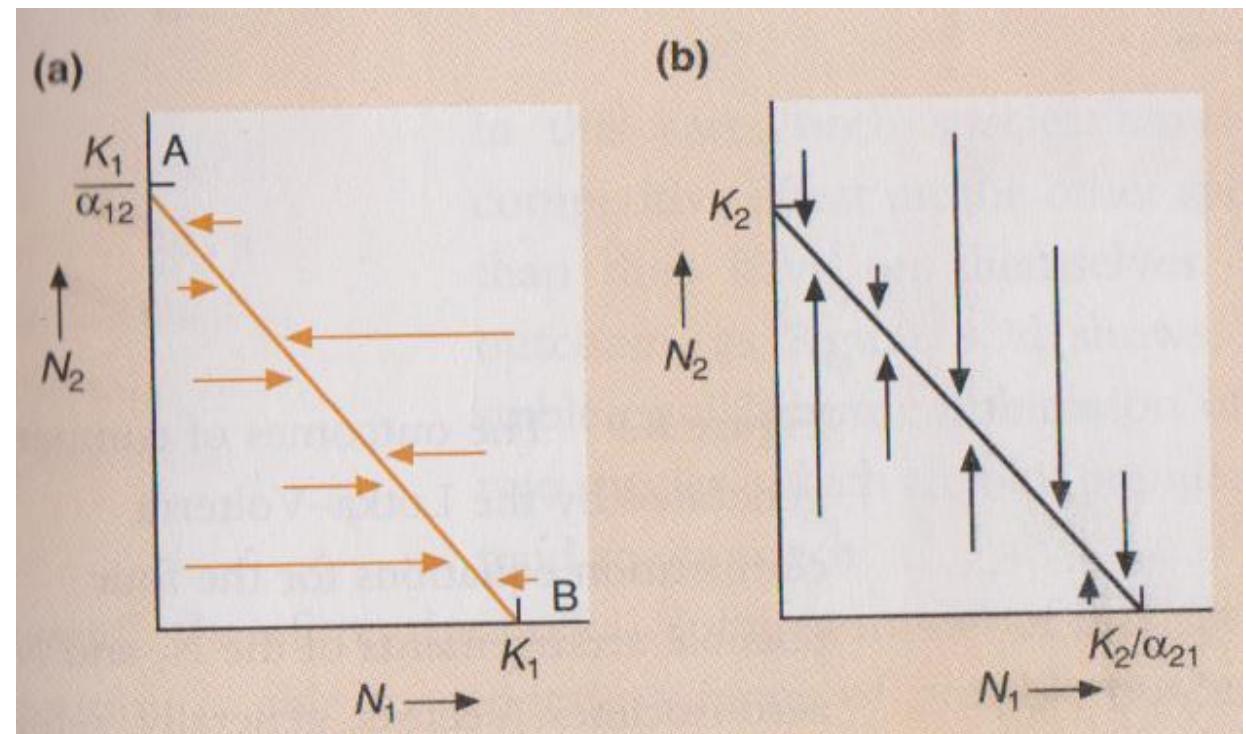
Logistic growth for two species modified to account for effect of interspecific competition:

$$\frac{dN_1}{dt} = r_1 N_1 \frac{K_1 - N_1 - \alpha_{12} N_2}{K_1}$$

$$\frac{dN_2}{dt} = r_2 N_2 \frac{K_2 - N_2 - \alpha_{21} N_1}{K_2}$$

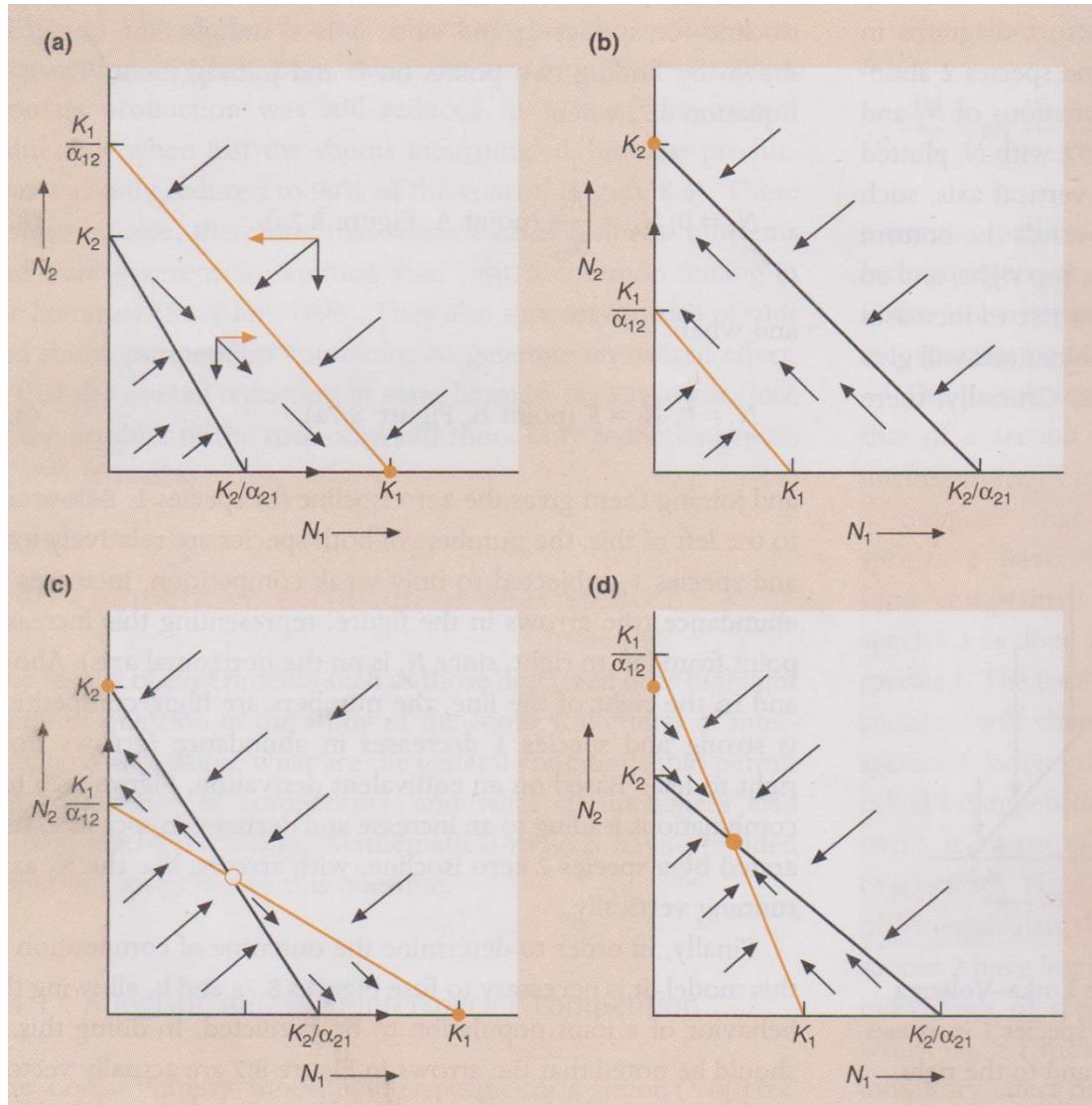
α_{12} = competitive effect of species 2 on species 1

Zero-growth isoclines:



From Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing.

Competition: Lotka-Volterra Model

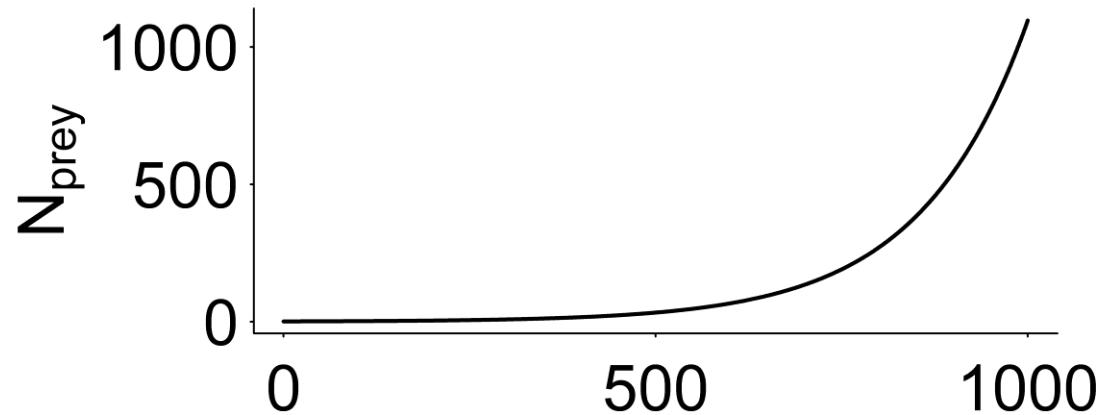


When $\frac{K_1}{\alpha_{12}} > K_2$ and $K_1 > \frac{K_2}{\alpha_{21}}$, or $K_1 > K_2\alpha_{12}$ and $K_1\alpha_{21} > K_2$, species 1 self-regulates more strongly than species 2 regulates it, and species 1 regulates species 2 more strongly than species 2 regulates itself. Therefore, species 1 outcompetes species 2

When $\frac{K_1}{\alpha_{12}} > K_2$ and $\frac{K_2}{\alpha_{21}} > K_1$, or $K_1 > K_2\alpha_{12}$ and $K_2 > K_1\alpha_{21}$, both species self-regulate more strongly than they affect each other, so co-exist stably

From Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing.

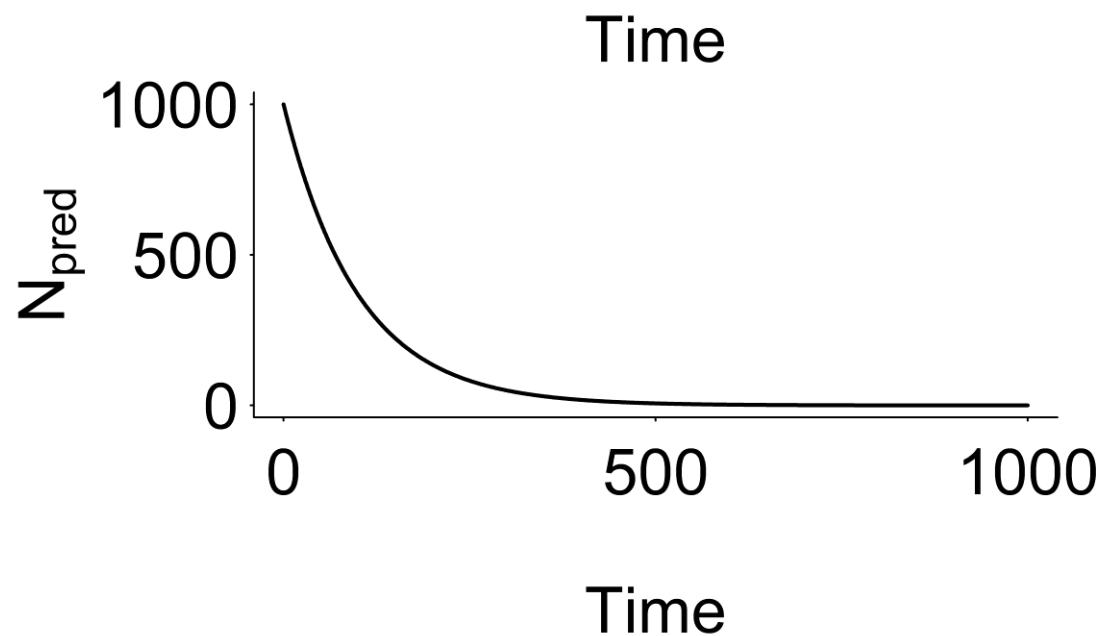
Predation: Lotka-Volterra Model



In the absence of interactions:

Exponential growth of prey:

$$\frac{dR}{dt} = rR$$



Constant per capita loss of predators through mortality:

$$\frac{dC}{dt} = -mC$$

R = Prey abundance, C = predator abundance, m = predator mortality rate

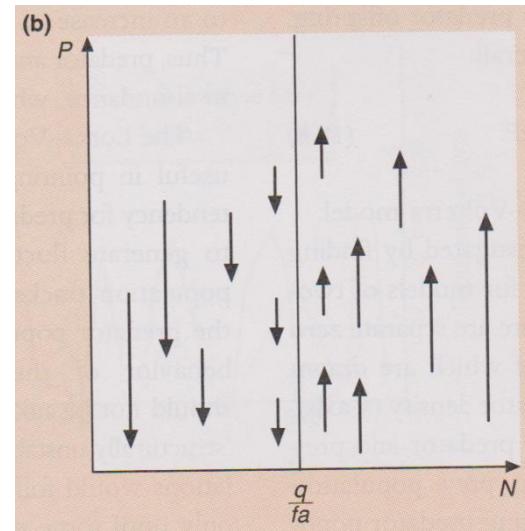
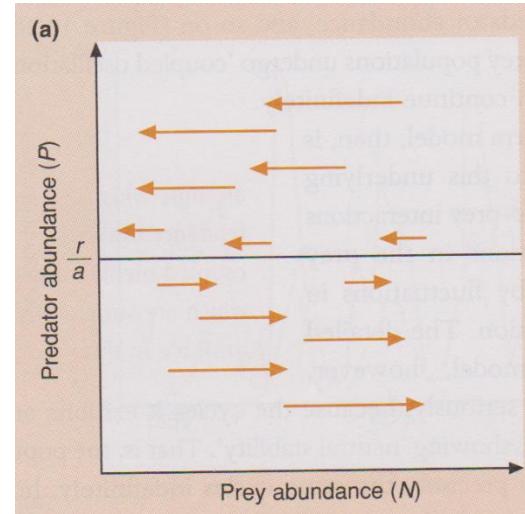
Predation: Lotka-Volterra Model

With interactions between predators and prey:

$$\frac{dR}{dt} = rR - \alpha_{rp}CR$$

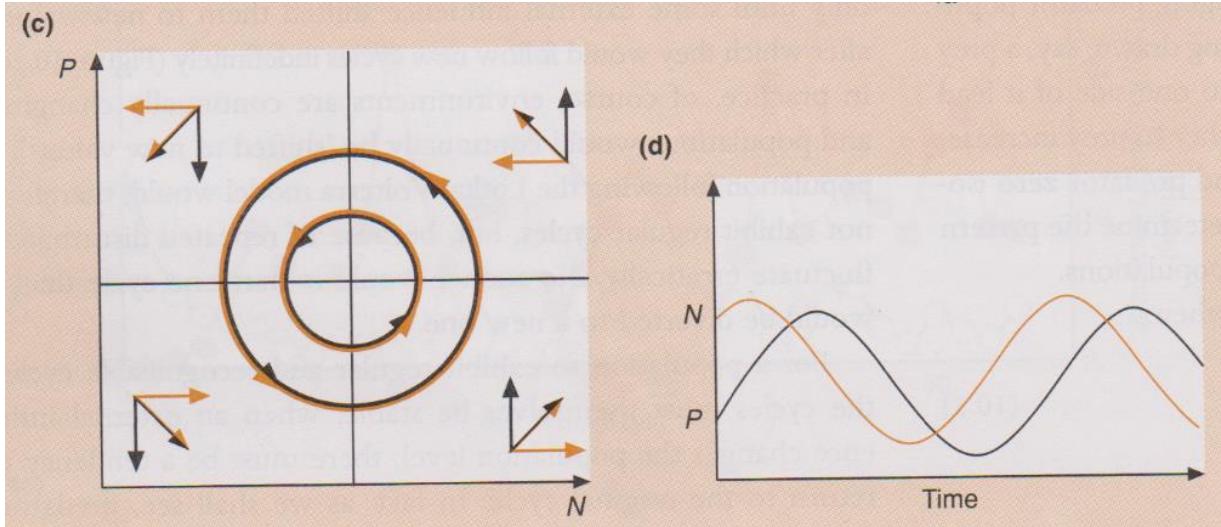
$$\frac{dC}{dt} = e\alpha_{rp}CR - mC$$

e = predation conversion efficiency



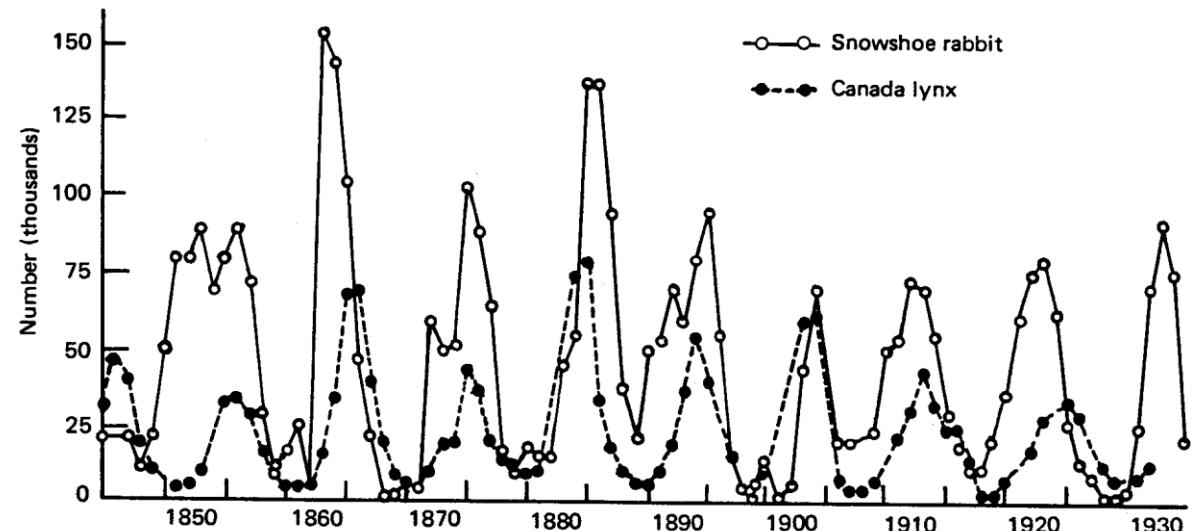
From Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing.

Predation: Lotka-Volterra Model



Lynx and snowshoe hare, from MacLulick (1937)

From Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing.



How fast can species eat?

When prey are scarce, predation rate might increase linearly with prey density

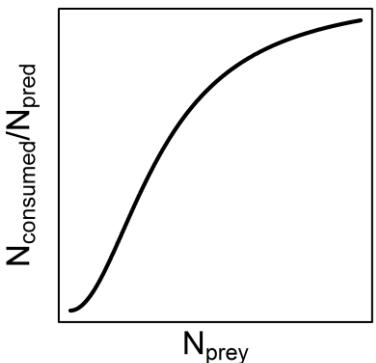
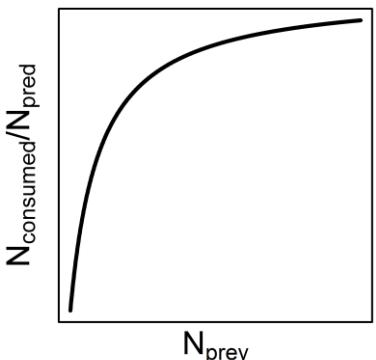
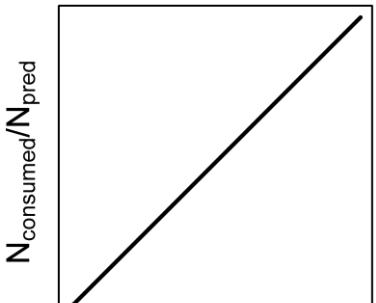


When prey are abundant, predators might be limited by handling time



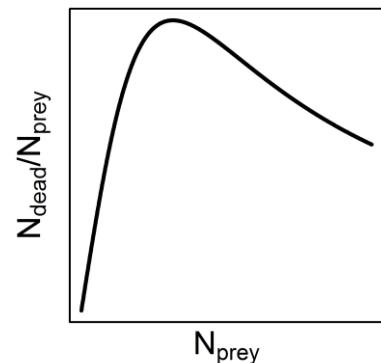
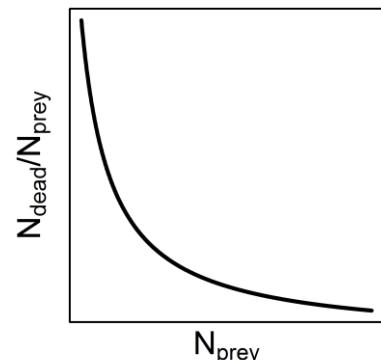
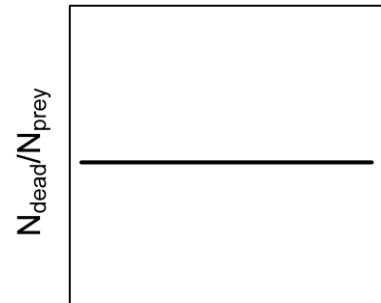
pats0n.livejournal.com

Functional Responses



Type	Predator per capita prey consumption rate	Prey per capita predation mortality
I	aR	Ca
II	$\frac{aR}{1 + ahR}$	$C \frac{a}{1 + ahR}$
III	$\frac{aR^q}{1 + ahR^q}, 1 < q < 2$	$C \frac{aR^{q-1}}{1 + ahR^q}, 1 < q < 2$

a = predator attack rate, R = prey abundance, C = predator abundance, h = handling time, q = prey-abundance exponent



Functional Responses – multiple prey

Type	Predator per capita prey consumption rate	Prey per capita predation mortality
I	aR	Ca
II	$\frac{aR}{1 + \sum_{r \in S_r} a_r h_r R_r}$	$C \frac{a}{1 + \sum_{r \in S_r} a_r h_r R_r}$
III	$\frac{aR^q}{1 + \sum_{r \in S_r} a_r h_r R_r^q},$ $1 < q < 2$	$C \frac{aR^{q-1}}{1 + \sum_{r \in S_r} a_r h_r R_r^q},$ $1 < q < 2$

S_r is the set of species that the predator can consume

Functional Responses – generalized form

$$\text{Consumption rate} = \frac{aR^q}{1 + \sum_{r \in S_r} a_r h_r R_r^q}$$

$$\text{Mortality rate} = C \frac{aR^{q-1}}{1 + \sum_{r \in S_r} a_r h_r R_r^q}$$

Type I: $h = 0, q = 1$

Type II: $h > 0, q = 1$

Type III: $h > 0, 1 < q < 2$

Predation and competition: Generalized Rosenzweig-MacArthur Model

$$\frac{dN_i}{dt} = N_i \left(r_i(t) + \sum_{j=1}^s \tilde{\alpha}_{ij} N_j \right)$$

Exponential growth

$$\frac{dN_i}{dt} = N_i r_i(t) - N_i \sum_{j \in L(i)} \alpha_{ij} N_j$$

Competition (including intraspecific, when $i=j$)

$$-N_i \sum_{j \in C(i)} \left(N_j \frac{h_{ij} \alpha_{ij} N_i^{q_{ij}-1}}{1 + \sum_{n \in R(j)} T_{nj} h_{nj} \alpha_{nj} N_n^{q_{nj}}} \right)$$

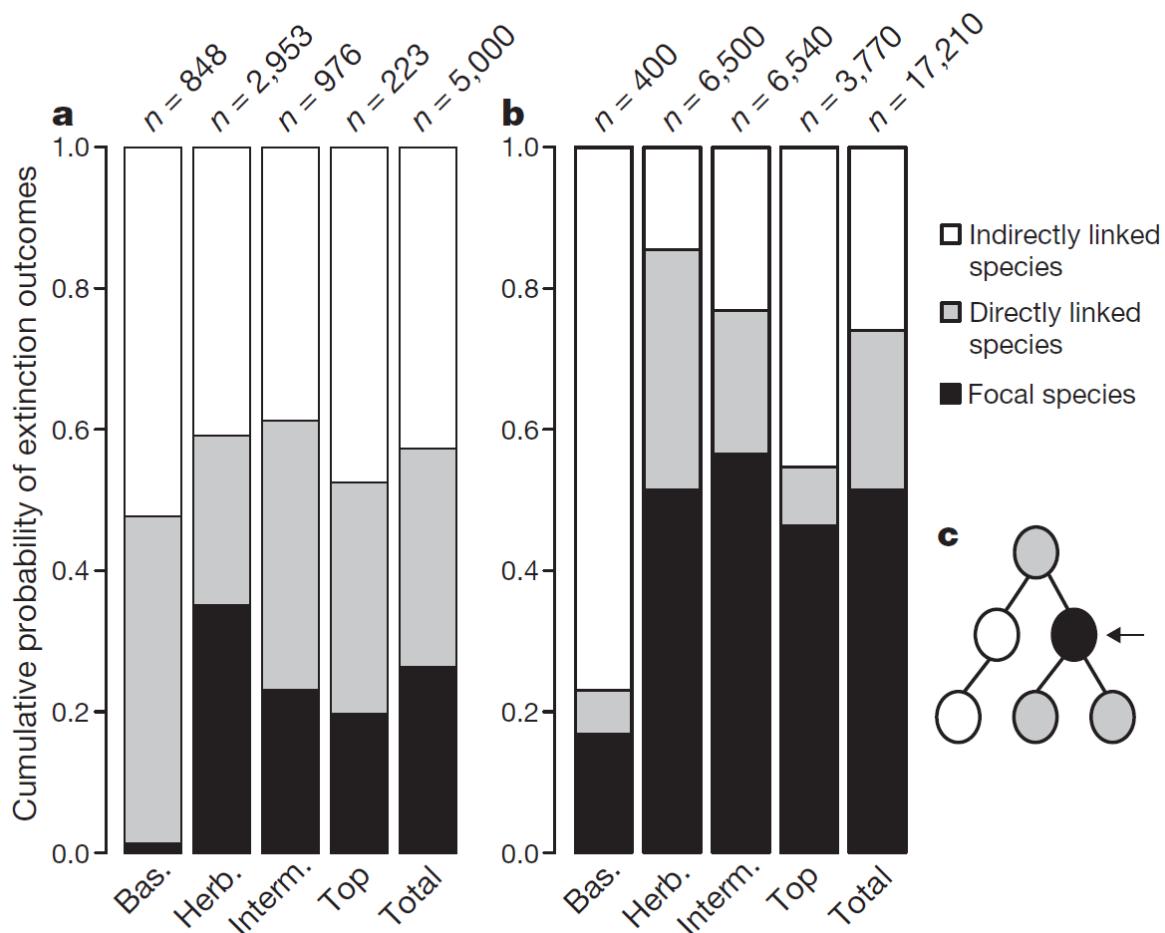
Being predated upon

$$+N_i \sum_{j \in R(i)} \left(e_{ji} \frac{h_{ji} \alpha_{ji} N_j^{q_{ji}}}{1 + \sum_{n \in R(i)} T_{ni} h_{ni} \alpha_{ni} N_n^{q_{ni}}} \right)$$

Predating

$L(i)$ is the set of species competing with i , $C(i)$ is the set of species consuming i , and $R(i)$ is the set of species eaten by i .

Applications of simple community models: extinction risk in ecological networks

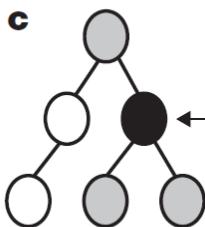


Generalized Rosenzweig-MacArthur model

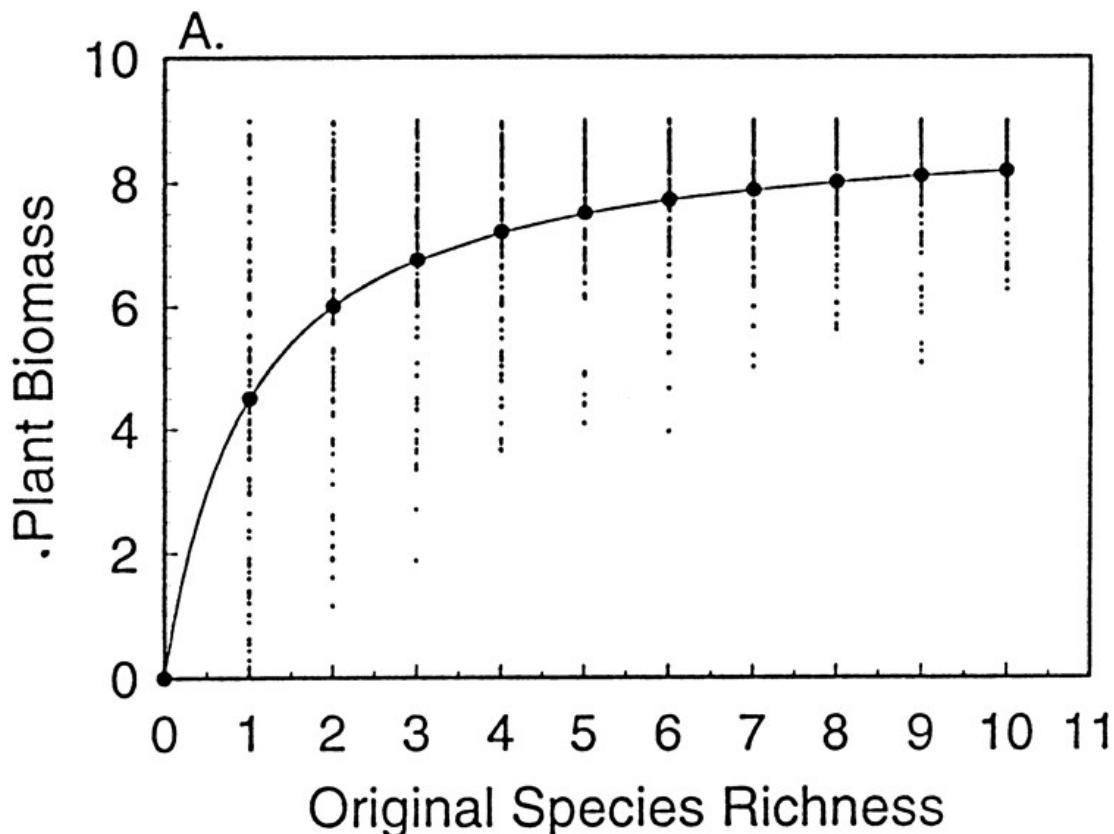
Mortality rate of one species is increased until any species goes extinct

First species to go extinct is often not the species with the increased mortality rate

‘Functional extinction’ before actual extinction



Biodiversity and ecosystem functioning

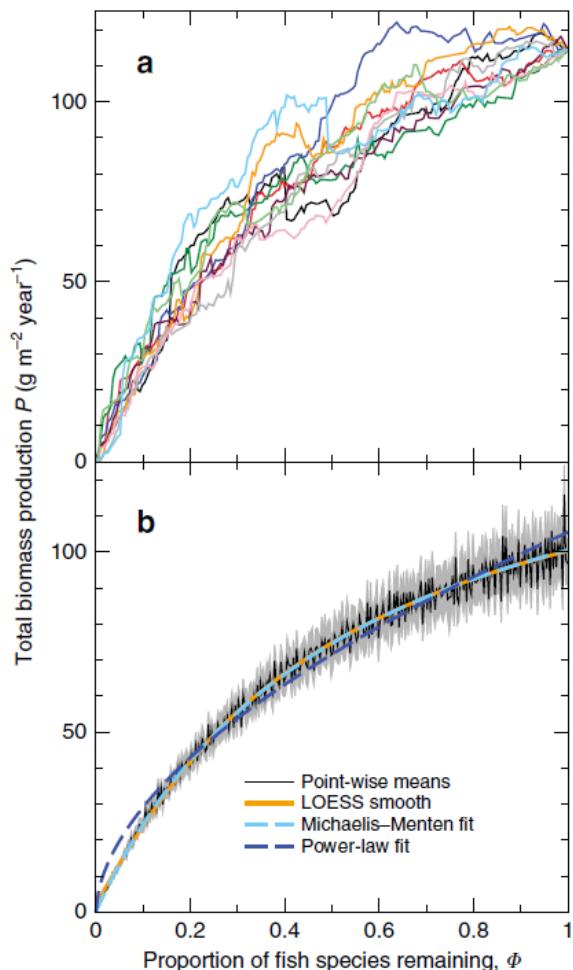


A big question in ecology is whether increased biodiversity supports increased ecosystem function

Empirical tests have tended to focus on grasslands in temperate environments

Simple community models can help to address this question

Applications of simple community models: biodiversity and ecosystem functioning



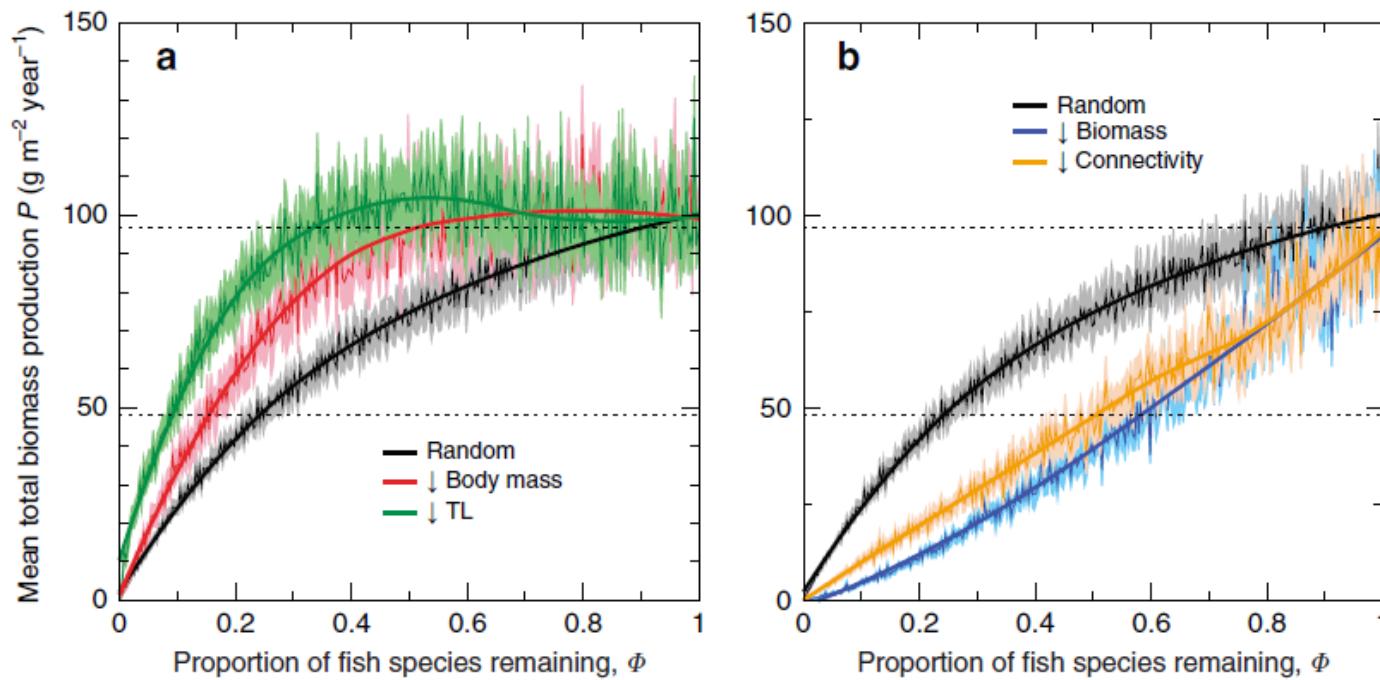
Marine food-web model with thousands of species

Competition: Lotka-Volterra

Predator-prey relationships:
Holling Type II functional response

Loss of species led to loss of fish production

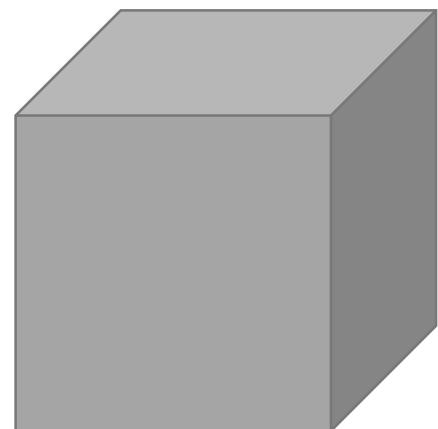
Applications of simple community models: biodiversity and ecosystem functioning



If large or high-trophic-level species were removed first, small species losses had little effect on production

If the species of highest biomass or highest connectivity were removed first, species losses had steep effect on production

Metabolic theory



$$\text{Surface area} \propto \text{Length}^2$$

$$\text{Volume} \propto \text{Mass} \propto \text{Length}^3$$

$$\text{Surface area} \propto \text{Mass}^{2/3}$$

Rubner (1883):

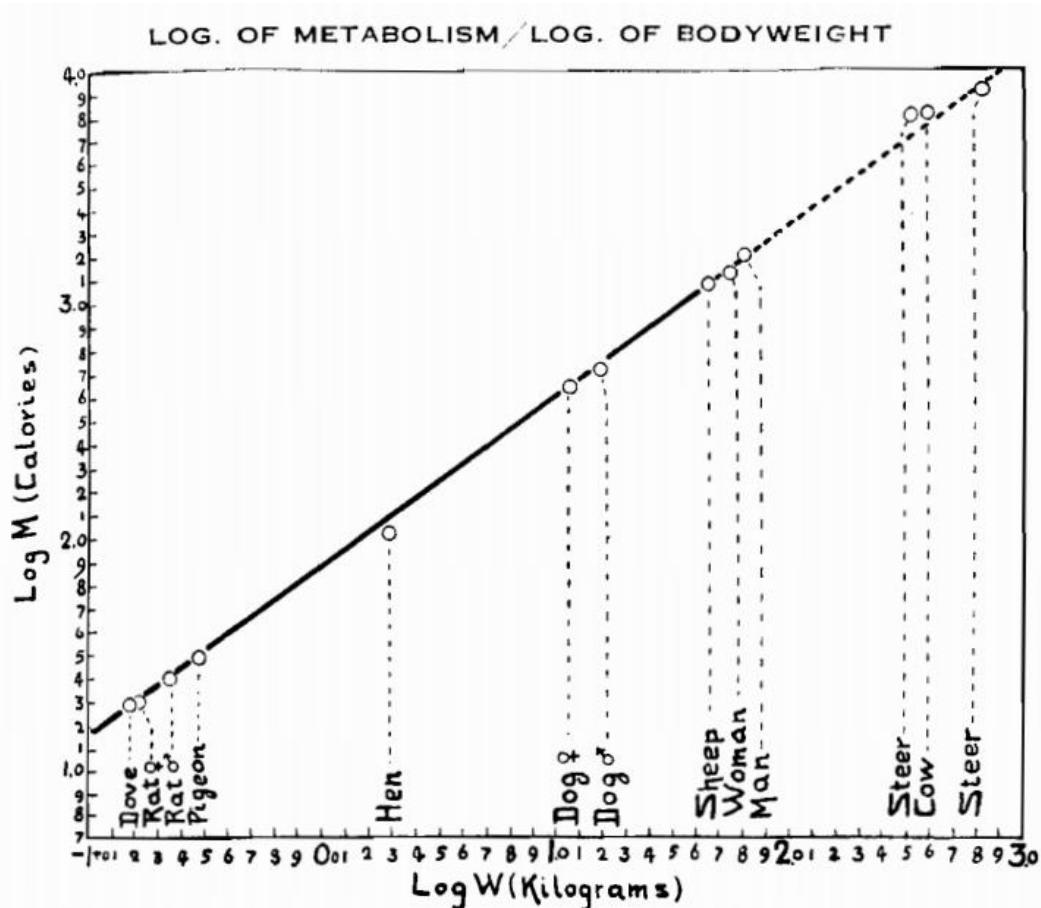
Metabolic rate of dogs divided by surface area independent of mass

Therefore:

$$B \propto M^{2/3}$$

Rubner (1883). *Zeitschrift für Biologie* 19: 536-562

Metabolic theory

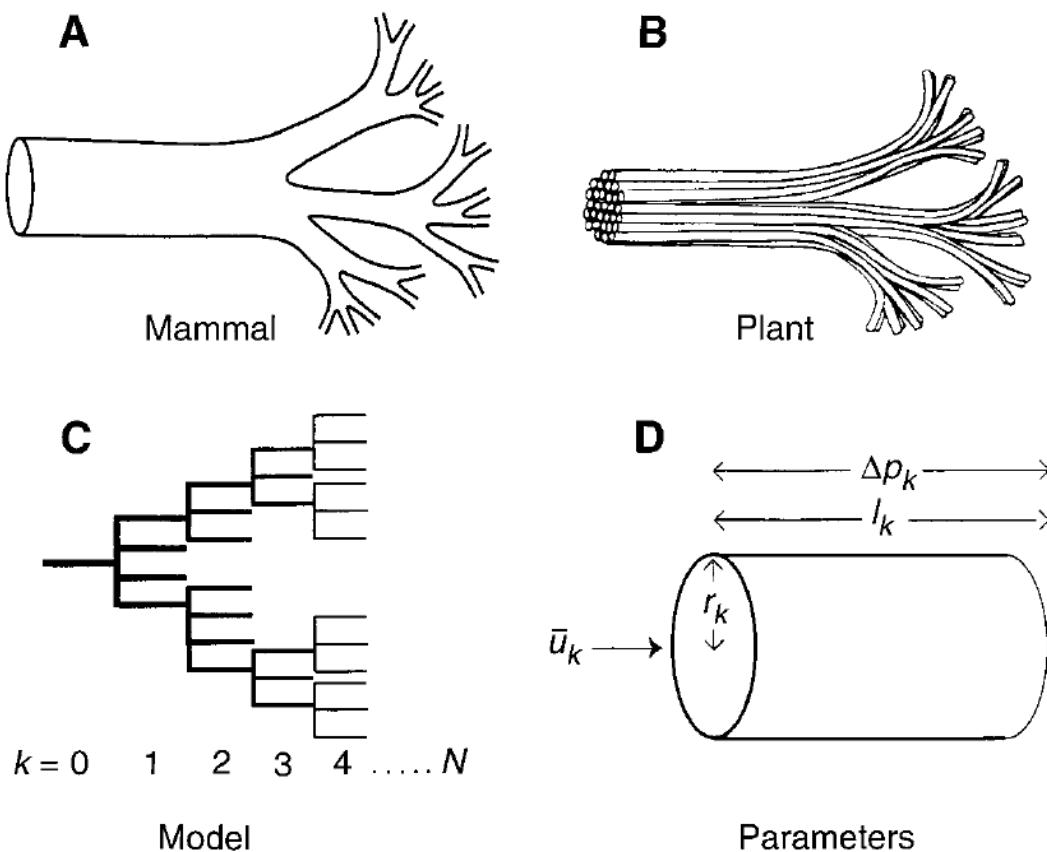


Kleiber (1932):

$$B \propto M^{3/4}$$

Assuming that metabolism scales with body surface area is overly simplistic

Metabolic theory

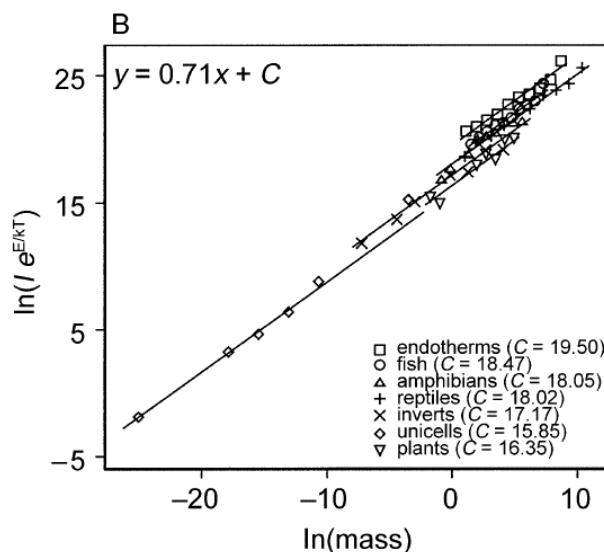
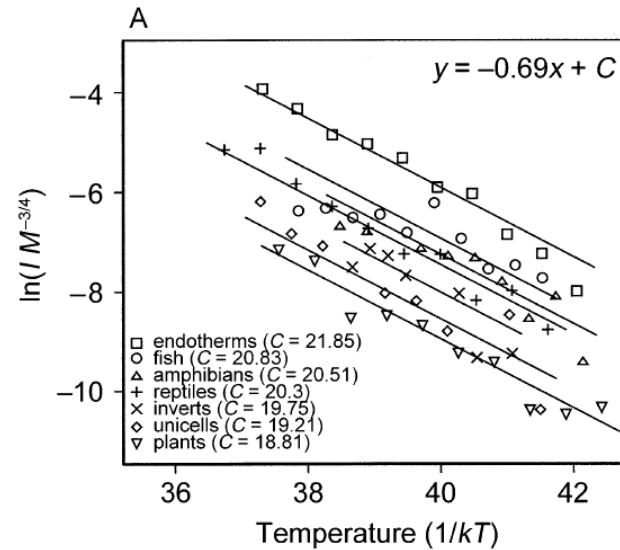


Transport through networks, e.g. capillaries, of resources required for metabolism scales with $M^{3/4}$

Makes some relatively straightforward assumptions

Predicts accurately the mass-scaling of properties of mammalian circulatory systems

Metabolic theory



Combined effects of mass and temperature:

$$B = b_0 M^{3/4} e^{-E/kT}$$

E = activation energy; T = temperature; k = Boltzmann constant; b_0 = constant

Critiques of metabolic theory

AN ILLUSION OF MECHANISTIC UNDERSTANDING

HÉLÈNE CYR¹ and STEVE C. WALKER

THE VALUE OF NULL THEORIES IN ECOLOGY

JOHN HARTE¹

METABOLIC ECOLOGY: LINKING INDIVIDUALS TO ECOSYSTEMS

PABLO A. MARQUET,^{1,3} FABIO A. LABRA,¹ and BRIAN A. MAURER²

DOES METABOLIC THEORY APPLY TO COMMUNITY ECOLOGY?
IT'S A MATTER OF SCALE

DAVID TILMAN,¹ JANNEKE HILLERISLAMBERS, STAN HARPOLE, RAY DYBZINSKI, JOE FARGIONE,
CHRIS CLARK, AND CLARENCE LEHMAN

CAN FUNCTION AT THE ORGANISMAL LEVEL EXPLAIN
ECOLOGICAL PATTERNS?

M. A. R. KOEHL¹ AND BRYCE D. WOLCOTT

A ONE-RESOURCE “STOICHIOMETRY”?

ROBERT W. STERNER¹

Ecology, Evolution and Behavior, University of Minnesota, St. Paul, Minnesota 55108 USA

The approach of Brown et al. (2004) might succeed or fail on two levels. On one level, it can be used as a purely statistical, predictive tool. Examples given by Brown and colleagues leave no doubt that temperature and body size “explain” (in the statistical sense) a great deal. We do need good predictive models for many reasons, one of them for incorporating more ecology

course, is less certain than is the existence of good statistical correlations.

Brown et al. view the “big three” variables to be temperature, body size, and stoichiometry. Temperature turns out to be approachable using decades-old formulations of Arrhenius, Boltzmann, and others. It

Main criticisms:

- Assumptions justified?
- Extent of applicability
- Many other important ecological processes
- Contingency
- Explanation of mechanisms, or just good fit to patterns?
- Usefulness to community dynamics
- Organisms face multiple limiting factors
- Is metabolic rate really $\propto M^{0.75}$?

Metabolic theory

Table 2. Ordinary least-squares (OLS) and reduced major axis (RMA) allometric regression parameters for the scaling of mammalian metabolic rate

	OLS		RMA		95% CI
	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	
SMR	4.17	0.675	3.85	0.689	0.013
BMR	3.98	0.686	3.61	0.706	0.014
RMR _t	3.66	0.712	3.33	0.729	0.013
FMR	9.99	0.73	4.53	0.75	0.04
RMR _{pp}	7.91	0.75	7.70	0.76	0.03
MMR _c	31.56	0.65	28.3	0.68	0.05
MMR _e	16.71	0.87	0.4	0.88	0.05

Mammalian metabolic rate (MR)= aM_b^b . All regressions are presented in standardised units (BMR in ml O₂ h⁻¹; M_b in g). SMR, standard metabolic rate; BMR, basal metabolic rate; RMR_t, thermoneutral resting metabolic rate; FMR, field metabolic rate; RMR_{pp}, peak postprandial resting metabolic rate; MMR_c, cold-induced maximum metabolic rate; MMR_e, exercise-induced maximum metabolic rate; see text for details.

But perhaps metabolic rates are not really $\propto M^{3/4}$

White & Seymour (2005): slopes vary depending on measures, methods, and exclusion of problematic large herbivores

Evidence to reject a slope of 2/3 not always strong

Metabolic theory

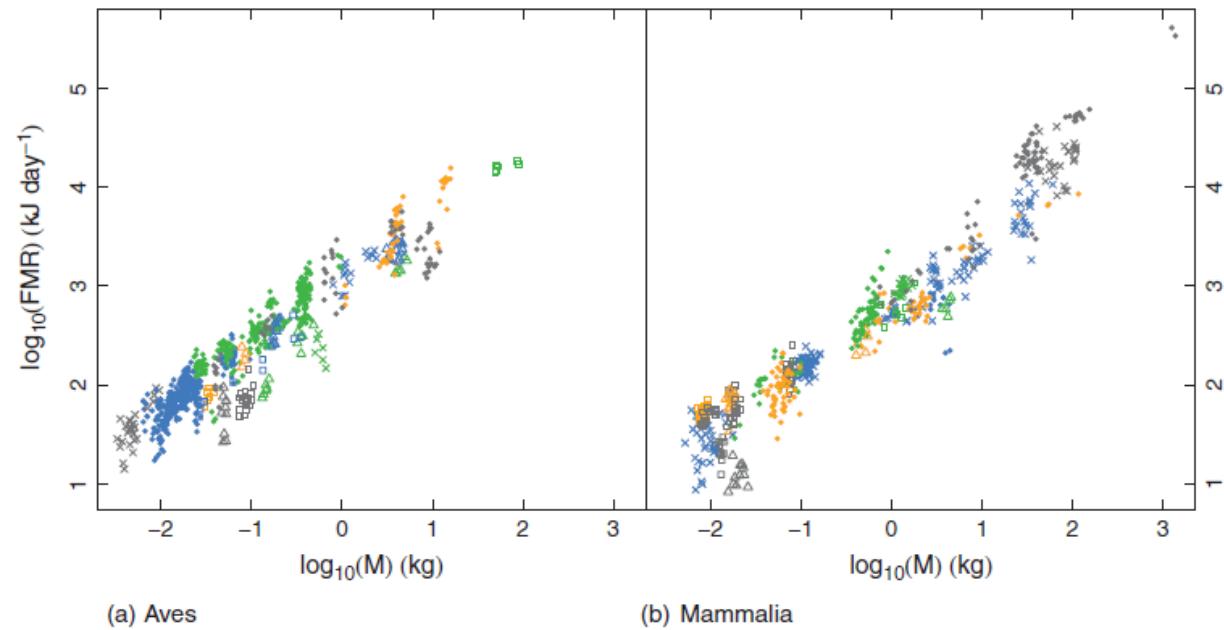
Hudson et al. (2013):

Wide taxonomic variation in slopes

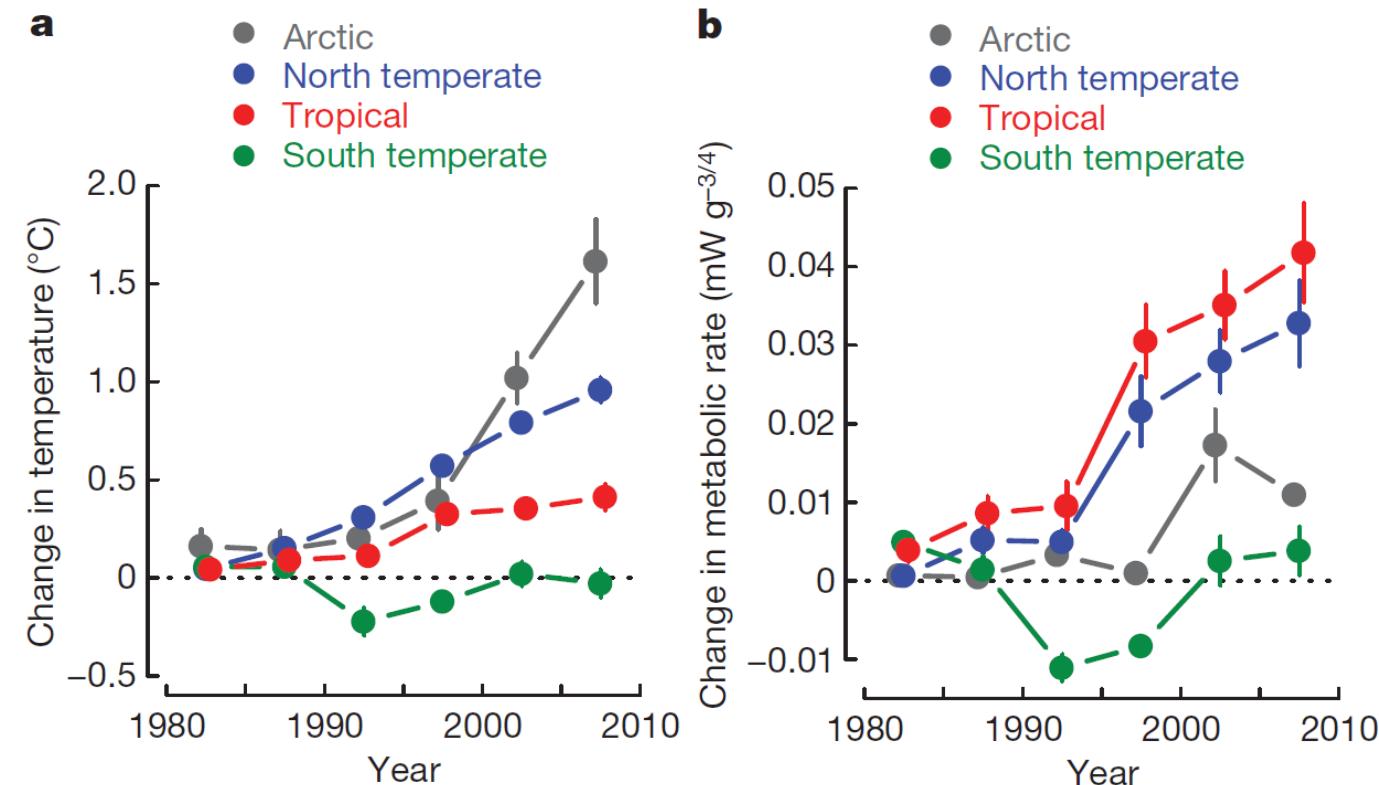
No evidence to reject slope of 2/3,
Sometimes can reject slope of 3/4

Legend:

Apodiformes	Falconiformes	Procellariiformes	Afrosoricida	Diprotodontia	Primates
Caprimulgiformes	Galliformes	Psittaciformes	Artiodactyla	Lagomorpha	Rodentia
Charadriiformes	Passeriformes	Sphenisciformes	Carnivora	Monotremata	Soricomorpha
Columbiformes	Pelecaniformes	Strigiformes	Chiroptera	Peramelemorphia	
Coraciiformes	Piciformes	Struthioniformes	Dasyuromorphia	Pilosa	



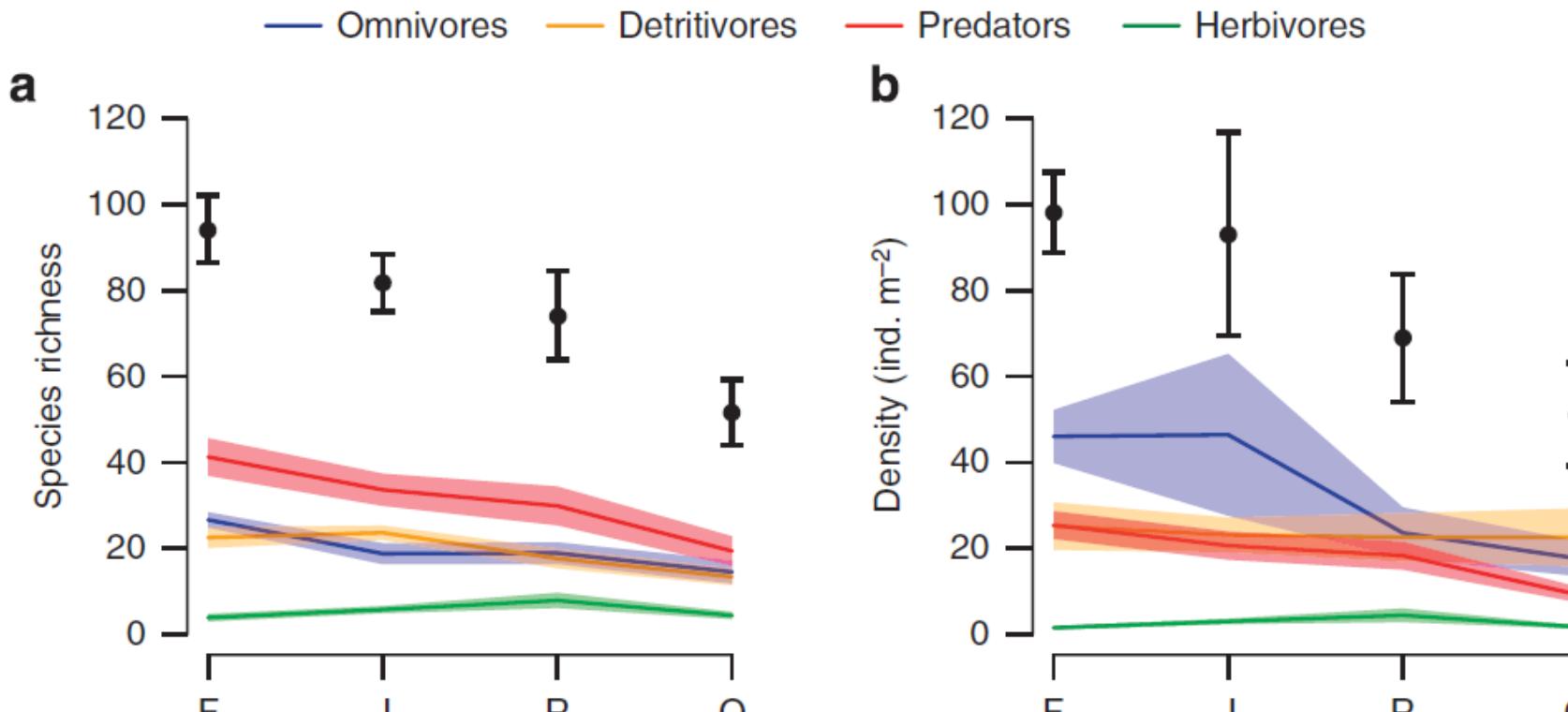
Applications of metabolic theory: effects of climate change



Mass-normalized metabolic rate based on weather-station temperature estimates

Arctic warmed fastest, but metabolic rates increased most in tropics

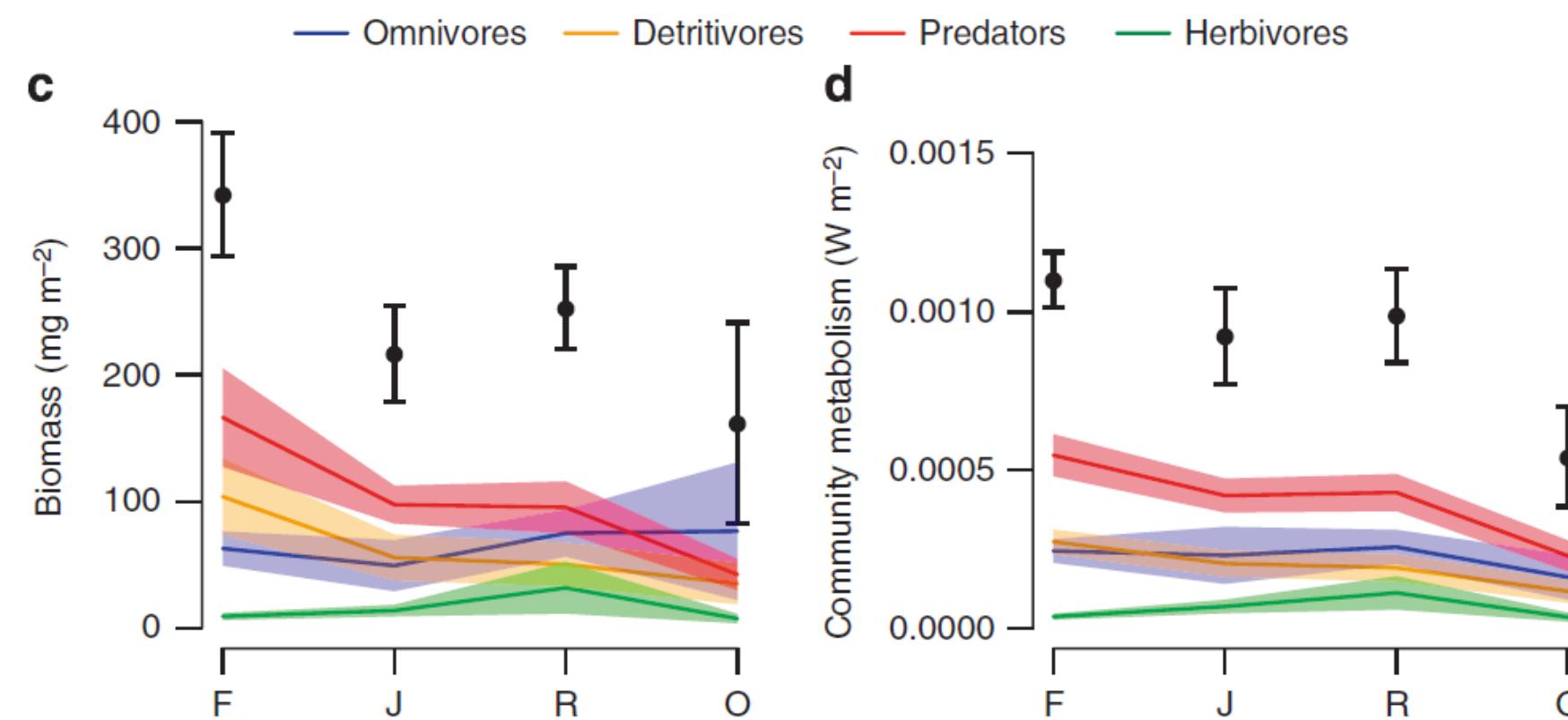
Applications of metabolic theory: biodiversity and ecosystem functioning again



F = Forest; J = Jungle rubber; R = Rubber plantation; O = Oil palm

Remember from
last lecture,
study showing
impacts of land
use on
biodiversity at
different trophic
levels

Applications of metabolic theory: biodiversity and ecosystem functioning again



They also calculated impacts on biomass and metabolic rates

Summary: Simple theoretical models

Useful for revealing general principles underlying ecological processes

Can make predictions about general patterns expected under environmental change

Often simple, deterministic and rely on sometimes unsupported assumptions

Don't account for complex interacting effects of environment, other organisms in community etc.

Therefore, predictions might be inaccurate in specific contexts

Reading list (I am not expecting you to read all of these!)

- Allen et al. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* **297**: 1545-1548.
- Barnes et al. (2014). Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications* **5**: 5351.
- Begon et al. (2006). *Ecology: From Individuals to Ecosystems*. Blackwell Publishing. [Sections on species-area relationships, life tables, competition, predation and functional responses].
- Black & McKane (2012). Stochastic formulation of ecological models and their applications. *Trends in Ecology & Evolution* **27**: 337-345.
- Brooks et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* **16**: 909-923.
- Brown et al. (2004). Toward a metabolic theory of ecology. *Ecology* **85**: 1771-1789.
- Daufresne et al. (2009). Global warming benefits the small in aquatic ecosystems. *PNAS* **106**: 12788-12793.
- Dillon et al. (2010). Global metabolic impacts of recent climate warming. *Nature* **467**: 704-706.
- Drakare et al. (2006). The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters* **9**: 215-227.

Reading list (I am not expecting you to read all of these!)

- Fung et al. (2015). Impact of biodiversity loss on production in complex marine food webs mitigated by prey-release. *Nature Communications* **6**: 6657.
- Hawkins et al. (2007). A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology* **88**: 1877-1888.
- He & Hubbell (2011). Species-area relationships always overestimate extinction rates from habitat loss. *Nature* **473**: 368-371.
- Holling (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist* **91**: 293-320.
- Hudson et al. (2013). The relationship between body mass and field metabolic rate among individual birds and mammals. *Journal of Animal Ecology* **82**: 1009-1020.
- MacArthur & Wilson (1967). *The Theory of Island Biogeography*. Princeton University Press.
- Munch & Salinas (2009). Latitudinal variation in lifespan within species is explained by the metabolic theory of ecology. *PNAS* **106**: 13860-13864.
- Pereira & Daily (2006). Modeling biodiversity dynamics in countryside landscapes. *Ecology* **87**: 1877-1885.
- Pimm et al. (1995). The future of biodiversity. *Science* **269**: 347-350.

Reading list (I am not expecting you to read all of these!)

Preston (1962). The canonical distribution of commonness and rarity. *Ecology* **43**: 185-215.

Reichenbach et al. (2007). Mobility promotes and jeopardizes biodiversity in rock-paper-scissors game. *Nature* **448**: 1046-1049.

Saterberg et al. (2013). High frequency of functional extinctions in ecological networks. *Nature* **499**: 468-470.

Terborgh (1974). Preservation of natural diversity: the problem of extinction prone species. *BioScience* **24**: 715-722.

Tilman et al. (1994). Habitat destruction and the extinction debt. *Nature* **371**: 65-66.

Wang & Loreau (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters* **19**: 510-518.

Wearn et al. (2012). Extinction debt and windows of conservation opportunity in the Brazilian Amazon. *Science* **337**: 228-232.

West et al. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**: 122-126.

White & Seymour (2005). Allometric scaling of mammalian metabolism. *Journal of Experimental Biology* **208**: 1611-1619.

Lecture Outline – Part 2: more complex systems models

Simpler systems-level models of ecosystems

Vegetation/plant-community models

Ocean ecosystem models

General ecosystem models

Relatively simple system-level models: coral reefs



Complex, interconnected
dynamics

Not ethical to experiment with the
effects of environmental change

Simple system-level model of coral reef dynamics

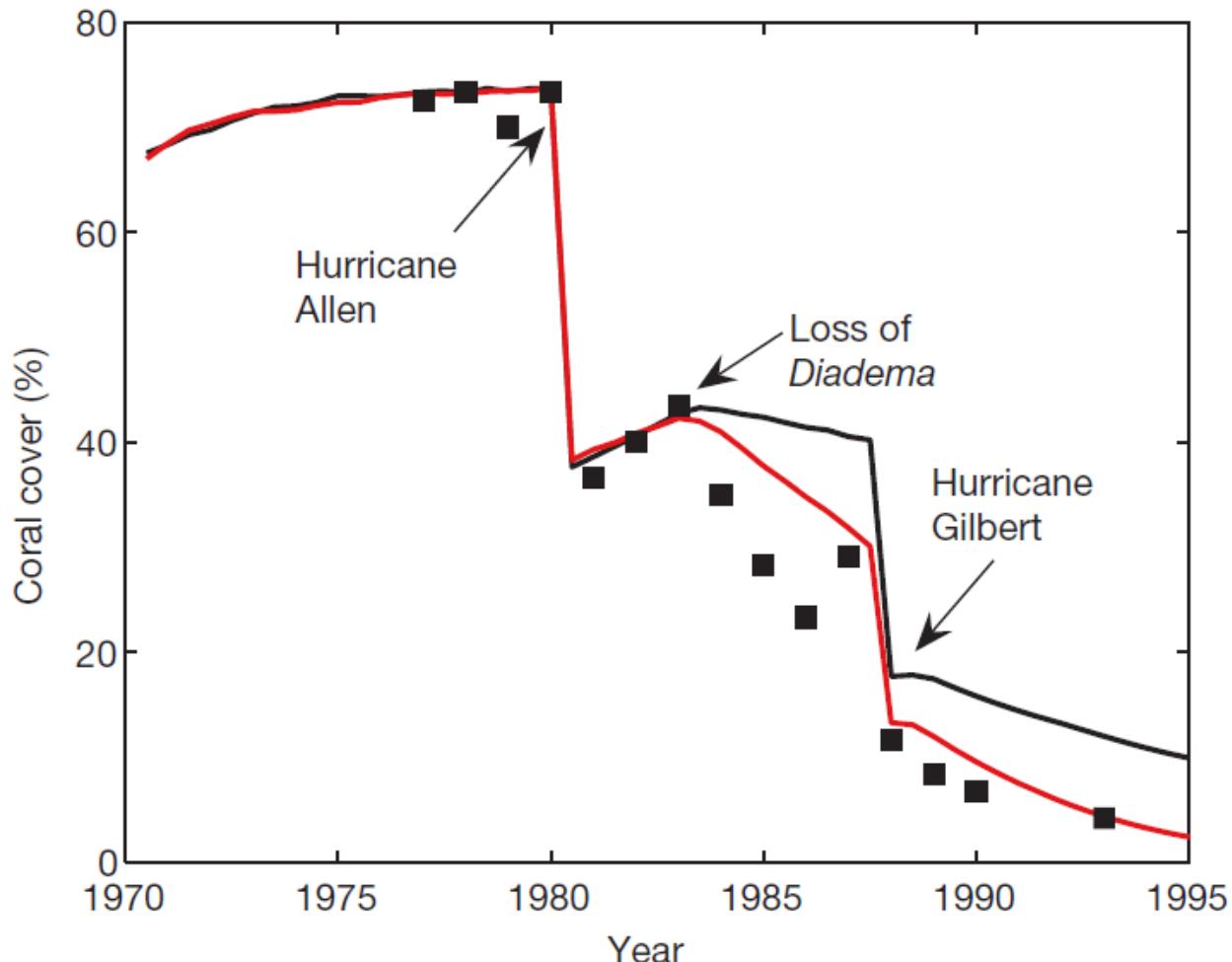
Model of cover of coral and algae

Processes (coral): recruitment, growth, reproduction, and competition (with corals and algae)

Processes (algae): colonization and growth

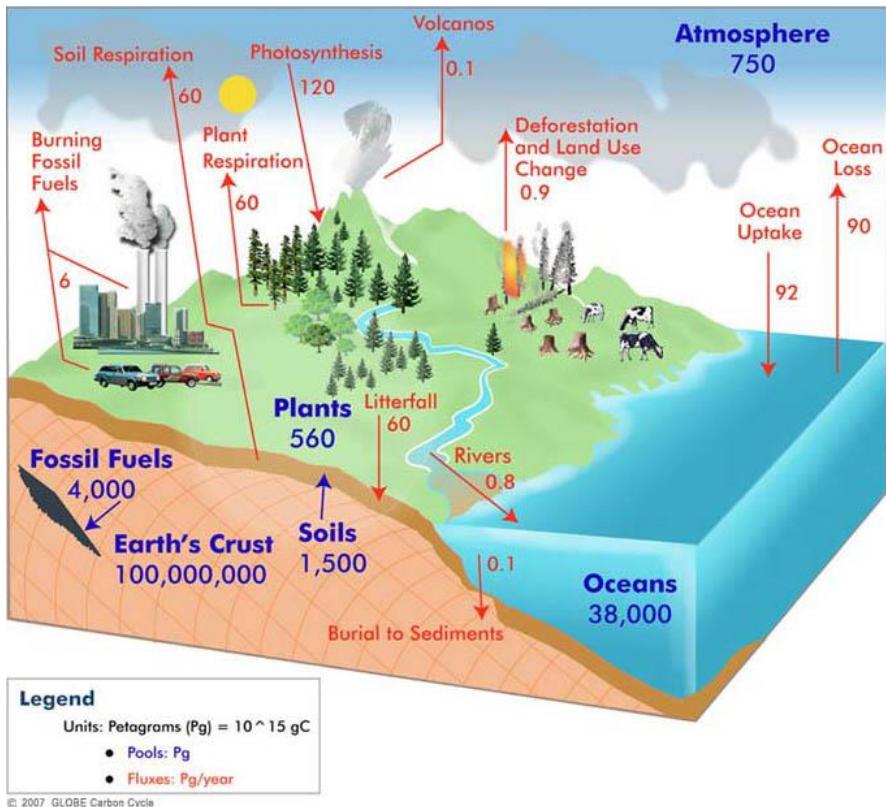
Processes (other): grazing by fish, fishing by humans

Model matches observed change in coral cover well

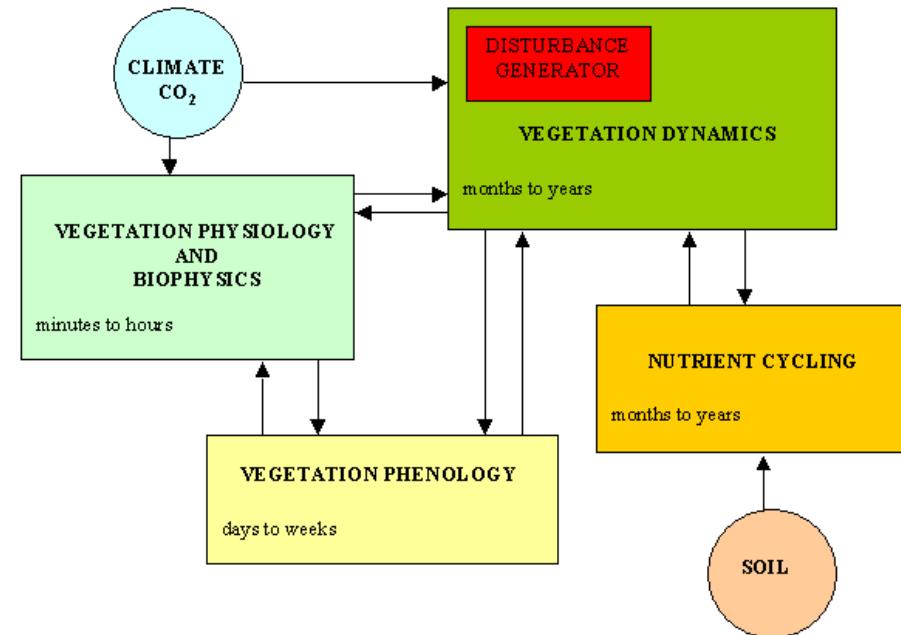


The importance of understanding vegetation dynamics

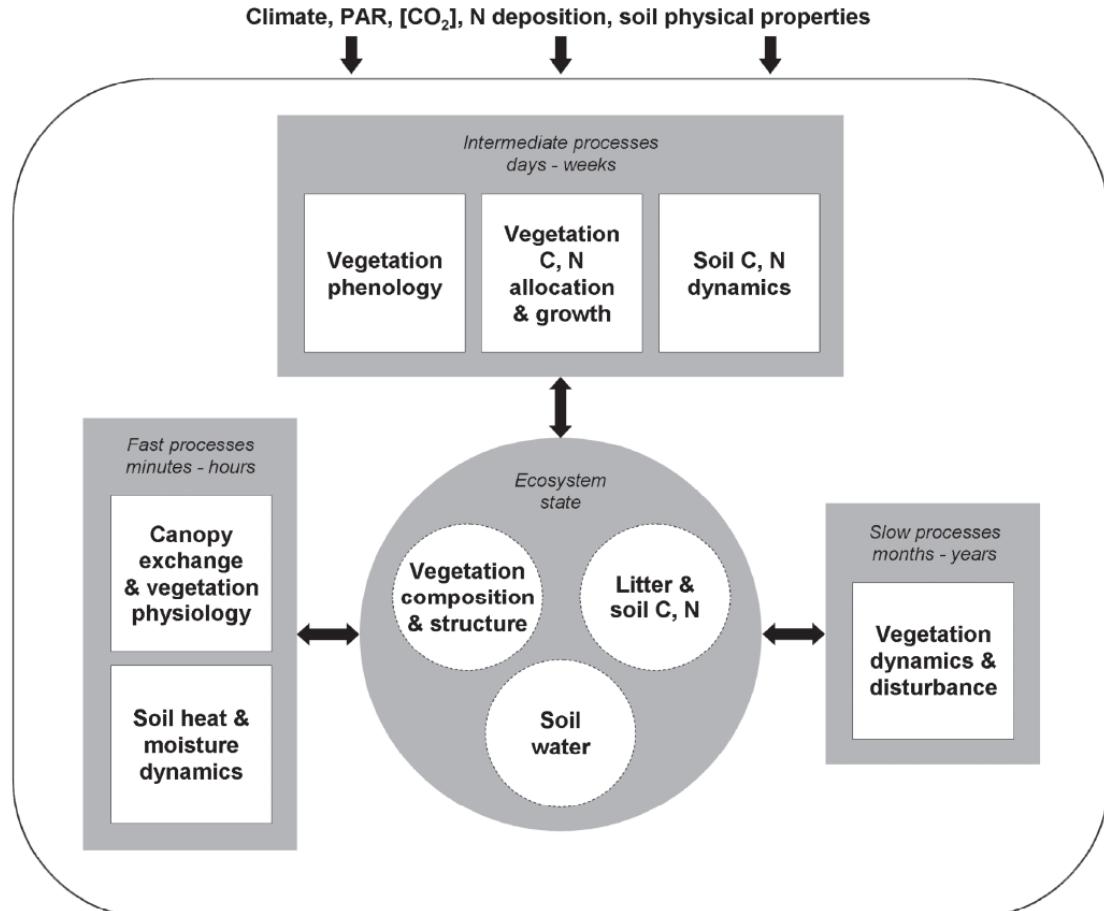
Vegetation plays an important role in the global carbon cycle



Dynamic Global Vegetation Models (DGVMs) are useful to understand and predict changes



Dynamic Global Vegetation Models

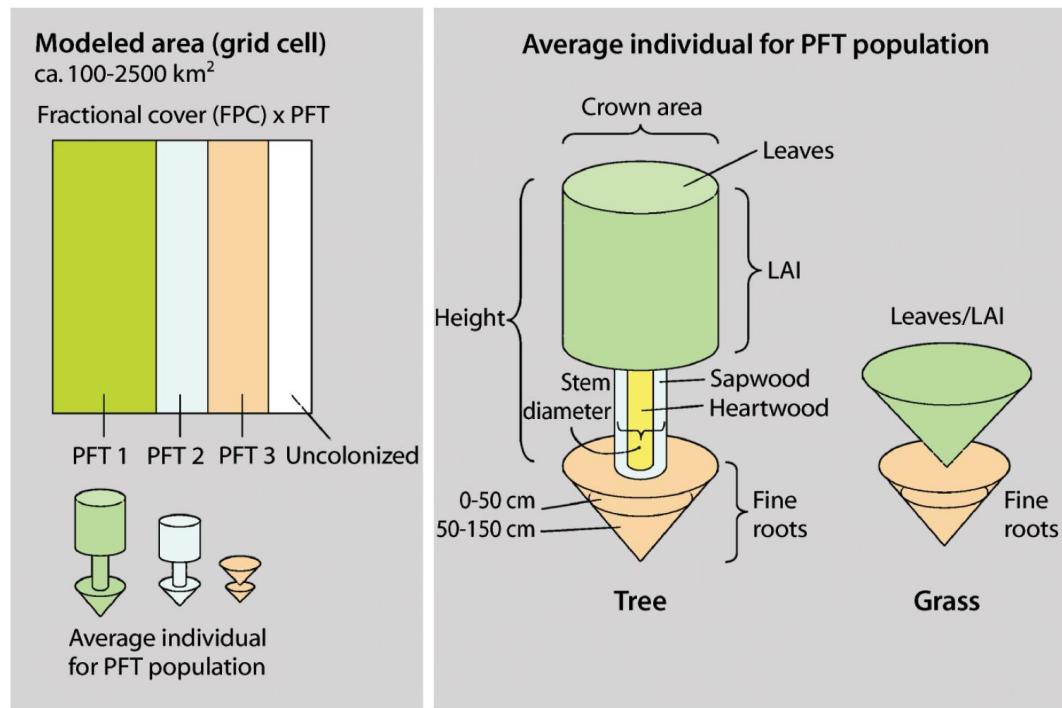


Four main process types: plant geography, plant physiology and biochemistry, vegetation dynamics, and biophysics

Increasingly capturing human disturbances

Generally capture only fractional cover of Plant Functional Types (PFTs), but sometimes also age/size structure

Dynamic Global Vegetation Models



All plants classified into small number (10+) functional types, characterized in terms of the average individual

PFT

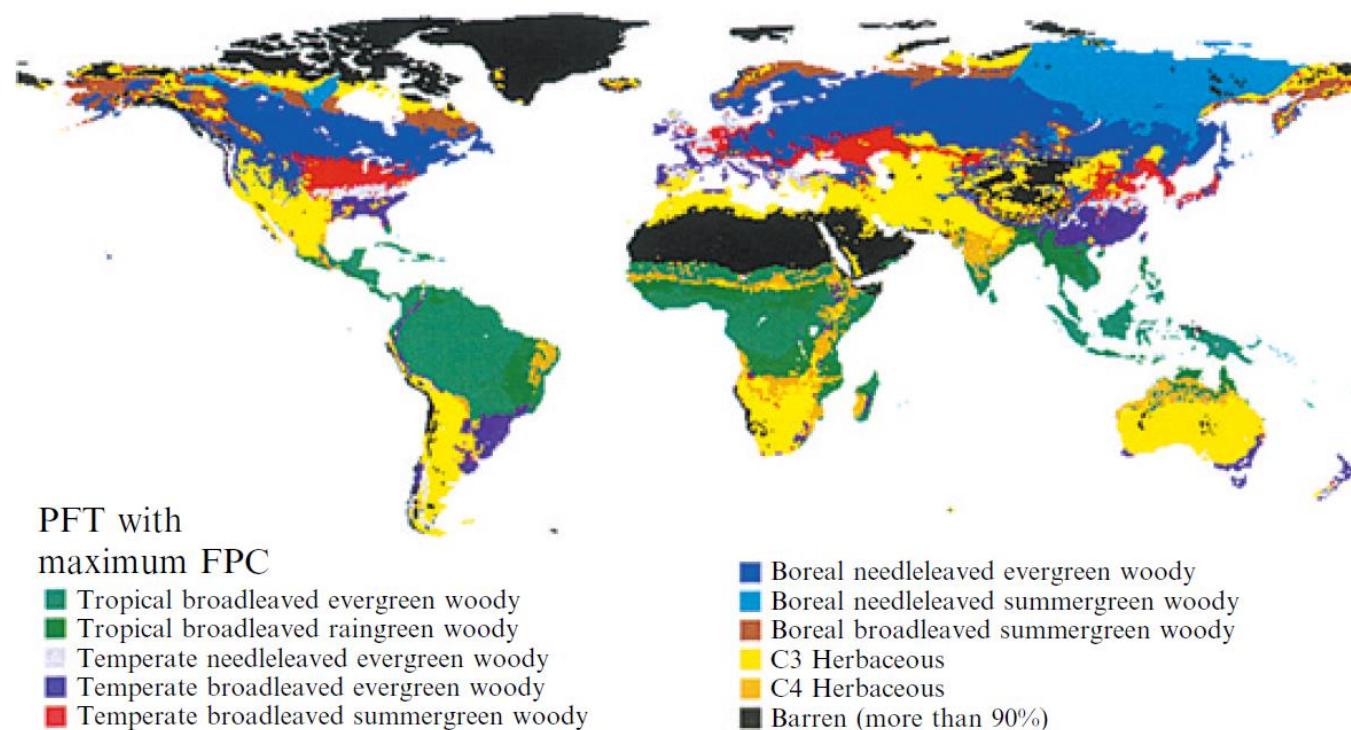
Tropical broad-leaved evergreen (TrBE)
Tropical broad-leaved raingreen (TrBR)
Temperate needle-leaved evergreen (TeNE)
Temperate broad-leaved evergreen (TeBE)
Temperate broad-leaved summergreen (TeBS)
Boreal needle-leaved evergreen (BoNE)
Boreal needle-leaved summergreen (BoNS)
Boreal broad-leaved summergreen (BoBS)
Temperate herbaceous (TeH)
Tropical herbaceous (TrH)

Prentice et al. (2007). In *Terrestrial Ecosystem in a Changing World*.

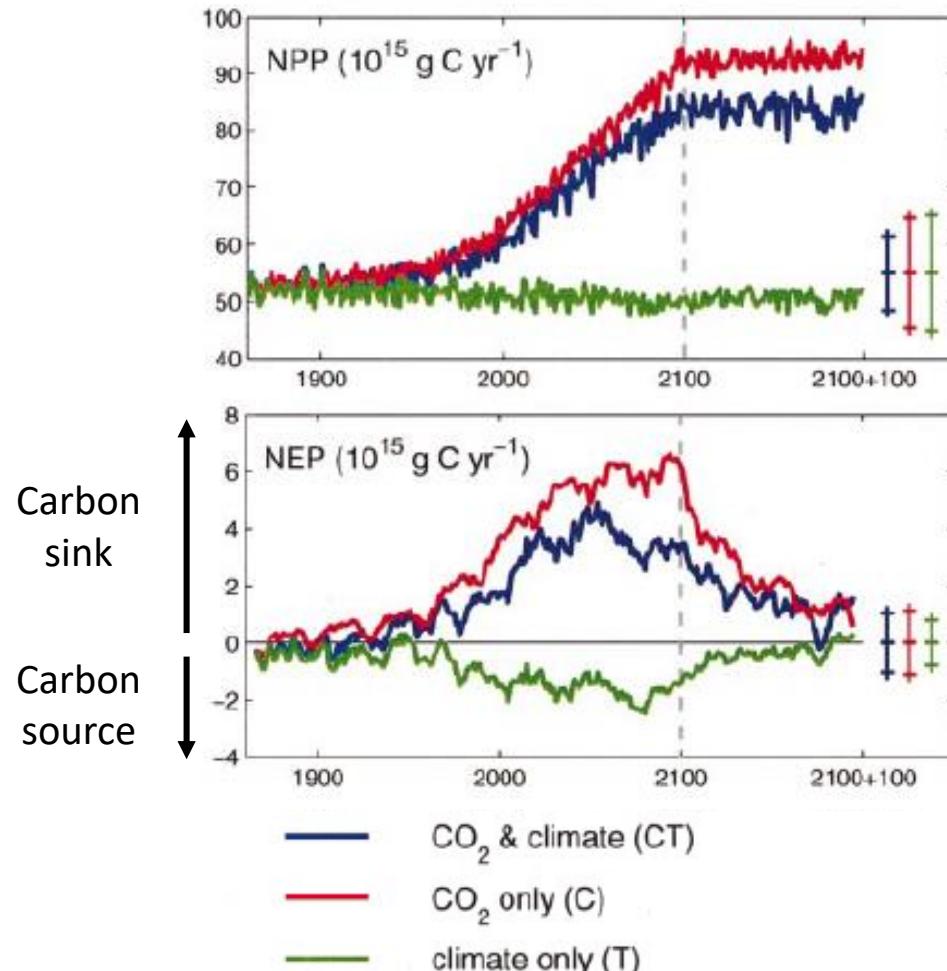
Sitch et al. (2003). *Global Change Biology* 9: 161-185.

Coarse coverage of PFTs is captured well

Lund-Potsdam-Jena (LPJ) DGVM estimation of dominant plant functional types:



Applications of Dynamic Global Vegetation Models: Climate change



6 DGVMs

Predicted under change in climate, CO₂ concentration, or both

Increased CO₂ concentration predicted to increase carbon sink potential

Offset by climate change: effect of CO₂ asymptotes, but effect of temperature on respiration continues

Plant communities are composed of individuals with large variation



Individual-based vegetation models: aDGVM

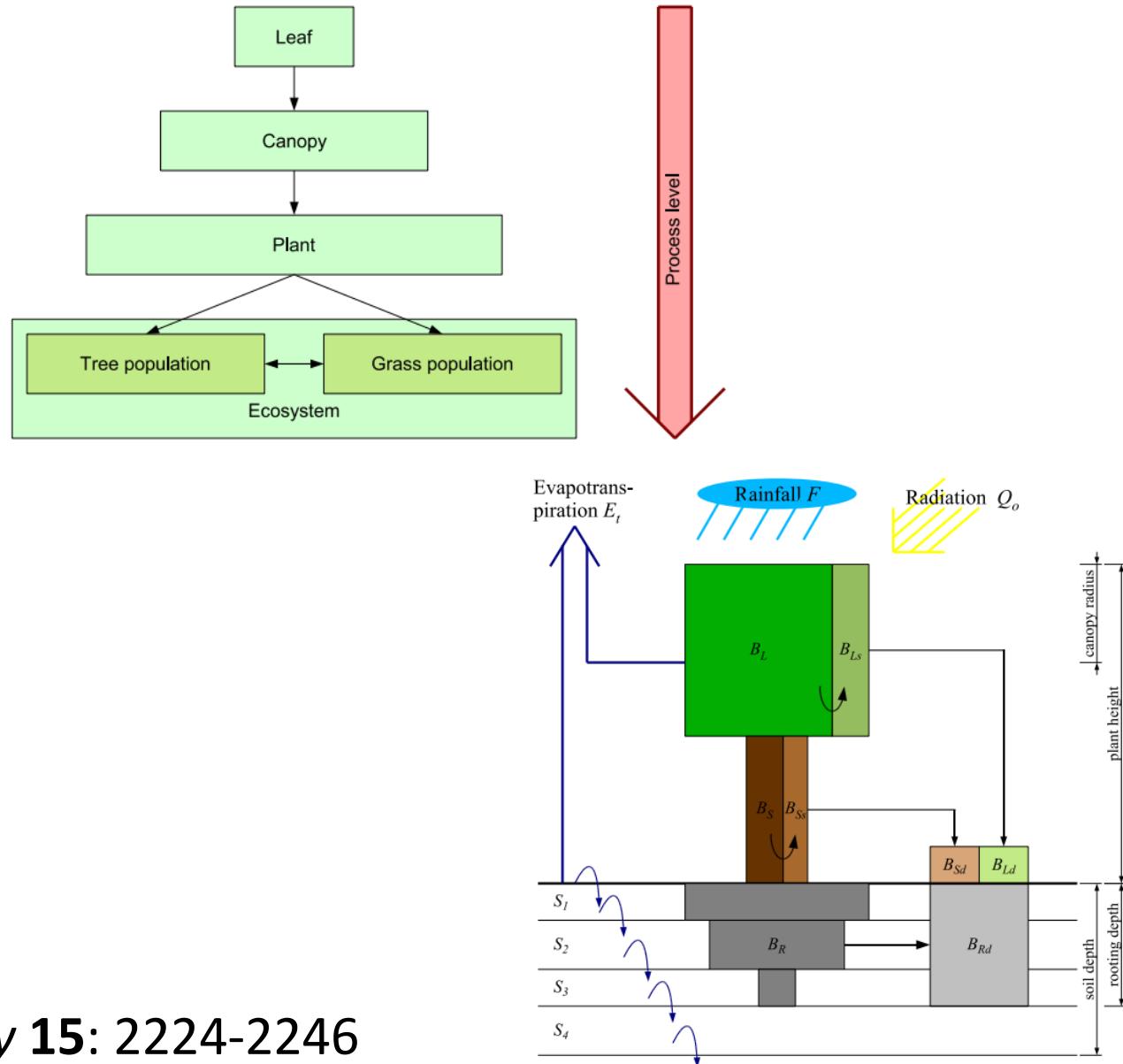
Adaptive Dynamic Global Vegetation
Model (aDGVM)

Leaf photosynthesis →

Canopy photosynthesis, respiration and
conductance →

Plant growth, allometry, competition,
reproduction and mortality

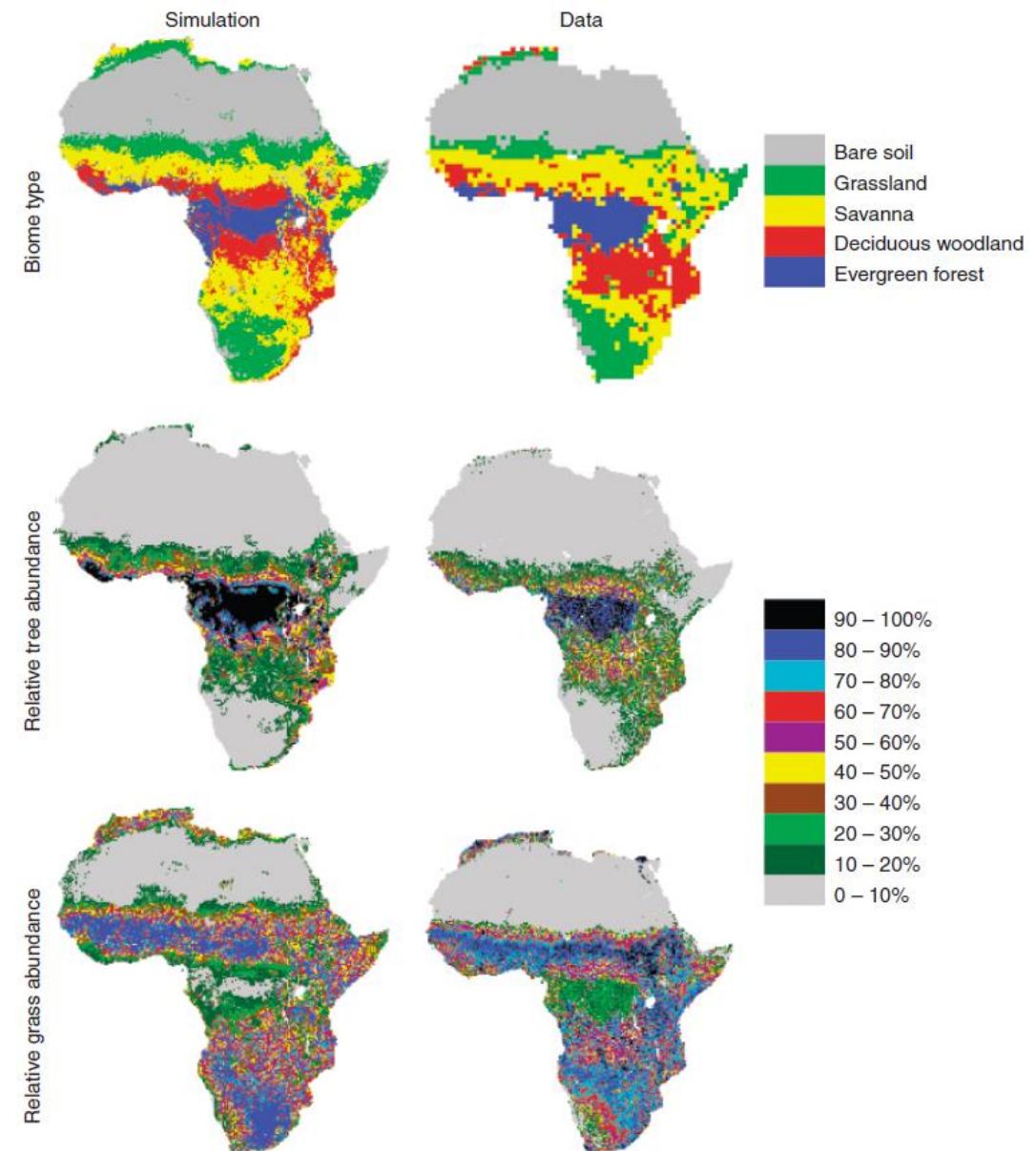
Representative 1-ha stands, scaled up to
 $\frac{1}{3}^\circ$



Individual-based vegetation models: aDGVM

Fits observed data fairly well

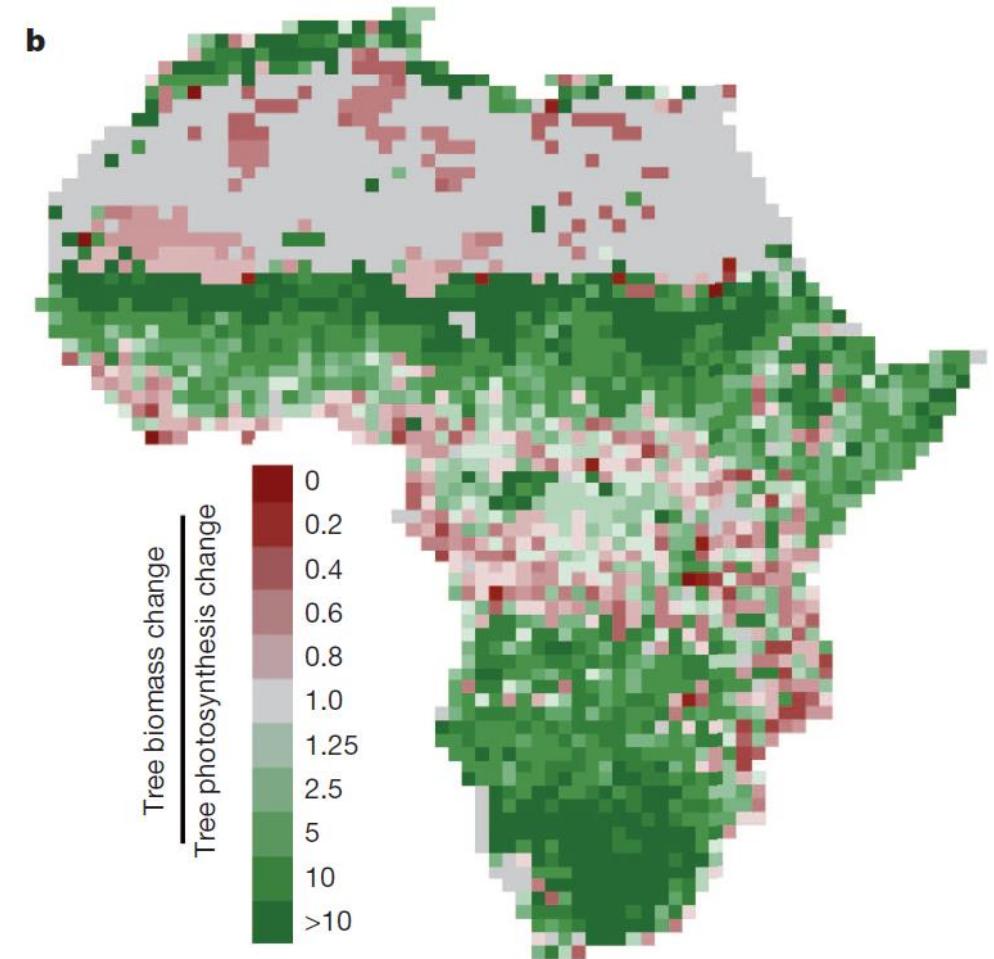
Fit generally better than models
based on coverage of plant
functional types



Applications of individual-based vegetation models: climate change

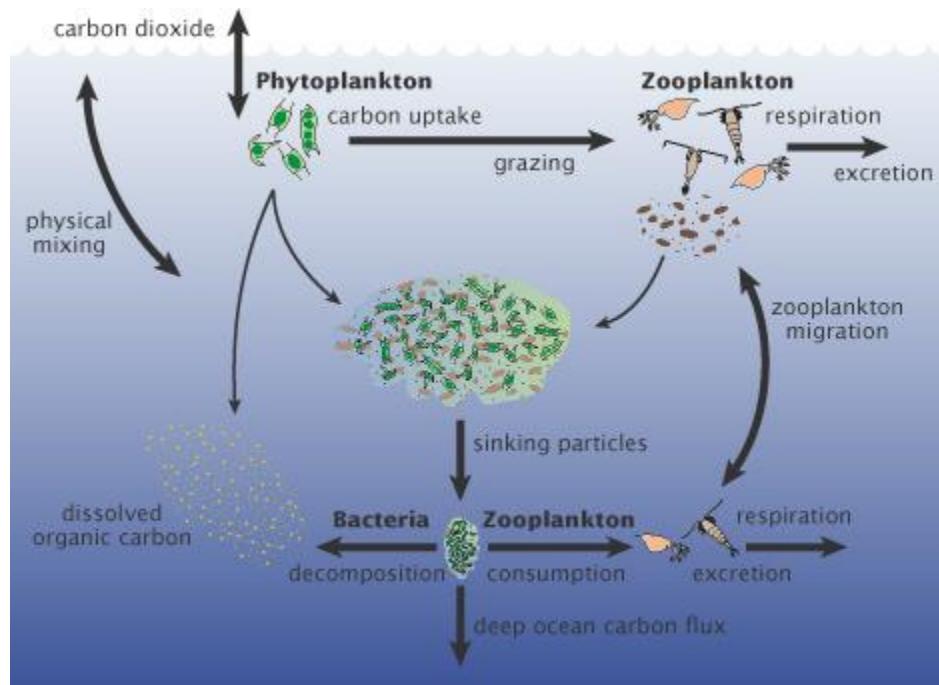
Predicted vegetation shifts from desert to grassland, grassland to savanna/woodland, and savanna to forest

Probability of a given state depended on historical conditions (hysteresis)



Ocean ecosystem models: more developed than on land

Understanding contribution of primary producers to the carbon cycle and climate



Managing fisheries



NPZ(D) Models: Nutrient-Phytoplankton-Zooplankton(-Detritus)

(Relatively) simple formulation

Captures photosynthesis and phytoplankton growth, grazing of phytoplankton by zooplankton, mortality and vertical movement

$$\frac{dN}{dt} = \omega P + gZ + \frac{(1-f)cP^2Z}{K + P^2} - \frac{\alpha(L_d, M_d, P)PN}{j + N} - (N - N_d)\zeta_N(M_d)/M_d,$$

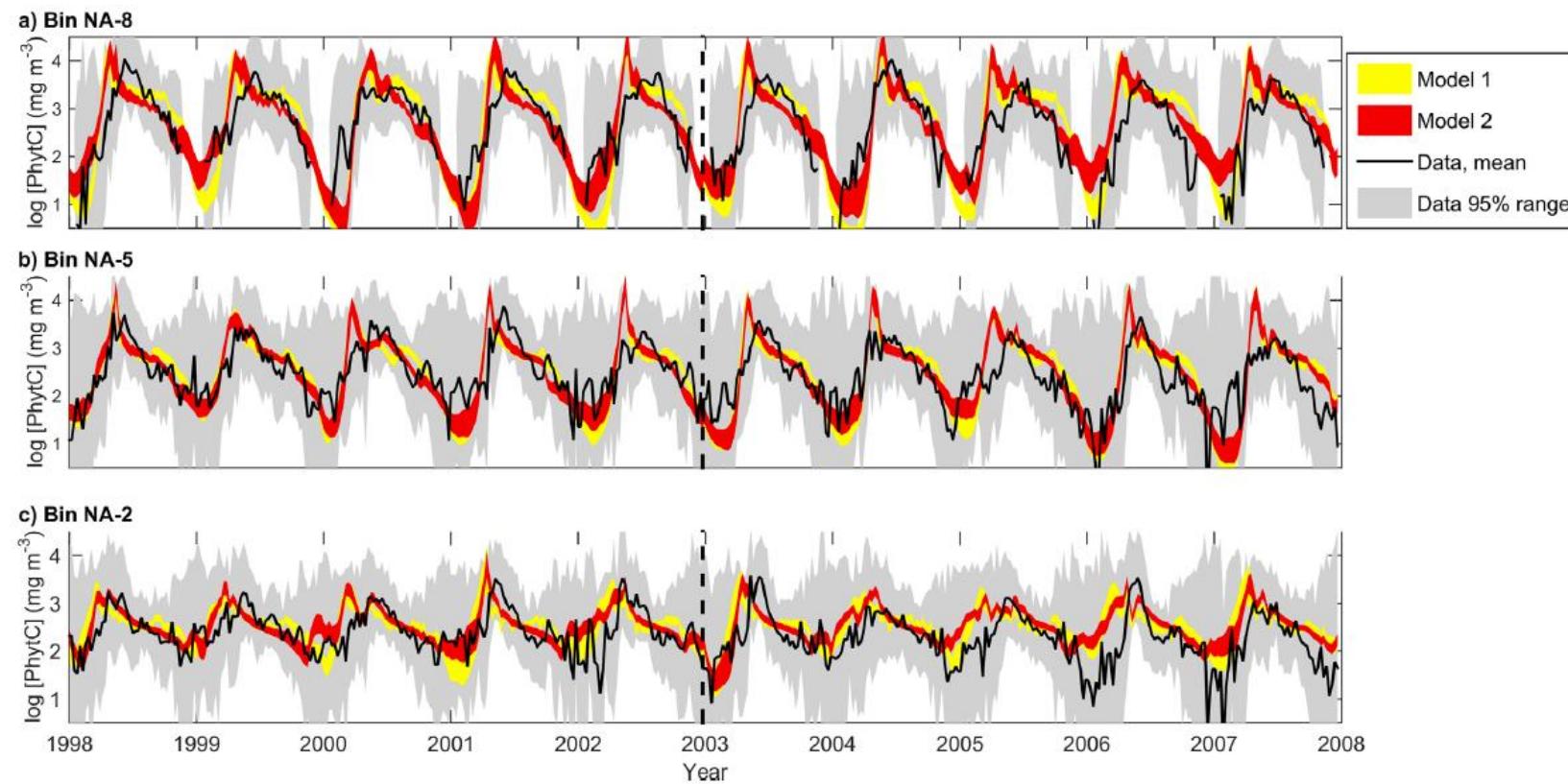
$$\frac{dP}{dt} = \frac{\alpha(L_d, M_d, P)PN}{j + N} - \omega P - \frac{cP^2Z}{K + P^2} - P\zeta_P(M_d)/M_d,$$

$$\frac{dZ}{dt} = \frac{fcP^2Z}{K + P^2} - gZ - Z\zeta_Z(M_d)/M_d,$$

Textual Definition	Symbol
Nitrate uptake half saturation	j
Phytoplankton background mortality rate	ω
Grazing half saturation	K
Maximum grazing rate	c
Grazing efficiency	f
Zooplankton background mortality rate	g
Maximum photosynthetic rate (supporting information Text S1)	Q
Lowlight photosynthetic slope (supporting information Text S1)	s
Light attenuation by water (supporting information Text S1)	k
Light attenuation by phytoplankton (supporting information Text S1)	l
Nitrate diffusion rate	m_N
Phytoplankton diffusion rate out of mixed layer	m_P
Nitrate conc. below the mixed layer	N_d

Can capture well observed phytoplankton concentrations

North Atlantic phytoplankton bloom



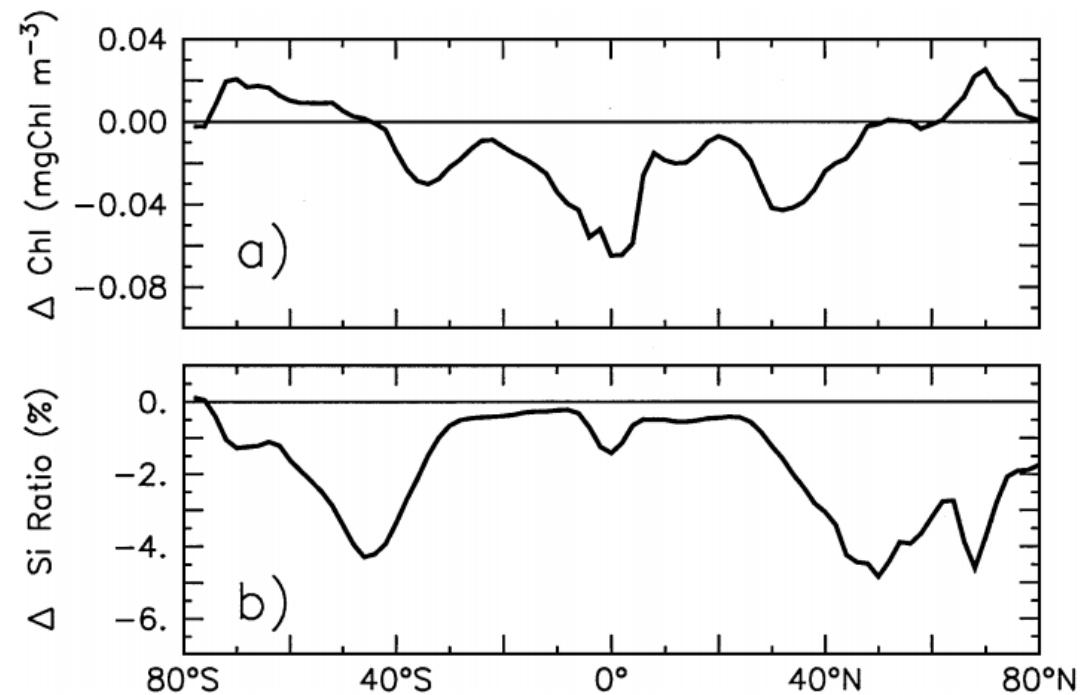
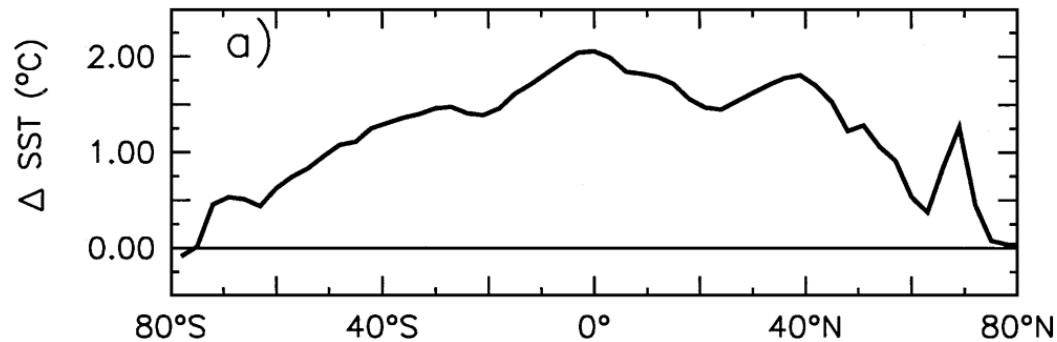
Application of NPZ models: climate change

Predicted effects of doubling of pre-industrial CO₂

Increase in Sea Surface Temperature at most latitudes

Overall decline (9%) in primary productivity, but increases at some latitudes

Decrease in representation of siliceous phytoplankton



Bopp et al. (2003). *Tellus B* 55: 11-22.

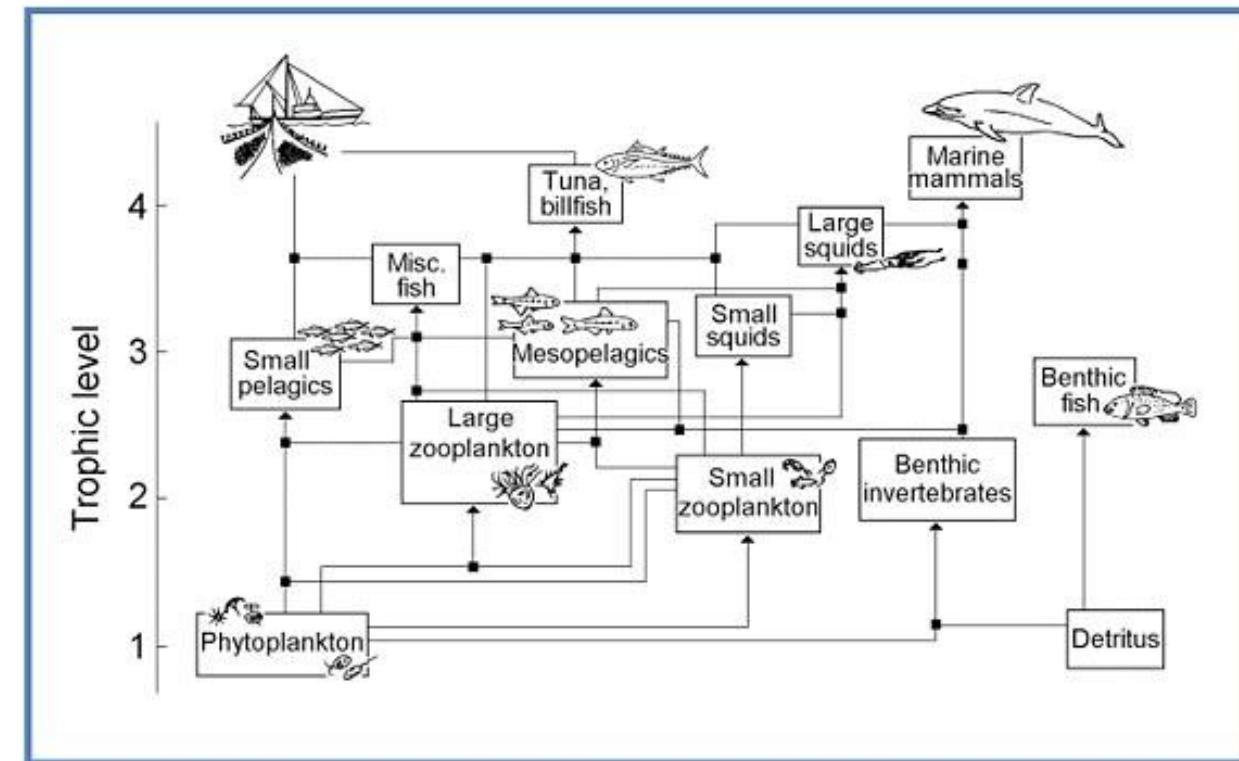
Summarized in Richardson (2008). *ICES J Marine Science* 65: 279-295.

Ecopath with Ecosim

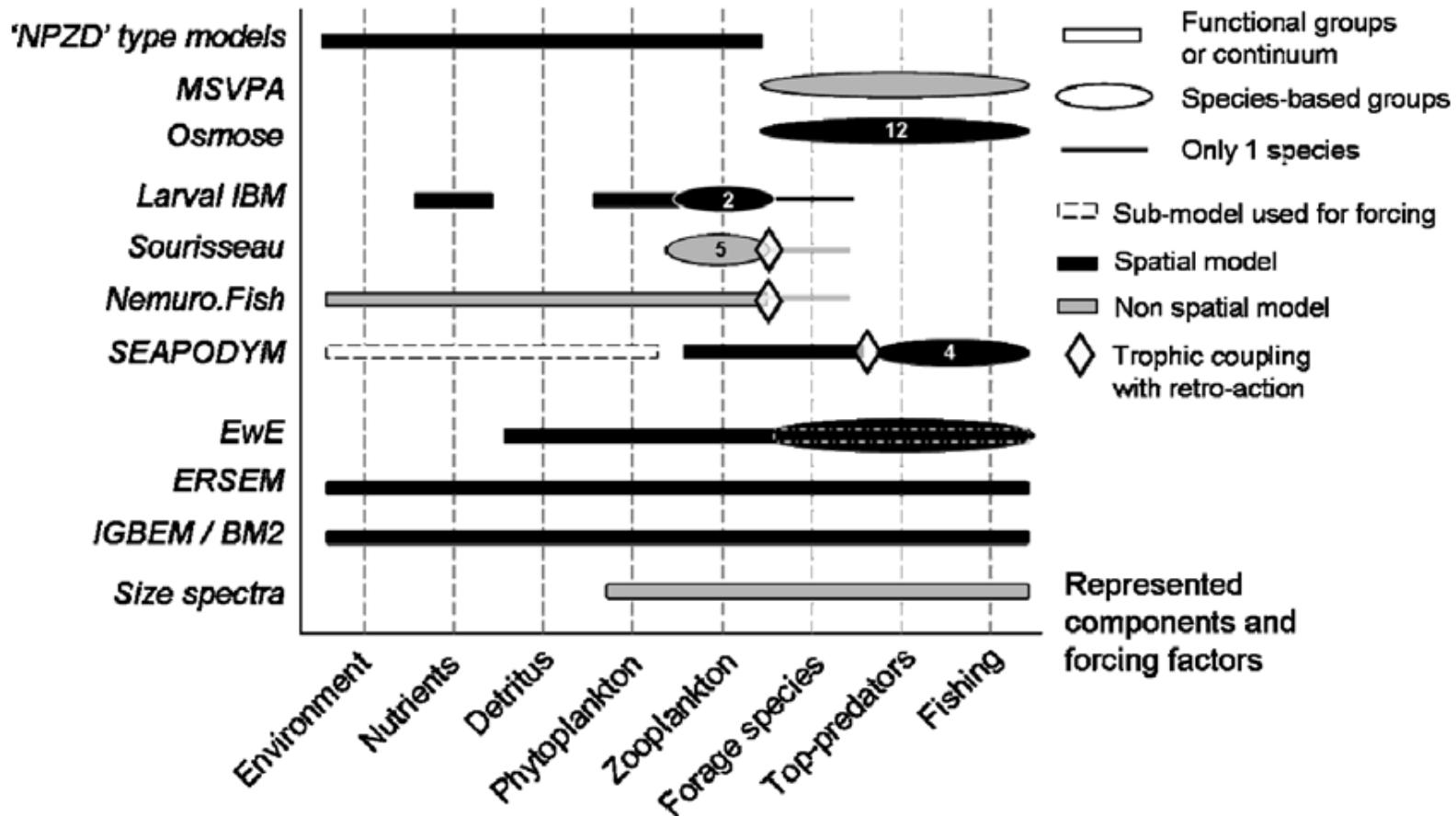
Ecopath: biomass stocks and trophic flows

Ecosim: coupled differential equations to simulate dynamics

Ecospace: spatial representation, including dispersal/migration



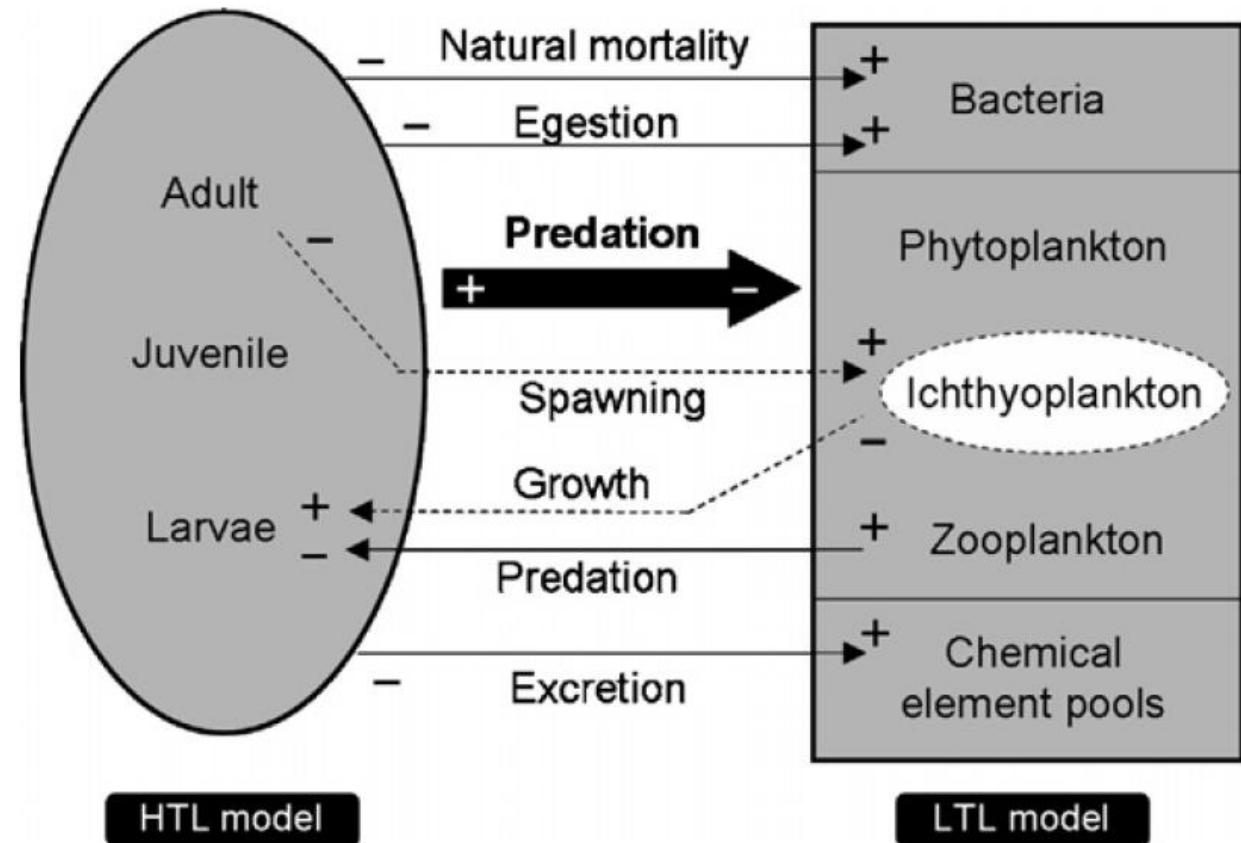
Many marine models only capture parts of the whole system



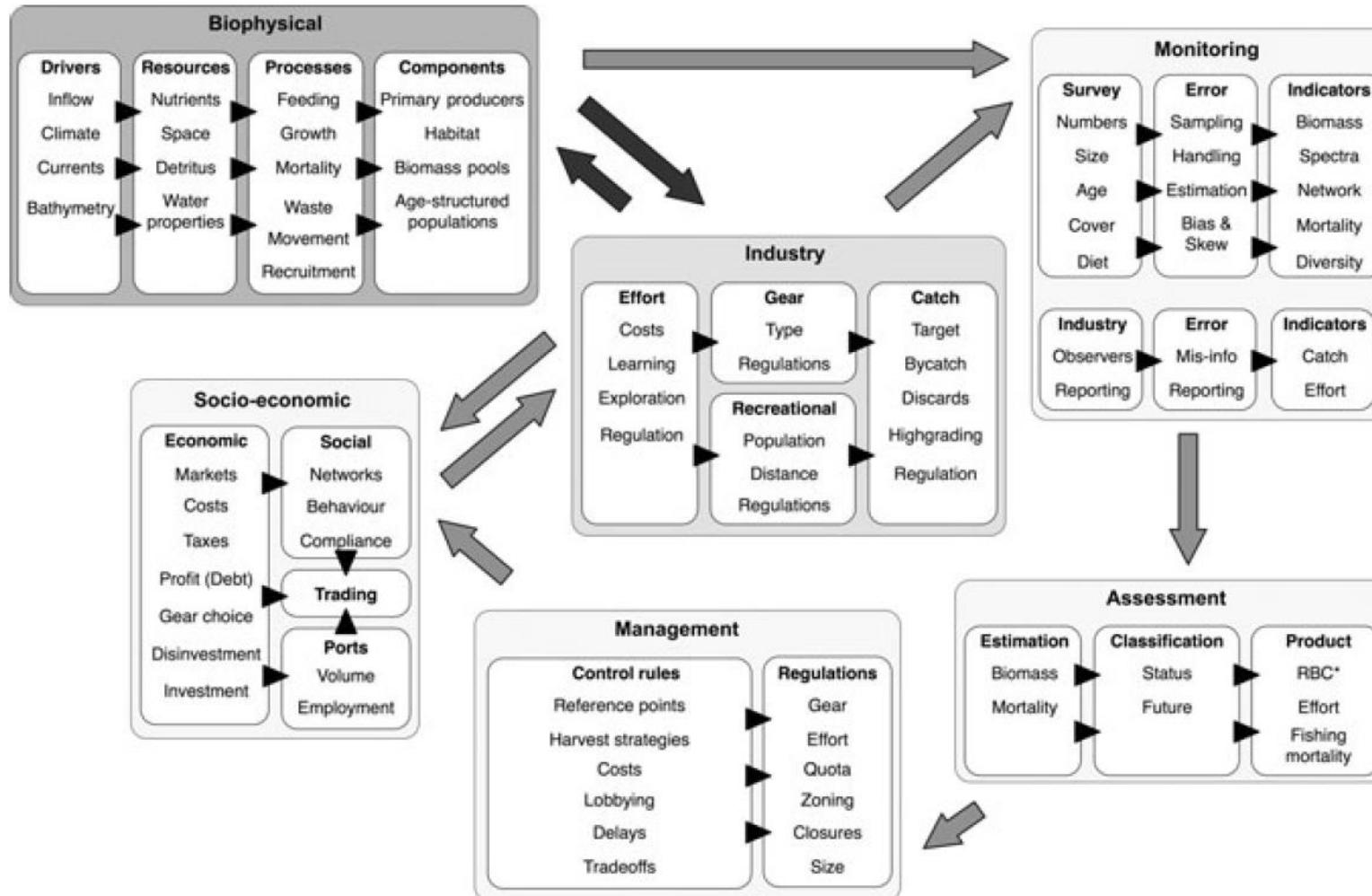
Many marine models only capture parts of the whole system

There exist some coupled models of low and high trophic levels

There is an increasing trend toward developing full 'end-to-end' ecosystem models

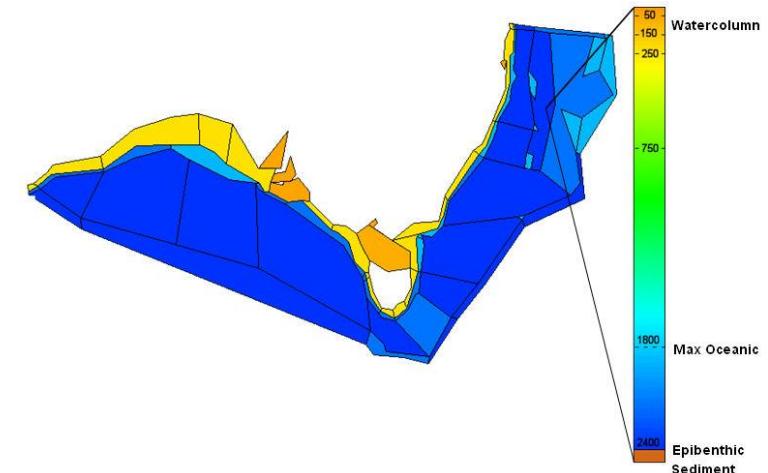


Atlantis: an end-to-end ecosystem model

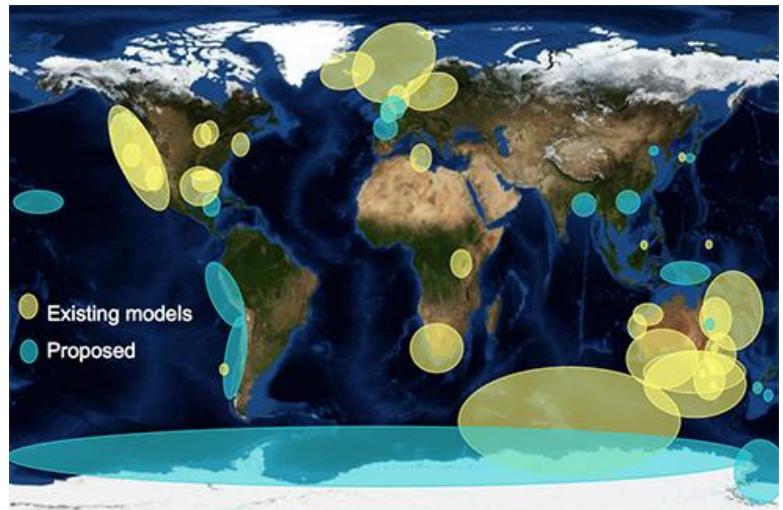


Atlantis: an end-to-end ecosystem model

Biophysical model spatially resolved into 3D, unequal-sized polygons



Ecological processes: consumption, production, movement and migration, predation, recruitment, habitat dependency and mortality



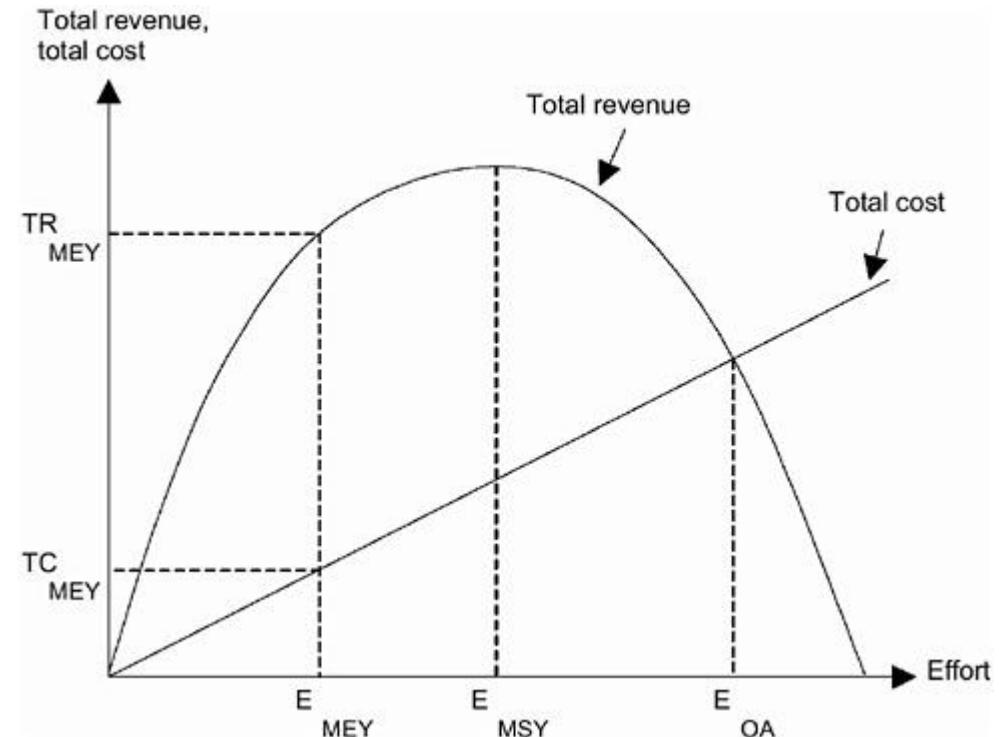
Human effects simulated as agents in the model

Applications of marine ecosystem models: fisheries management

Maximum sustainable yield

Has been dismissed several times over the years

But still has resonance



From Townsend & Wilson (1987). An economic view of the tragedy of the commons. In *The Question of the Commons: the Culture and Ecology of Communal Resources*

Applications of marine ecosystem models: fisheries management

Fisheries management is often based on single-species assessments (e.g. using population models)

Complex interactions might effect potential catches

Ecosystem models can be used to assess multi-species maximum sustainable yields

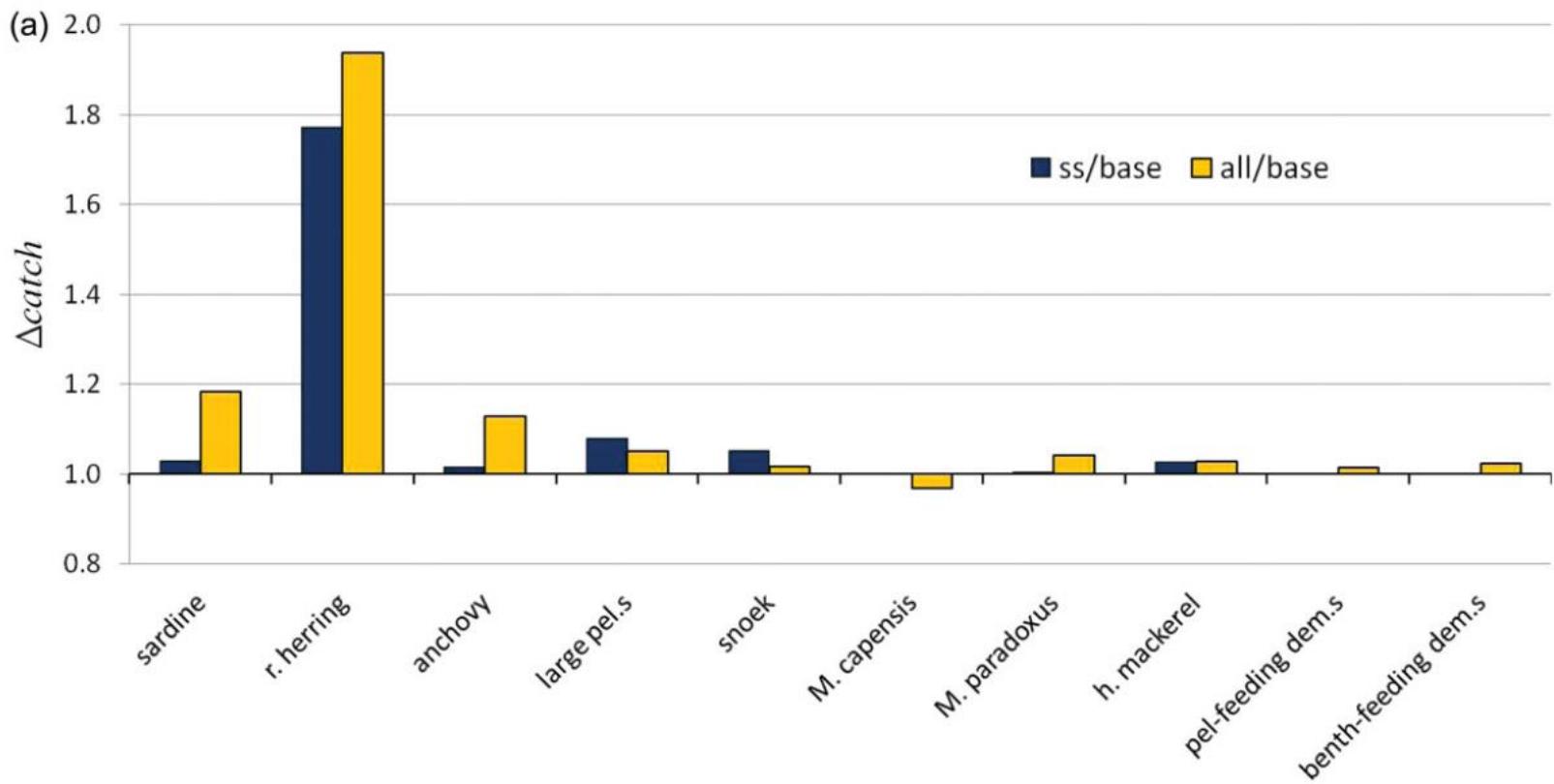


Applications of marine ecosystem models: fisheries management

Fisheries 9% more productive using single-species assessment

16% more productive with multi-species assessment

But benefits of multi-species assessments varied among species



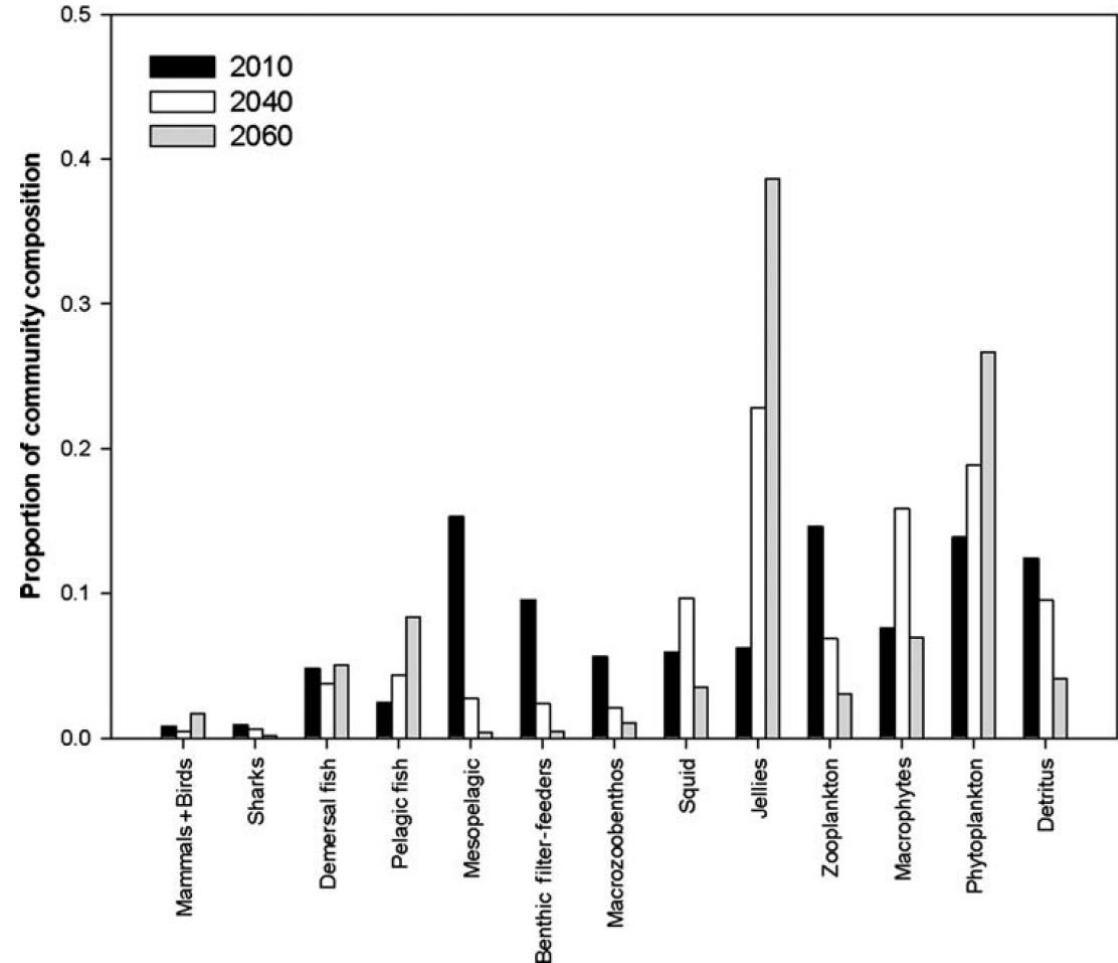
Applications of marine ecosystem models: climate change

3 modelling frameworks: Atlantis, Ecopath with Ecosim, InVitro

Models for 7 ecosystems

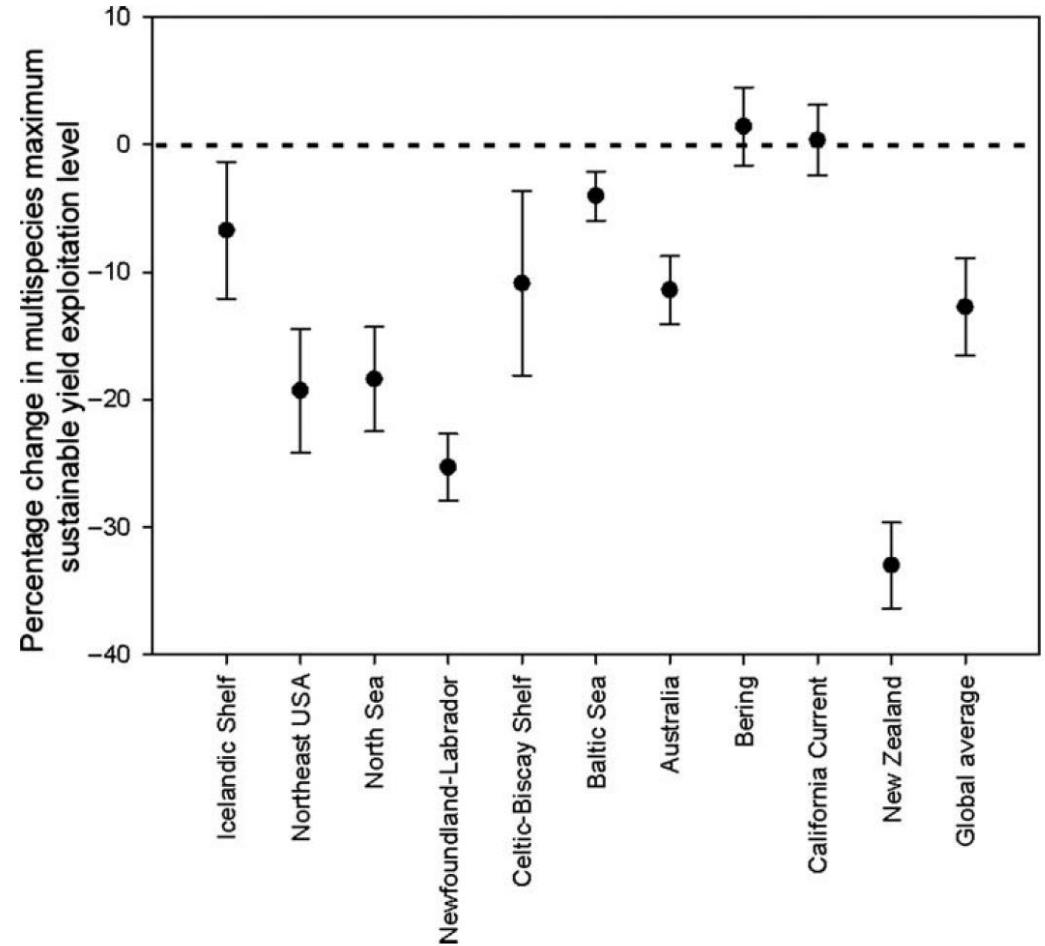
Climate and socio-economic projections under the SRES A2 scenario

Some functional groups increased and some decreased → big changes in community composition



Applications of marine ecosystem models: climate change

Multi-species maximum sustainable yield declined in most regions



Can we model everything?

All realms: marine, terrestrial, freshwater

Common set of ecological processes

All major ecosystem components

COMMENT

COMMUNICATION Sally Rockey reflects on two years of blogging at the NIH p.298

ECOLOGY Zoological travelogue tracks rare species worldwide p.300

WOMEN Calls to root out sexism in journals, conferences and experiments p.305

OBITUARY Rita Levi-Montalcini, nerve growth factor pioneer and science advocate p.306

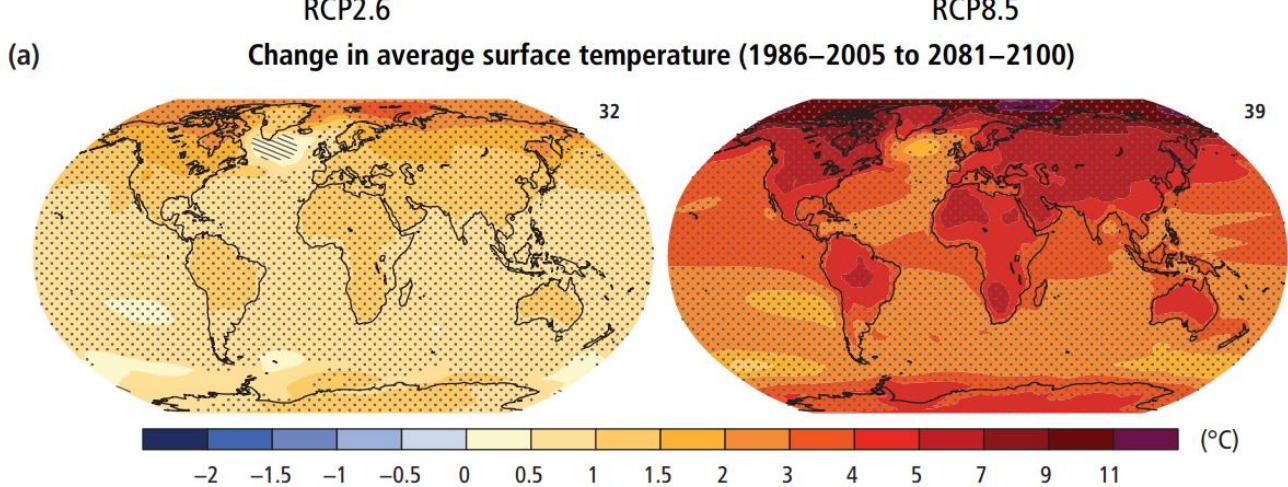
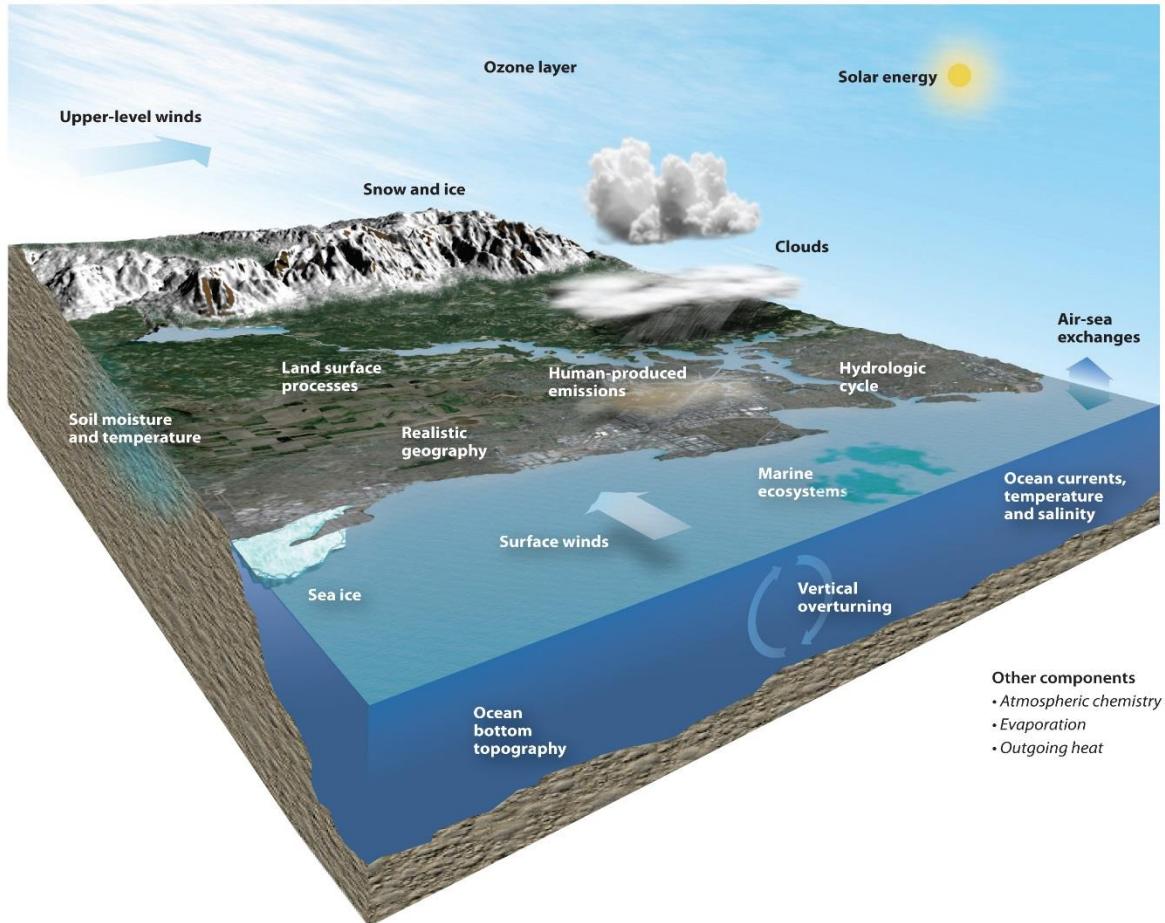


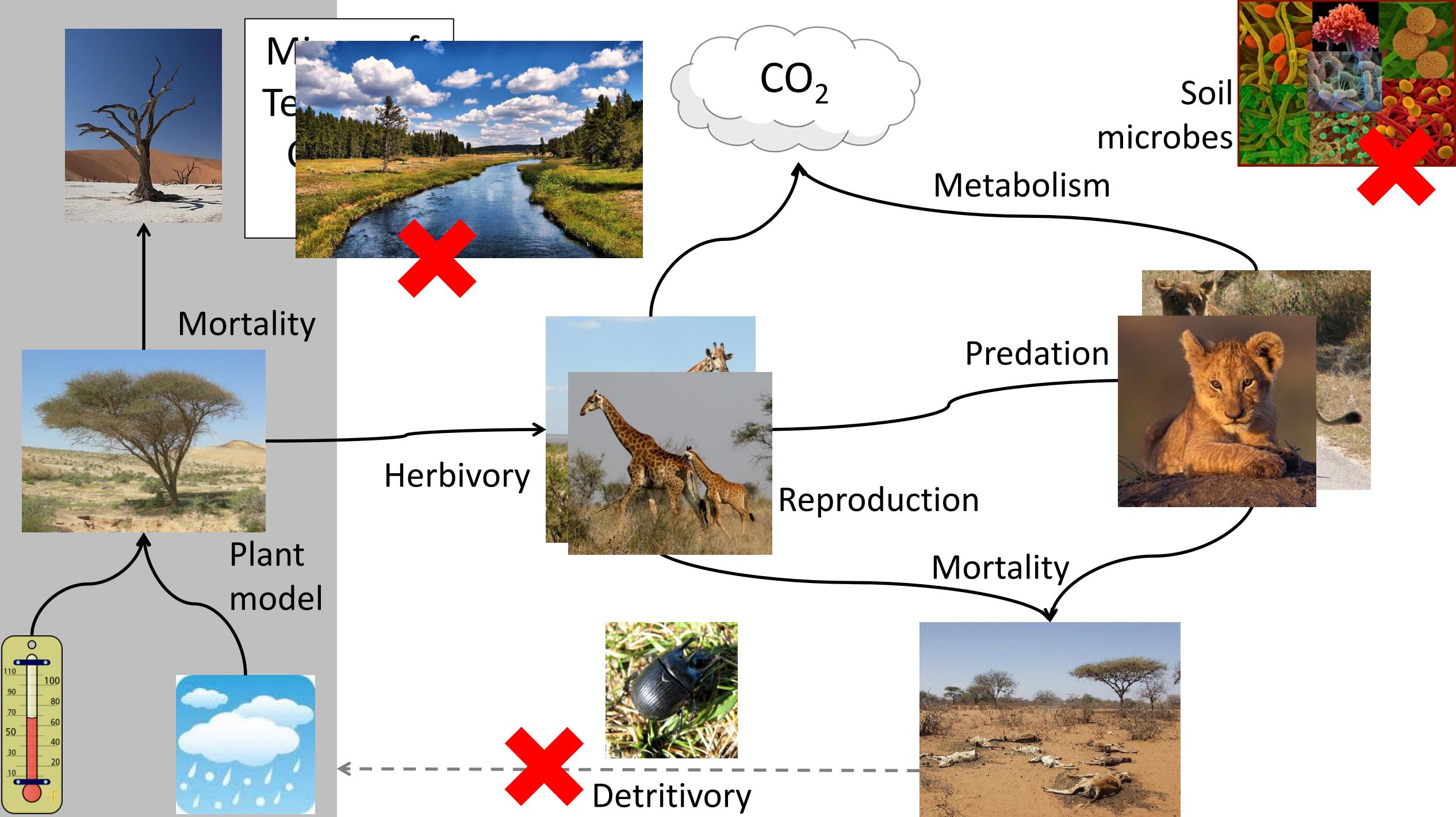
A hyena surveys a flock of flamingos in South Africa.

YI LIU/GETTY STOCK/COHES

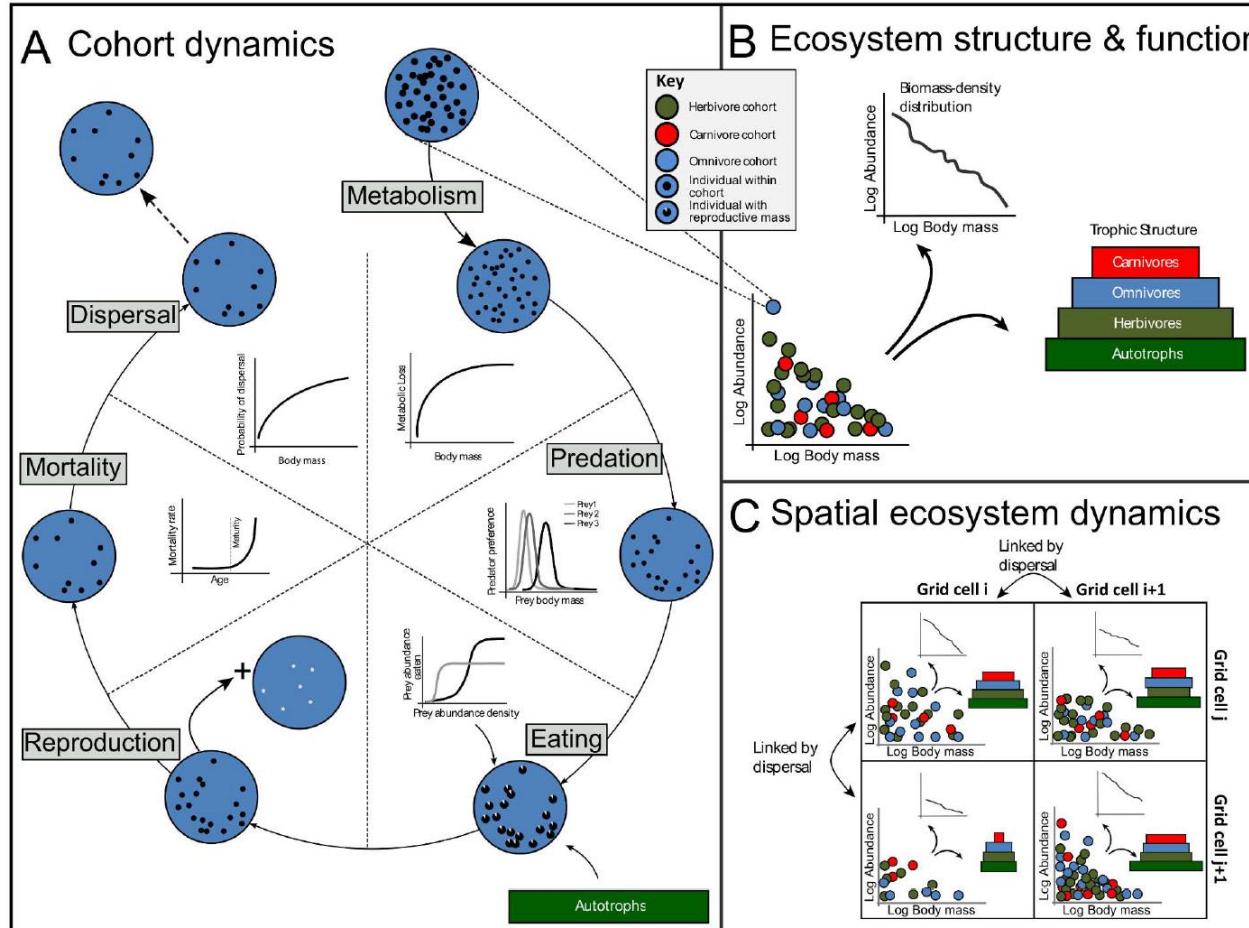
Time to model all life on Earth

Similar conceptually to global climate models





Ecological processes operate on individual cohorts; predictions are made about emergent ecosystem structure



Represents functional groups not species



Herbivore

Ectotherm

Semelparous

Mobile

Terrestrial

Carnivore

Endotherm

Iteroparous

Mobile

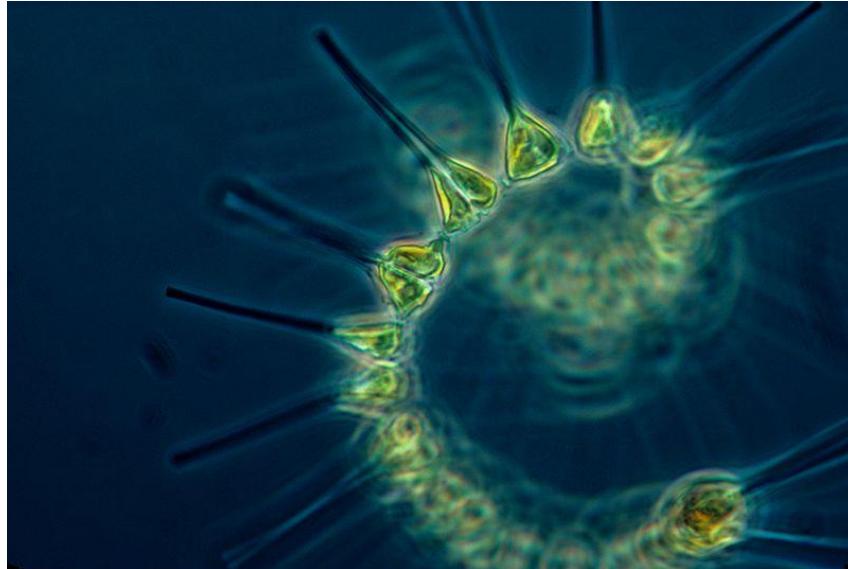
Terrestrial



Omnivore
Endotherm
Iteroparous
Mobile
Marine



An individual-based model would be computationally intractable



Millions per litre
(<http://www.cefas.defra.gov.uk>)



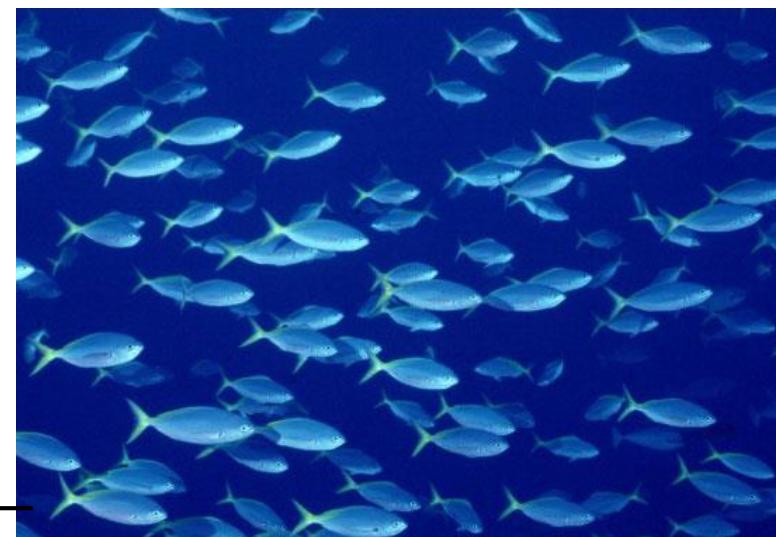
Up to c. 2500 per km²
(Goodman, 1998, *Zoology*)

Instead individuals are grouped into 'cohorts'



ID:	4520
Num. individuals:	1221
Individual mass:	450 kg
Age:	11.3 years
Functional group:	3

ID:	10,802
Num. individuals:	426
Individual mass:	5.6 kg
Age:	3.4 years
Functional group:	19

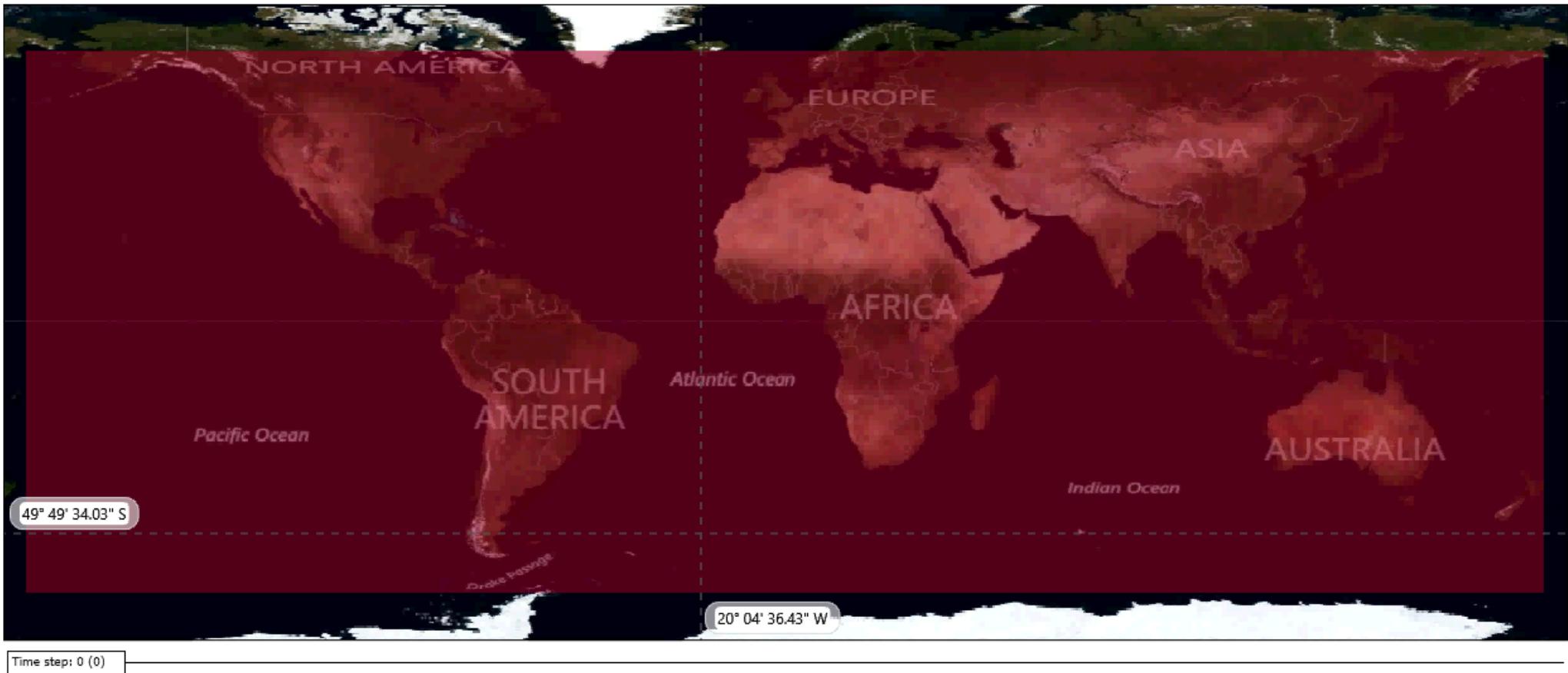


An individual-based model would be computationally intractable

Cohort-based model for a single ecosystem: ≈ 10 hours

Individual-based model: ≈ 47 billion years

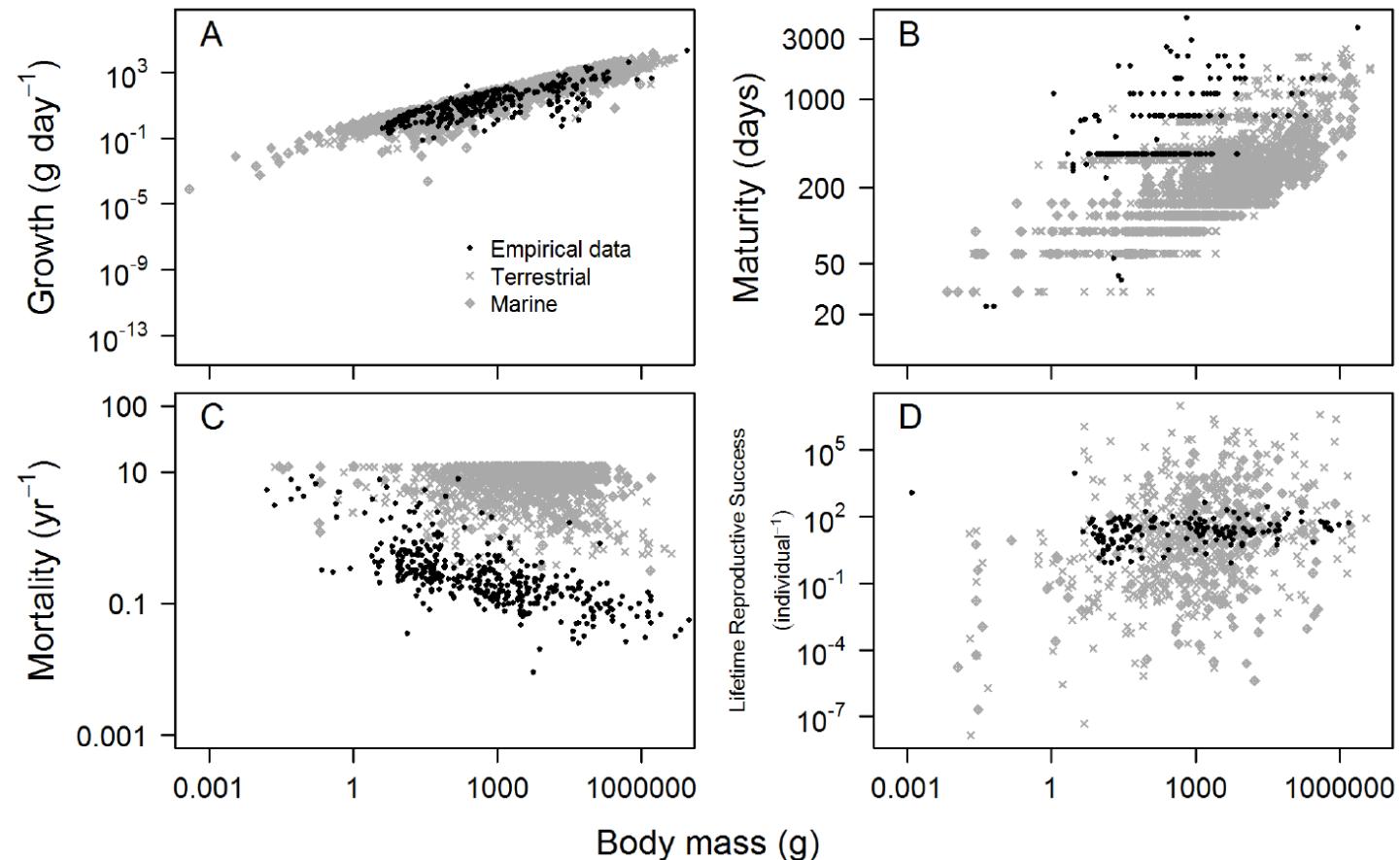
Emergent biomass patterns



Correspondence with empirical data: individual-level process rates

Empirical data on lifetime reproductive success are species averages, so much less variable than modelled cohorts

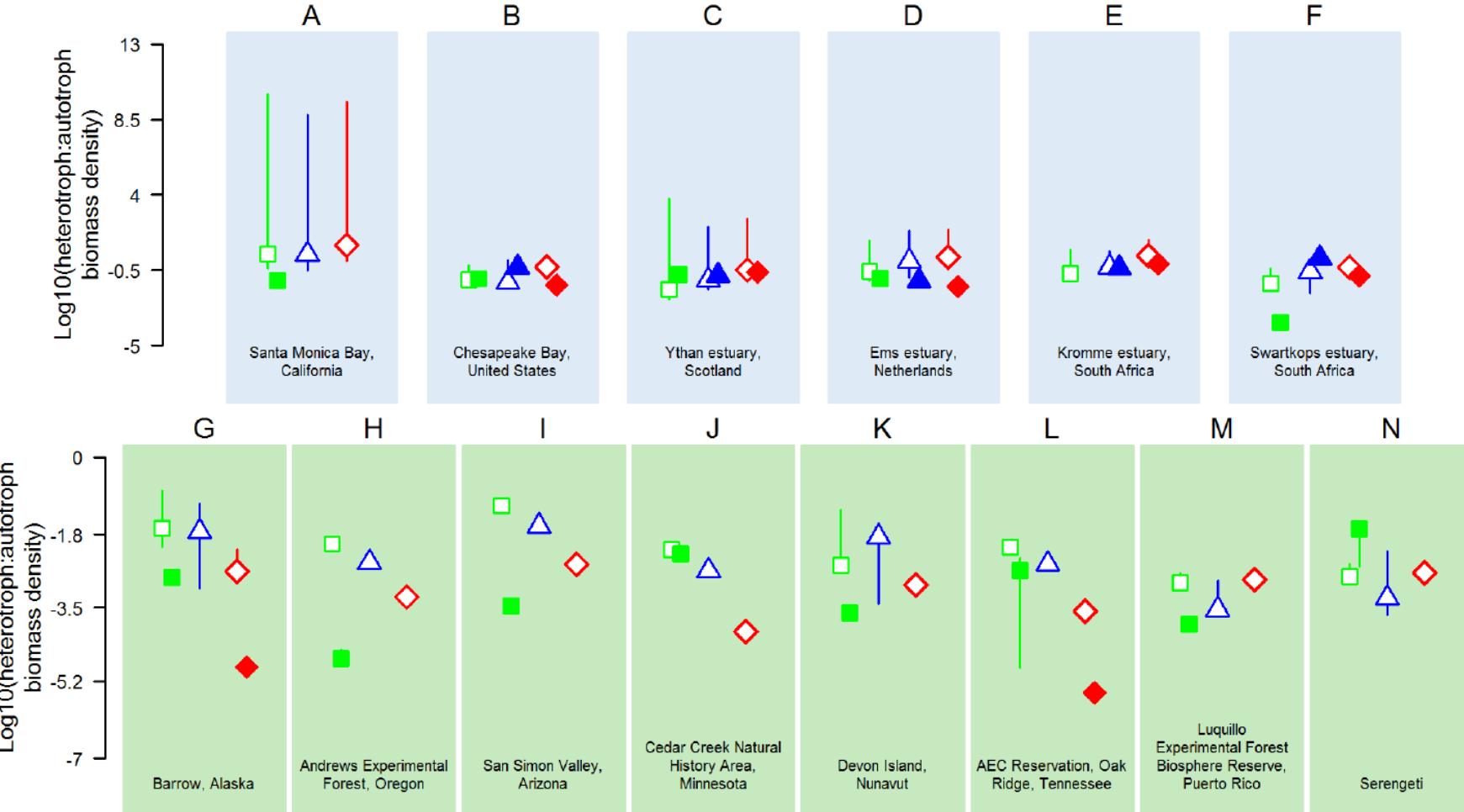
Mortality rates don't match observed scaling with mass



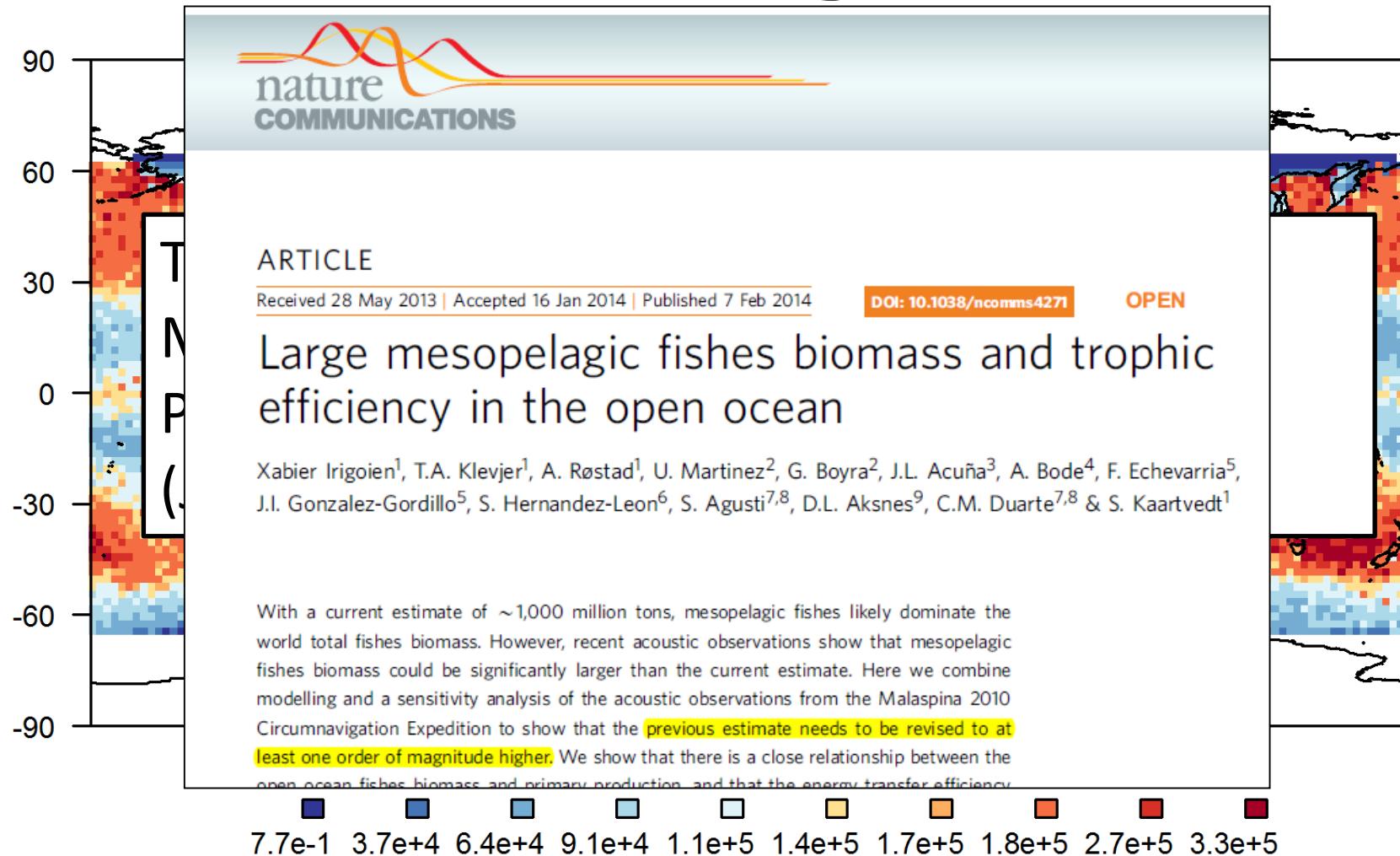
Correspondence with empirical data: individual-level process rates

Match with empirical data generally good in marine systems

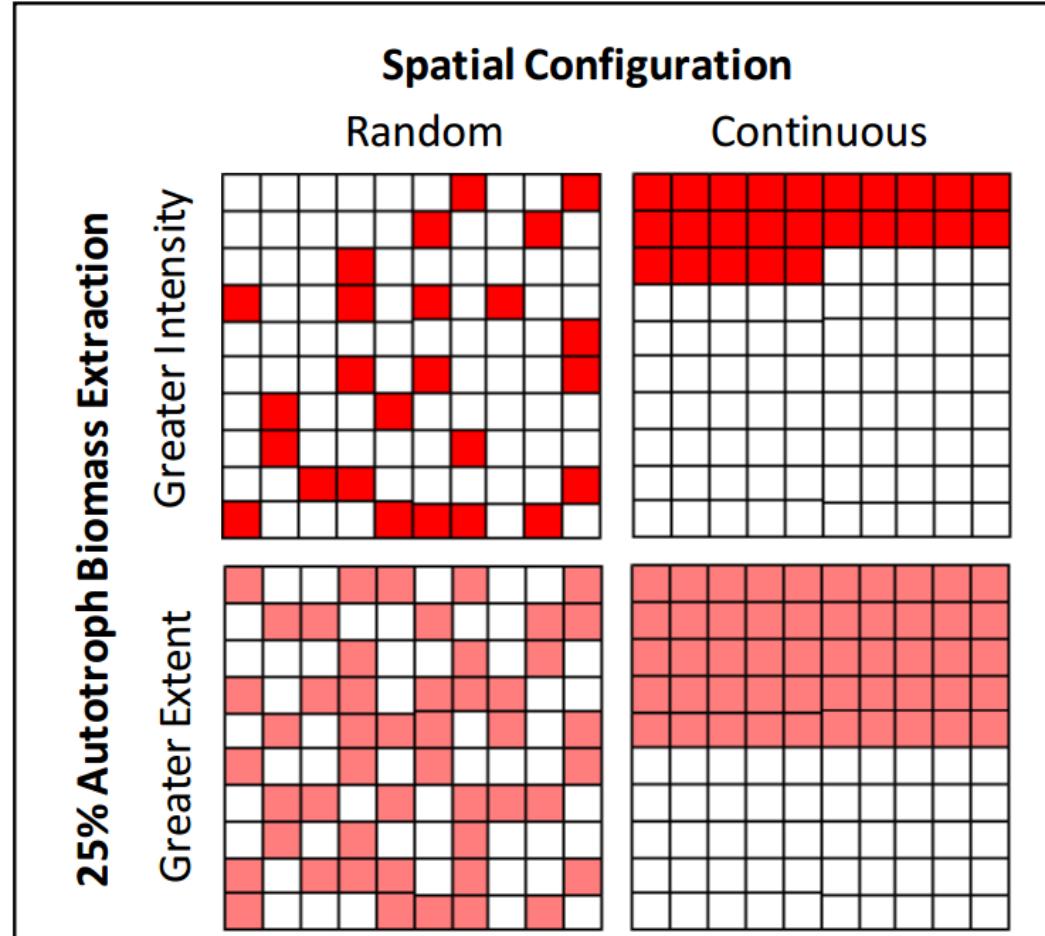
On land, better for grassland ecosystems than forests – vertical vegetation structure?



Not much data with which to evaluate biomass patterns at a global scale



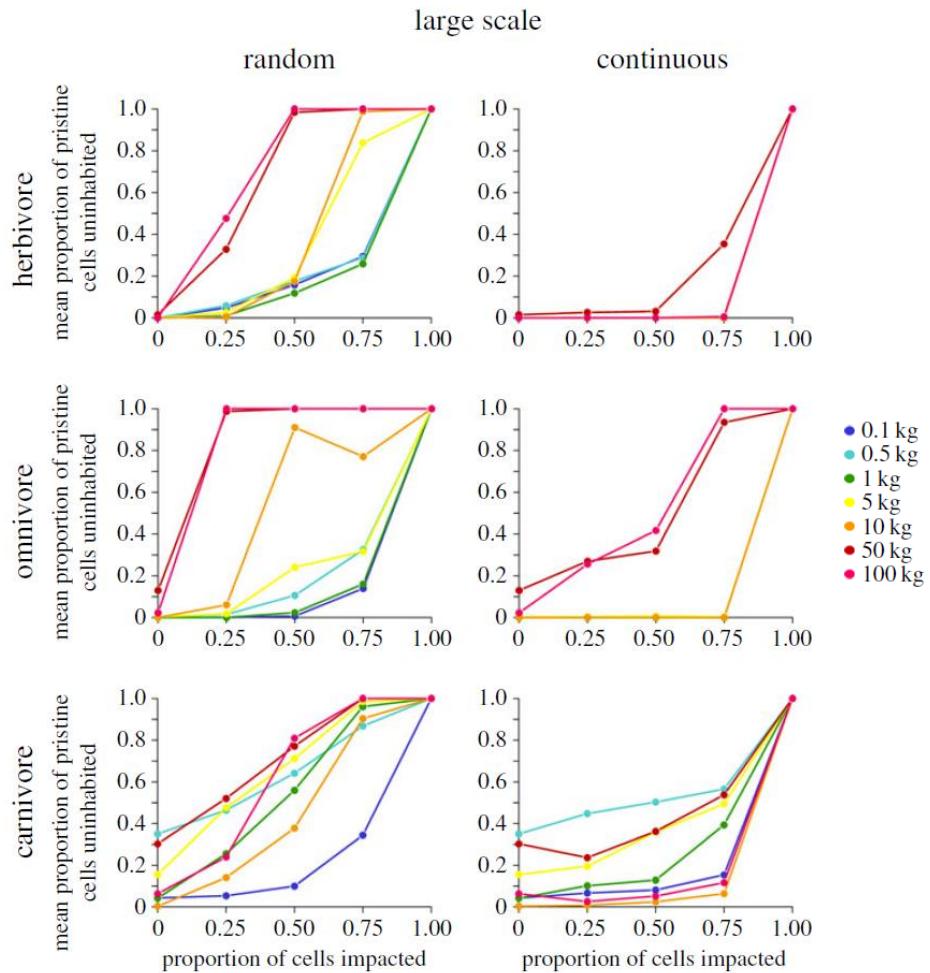
Applications of general ecosystem models: effects of habitat fragmentation



Plant biomass removed from Madingley-Model ecosystems in different extents, intensities and configurations

Simulated impacts on higher trophic levels, for organisms of different body mass

Applications of general ecosystem models: effects of habitat fragmentation



Impacts depended on fragmentation scenario

Higher trophic levels and large organisms generally more likely to be lost

Losses generally greater under fragmented than continuous habitat loss

Summary: complex ecosystem models

System-level models can capture the multiple interacting entities that make up ecological systems

Some outcomes of environmental change can be a product of the interactive nature of ecosystems

These interactive effects can lead to abrupt changes/tipping points

A challenge for systems-level model is obtaining enough information on all of the relevant processes

General summary

No model is perfect (not even close)

The right model depends on the questions being asked

No amount of model sophistication will correct for bad assumptions/data/model structure

It is important to constantly question the assumption of models and to confront models with empirical data

Reading list (I am not expecting you to read all of these!)

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Smith et al. (2015). Inferred support for disturbance-recovery hypothesis of North Atlantic phytoplankton blooms. *J of Geophysical Research: Oceans* **120**: 7067-7090.

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