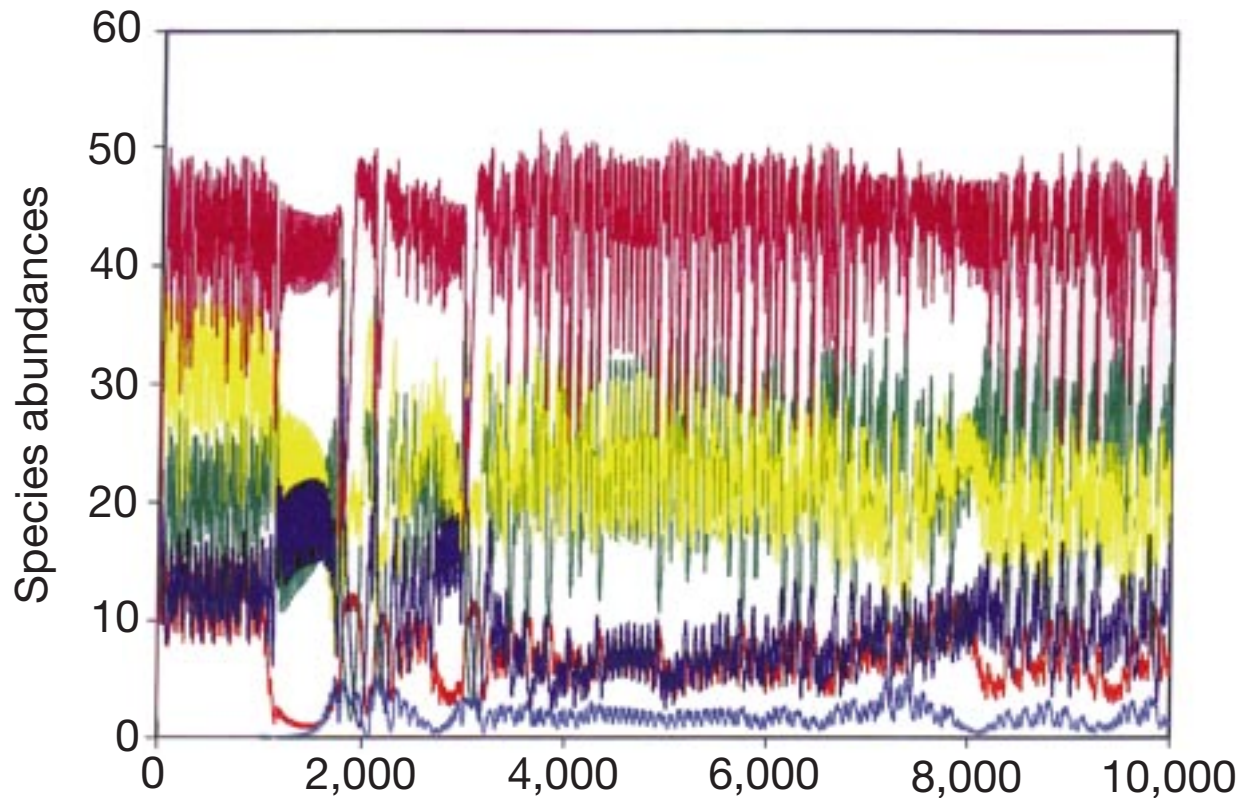


# Non equilibrium co-existence



Competitive chaos and  
the coexistence of 12  
species on five resources

Biodiversity has both fascinated and puzzled biologists. A simple resource competition model can generate oscillations and chaos when species compete for three or more resources. These oscillations and chaotic fluctuations in species abundances allow the coexistence of many species on a handful of resources. [Huisman & Weissing, Nature, 1999]

# Density dependent predation

## Toward a trophic theory of species diversity

**John W. Terborgh<sup>1</sup>**

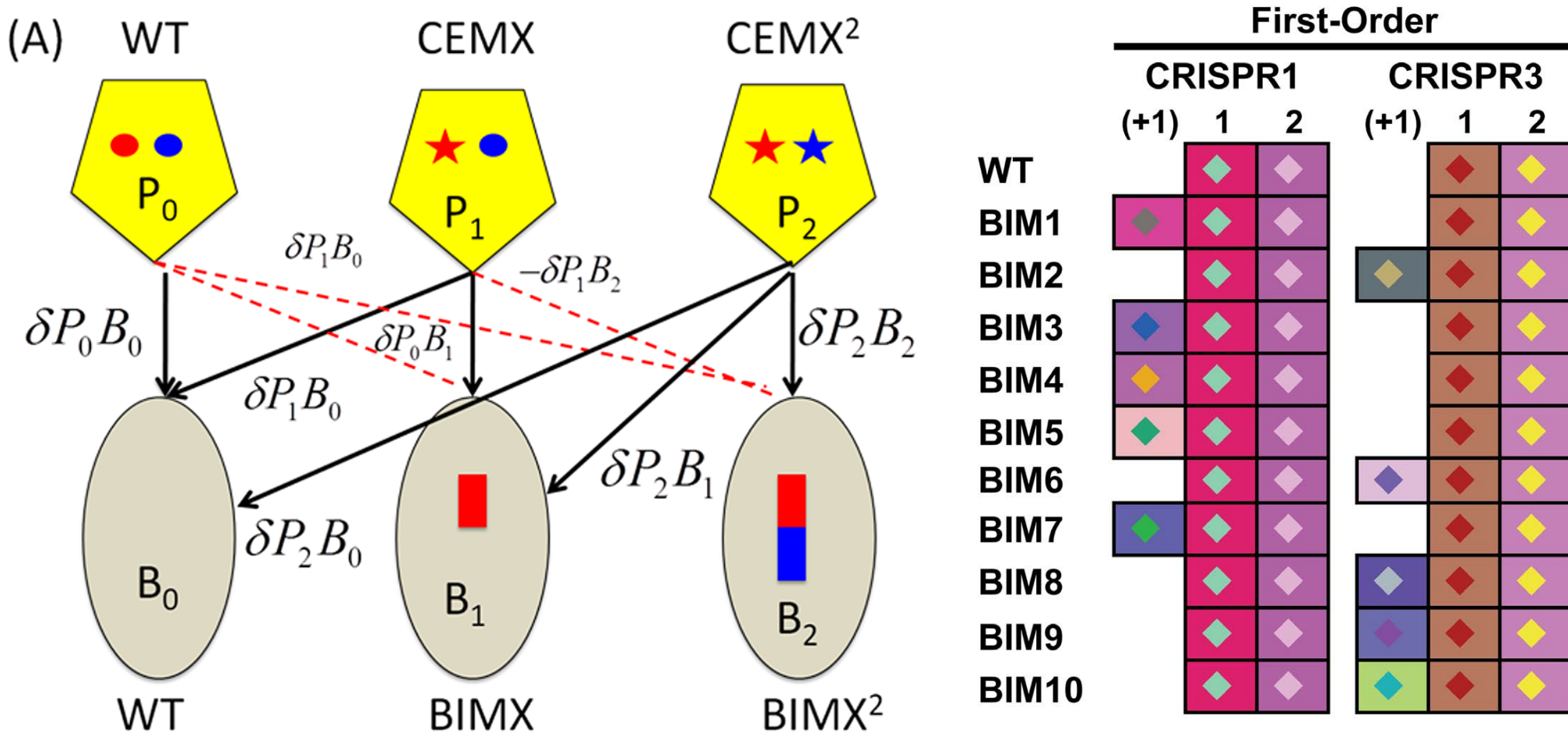
*Center for Tropical Conservation, Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27708*

Edited by Simon A. Levin, Princeton University, Princeton, NJ, and approved August 10, 2015 (received for review February 6, 2015)

Efforts to understand the ecological regulation of species diversity via bottom-up approaches have failed to yield a consensus theory. Theories based on the alternative of top-down regulation have fared better. Paine's discovery of keystone predation demonstrated that the regulation of diversity via top-down forcing could be simple, strong, and direct, yet ecologists have persistently failed to perceive generality in Paine's result. Removing top predators destabilizes many systems and drives transitions to radically distinct alternative states. These transitions typically involve community reorganization and loss of diversity, implying that top-down forcing is crucial to diversity maintenance. Contrary to the expectations of bottom-up theories, many terrestrial herbivores and mesopredators are capable of sustained order-of-magnitude population increases following release from predation, **negating the assumption that populations of primary consumers are resource limited** and at or near carrying capacity. Predation *sensu lato* (to include Janzen–Connell mortality agents) has been shown to promote diversity in a wide range of ecosystems, including rocky intertidal shelves, coral reefs, the nearshore ocean, streams, lakes, temperate and tropical forests, and arctic tundra. The compelling variety of these ecosystems suggests that top-down forcing plays a universal role in regulating diversity. This conclusion is further supported by studies showing that the reduction or absence of predation leads to diversity loss and, in the more dramatic cases, to catastrophic regime change. Here, I expand on the thesis that diversity is maintained by the interaction between predation and competition, such that strong top-down forcing reduces competition, allowing coexistence.

carrying capacity | interspecific competition | predation | species diversity | trophic cascades

# CRISPR mediated immunity



Bacteria pick up DNA fragments from phages. They 'store' these fragments in their own genome to become immune to phages expressing these sequences [Levin *et al.* PLoS Genetics 2013]

# Group formation and predator-prey dynamics



Lions living in groups have a lower food intake but have better stability.  
But is this an ESS? [Fryxell *et al.* Science, 2007]

# Apparent competition structures ecological assemblages

**M. B. Bonsall & M. P. Hassell**

*Department of Biology and the NERC Centre for Population Biology,  
Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, UK*



Nature 1997

We find that whereas the two separate, single host-single parasitoid interactions are persistent, the three-species system with the parasitoid attacking both hosts species (which are not allowed to compete directly) is unstable. One of the host species is eliminated owing to the effects of apparent competition.

Also study equal predation

# Competitive exclusion and parasitism

We studied the effect of a pathogen on winning species:

$$S_j' = bN_j(1 - N_j/k) - d_j S_j - \beta S_j I_j$$

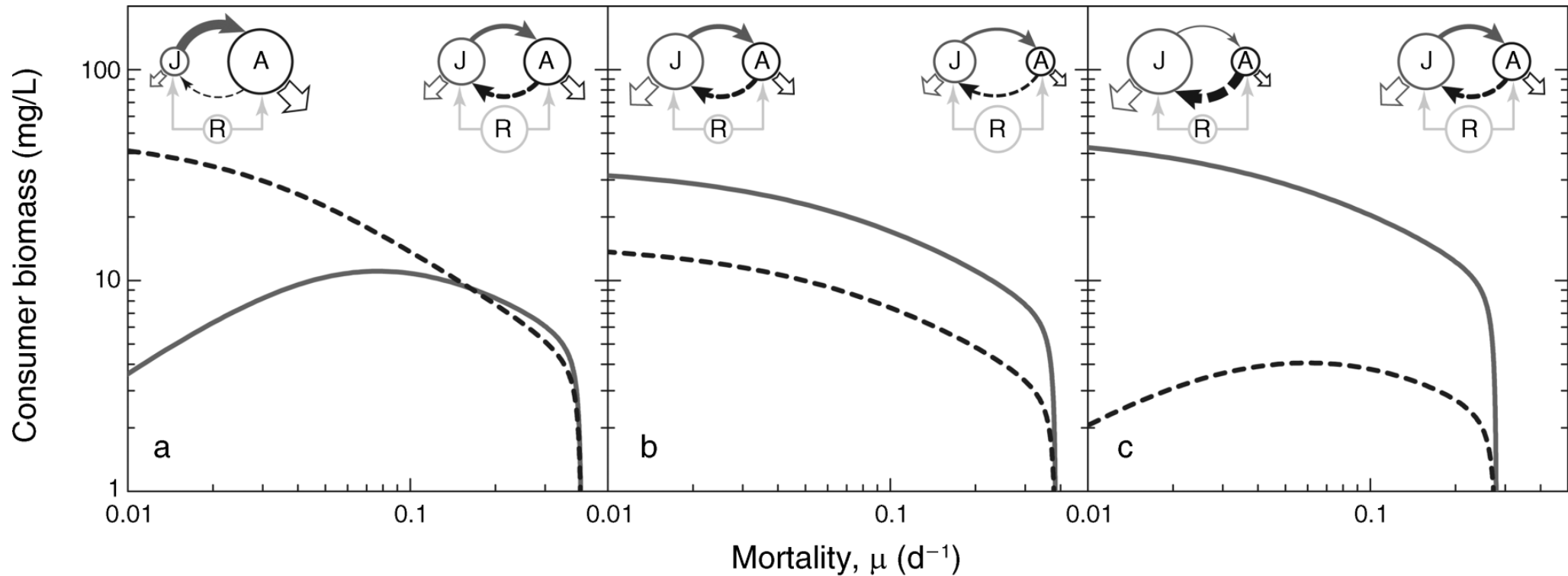
$$I_j' = \beta S_j I_j - (d_j + \delta) I_j$$

Janzen-Connell hypothesis: parasites evolve towards most dominant species (negative density dependence)

[Bagchi *et al.*, Nature, 2014]

What is the effect of pathogens on co-existence?

# Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults



Persson & De Roos Ecology 2013; De Roos & Persson, Princeton UP, 2013

Ontogenetic development for dummies, try to repeat these results with:

$$R = K - c_1 J - c_2 A, \quad \frac{dJ}{dt} = \frac{eAR}{h_2 + R} - \frac{mJR}{h_1 + R} - \mu d_1 J \quad \text{and} \quad \frac{dA}{dt} = \frac{mJR}{h_1 + R} - \mu d_2 A$$

# Long term effects of vaccination

Fire

Elephants

Wildebeest

Rainfall



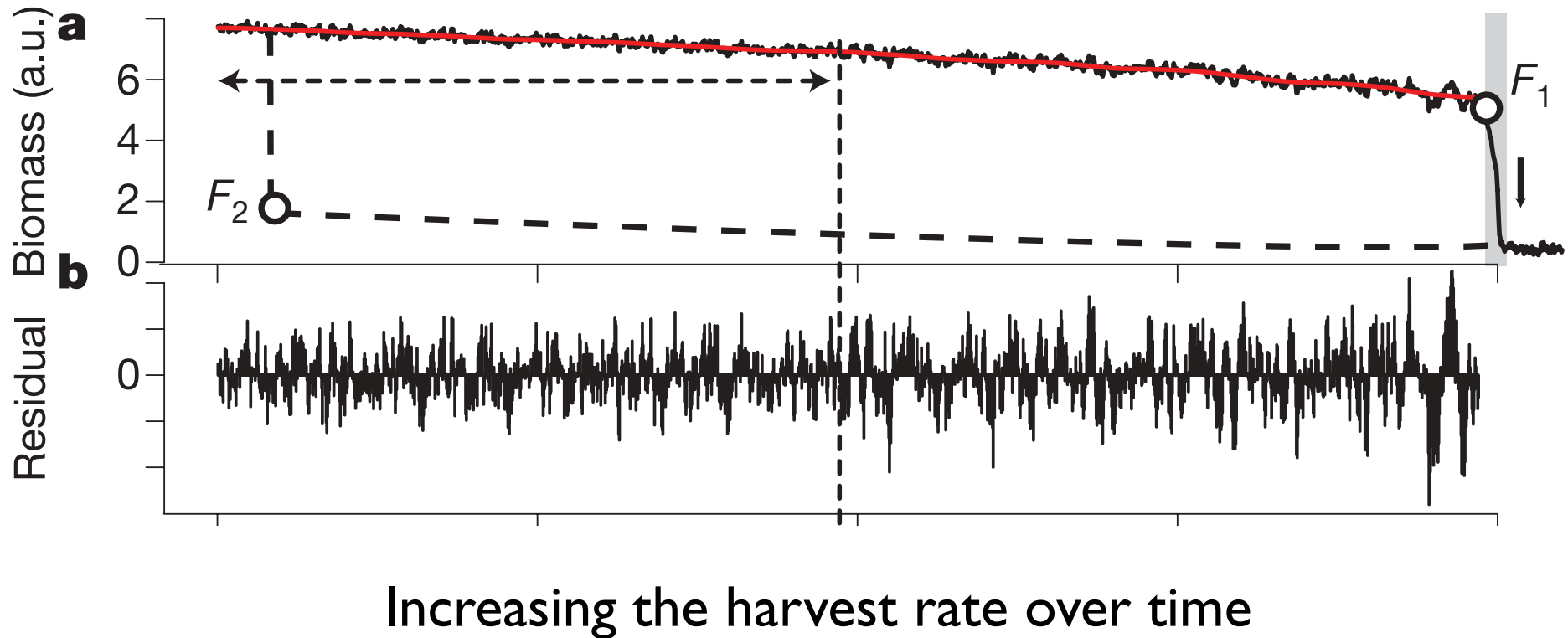
Getz, PLoS Biol 2009

The effect of elephants is through regular browsing and coppicing of trees, fire through episodic burns linked to fuel load, wildebeest after being released from the suppressing effects of endemic rinderpest (a morbillivirus of artiodactyls), and rain through its connections to all system components.

Holdo et al. [2009] demonstrate that eradication of rinderpest is responsible for the Serengeti switch from a net source to net accumulator of carbon.

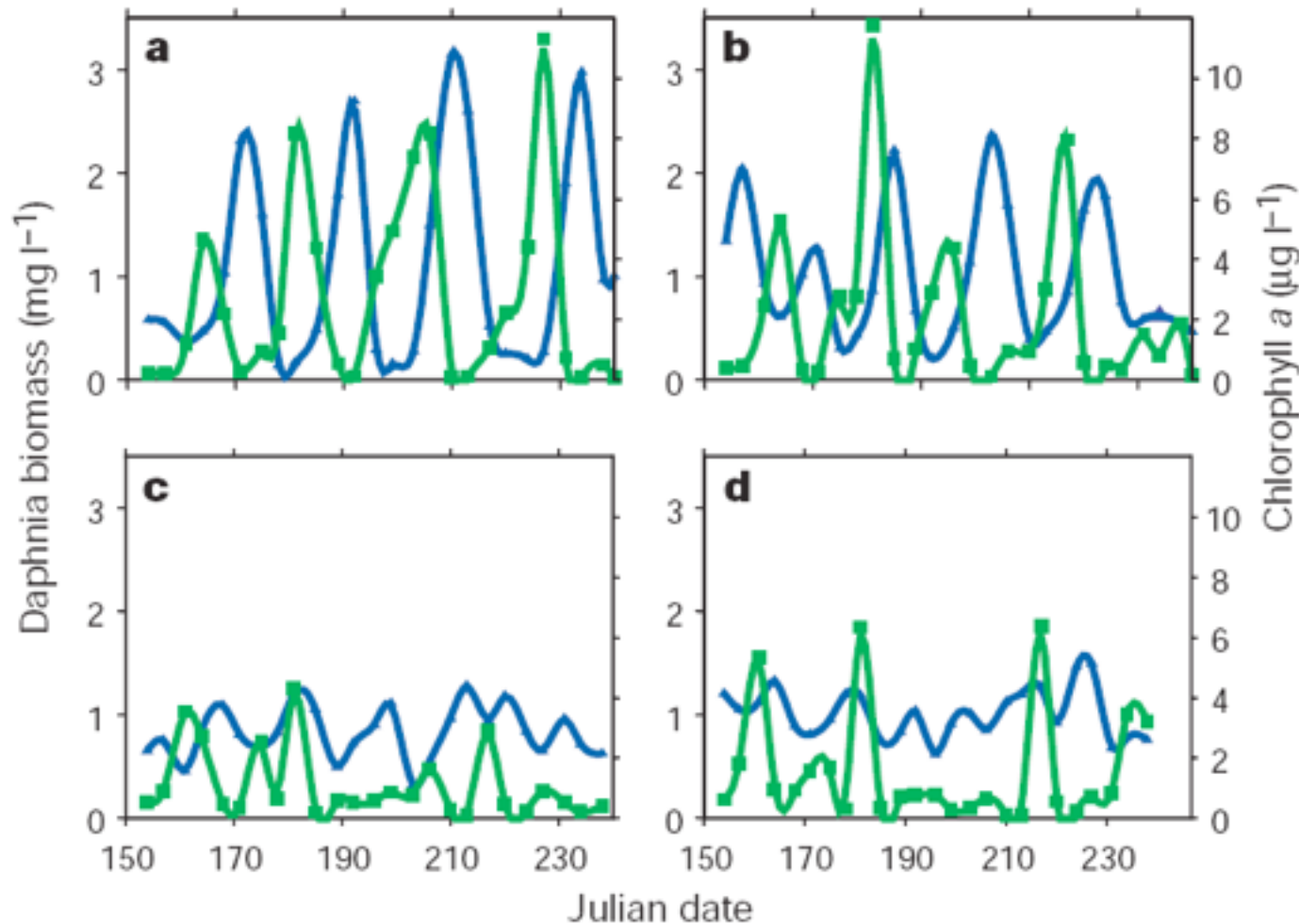


# Early-warning signals for critical transitions



Ecosystems can have tipping points at which a sudden shift to a contrasting dynamical regime may occur. Although predicting such critical points is extremely difficult, generic early-warning signals may indicate that a critical threshold is approaching [Scheffer Nature 2009]

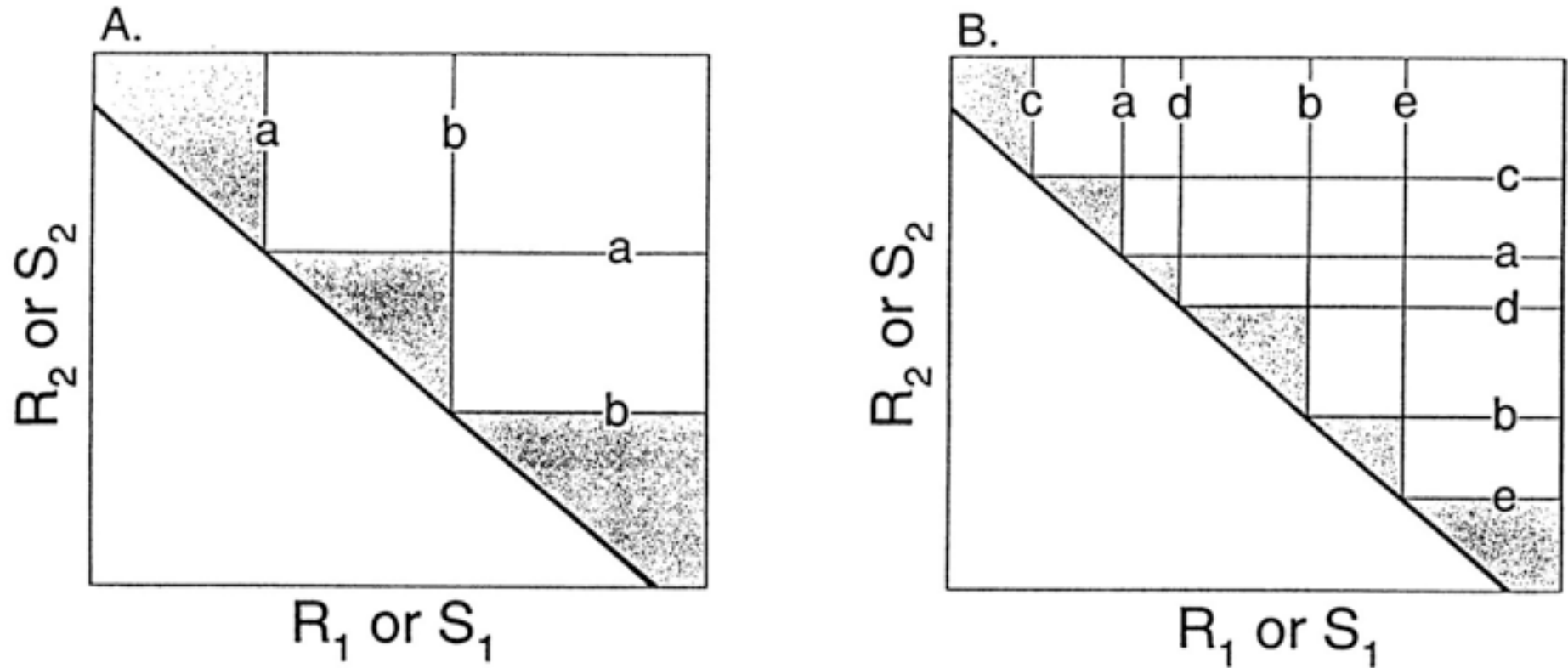
# Large-amplitude cycles of *Daphnia* and its algal prey in enriched environments



McCauley et al Nature 1999

$$f(R) = \frac{2R}{H + R + \sqrt{(H + R)^2 - 4\gamma HR}}$$

# Tilman's competition model: famous 1982 Princeton book, and PNAS 1997



What is the relation between diversity and productivity?

See also recent experimental tests:

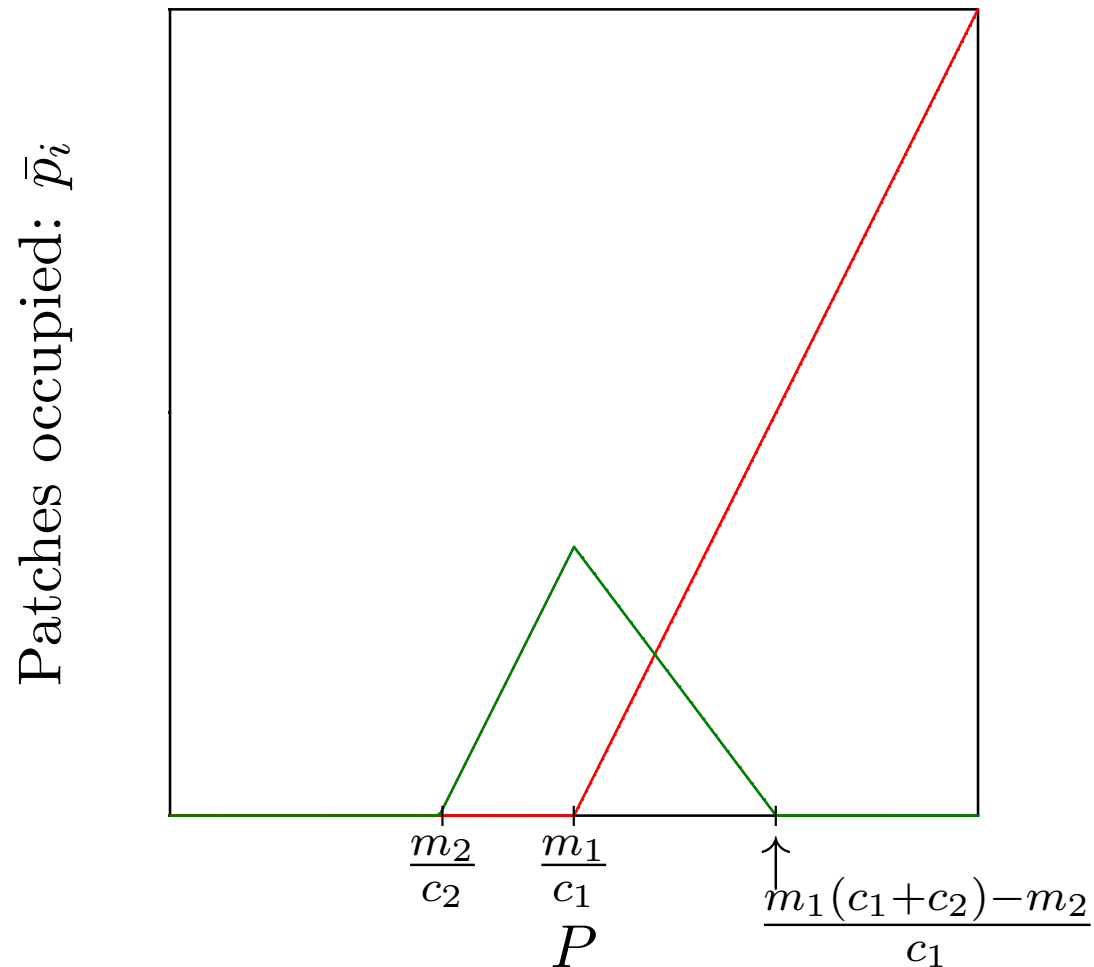
Dybziński & Tilman, *American Naturalist* 2007 & Adler et al. *Science* 2011

# Tilman's metapopulation model

## Habitat destruction and the extinction debt

David Tilman\*, Robert M. May†,  
Clarence L. Lehman\* & Martin A. Nowak†

Nature 1994



# Influenza strain replacement

## Mapping the Antigenic and Genetic Evolution of Influenza Virus

Derek J. Smith,<sup>1,2\*†</sup> Alan S. Lapedes,<sup>3\*</sup> Jan C. de Jong,<sup>2</sup>  
Theo M. Bestebroer,<sup>2</sup> Guus F. Rimmelzwaan,<sup>2</sup>  
Albert D. M. E. Osterhaus,<sup>2</sup> Ron A. M. Fouchier<sup>2\*</sup>

Study strain replacement within a season,  
and how this depends on the vaccine  
coverage at the start of the season.

