

# An introduction to ecological modelling

## 3. (More) Complex Models of Ecological Systems

# Lecture outline

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

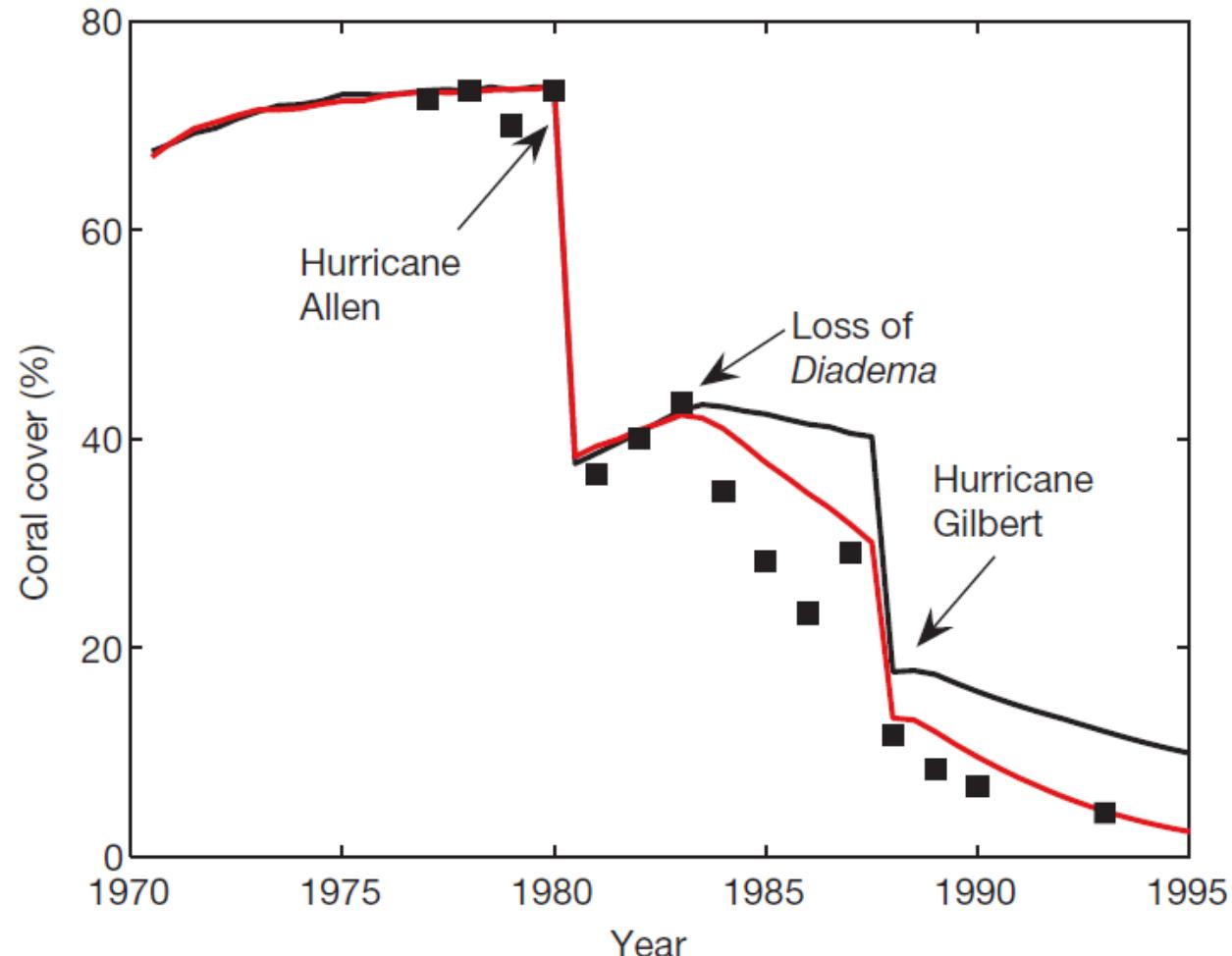
Model of cover of coral and algae

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

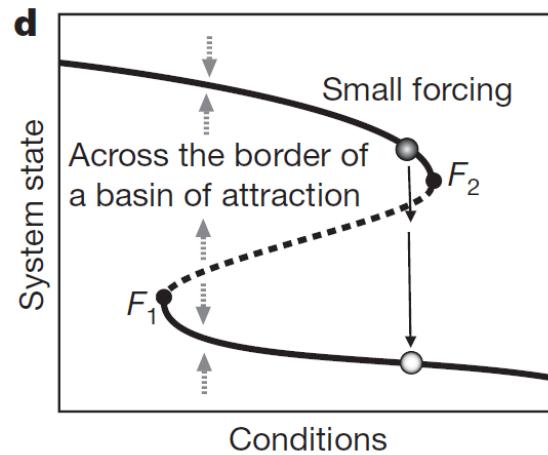
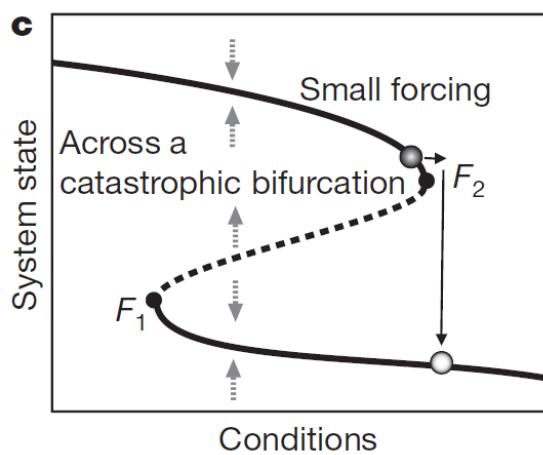
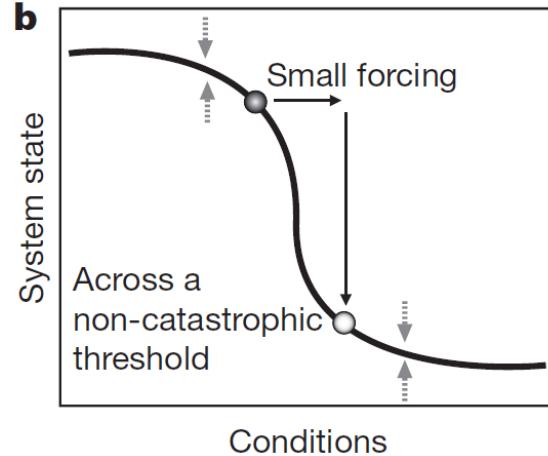
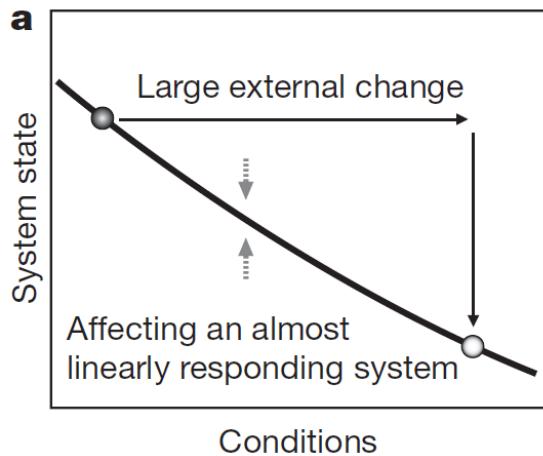
Processes (algae): colonization and growth

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

Model matches observed change in coral cover well



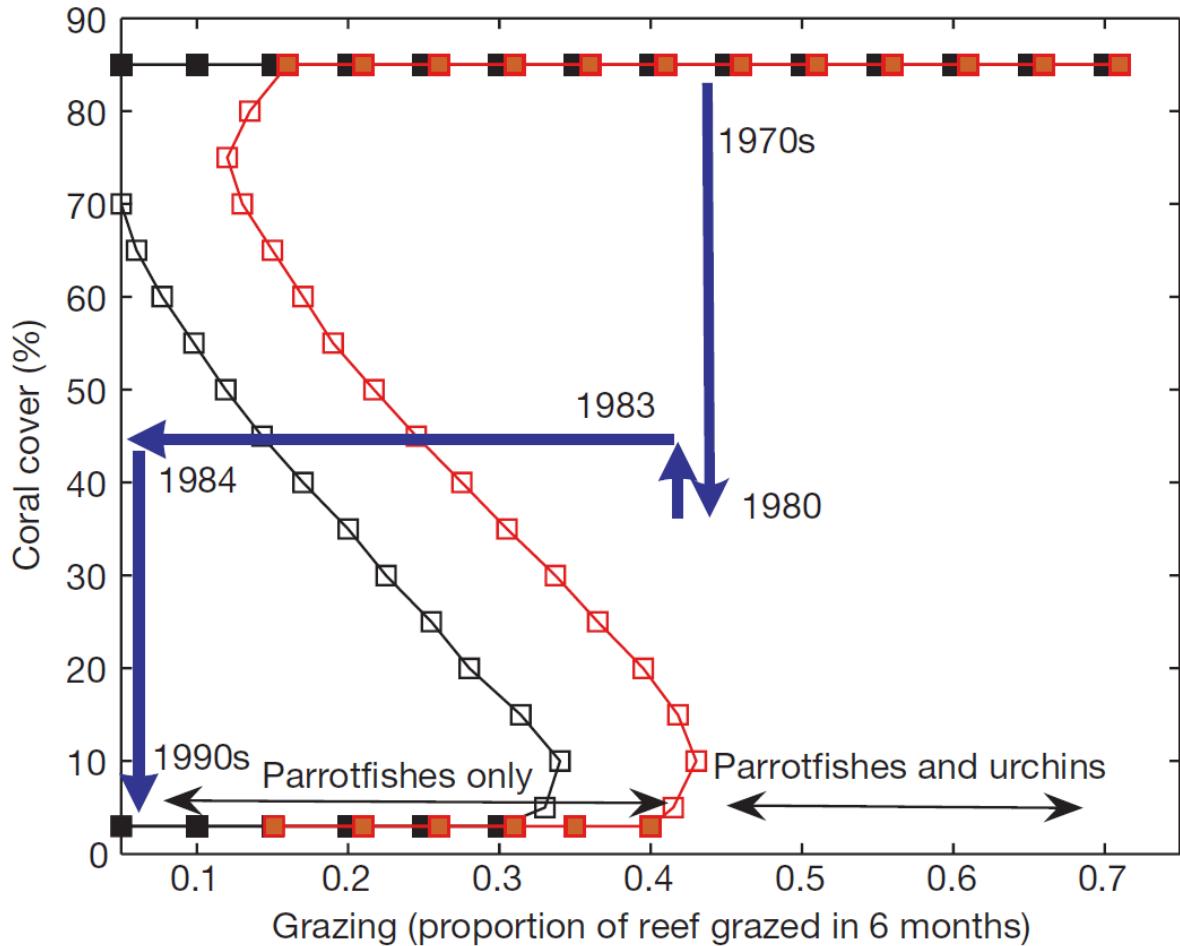
# Ecosystem regime shifts



If conditions change beyond a certain point, ecosystems can abruptly shift to a new state

Reversing the conditions might not be enough to cause the ecosystem state to revert ('hysteresis')

# Simple system-level model of coral reef dynamics



System has unstable equilibria (open squares)

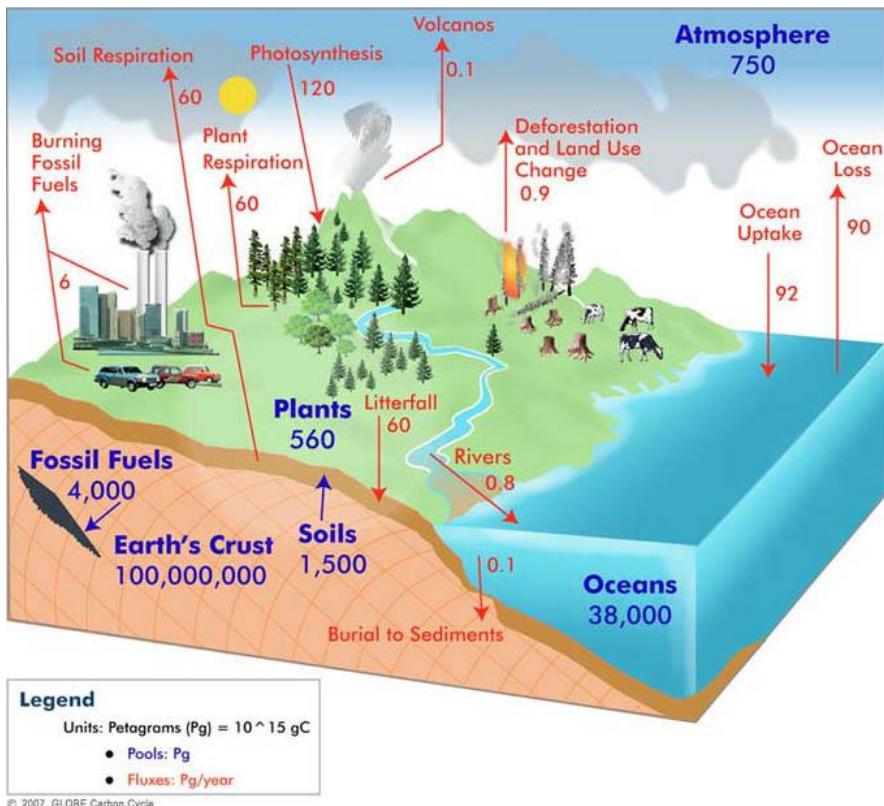
Grazing reduced after loss of urchins

Makes system less resilient to disturbance (e.g. by hurricanes)

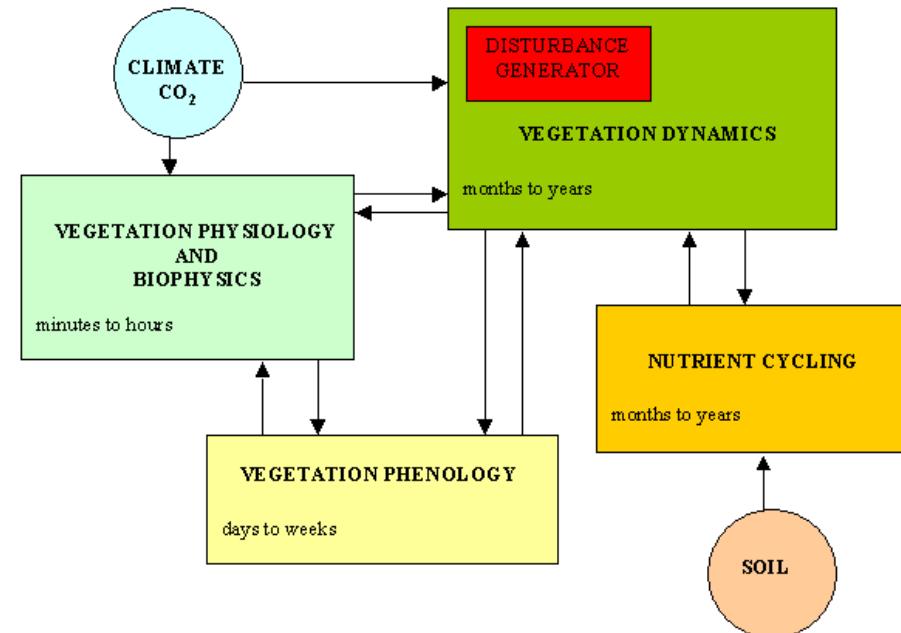
Switch to stable algal-dominated state more likely

# The importance of understanding vegetation dynamics

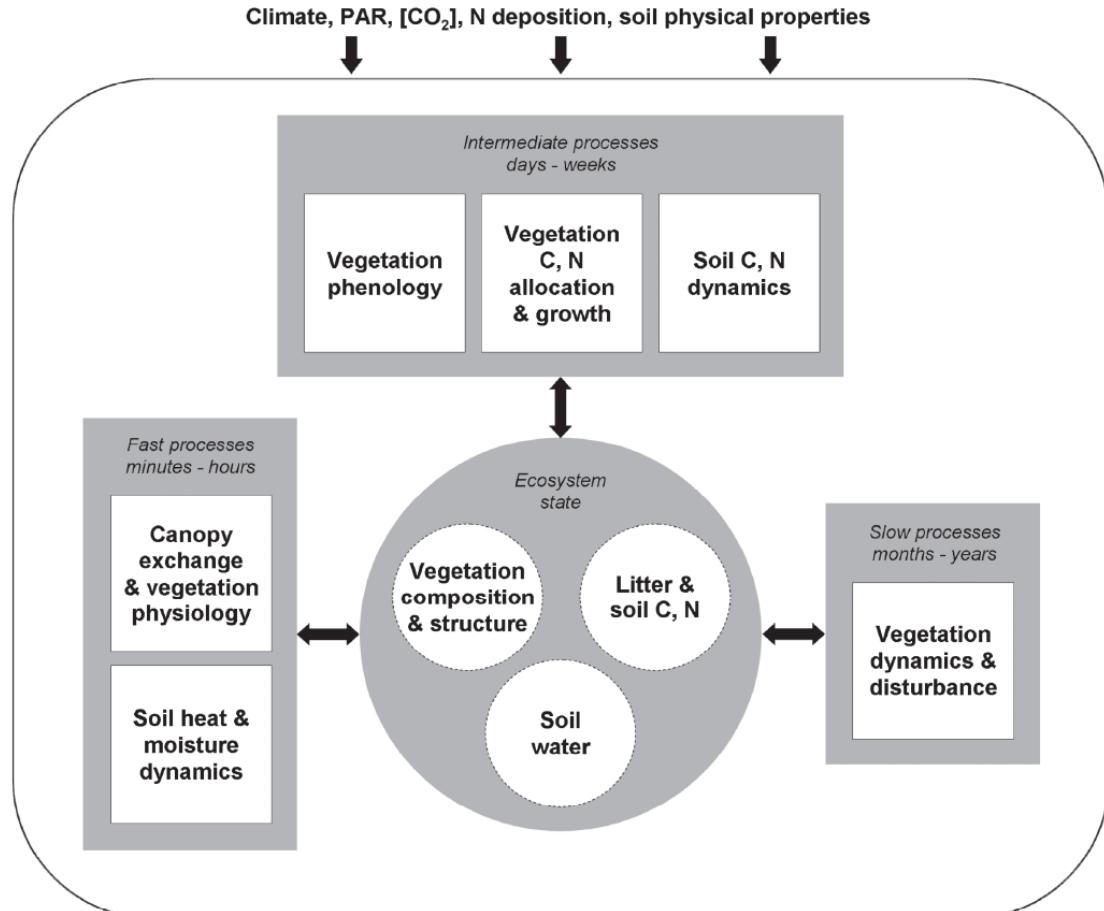
Vegetation plays an important role in the global carbon cycle



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



# Dynamic Global Vegetation Models

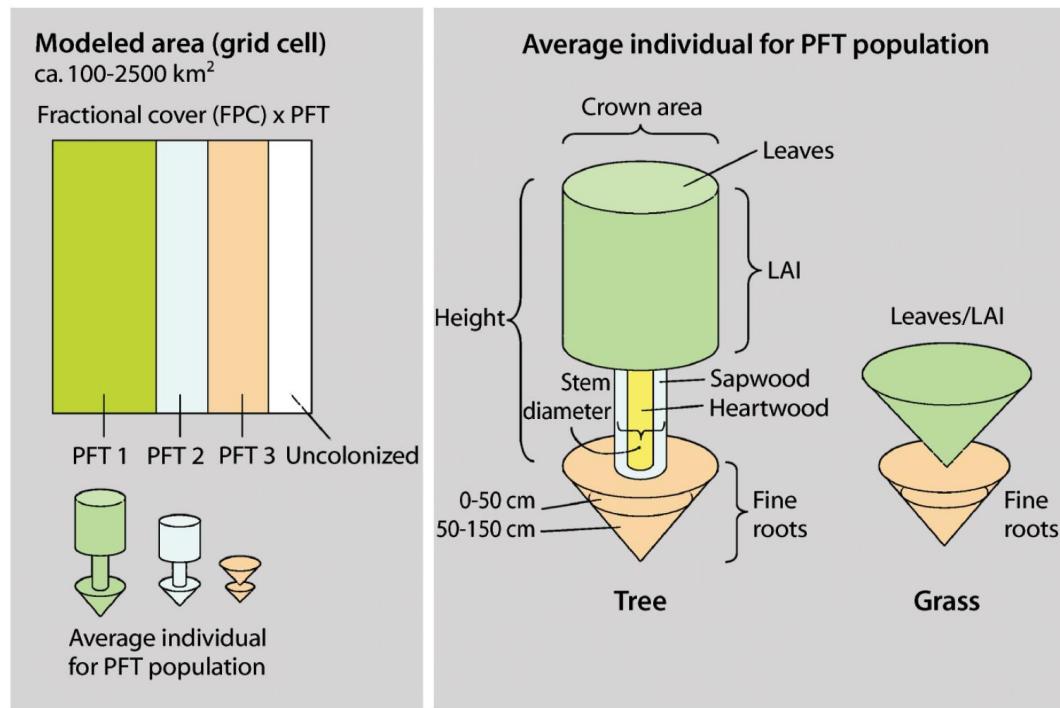


Four main process types: plant geography, plant physiology and biochemistry, vegetation dynamics, and biophysics

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

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## PFT

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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)

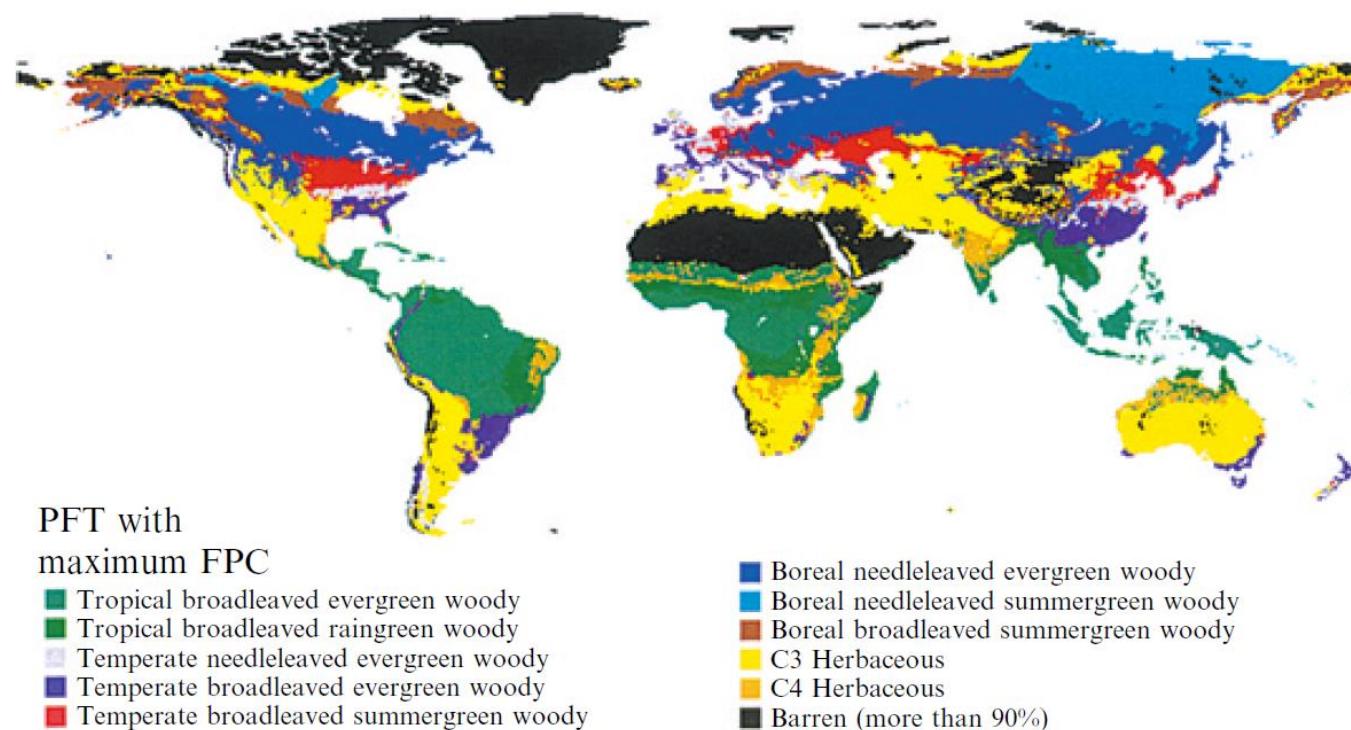
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Prentice et al. (2007). In *Terrestrial Ecosystem in a Changing World*.

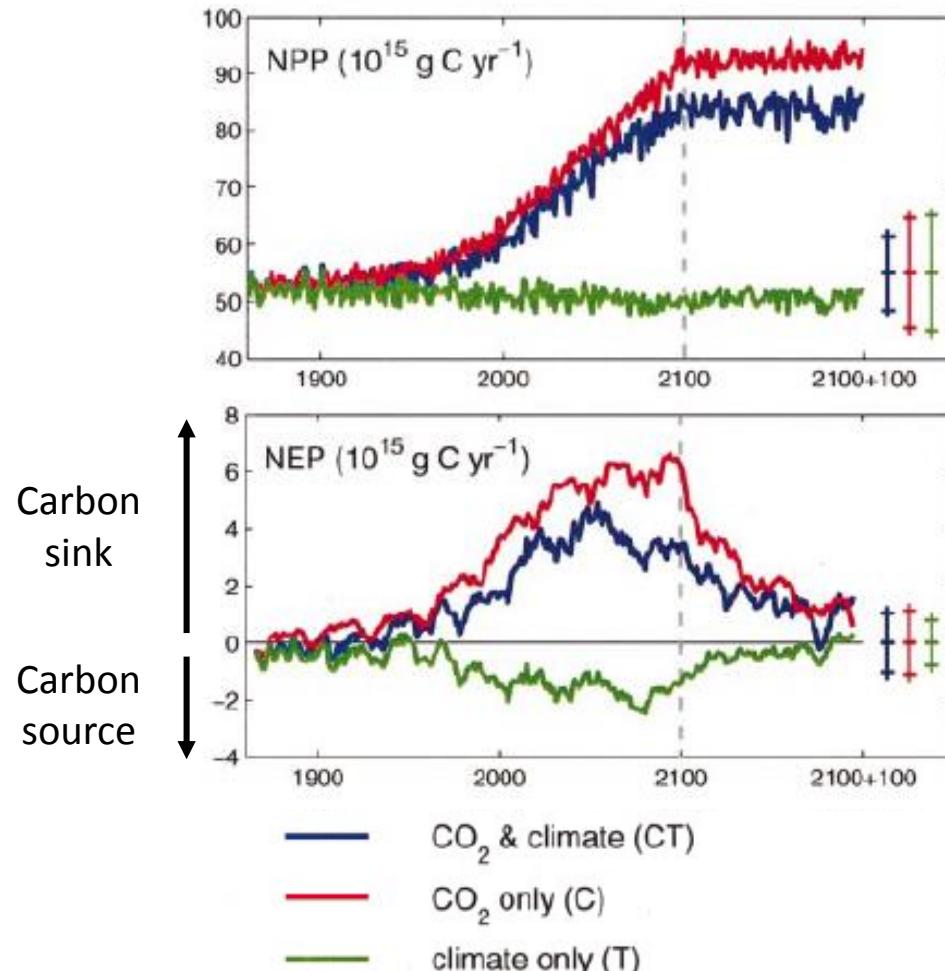
Sitch et al. (2003). *Global Change Biology* 9: 161-185.

# 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



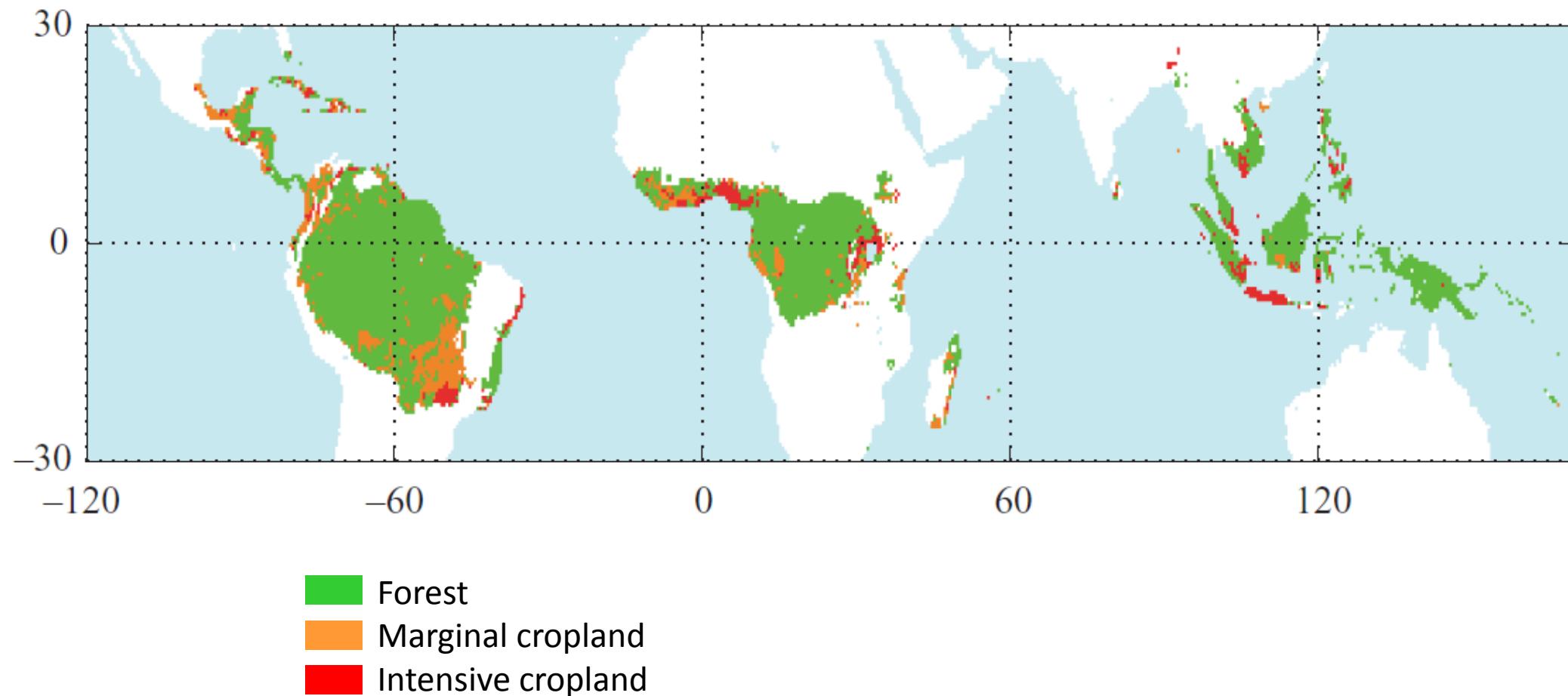
6 DGVMs

Predicted under change in climate, CO<sub>2</sub> concentration, or both

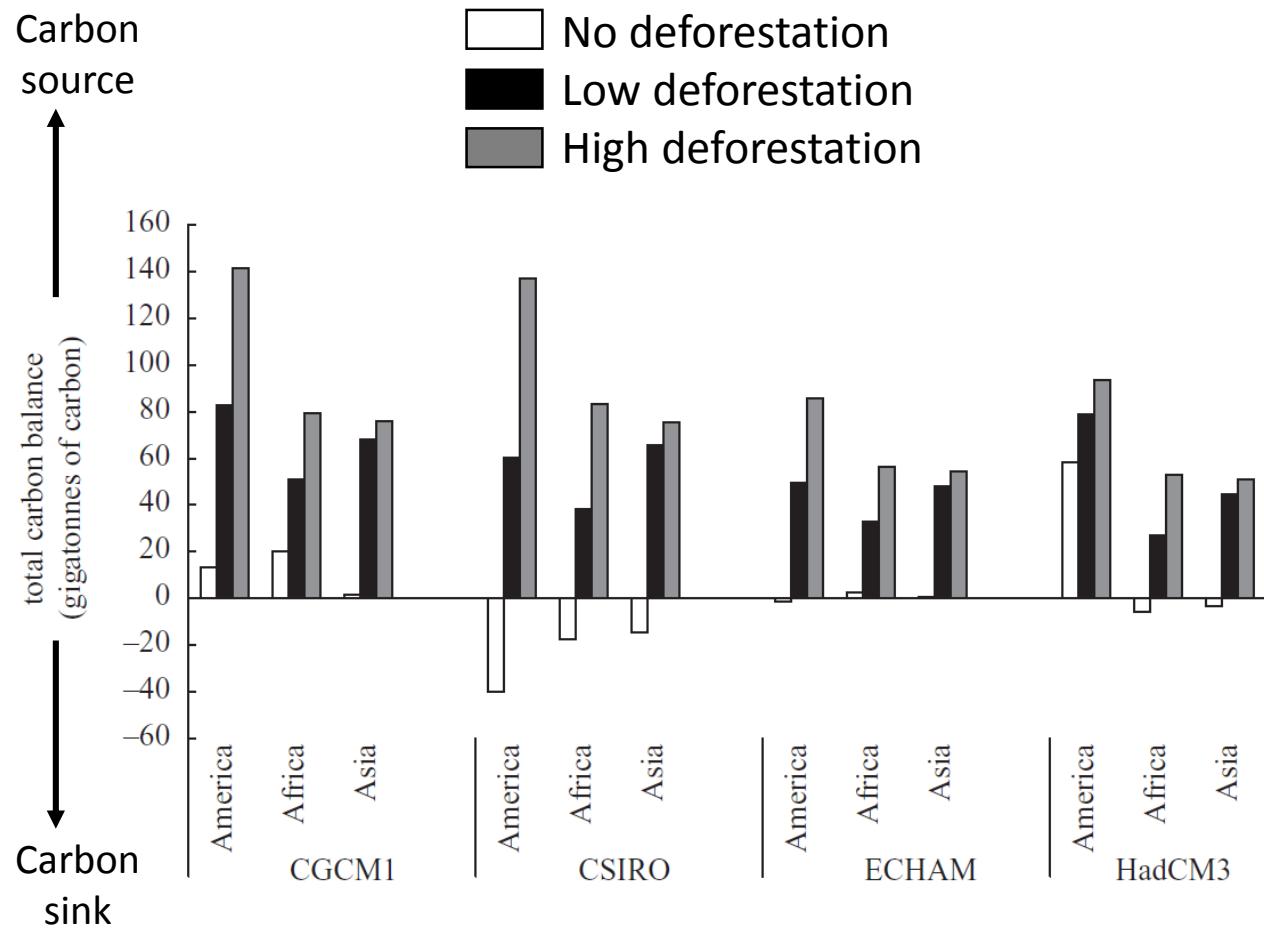
Increased CO<sub>2</sub> concentration predicted to increase carbon sink potential

Offset by climate change: effect of CO<sub>2</sub> asymptotes, but effect of temperature on respiration continues

# Applications of Dynamic Global Vegetation Models: Climate change and deforestation



# Applications of Dynamic Global Vegetation Models: Climate change and deforestation



One DGVM (LPJ)

Predicted vegetation and carbon balance of tropical forest

No, low and high deforestation scenarios

Carbon source over 21<sup>st</sup> Century under most scenarios, especially with deforestation

# Plant communities are composed of individuals with large variation



# Individual-based vegetation models: aDGVM

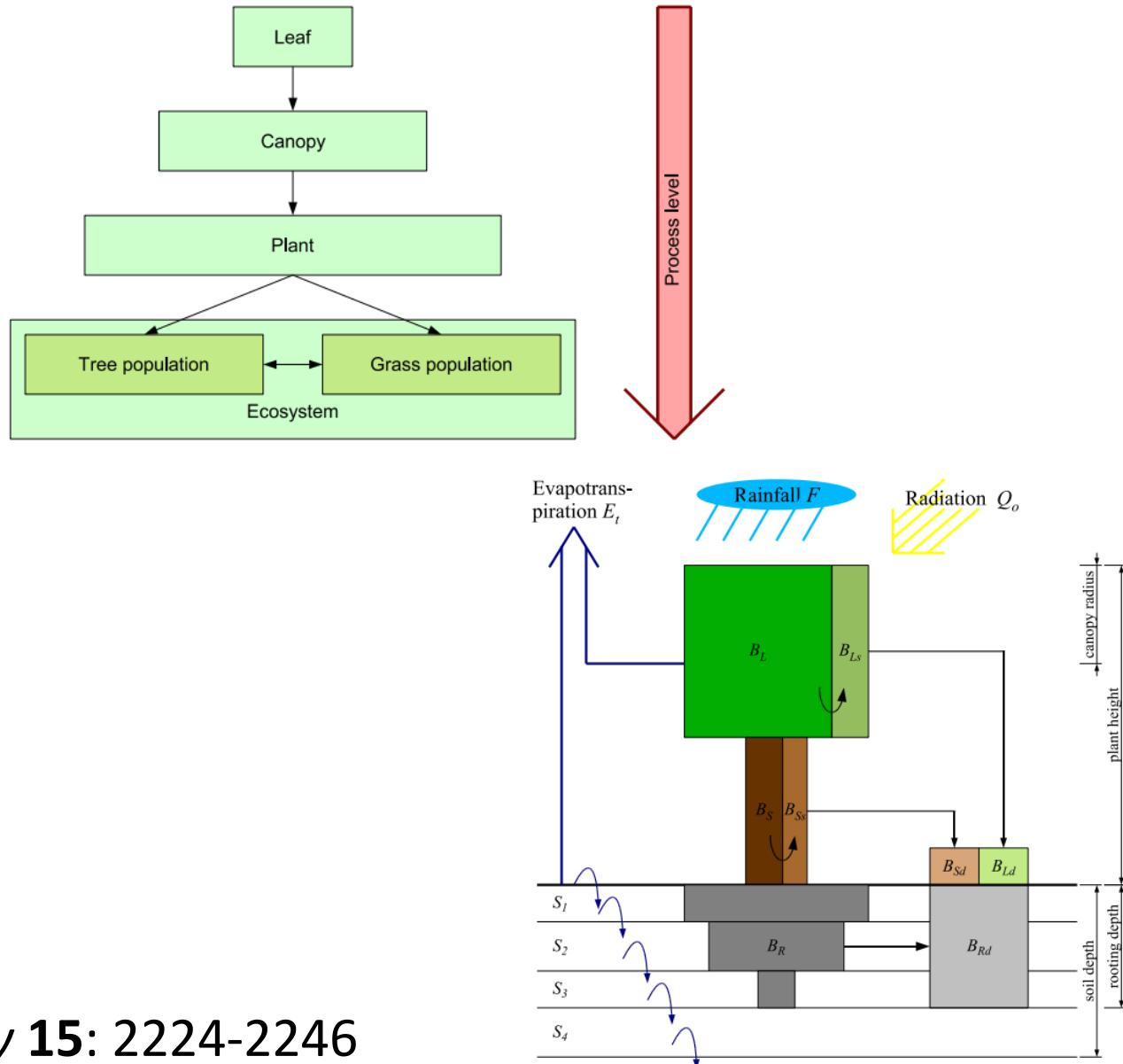
Adaptive Dynamic Global Vegetation  
Model (aDGVM)

Leaf photosynthesis →

Canopy photosynthesis, respiration and  
conductance →

Plant growth, allometry, competition,  
reproduction and mortality

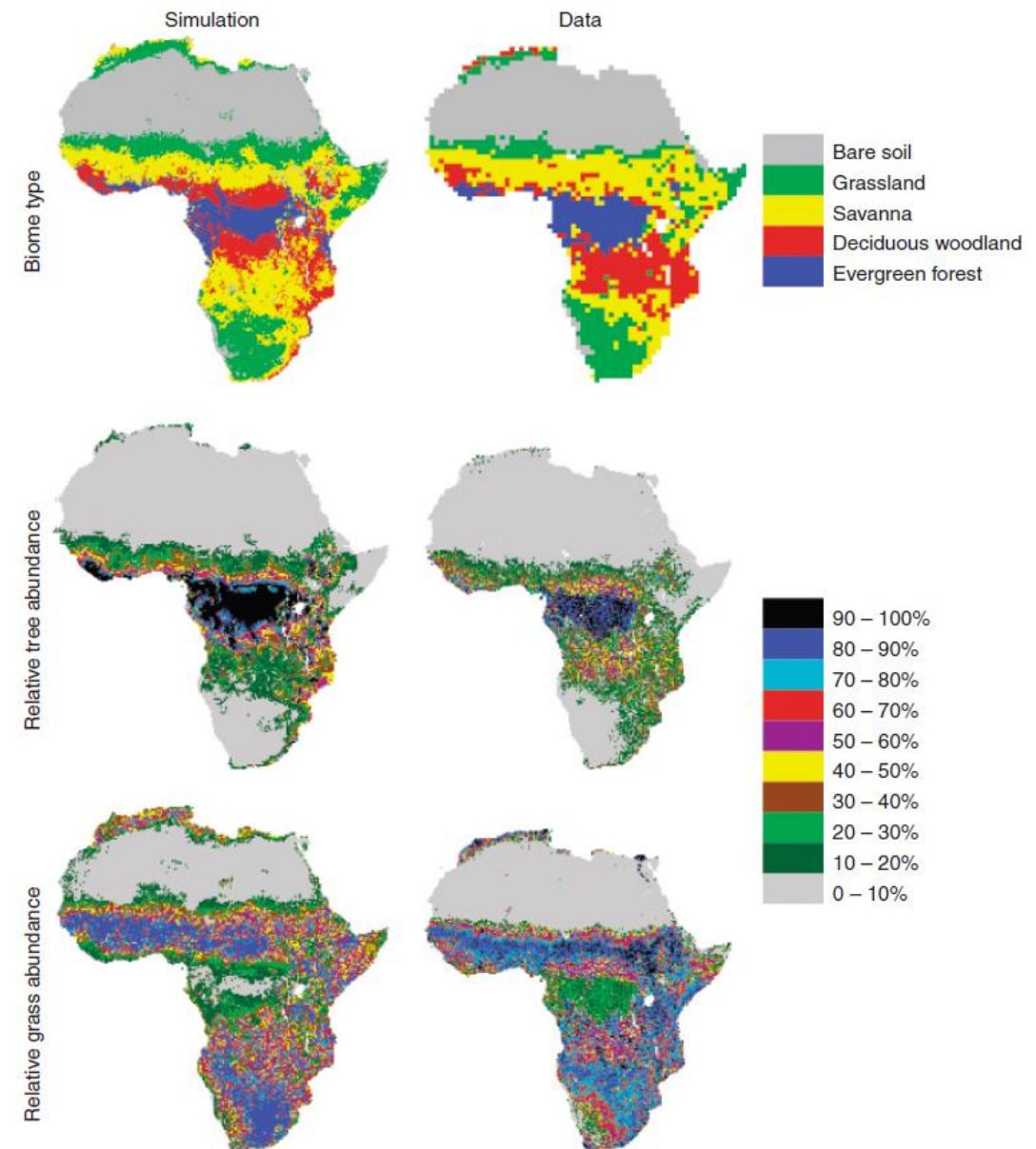
Representative 1-ha stands, scaled up to  
 $\frac{1}{3}^\circ$



# Individual-based vegetation models: aDGVM

Fits observed data fairly well

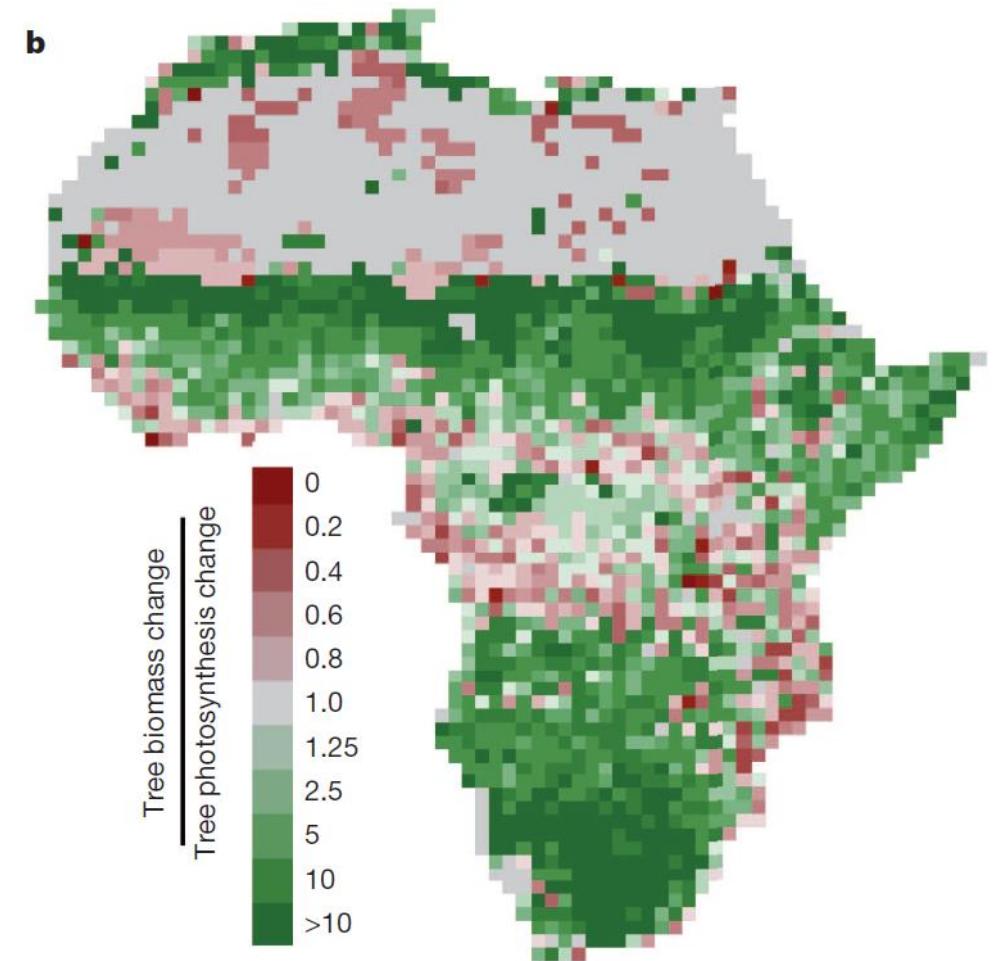
Fit generally better than models  
based on coverage of plant  
functional types



# Applications of individual-based vegetation models: climate change

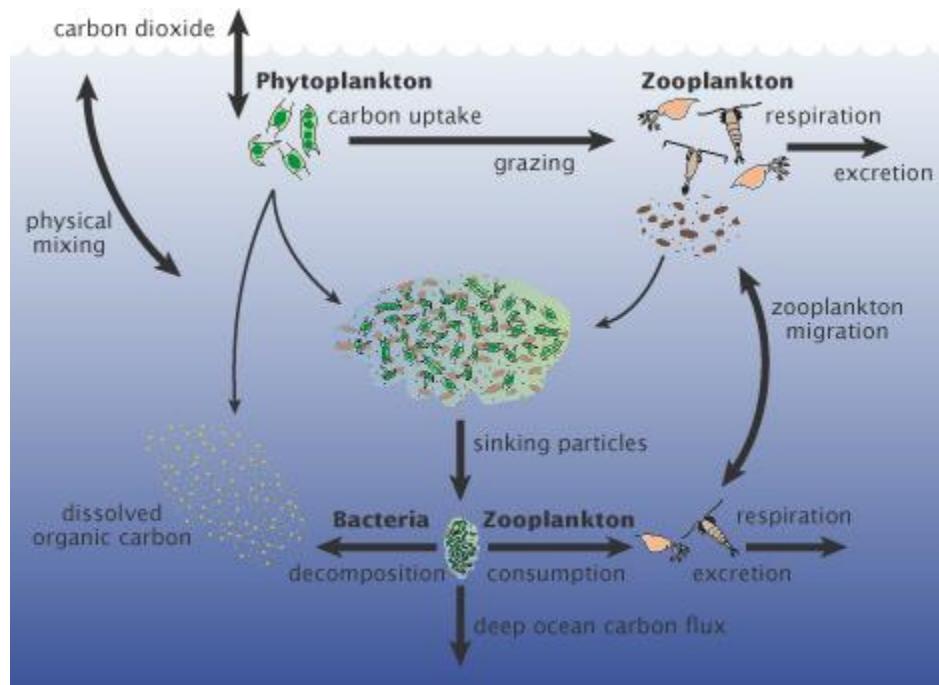
Predicted vegetation shifts from desert to grassland, grassland to savanna/woodland, and savanna to forest

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

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

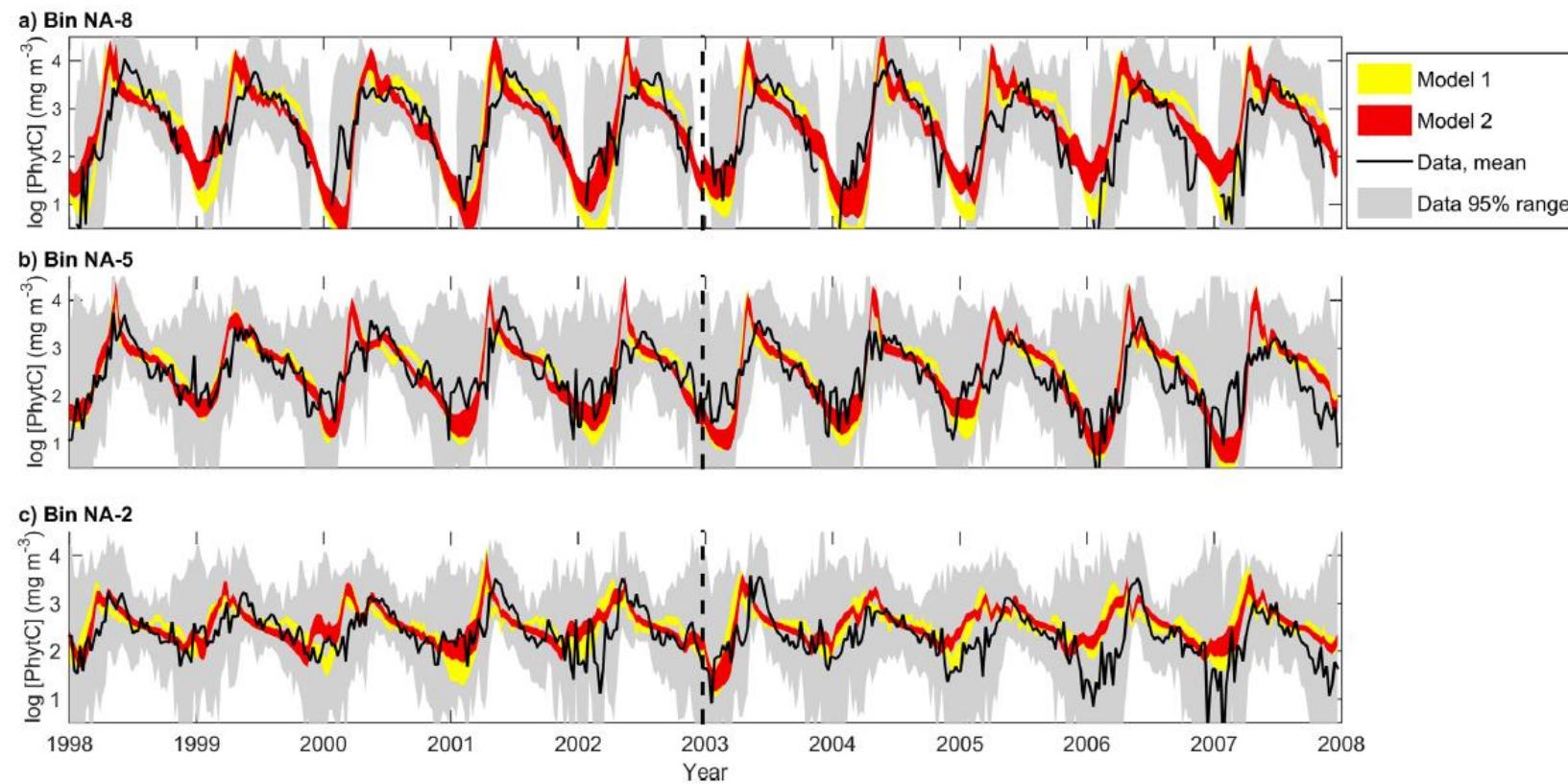
$$\frac{dP}{dt} = \frac{\alpha(L_d, M_d, P)PN}{j + N} - \omega P - \frac{cP^2Z}{K + P^2} - P\zeta_P(M_d)/M_d,$$

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

Textual Definition	Symbol
Nitrate uptake half saturation	$j$
Phytoplankton background mortality rate	$\omega$
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



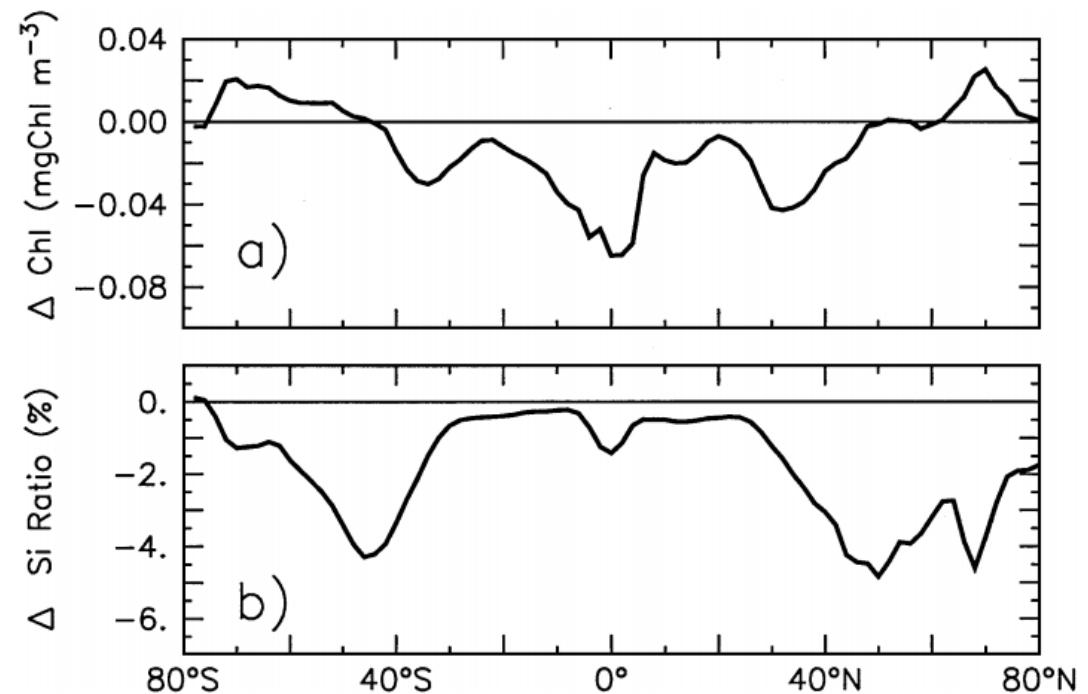
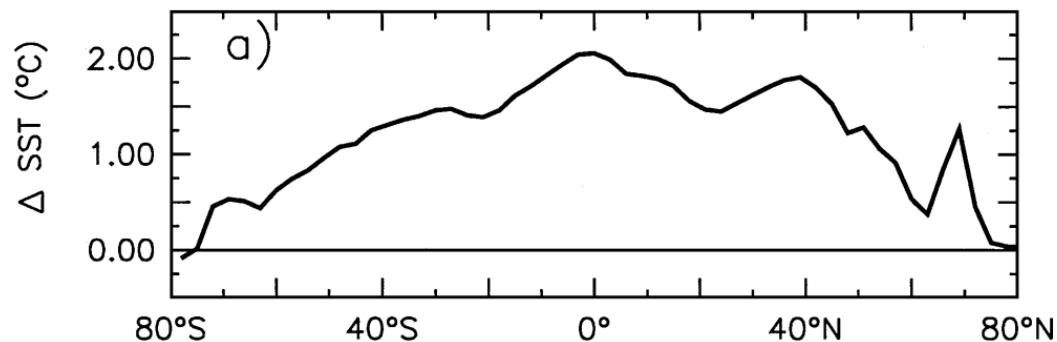
# Application of NPZ models: climate change

Predicted effects of doubling of pre-industrial CO<sub>2</sub>

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.

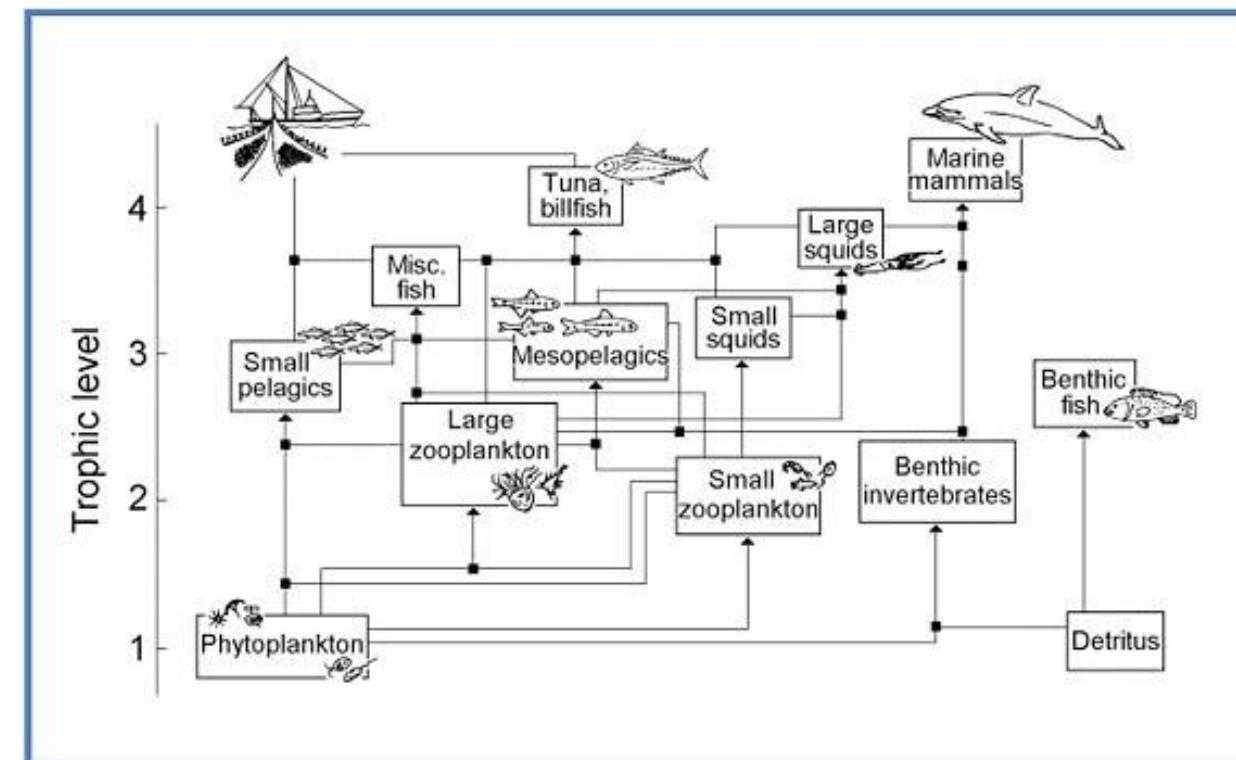
Summarized in Richardson (2008). *ICES J Marine Science* 65: 279-295.

# Ecopath with Ecosim

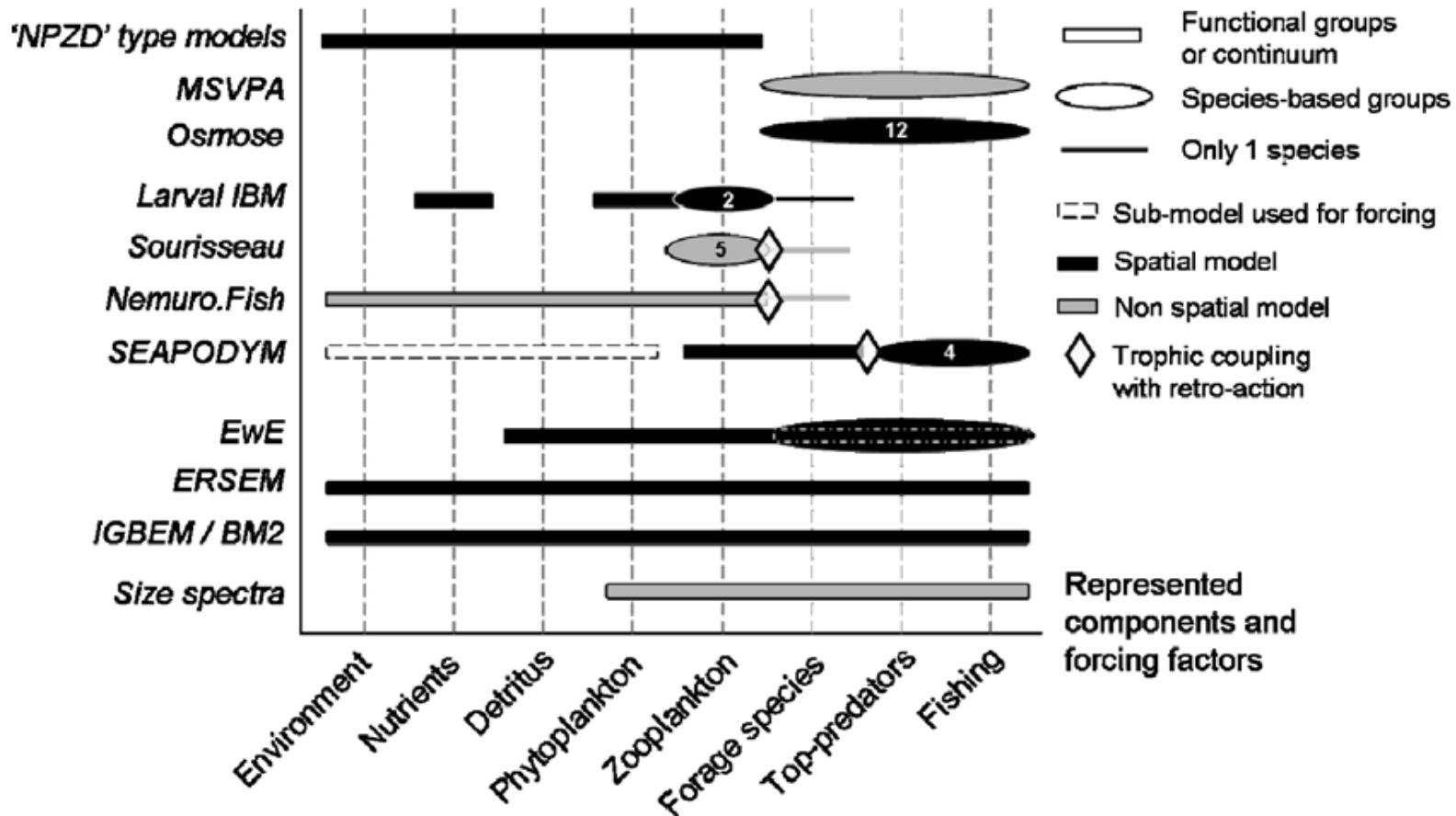
Ecopath: biomass stocks and trophic flows

Ecosim: coupled differential equations to simulate dynamics

Ecospace: spatial representation, including dispersal/migration



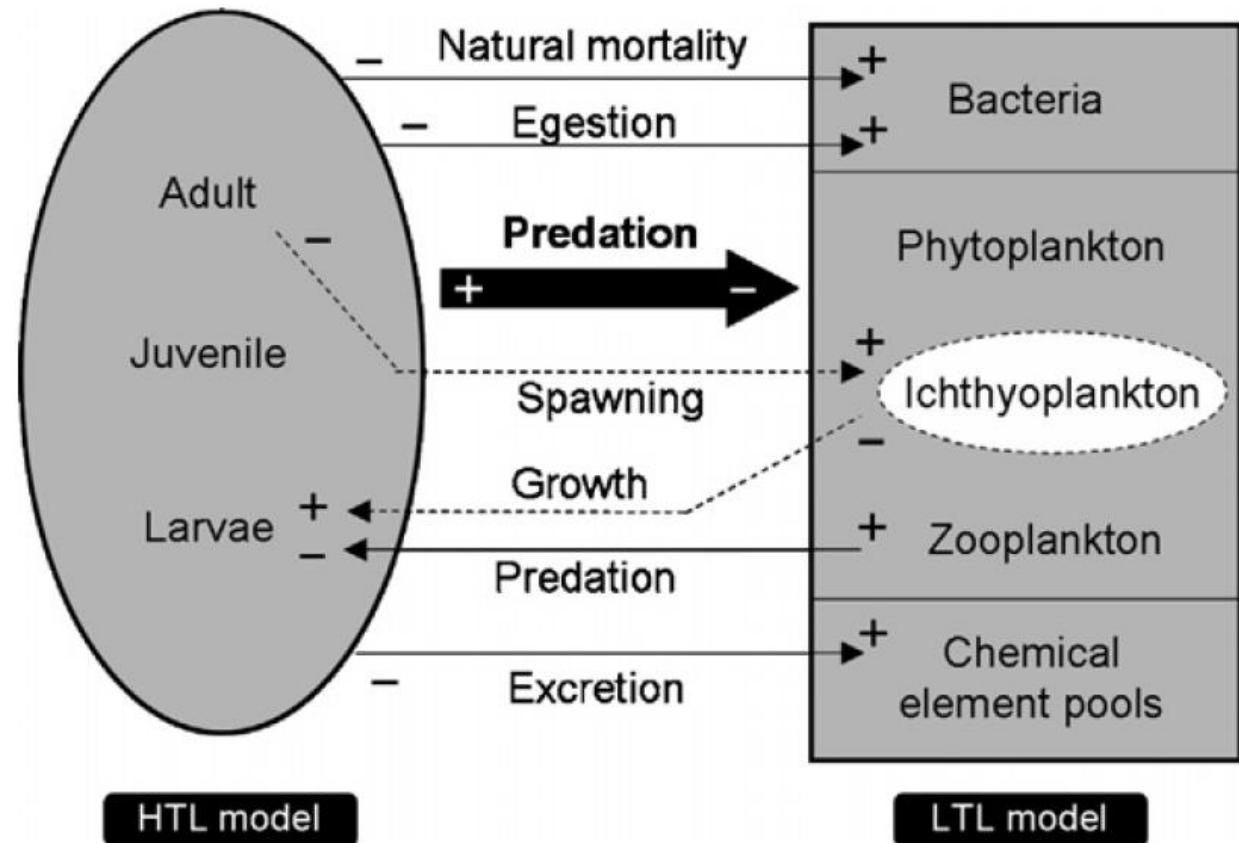
# Many marine models only capture parts of the whole system



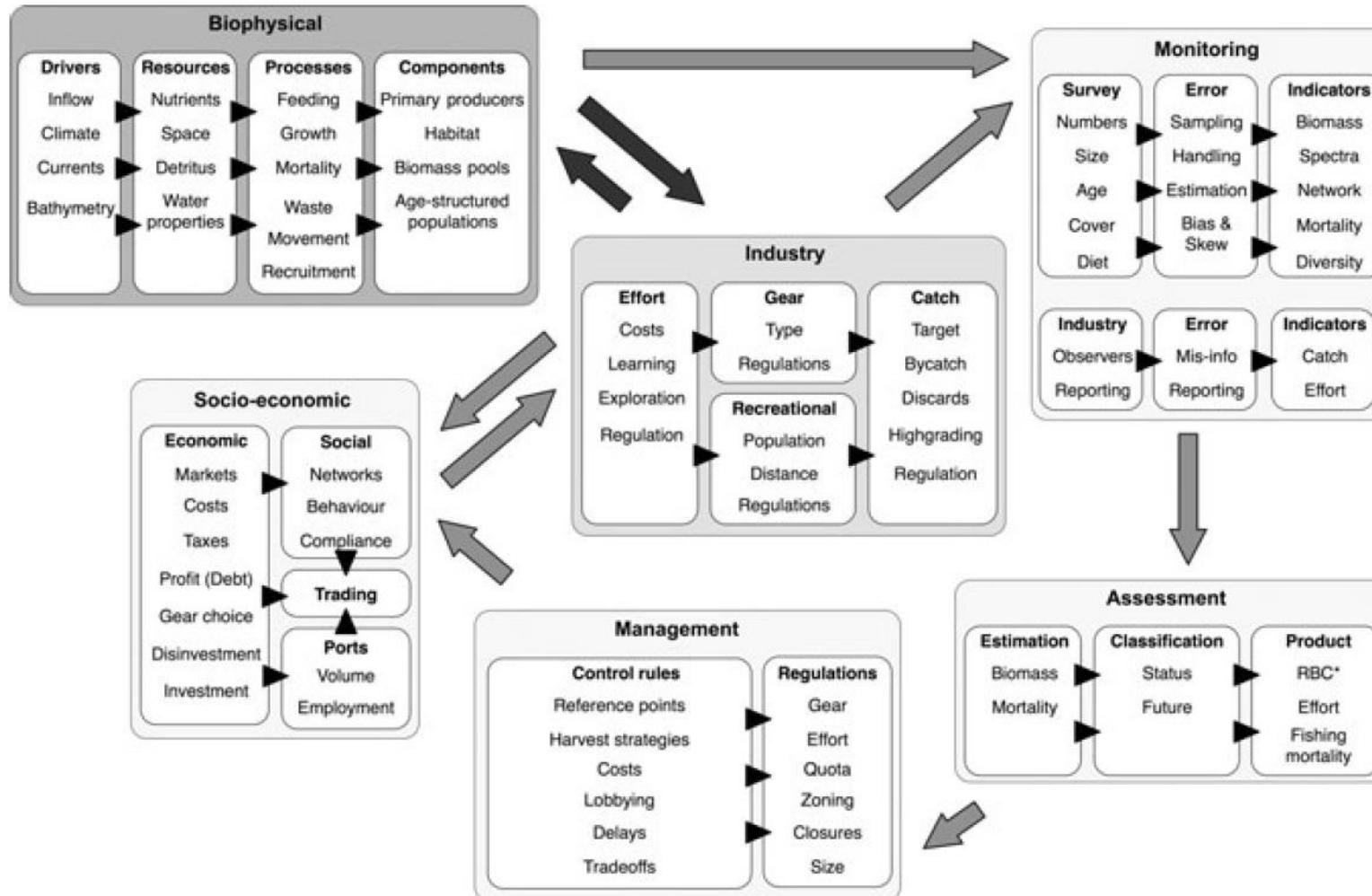
# Many marine models only capture parts of the whole system

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

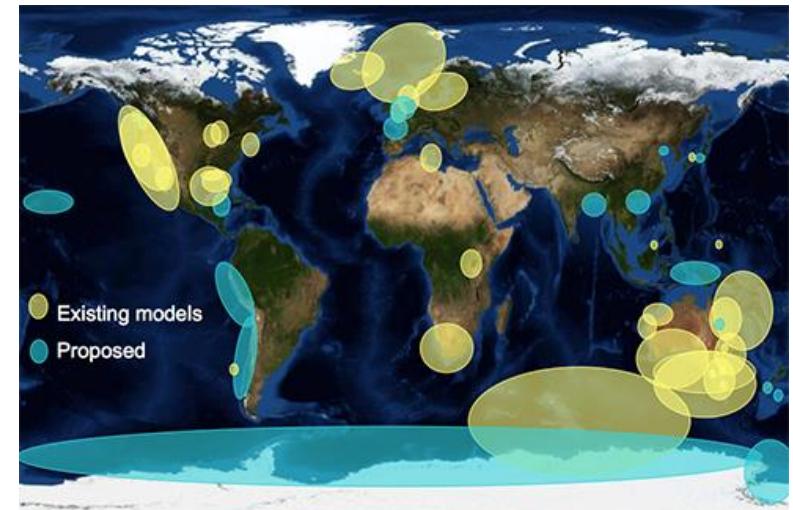
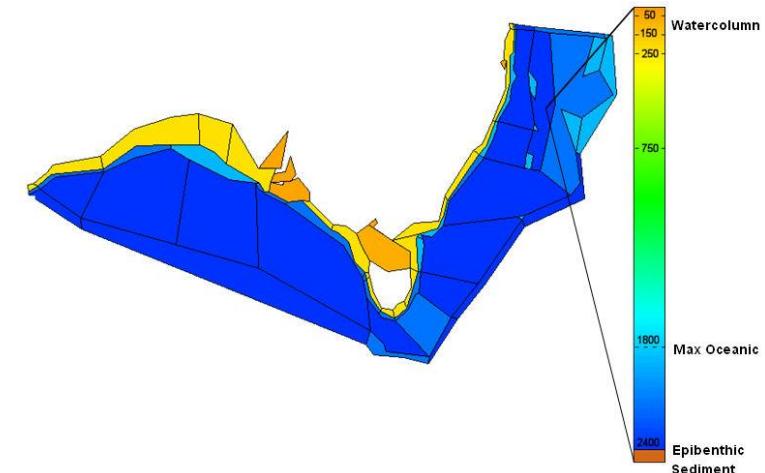


# Atlantis: an end-to-end ecosystem model

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

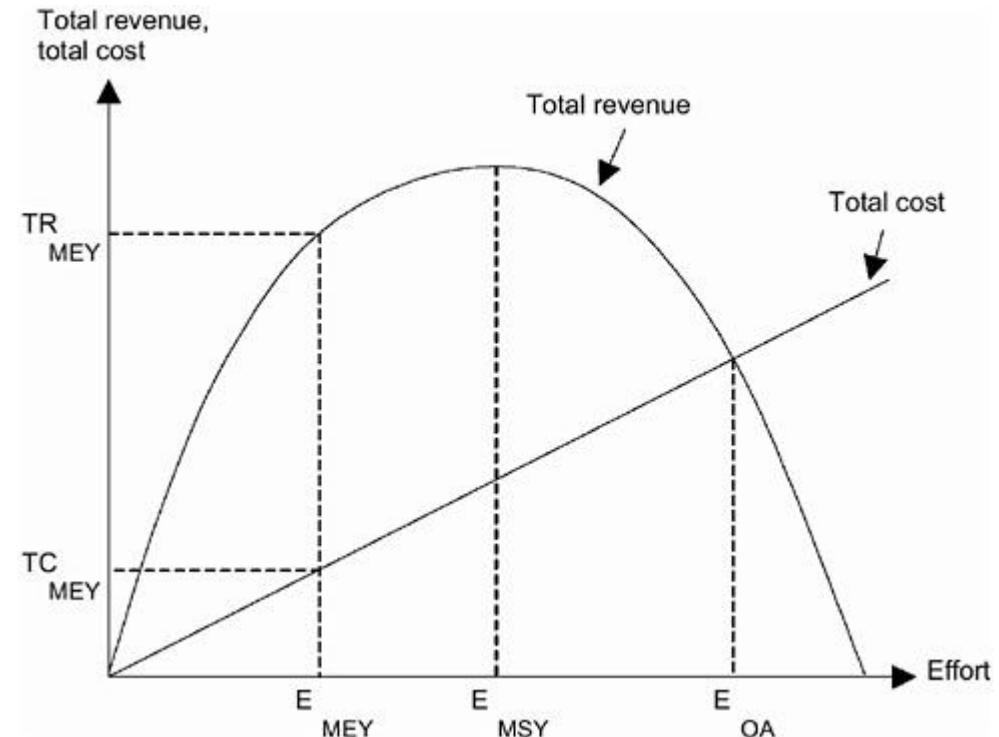


# Applications of marine ecosystem models: fisheries management

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

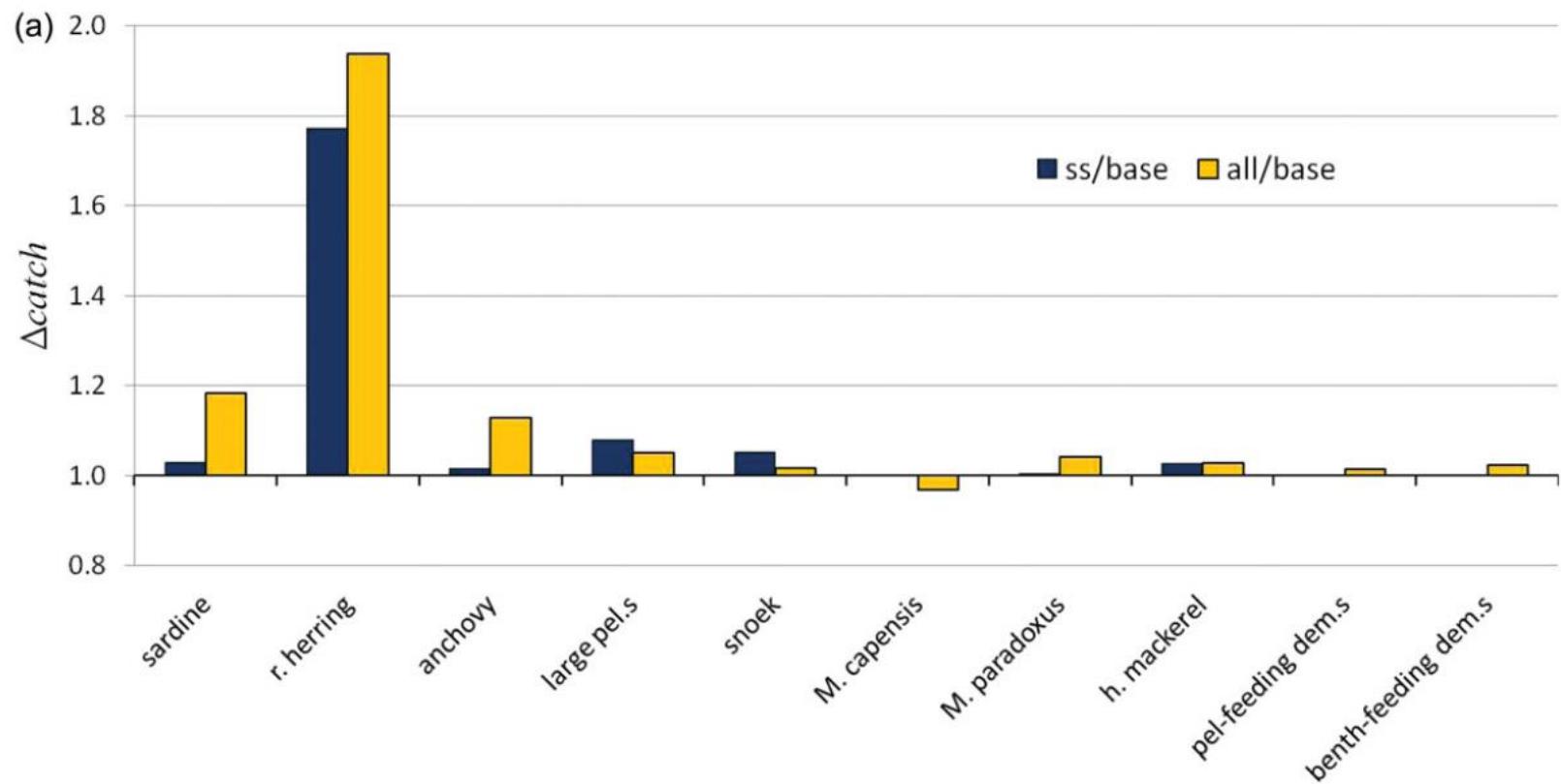


# Applications of marine ecosystem models: fisheries management

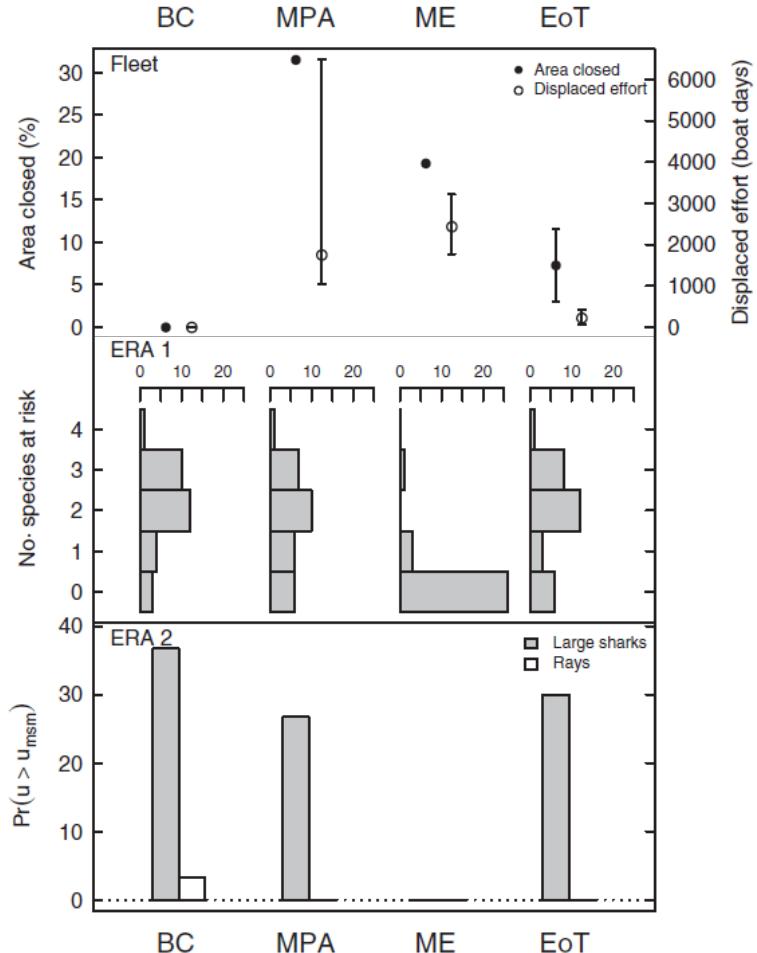
Fisheries 9% more productive using single-species assessment

16% more productive with multi-species assessment

But benefits of multi-species assessments varied among species



# Applications of marine ecosystem models: conservation strategies



Four scenarios: ‘business-as-usual’ (BC), marine protected areas (MPA), strategic attempt to reduce risk of particularly threatened groups (ME), and adaptive closures to reduce impacts on benthos (EoT)

Outcomes simulated using Ecopath with Ecosim

Targeting at-risk groups was most effective at conserving those groups

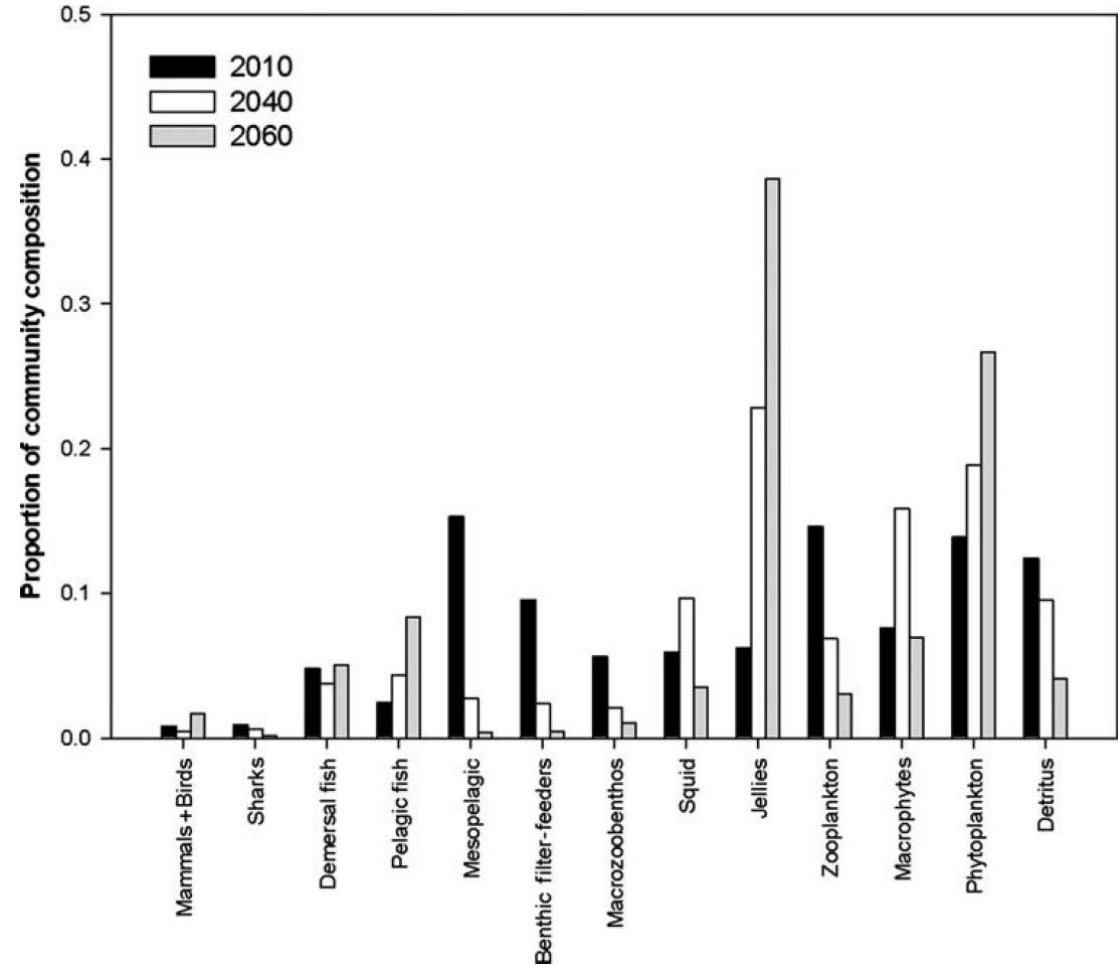
# Applications of marine ecosystem models: climate change

3 modelling frameworks: Atlantis, Ecopath with Ecosim, InVitro

Models for 7 ecosystems

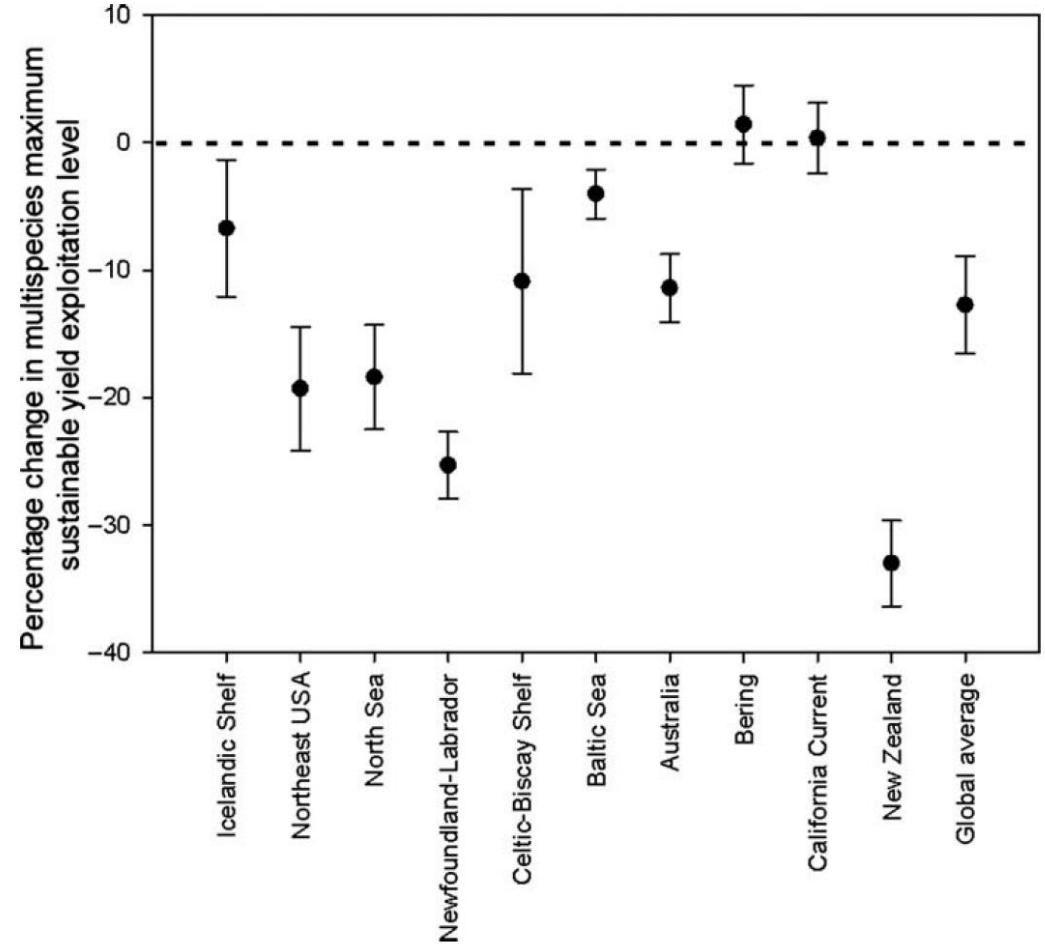
Climate and socio-economic projections under the SRES A2 scenario

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

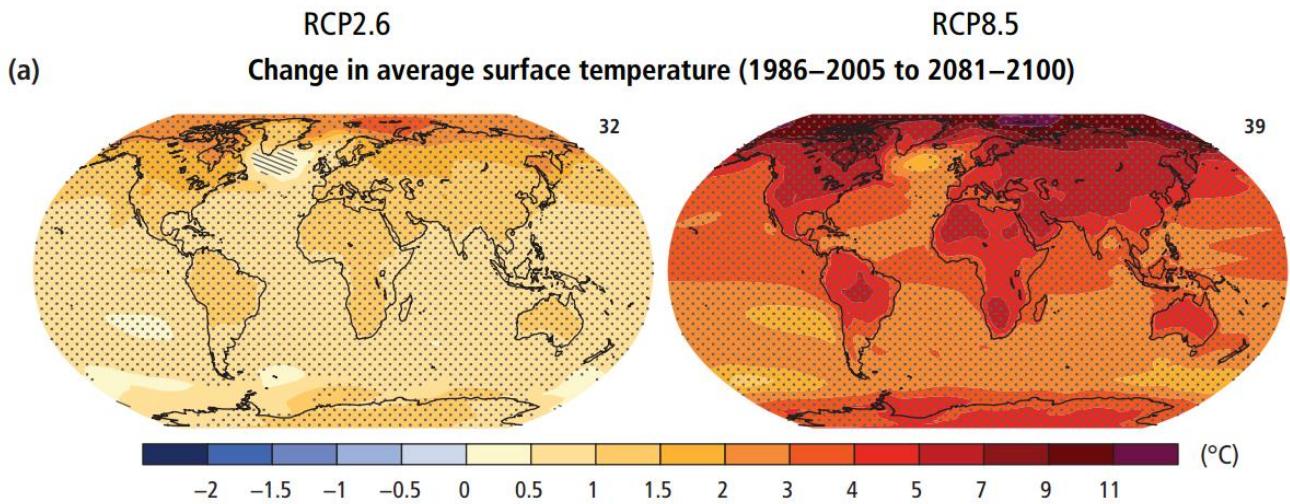
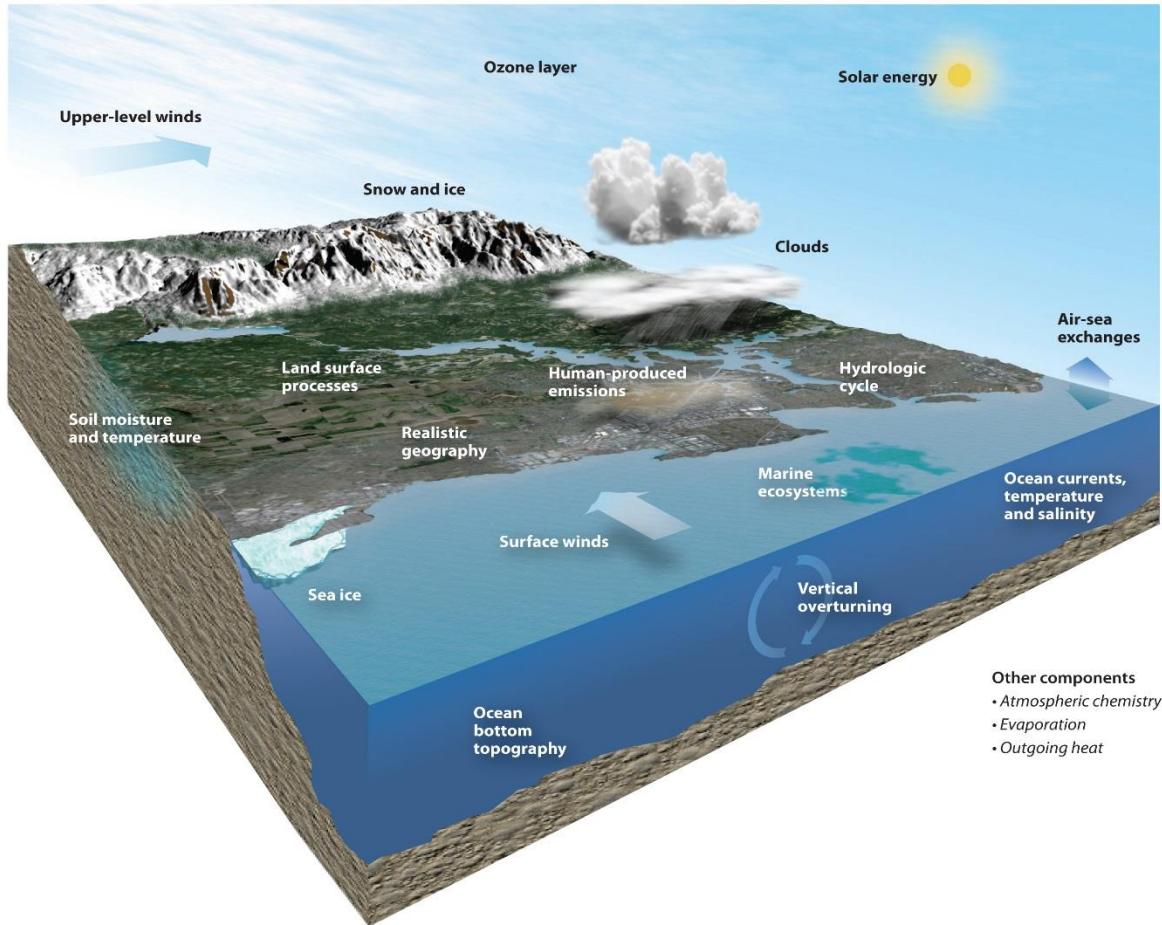


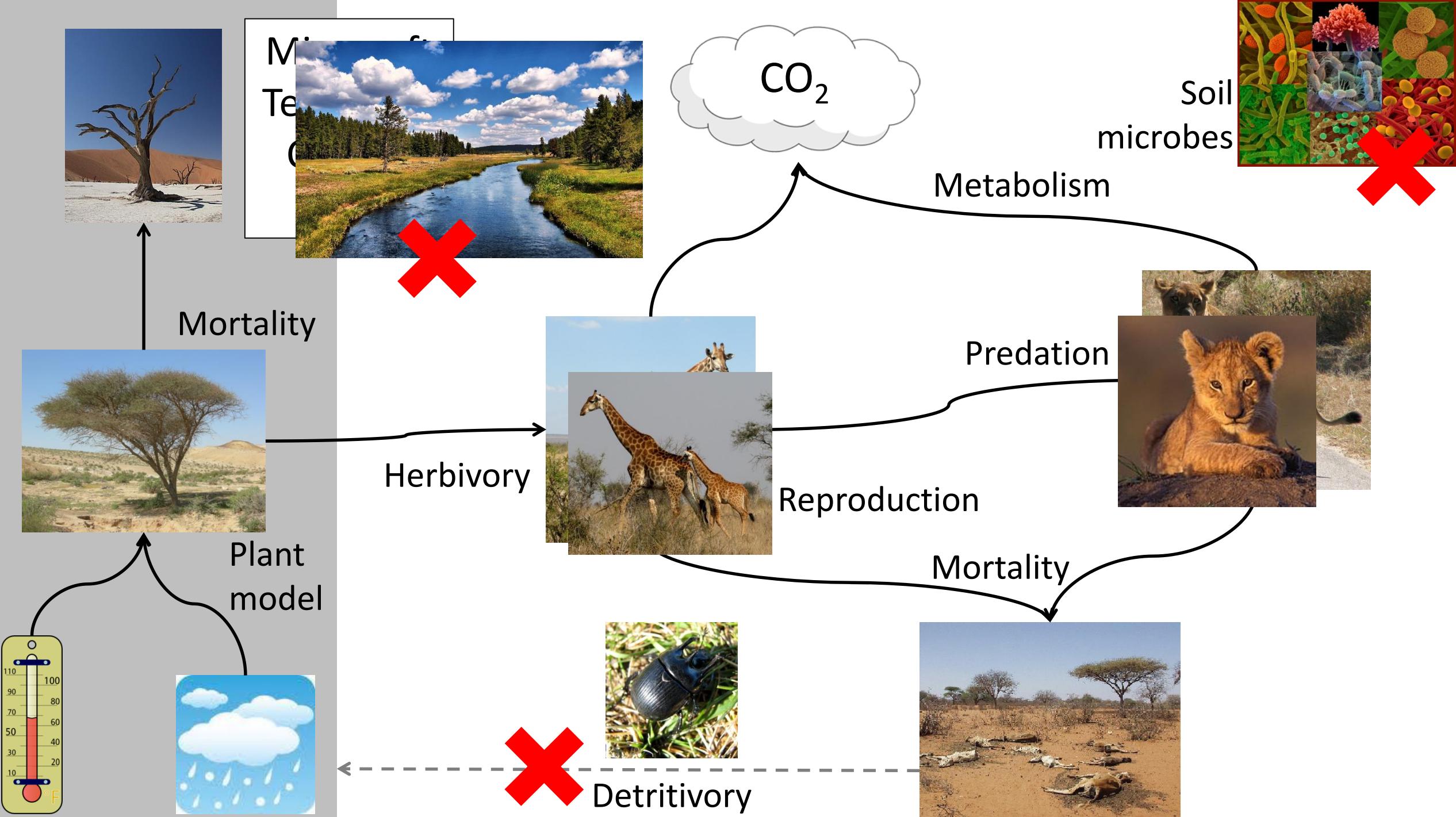
A hyena surveys a flock of flamingos in South Africa.

YI LIU/GETTY IMAGES

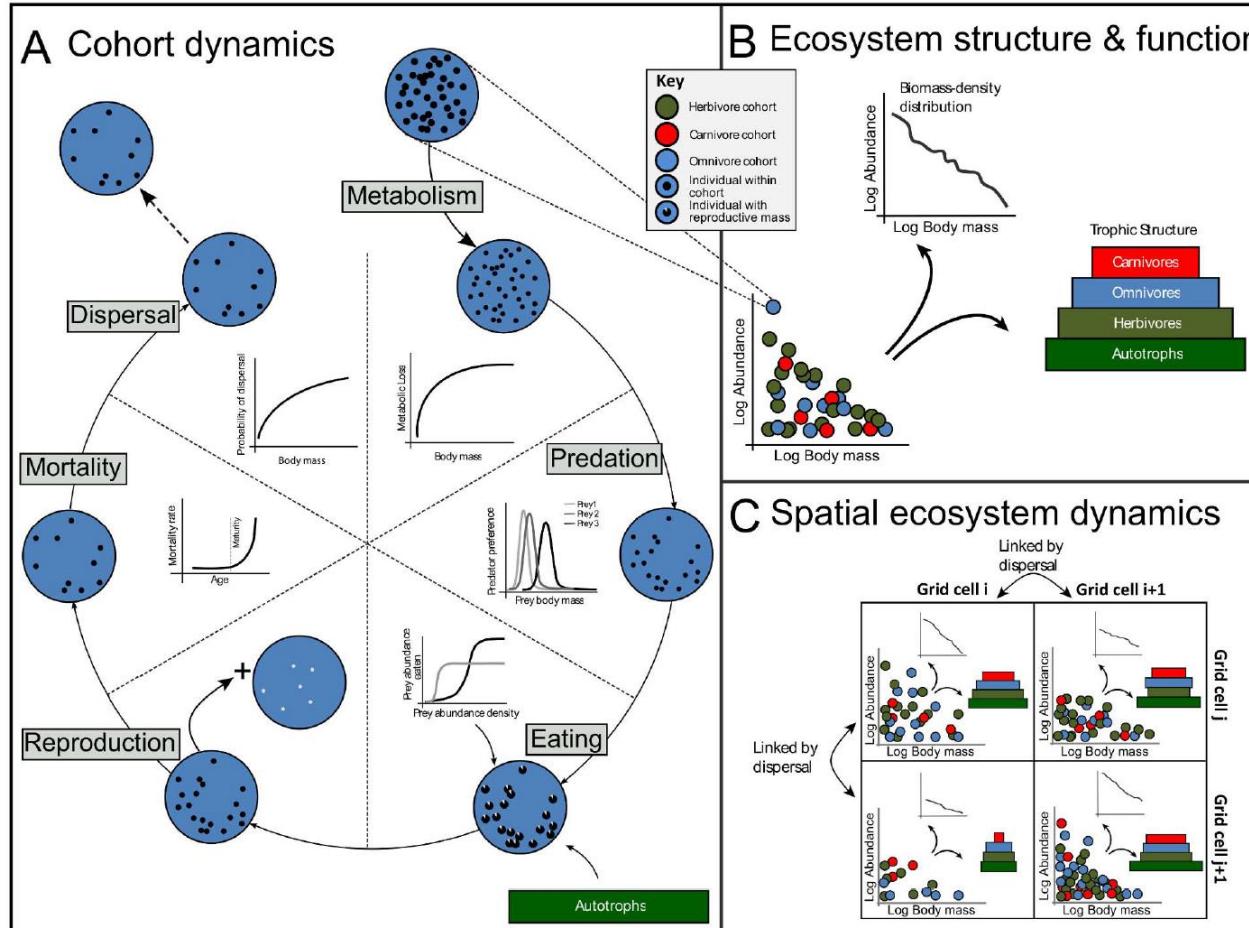
Time to model all life on Earth

# 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

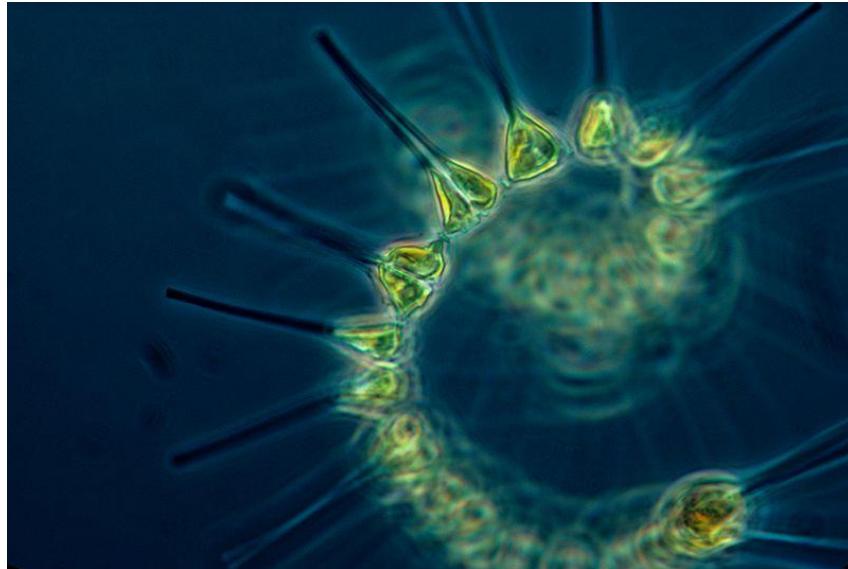
Iteroparous

Mobile

Marine



# An individual-based model would be computationally intractable



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



Up to c. 2500 per km<sup>2</sup>  
(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

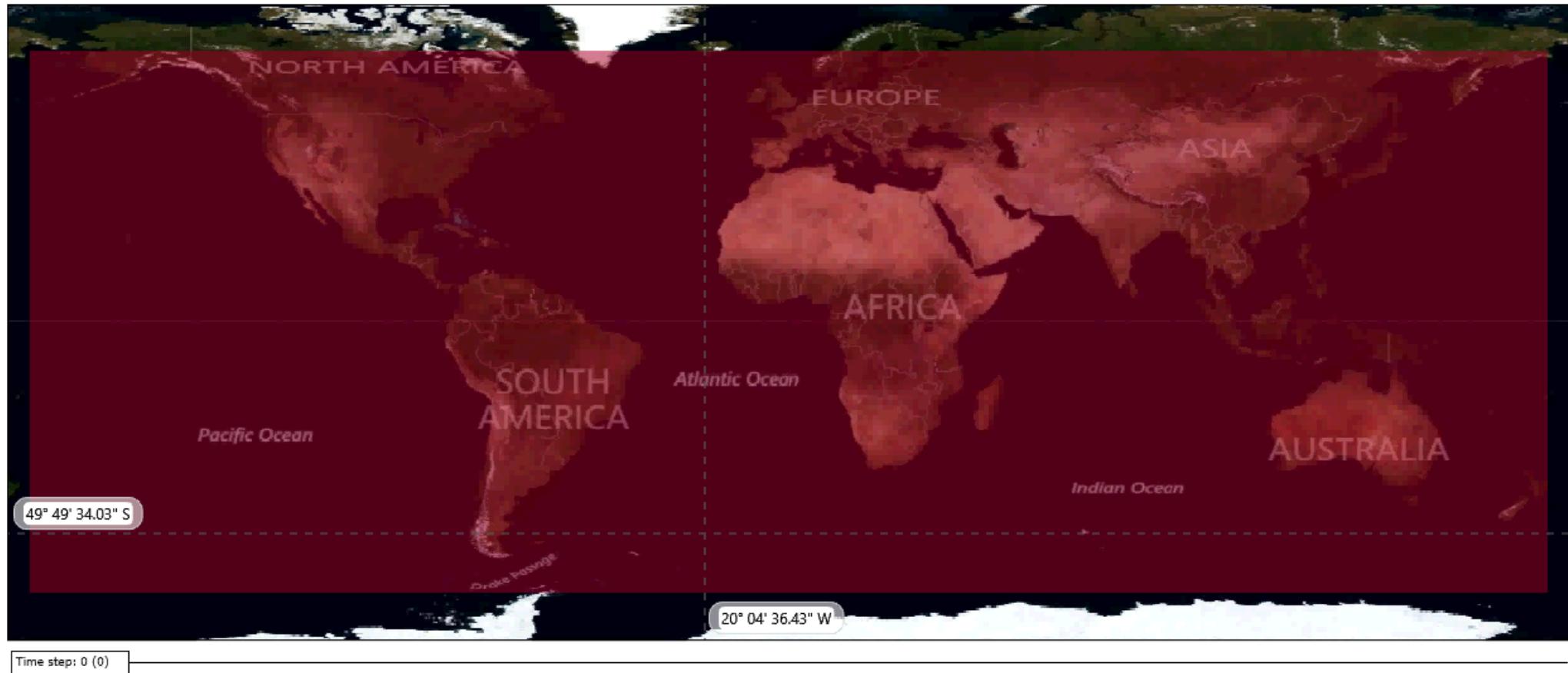


# An individual-based model would be computationally intractable

Cohort-based model for a single ecosystem:  $\approx 10$  hours

Individual-based model:  $\approx 47$  billion years

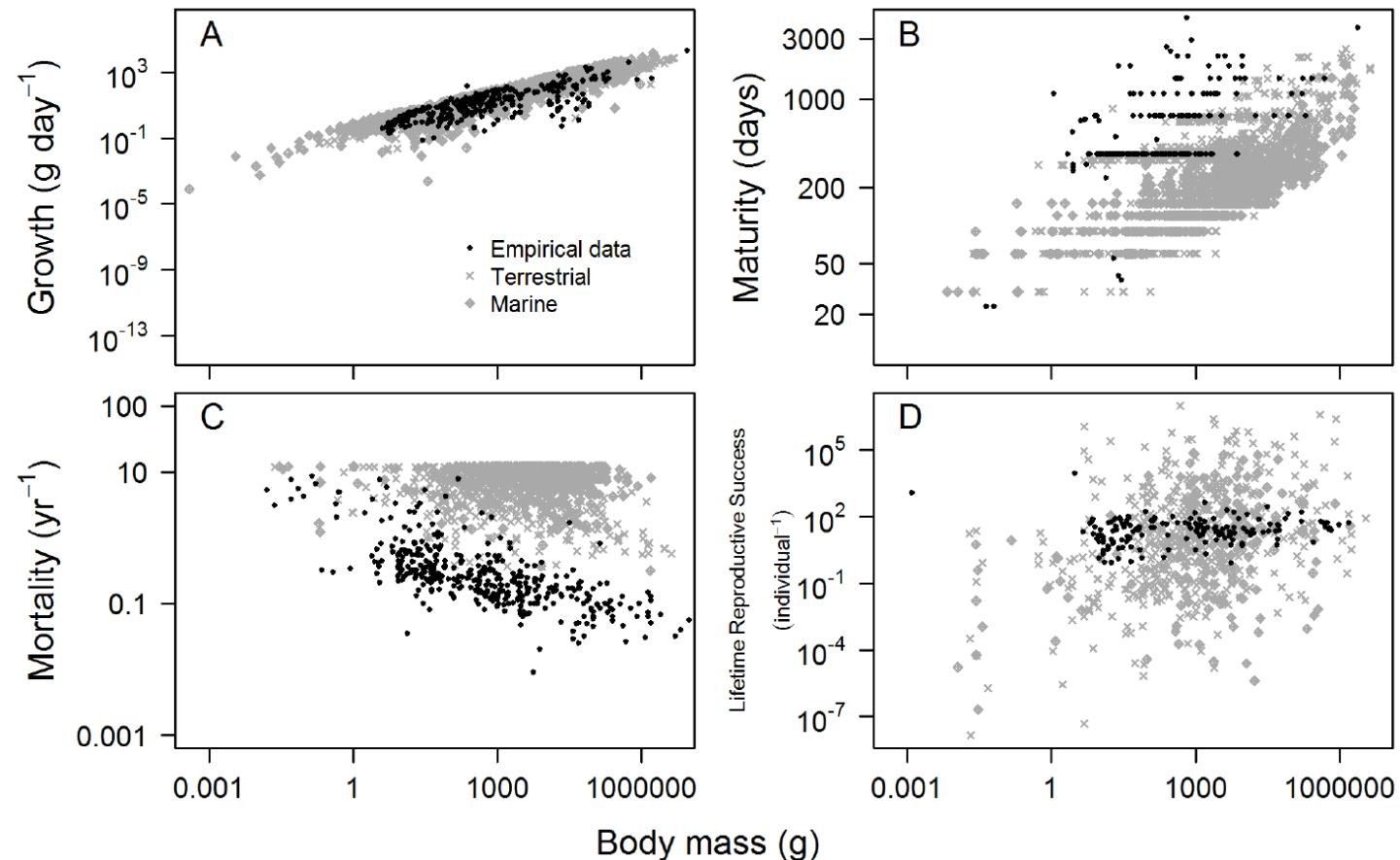
# Emergent biomass patterns



# Correspondence with empirical data: individual-level process rates

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

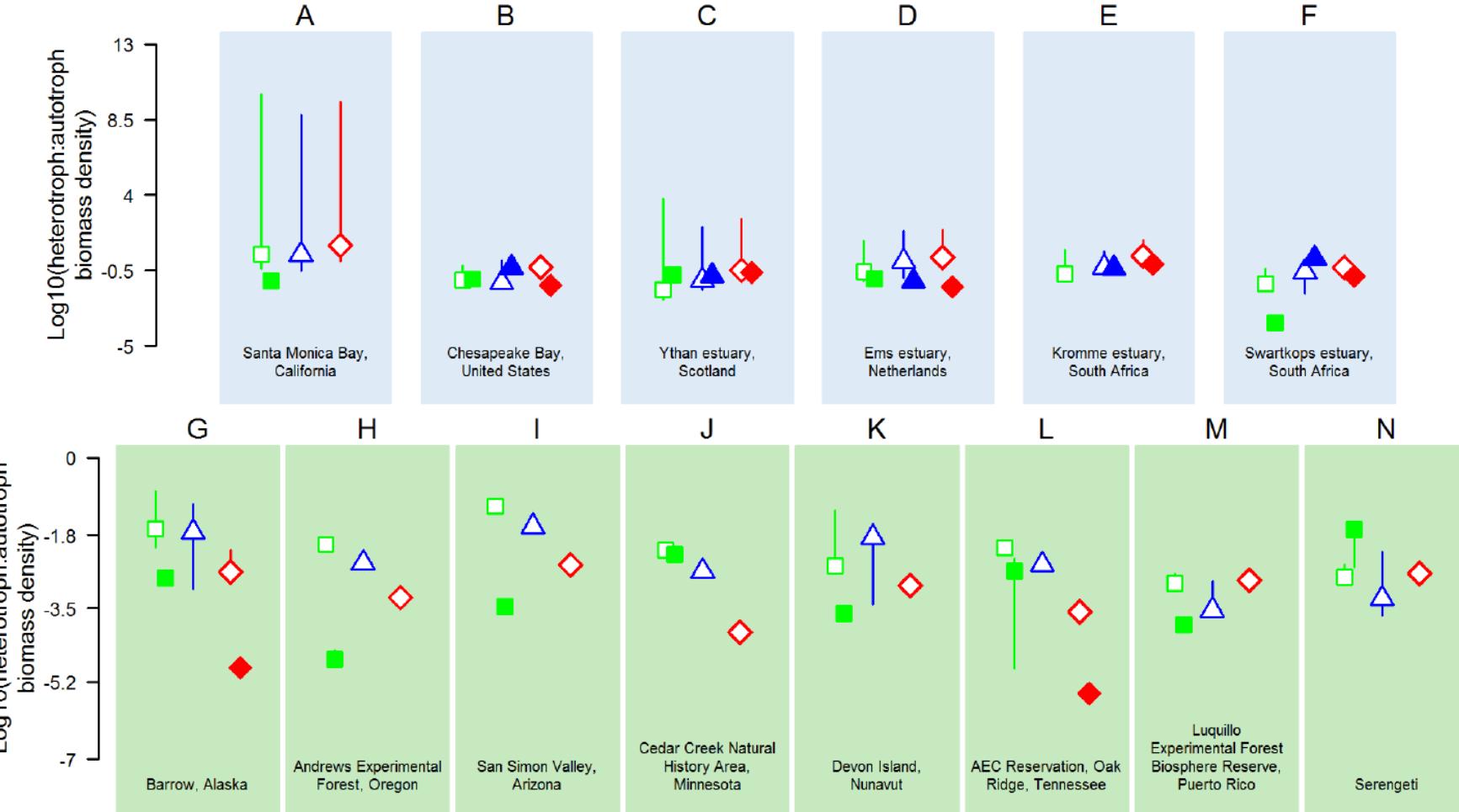
Mortality rates don't match observed scaling with mass



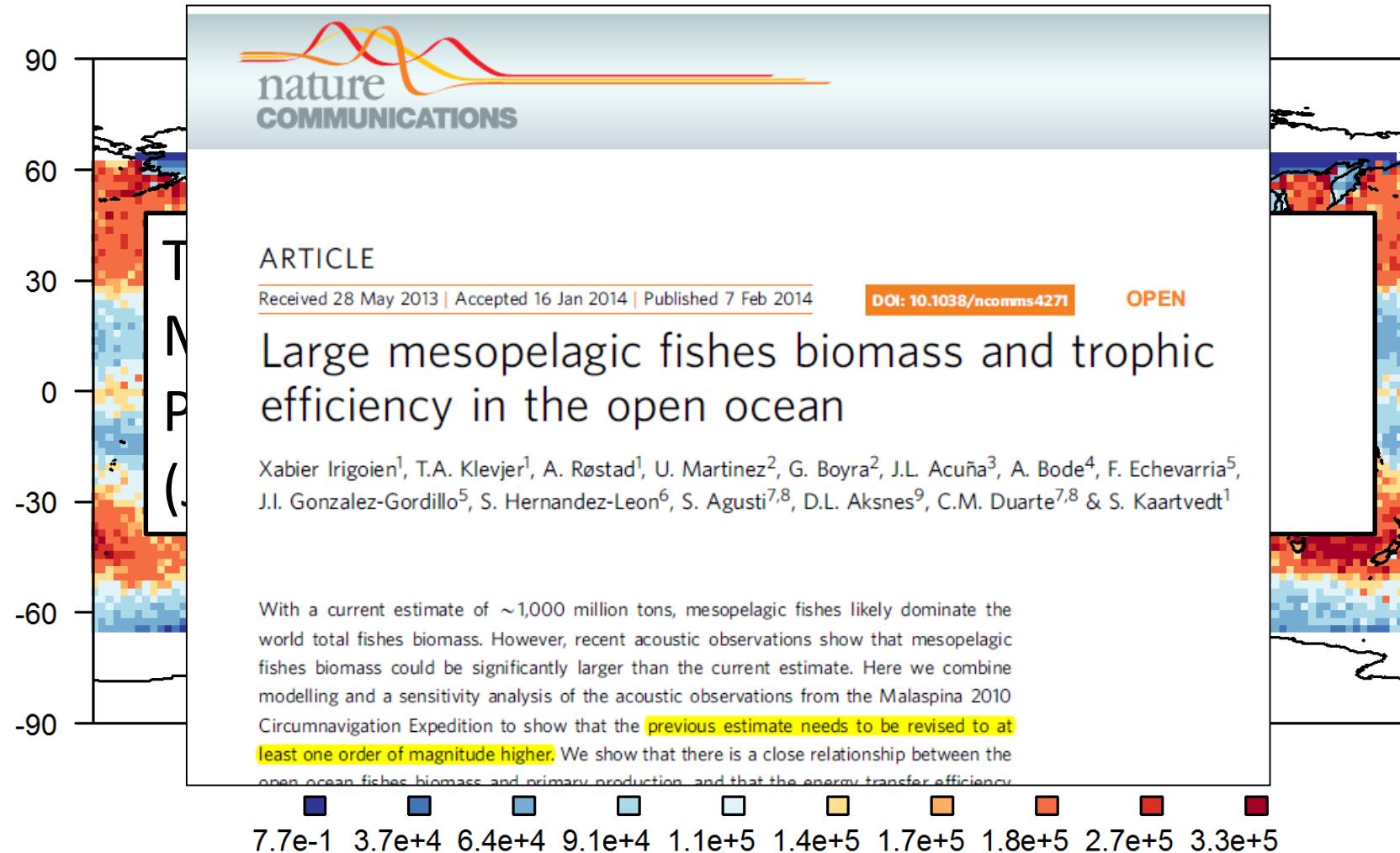
# Correspondence with empirical data: individual-level process rates

Match with empirical data generally good in marine systems

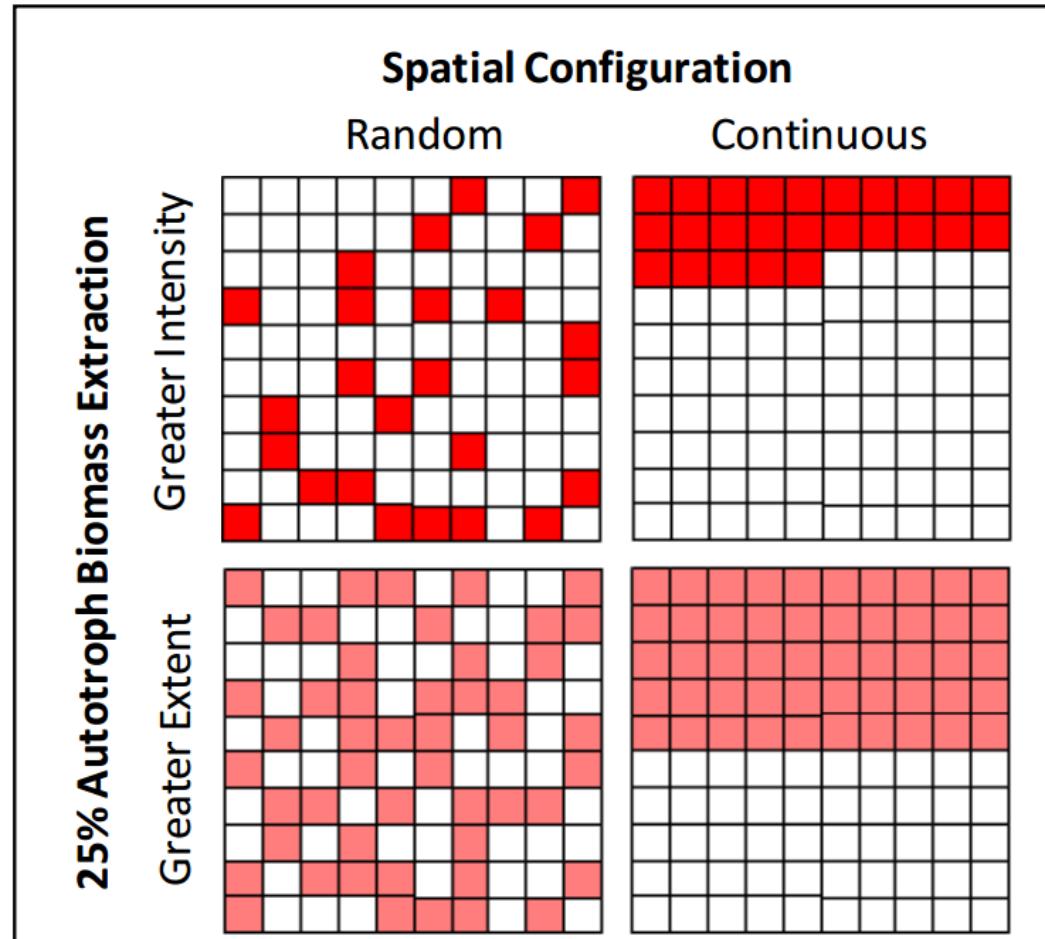
On land, better for grassland ecosystems than forests – vertical vegetation structure?



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



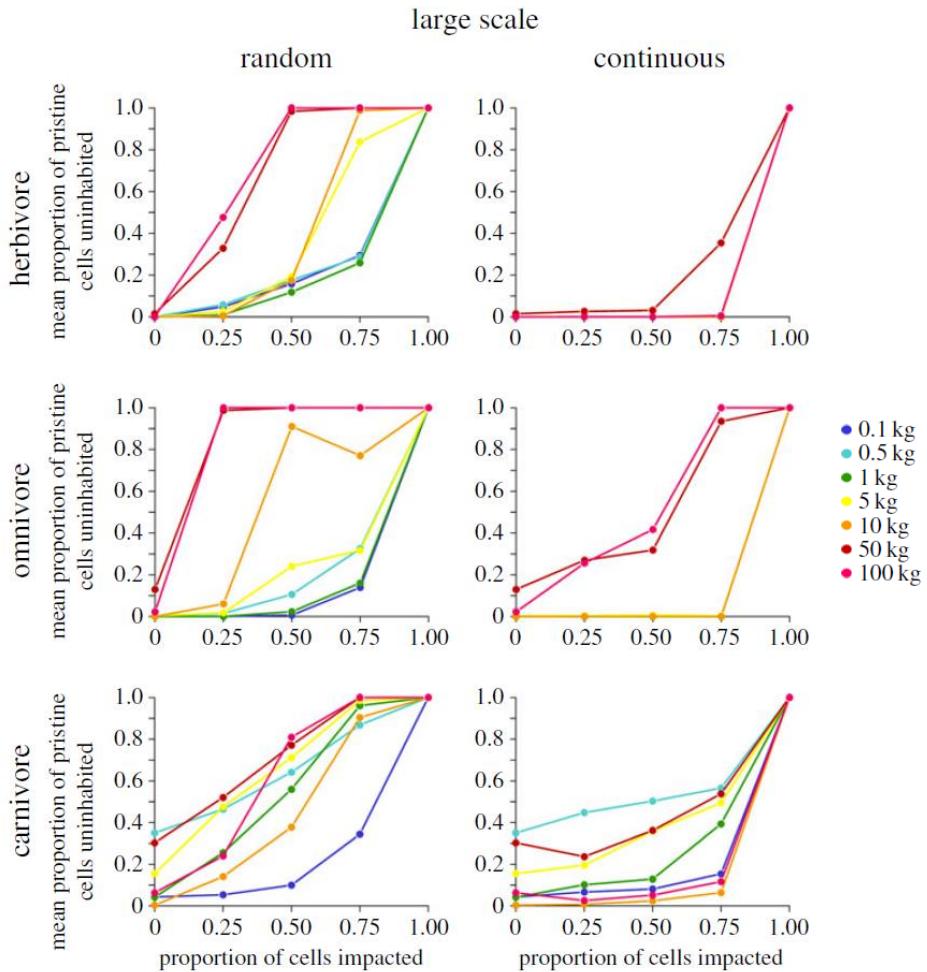
# Applications of general ecosystem models: effects of habitat fragmentation



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!)

- Bartlett et al. (2016). Synergistic impacts of habitat loss and fragmentation on model ecosystems. *Proceedings of the Royal Society of London, Series B* **283**: 20161027.
- Christensen & Walters (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**: 109-139.
- Cramer et al. (2001). Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**: 357-373.
- Cramer et al. (2004). Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. *Philosophical Transactions of the Royal Society, Series B* **359**: 331-343.
- Dichmont et al. (2013). Evaluating marine spatial closures with conflicting fisheries and conservation objectives. *Journal of Applied Ecology* **50**: 1060-1070.
- Fulton et al. (2011). Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish & Fisheries* **12**: 171-188.
- Fulton (2011). Interesting times: winners, losers, and system shifts under climate change around Australia. *ICES J Marine Science* **68**: 1329-1342.

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- Harfoot et al. (2014). Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. *PLoS Biology* **12**: e1001841.
- Higgins & Scheiter (2012). Atmospheric CO<sub>2</sub> forces abrupt vegetation shifts locally, but not globally. *Nature* **488**: 209-212.
- Mumby et al. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature* **450**: 98-101.
- Prentice et al. (2007). Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In *Terrestrial Ecosystems in a Changing World*. Springer.
- Purves et al. (2013). Time to model all life on Earth. *Nature* **493**: 295-297.
- Richardson (2008). In hot water: zooplankton and climate change. *ICES Journal of Marine Science* **65**: 279-295.
- Scheiter & Higgins (2009). Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Global Change Biology* **15**: 2224-2246.
- Sitch et al. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* **9**: 161-185.
- Smith et al. (2015). An investigation into fisheries interaction effects using Atlantis. *ICES Journal of Marine Science* **72**: 275-283.

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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.

Travers et al. (2007). Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography* **75**: 751-770.