Biodiversity and stability of ecological systems: New perspectives on an old debate

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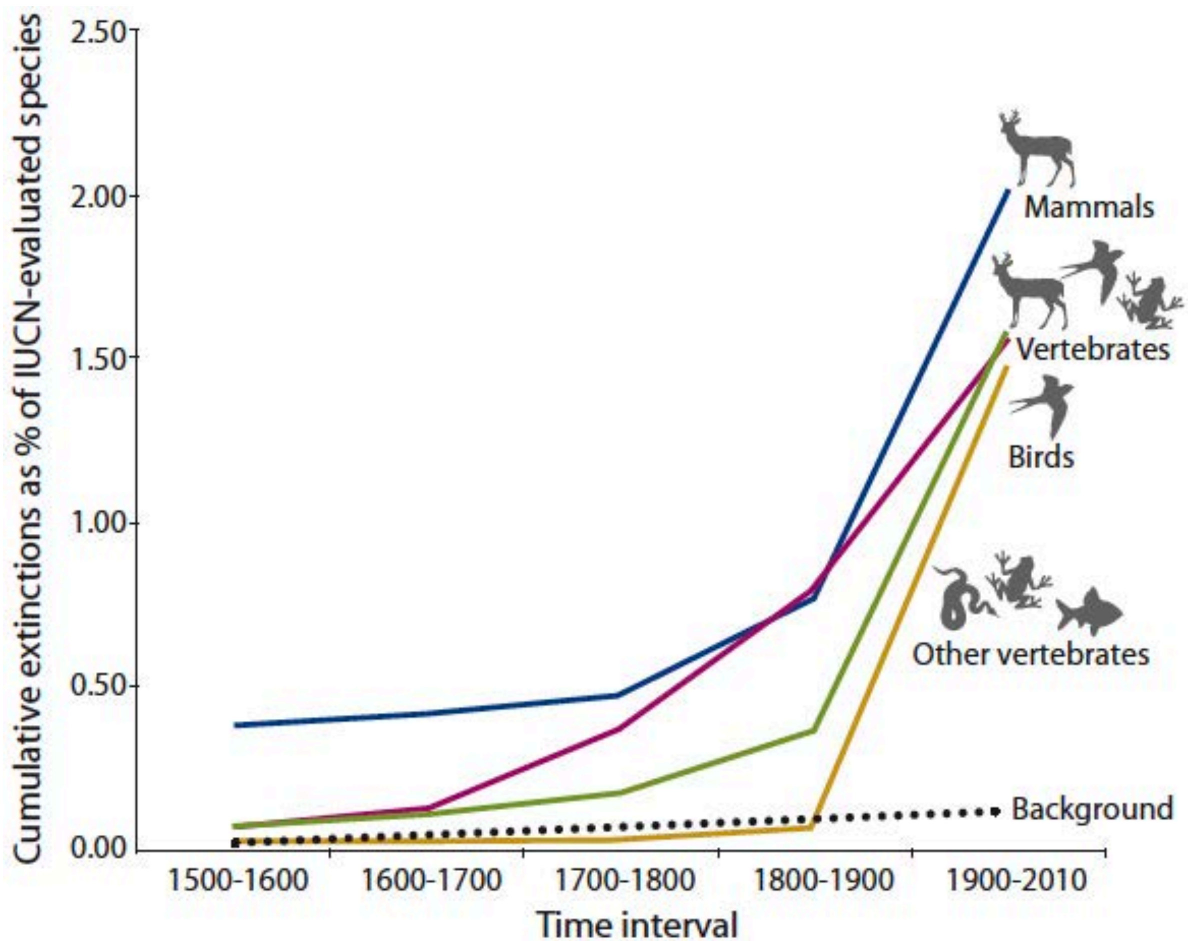
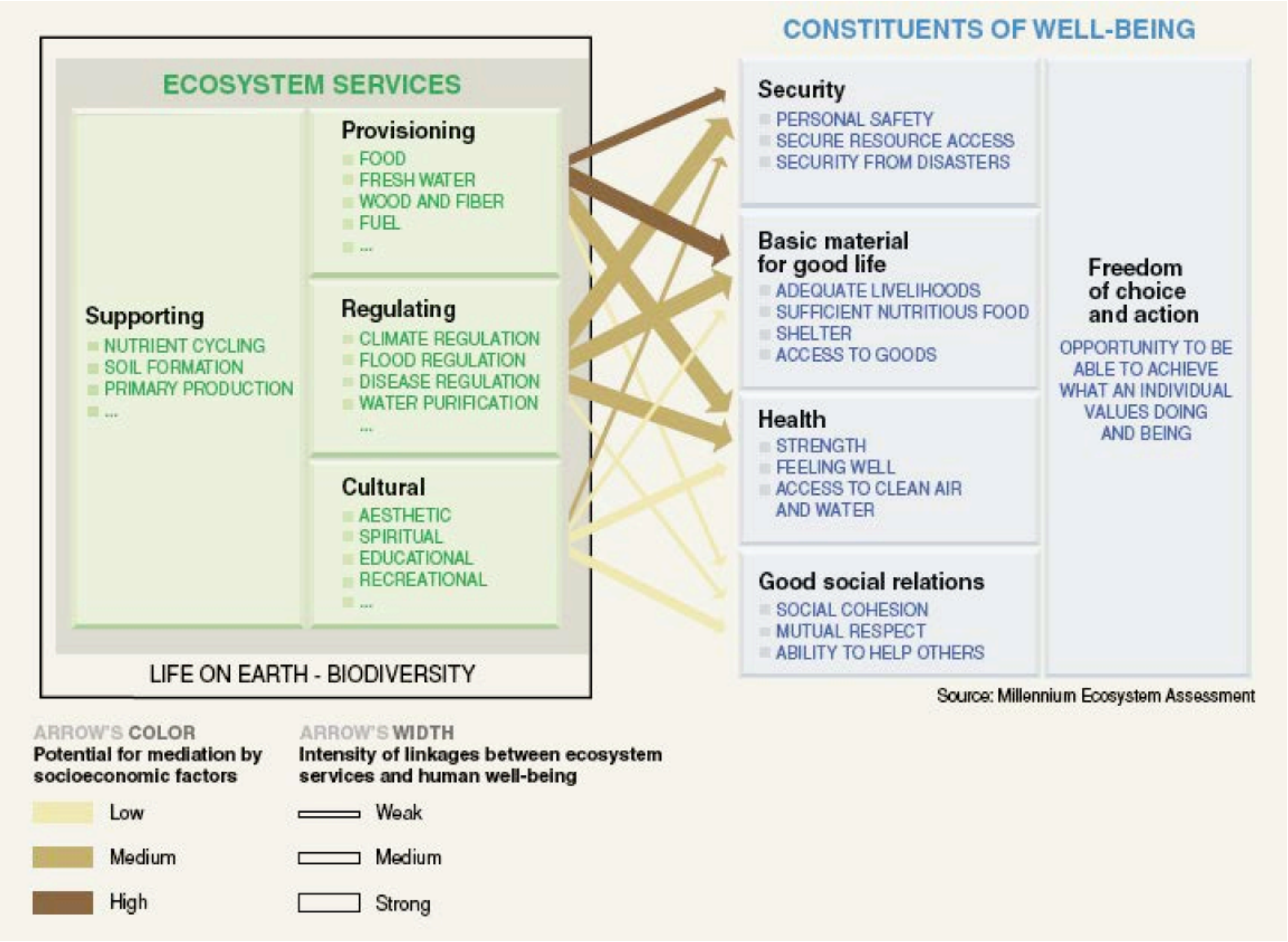
Heading for a sixth mass extinction



Ceballos et al., *Sci. Adv.* 1: e1400253 (2015)

How will biodiversity loss affect ecosystem functioning and human well-being?



Effects of biodiversity on ecosystem services

Category of service	Measure of service provision	SPU	Diversity level	Source	Study type	N	Relationship: Predicted	Relationship: Actual
Provisioning								
Crops	Crop yield	Plants	Genetic	DS	Exp	575	↗	↗
			Species	DS	Exp	100	↗	
Fisheries	Stability of fisheries yield	Fish	Species	PS	Obs	8	↗	↗
Wood	Wood production	Plants	Species	DS	Exp	53	↗	↗
Fodder	Fodder yield	Plants	Species	DS	Exp	271	↗	↗
Regulating								
Biocontrol	Abundance of herbivorous pests (bottom-up effect of plant diversity)	Plants	Species	DS*	Obs	40	↘	↘
		Plants	Species	DS†	Exp	100	↘	↘
		Plants	Species	DS‡	Exp	287	↘	
		Plants	Species	DS§	Exp	100	↘	0
	Abundance of herbivorous pests (top-down effect of natural enemy diversity)	Natural enemies	Species/trait	DS*	Obs	18	↘	↘
		Natural enemies	Species	DS†	Exp/Obs	266	↘	↘
		Natural enemies	Species	DS‡	Exp	38	↘	
	Resistance to plant invasion	Plants	Species	DS	Exp	120	↗	↗
	Disease prevalence (on plants)	Plants	Species	DS	Exp	107	↘	↘
	Disease prevalence (on animals)	Multiple	Species	DS	Exp/Obs	45	↘	
Climate	Primary production	Plants	Species	DS	Exp	7	↗	0
	Carbon sequestration	Plants	Species	DS	Exp	479	↗	↗
	Carbon storage	Plants	Species/trait	PS	Obs	33	↗	
Soil	Soil nutrient mineralization	Plants	Species	DS	Exp	103	↗	↗
	Soil organic matter	Plants	Species	DS	Exp	85	↗	↗
Water	Freshwater purification	Multiple	Genetic/species	PS	Exp	8	↗	0
Pollination	Pollination	Insects	Species	PS	Obs	7	↗	

Cardinale et al., *Nature* 486: 59–67 (2012)

What about the stability of ecosystem services?

- Large fluctuations in ecosystem services are harmful because the negative effects of scarcity are generally stronger than the positive effects of abundance

- Risk aversion is widespread, as attested by the importance of portfolios and insurance

- A positive effect of biodiversity on the stability of ecosystem services would be a powerful additional argument for biodiversity conservation

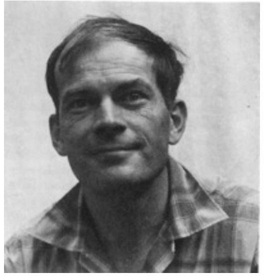
Diversity and stability of ecological systems: An old debate

The "conventional wisdom":
Diversity and complexity beget stability

- Regularity of species-rich ecosystems, "balance of nature" worldview
- Instability of simple theoretical and experimental models
- Fragility of species-poor island and human-modified ecosystems to biological invasions
- Stability conferred by alternative energy paths in food webs

Charles Elton

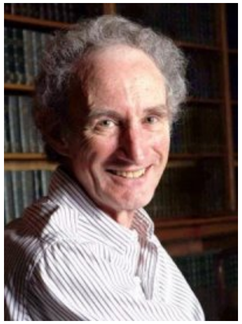
Eugene Odum



Robert MacArthur

Diversity and stability of ecological systems: An old debate

The new paradigm:
Diversity and complexity beget instability

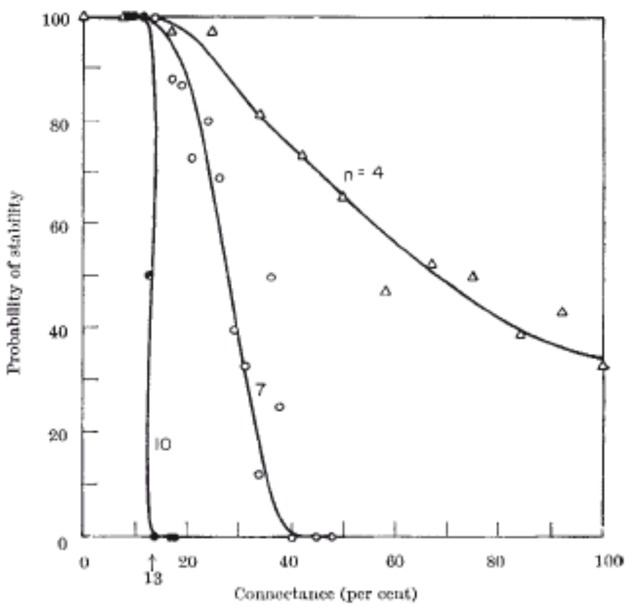


Robert May

Large complex systems that are assembled at random are almost certain to be stable up to a critical level of complexity, and then to suddenly become unstable, yielding the stability condition:

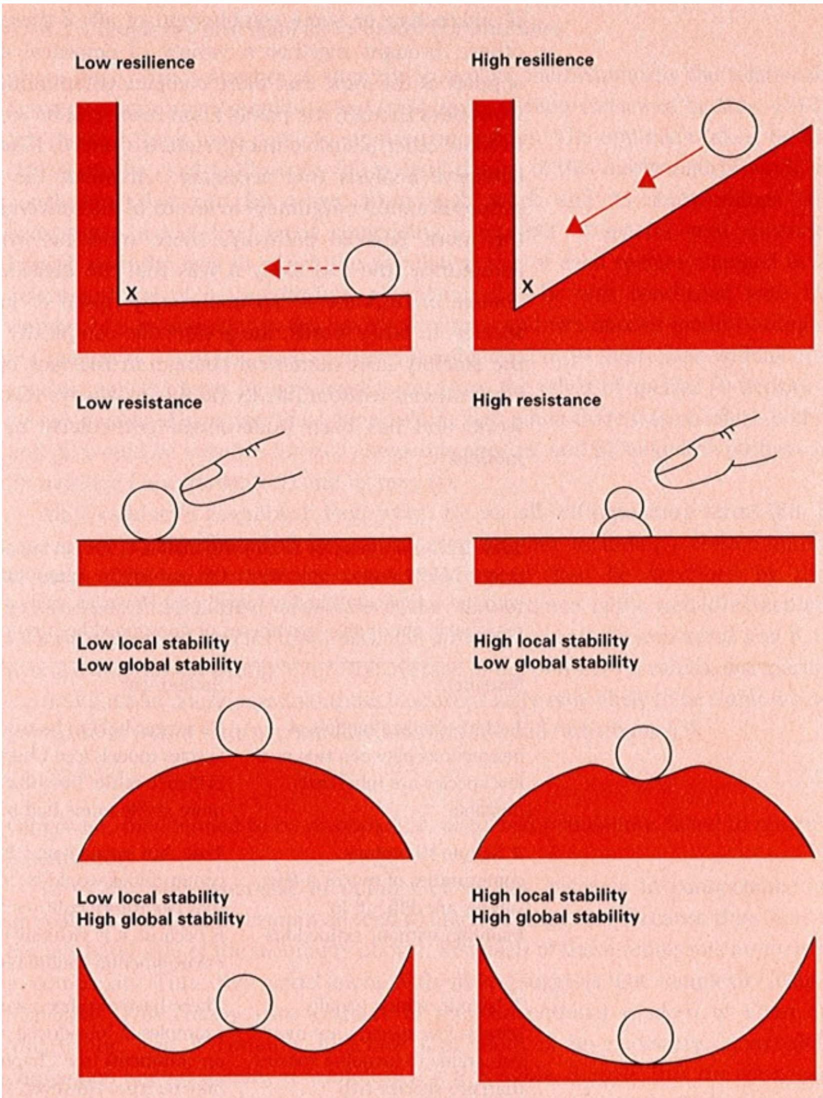
$$\overline{\beta}\sqrt{SC} < 1$$

S = number of species (diversity)
C = connectance
$\overline{\beta}$ = average interaction strength

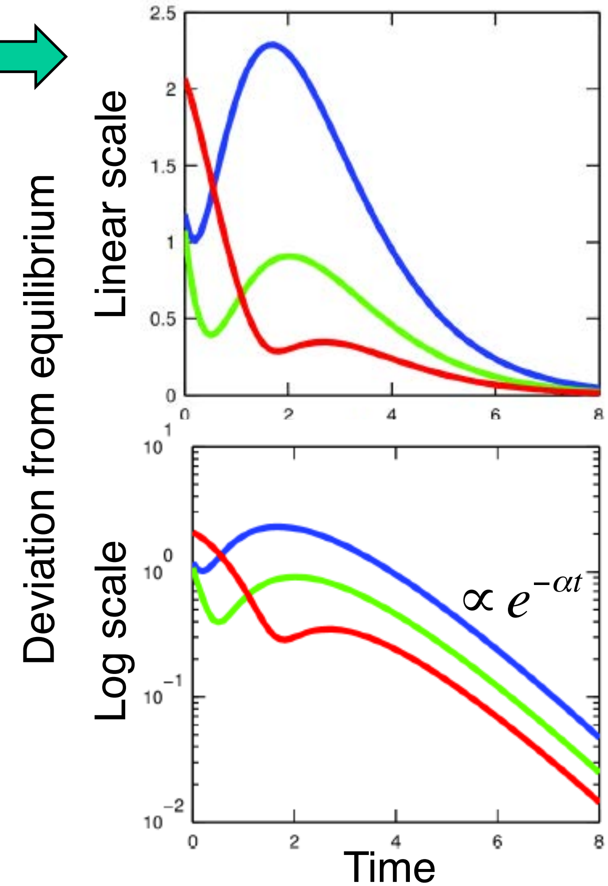


Gardner & Ashby, *Nature* 228: 784 (1970)

How theoreticians see the world

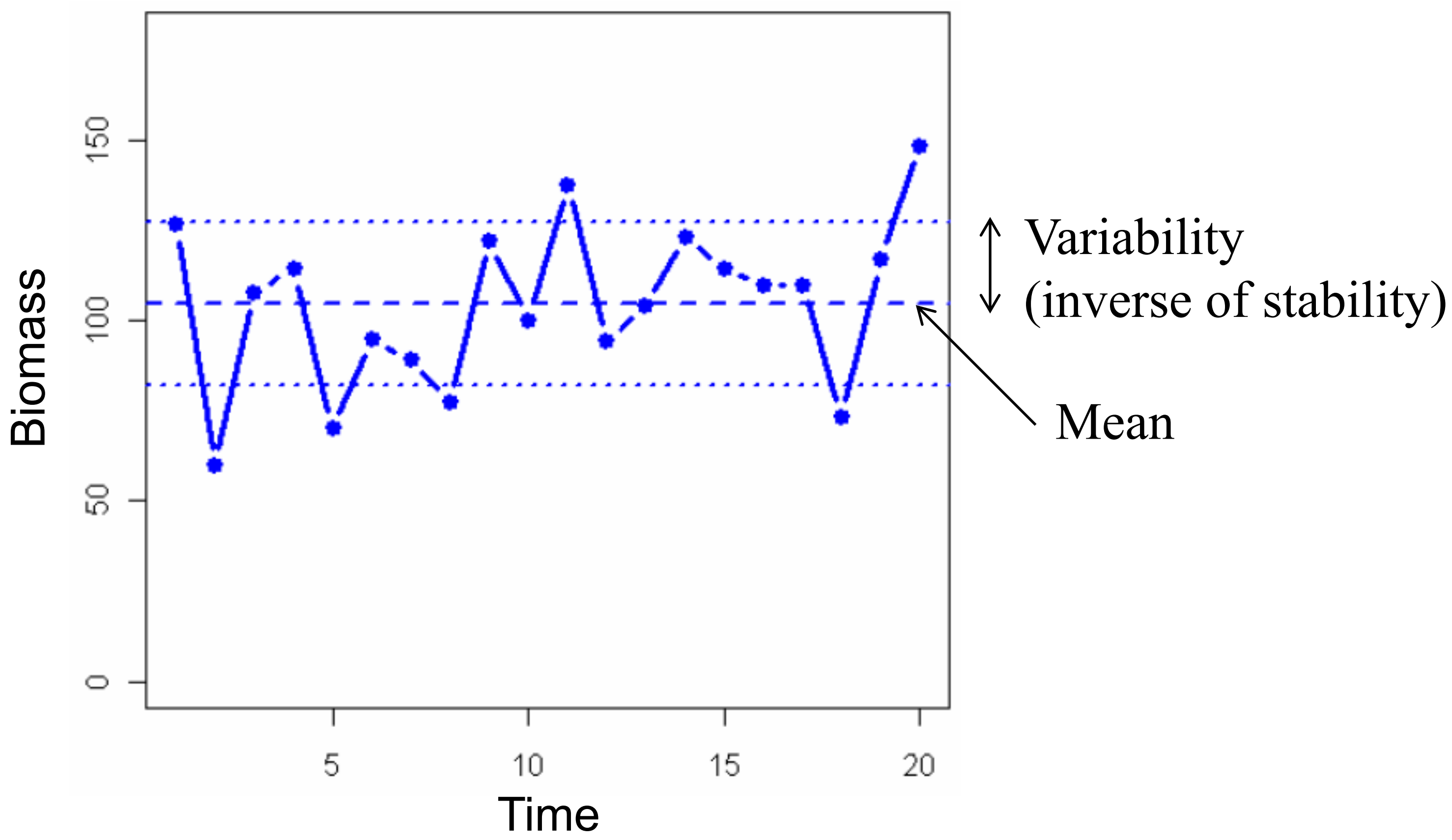


Begon et al., *Ecology*, 3rd ed. (1986)

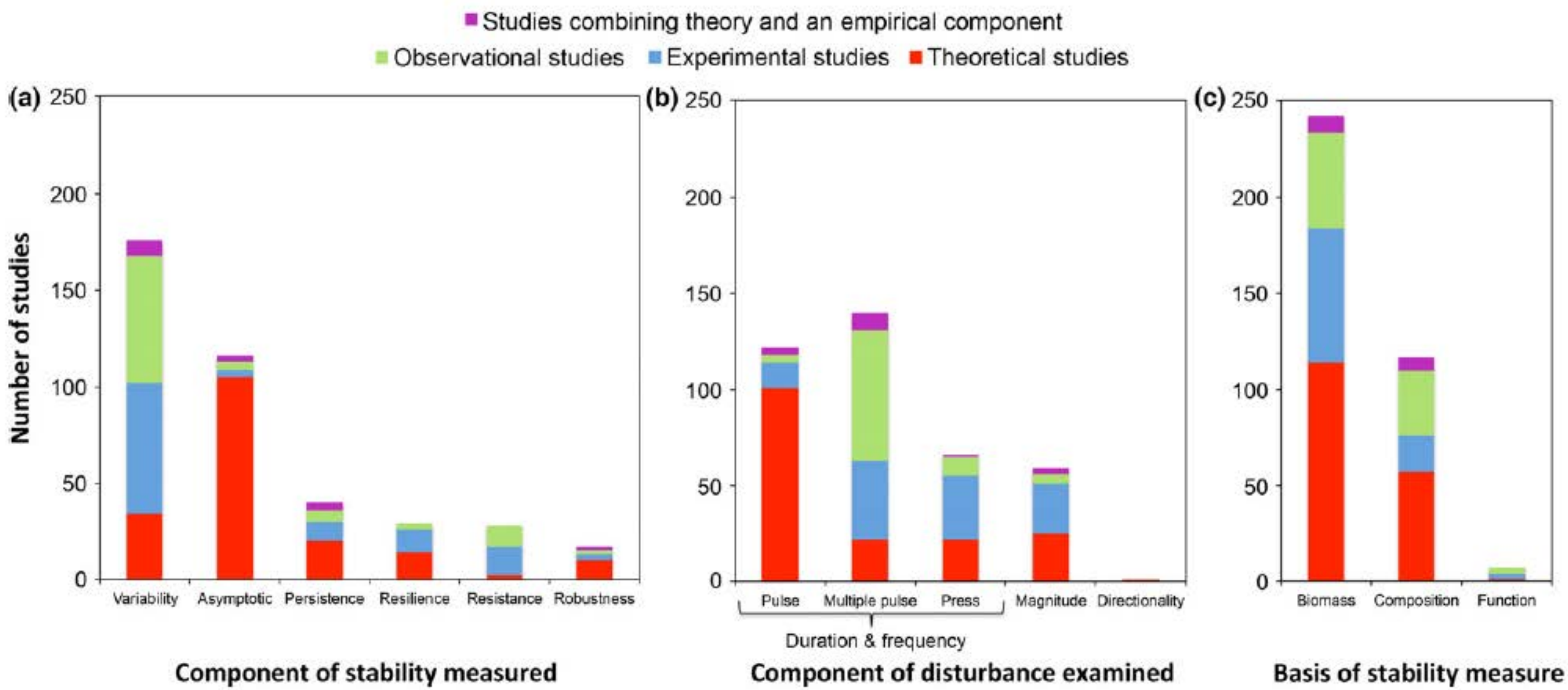


Asymptotic resilience $\alpha = -$ Real part of dominant eigenvalue of the linearised (Jacobian) matrix near equilibrium

How empiricists see the world

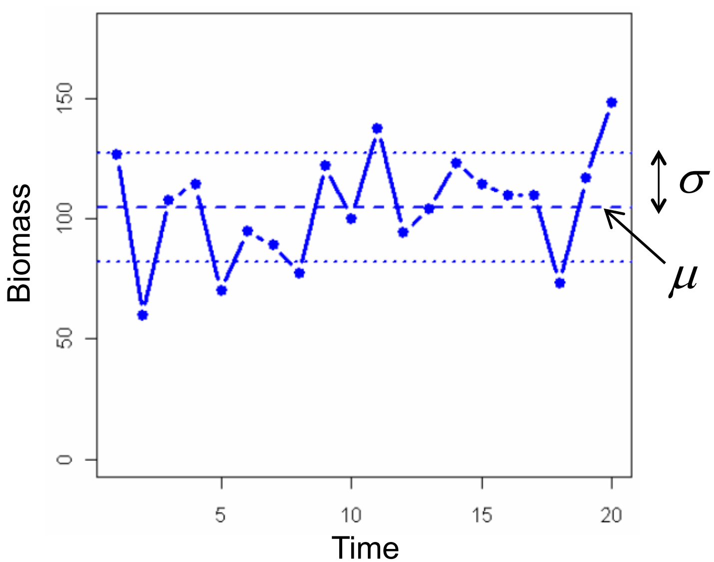


Theoreticians and empiricists study different components of stability



Donohue et al., *Ecol. Lett.* 19: 1172–1185 (2016)

Measuring variability and invariability



The variance typically scales as the square of the mean:

Variance(x) = Mean(x^2) – Mean^2(x)

$$\sigma^2 = \overline{x^2} - \mu^2$$

Variability (instability)

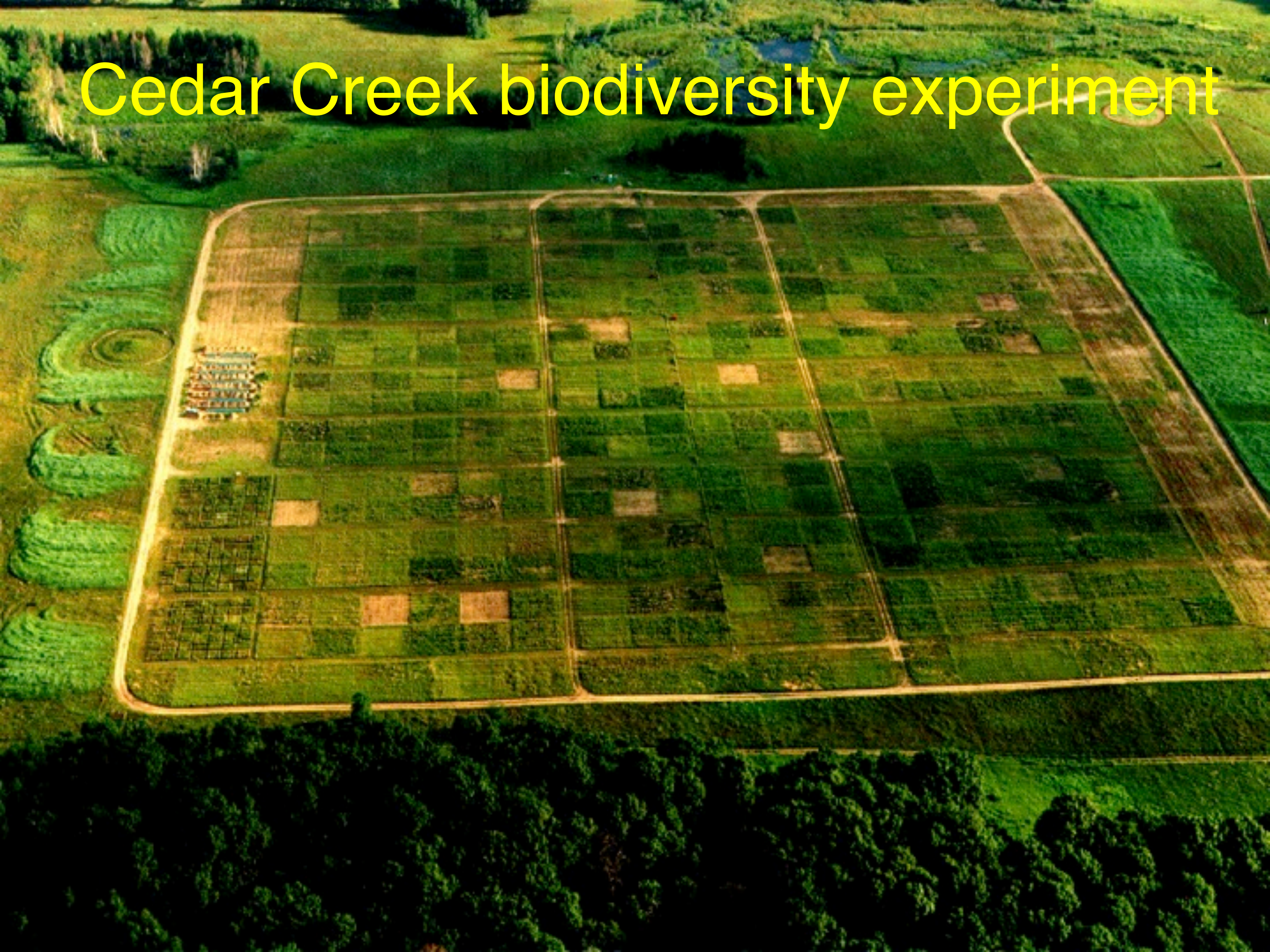
$$CV = \frac{\sigma}{\mu}$$

$$CV^2 = \frac{\sigma^2}{\mu^2}$$

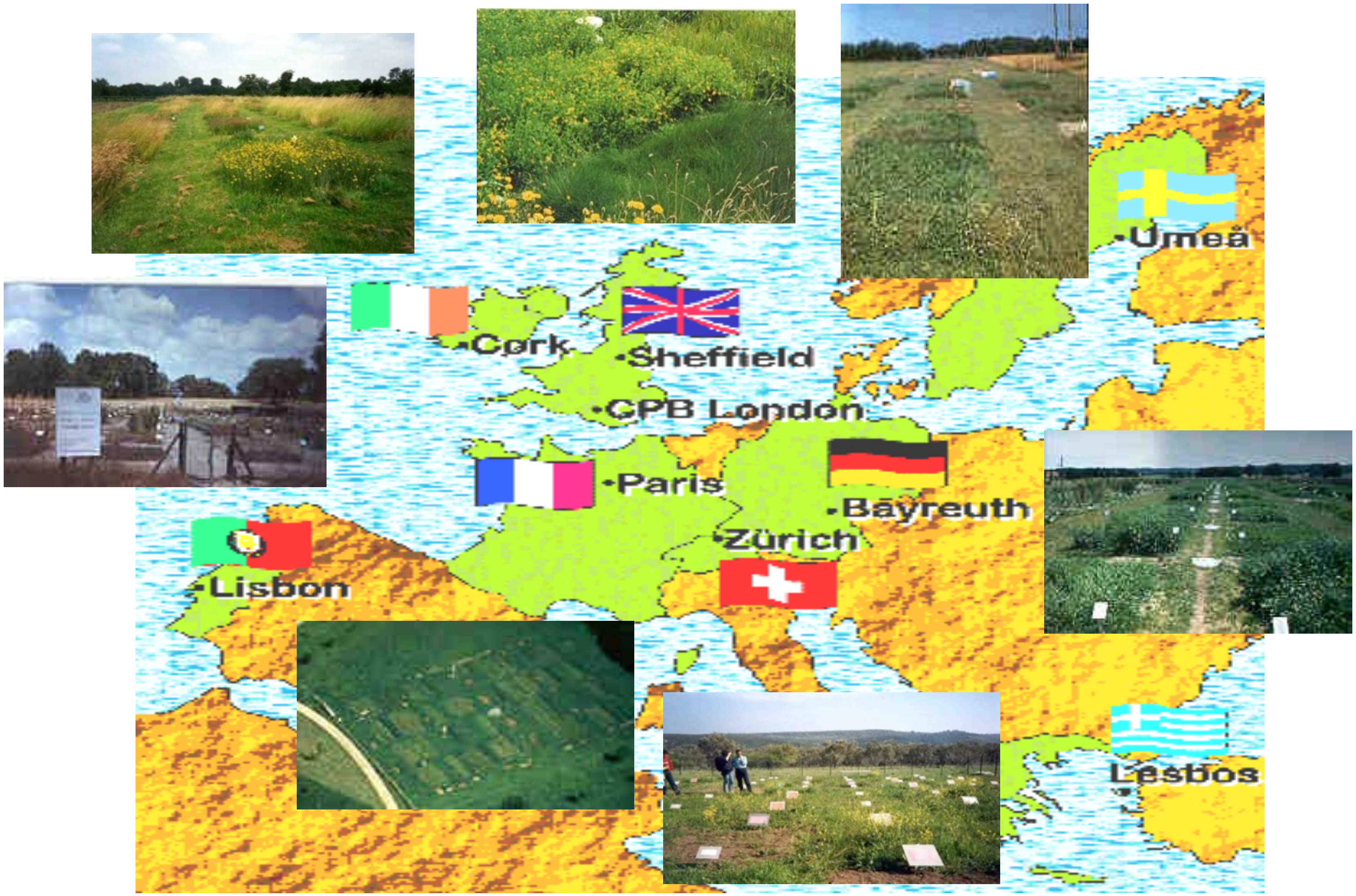
Invariability (stability)

$$\frac{1}{CV} = \frac{\mu}{\sigma}$$

$$\frac{1}{CV^2} = \frac{\mu^2}{\sigma^2}$$

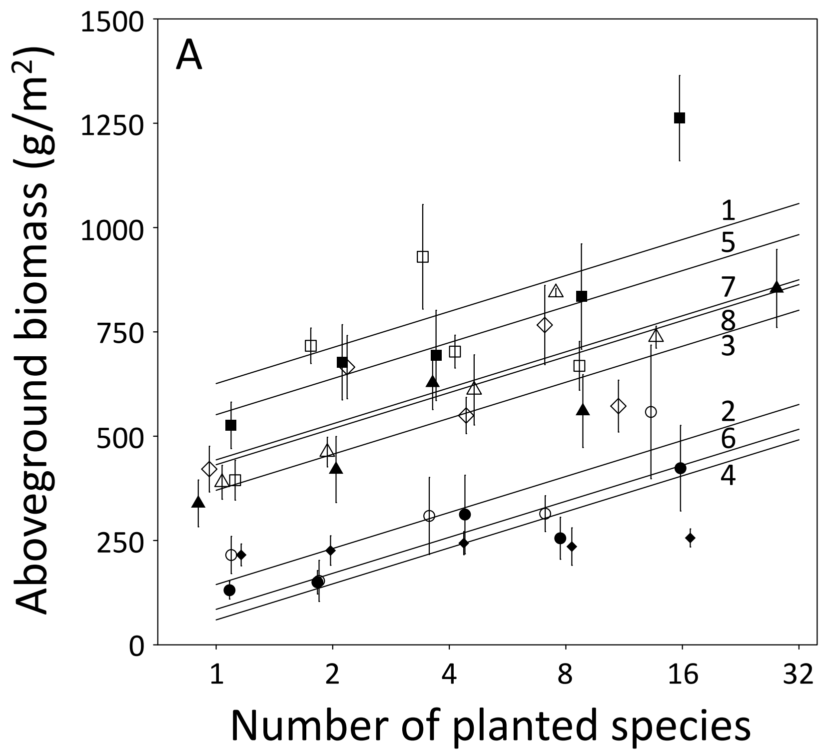

Cedar Creek biodiversity experiment

BIODEPTH biodiversity experiment

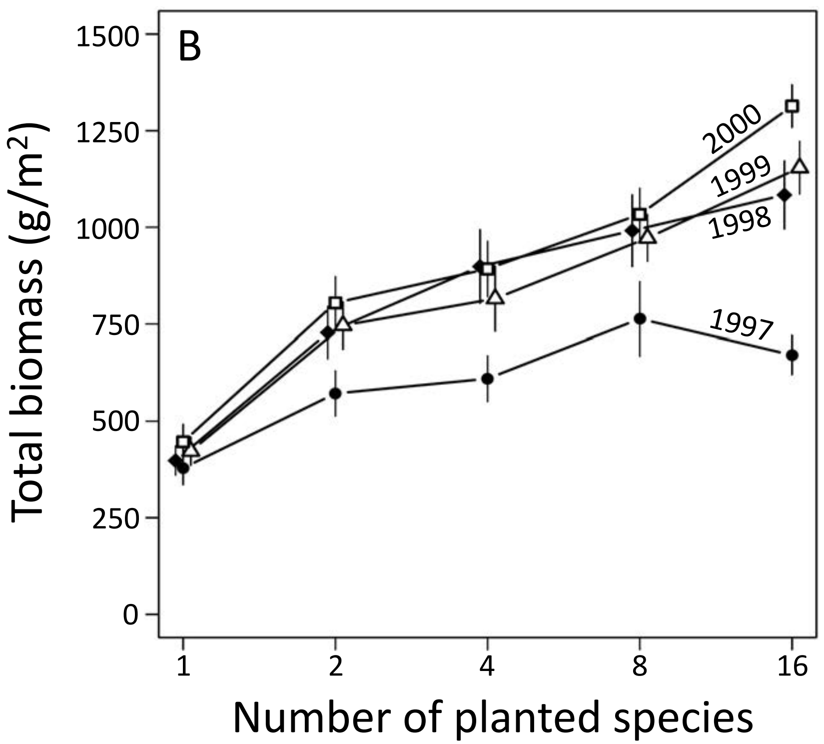


Species diversity increases plant biomass production in grasslands

BIODEPTH



Cedar Creek

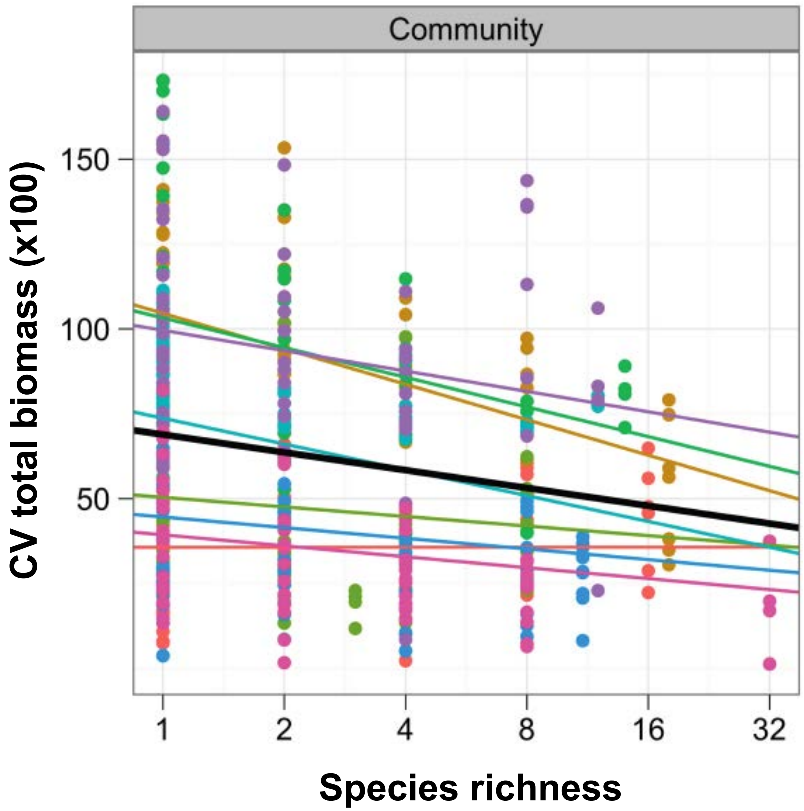


Based on Hector et al., *Science* 286: 1123–1127 (1999)

Based on Tilman et al., *Science* 294: 843–845 (2001)

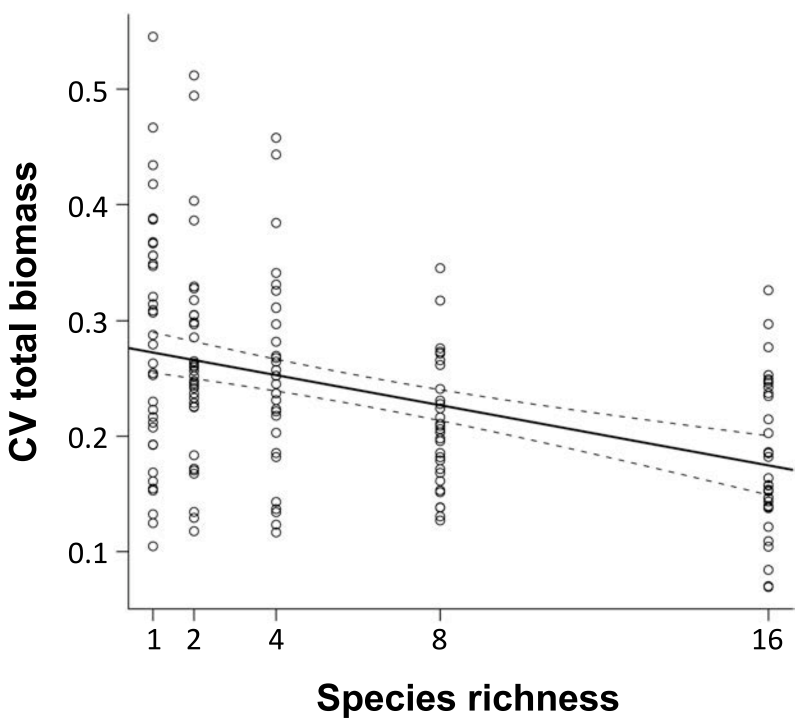
Species diversity also stabilises plant biomass production in grasslands

BIODEPTH



Hector et al., *Ecology* 441: 629–632 (2010)

Cedar Creek



Based on Tilman et al., *Nature* 441: 629–632 (2006)

The stabilising effect of diversity conflicts with the new paradigm

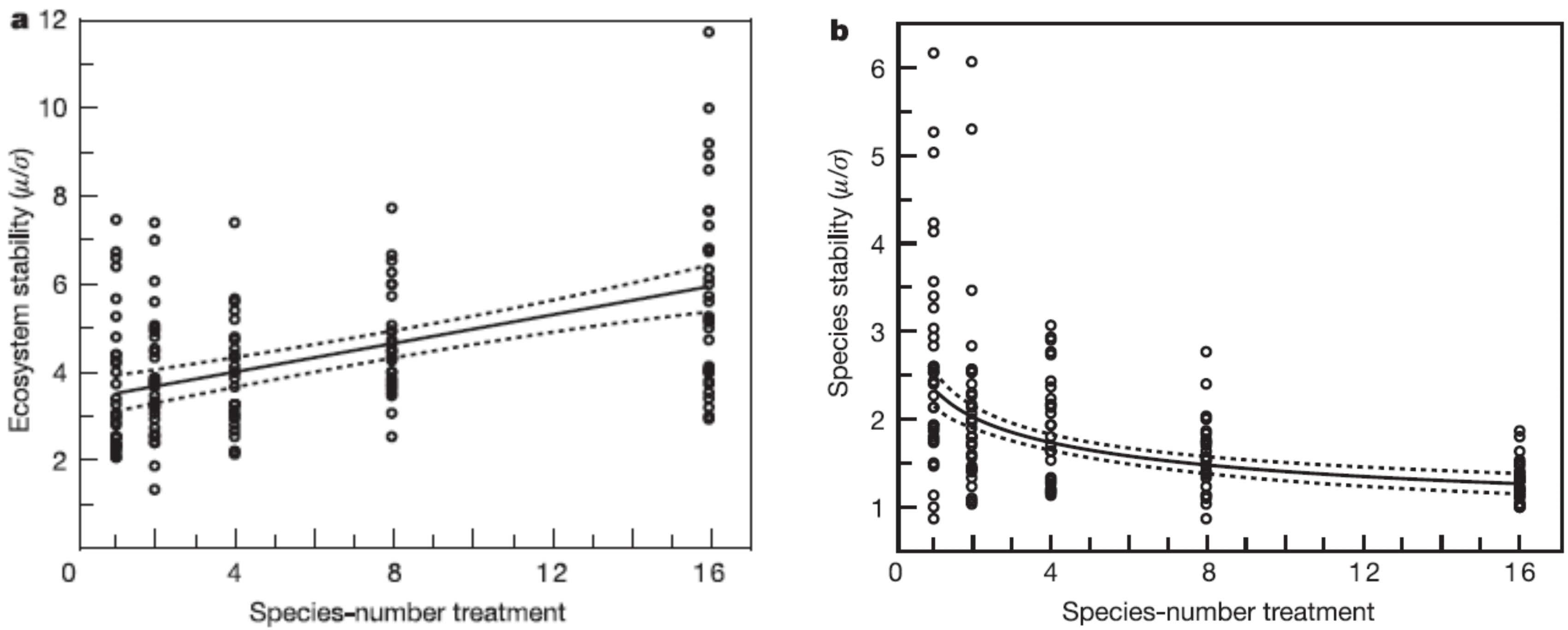
Some limitations of the new paradigm:

- There are many components of "stability": local stability, variability, resistance, resilience, reactivity…
- These stability properties may differ between each other and between levels of organisation: May's theory applies to communities as sets of interacting populations, not to aggregate ecosystem properties

A major current challenge is to develop a theory of ecological stability that spans multiple scales and levels of organisation and that is directly relevant to empirical work

Population vs. ecosystem stability in grasslands

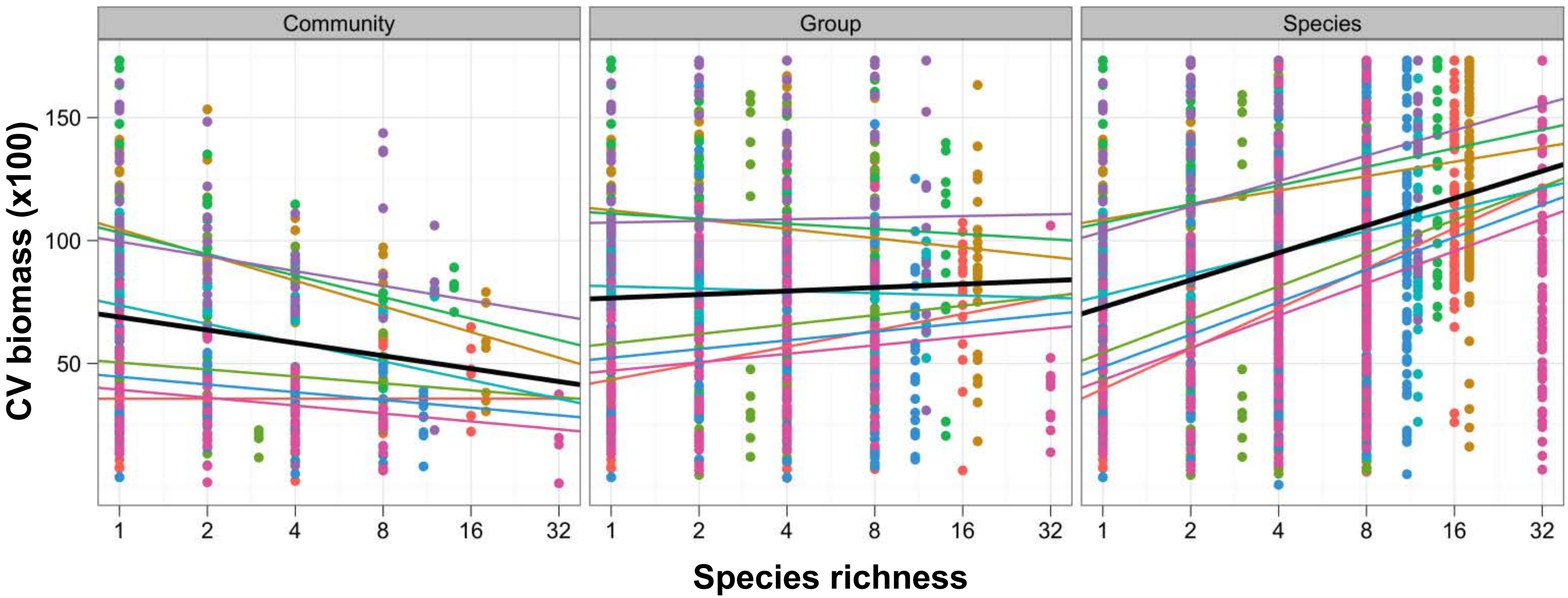
Cedar Creek



Tilman et al., *Nature* 441: 629–632 (2006)

Population vs. ecosystem stability in grasslands

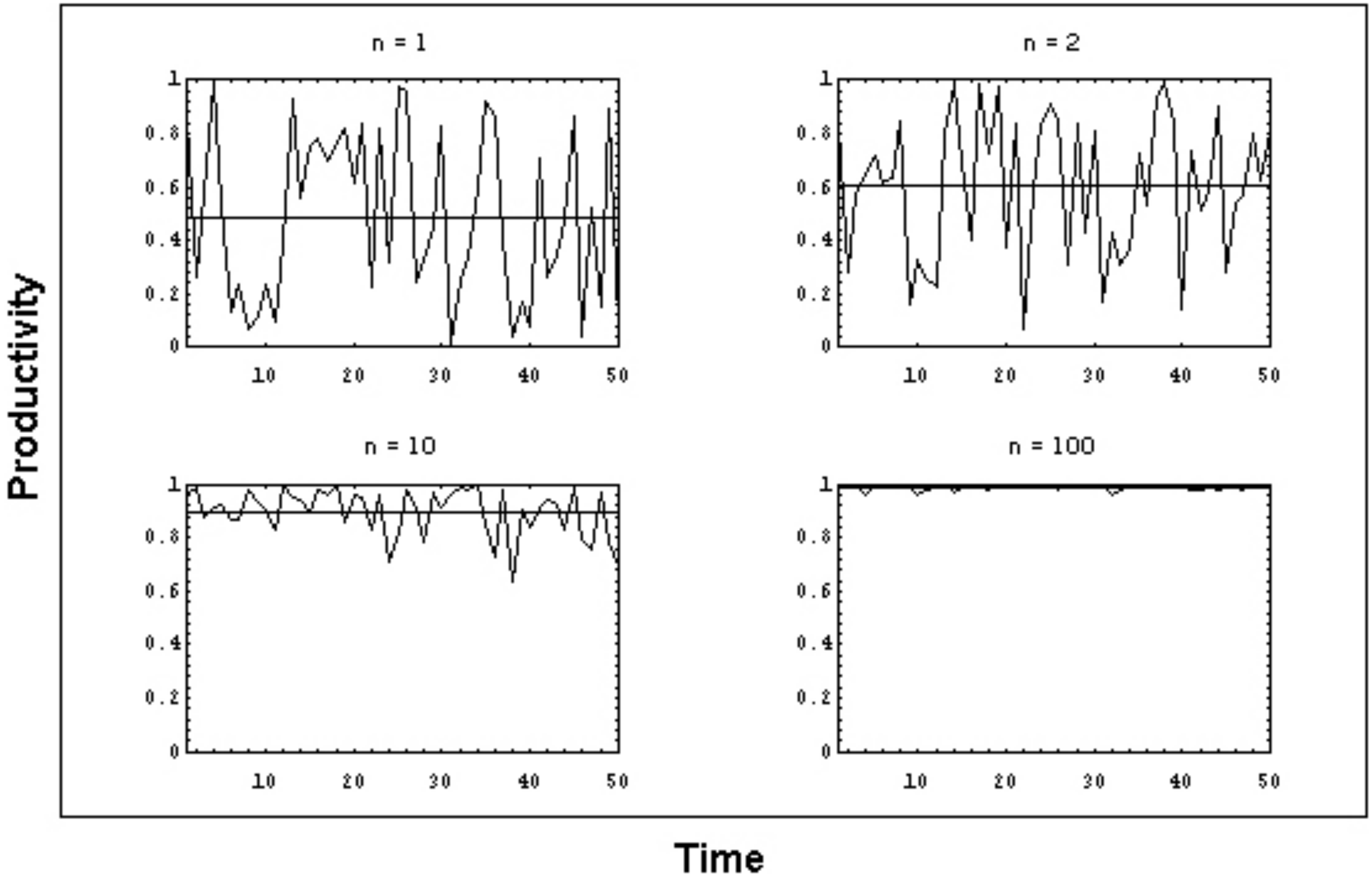
BIODEPTH



The whole is the sum of its parts, but it obeys different rules

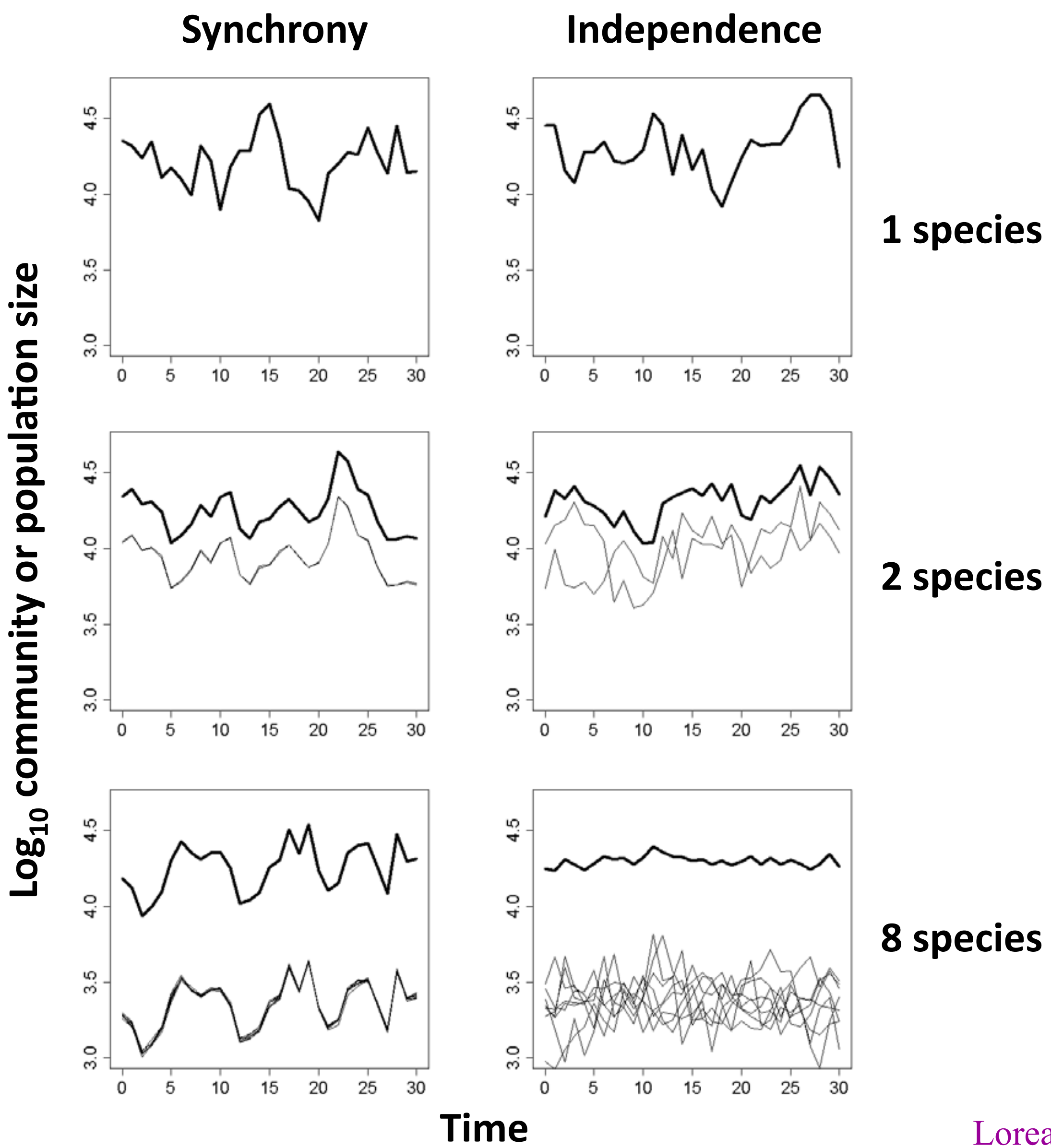
Hector et al., *Ecology* 441: 629–632 (2010)

The insurance hypothesis



Yachi & Loreau, *PNAS* 96: 1463–1468 (1999)

The insurance hypothesis



Main mechanism:
Asynchrony of species responses to environmental variations (= complementarity in response niches)

Loreau, *From Populations to Ecosystems* (2010)

Mechanistic approach based on stochastic community dynamics

Per capita population growth rate:

$$r_i(t) = \ln N_i(t+1) - \ln N_i(t)$$

$$= r_{mi}\left[1 - \frac{N_i(t)}{K_i} - \sum_{j \neq i} \frac{\beta_{ij} N_j(t)}{K_j}\right] + \sigma_{ei} u_{ei}(t) + \frac{\sigma_{di} u_{di}(t)}{\sqrt{N_i(t)}}$$

Intra- and interspecific competition | **Environmental stochasticity** | **Demographic stochasticity**

Loreau & de Mazancourt, *Am. Nat.* 172: E48–E66 (2008)
Loreau & de Mazancourt, *Ecol. Lett.* 16 (s1): 106–115 (2013)

Predicting ecosystem stability from community composition and biodiversity

Mechanisms driving the stabilising effect of diversity

Environmental stochasticity | **Demographic stochasticity** | **Observation error**

$$CV_{N_T}^2 \approx \varphi_e \Sigma_e^2 + \frac{\Sigma_d^2}{\overline{\overline{N_T}}} + \lambda \frac{\Sigma_o^2}{n_x}$$

Synchrony of species environmental responses

Mean total biomass

Simpson's concentration index

Insurance hypothesis

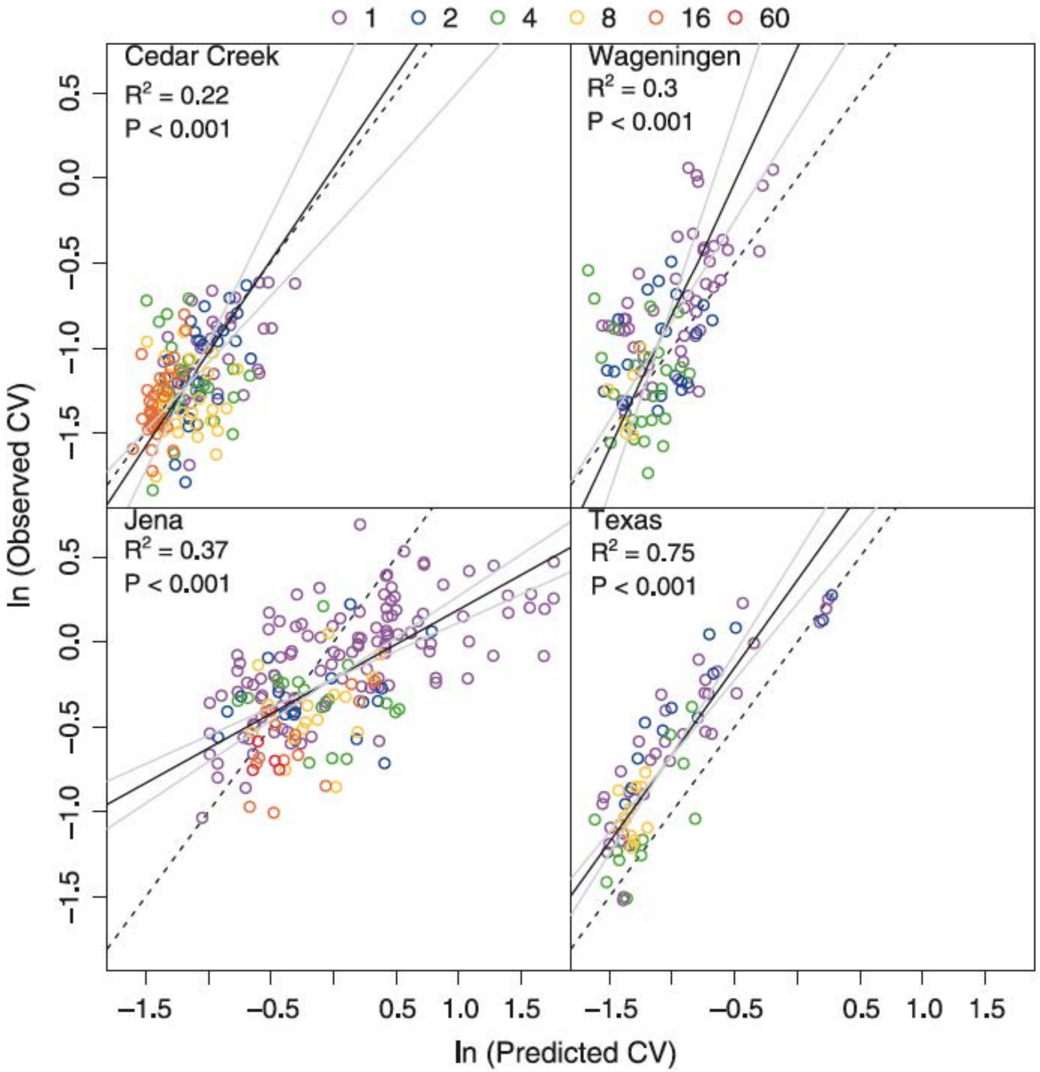
Overyielding effect

Error reduction

Species diversity

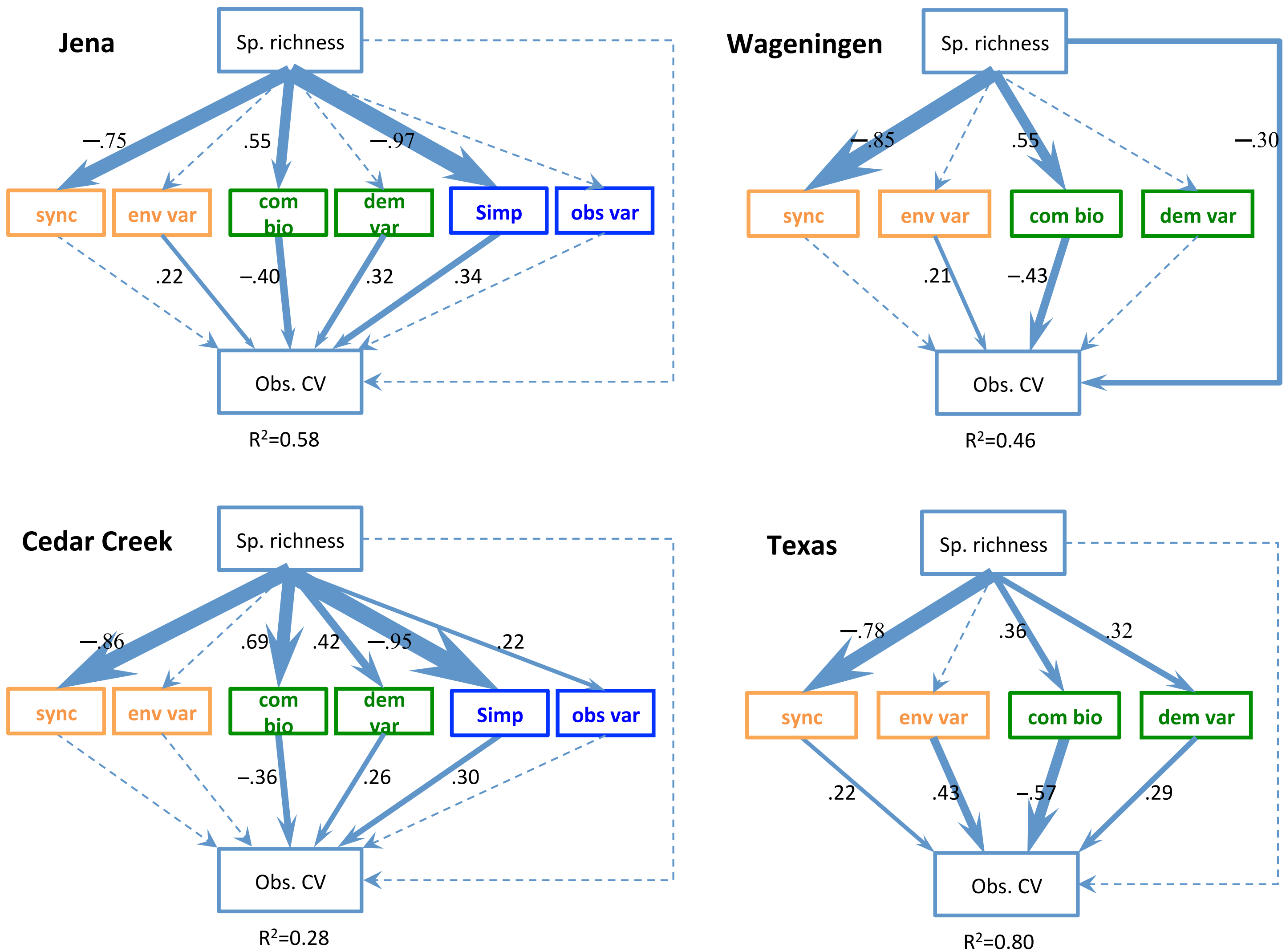
de Mazancourt et al., *Ecol. Lett.* 16: 617–625 (2013)

Testing prediction against data from four long-term grassland experiments



de Mazancourt et al., *Ecol. Lett.* 16: 617–625 (2013)

Mechanisms driving the stabilising effect of diversity in grassland experiments



de Mazancourt et al., *Ecol. Lett.* 16: 617–625 (2013)

Mechanisms driving the stabilising effect of diversity in grassland experiments

- Asynchrony of species environmental responses: **1/4**
- Overyielding reducing demographic stochasticity: **4/4**
- Reduction of observation error: **2/2**

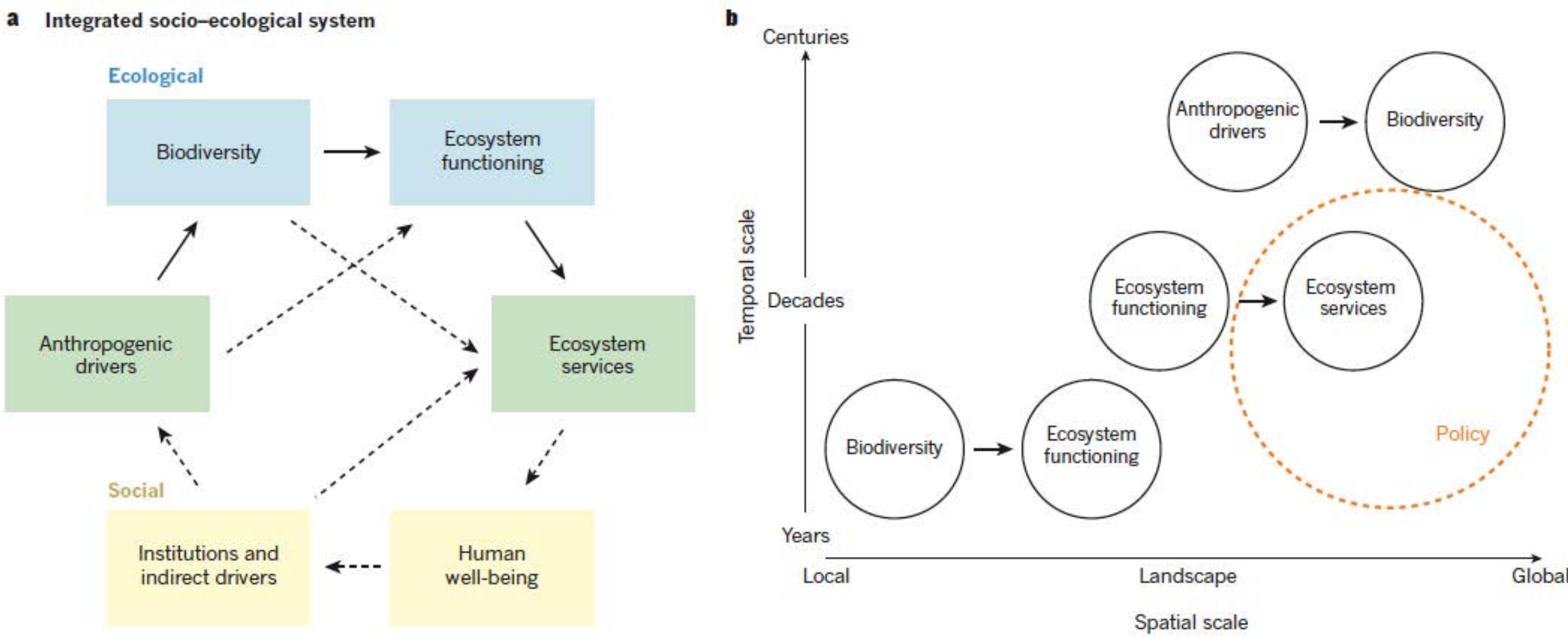
de Mazancourt et al., *Ecol. Lett.* 16: 617–625 (2013)

Mechanisms driving the stabilising effect of diversity in forest models

- Strong effect of species asynchrony, mostly due to responses to small-scale disturbances
- Weak effect of demographic stochasticity

Morin et al., *Ecol. Lett.* 17: 1526–1535 (2014)

Linking biodiversity, ecosystems and people: The scale mismatch



Isbell et al., *Nature* 546: 65–72 (2017)

Ecological stability across scales: α, β and γ variability

Gamma variability ($\gamma_{cv} = CV_M^2$)

$$\gamma_{cv} = \alpha_{cv} / \beta_1$$

Alpha variability ($\alpha_{cv} = CV_L^2$)

$$\alpha_{cv} = CV^2_{Species} \cdot \varphi_{Species}$$

Beta variability ($\beta_1 = 1/\varphi$)

- number of patches
- spatial unevenness
- community similarity between patches
- spatial correlation of environment
- dispersal

Species variability ($CV^2_{Species}$)

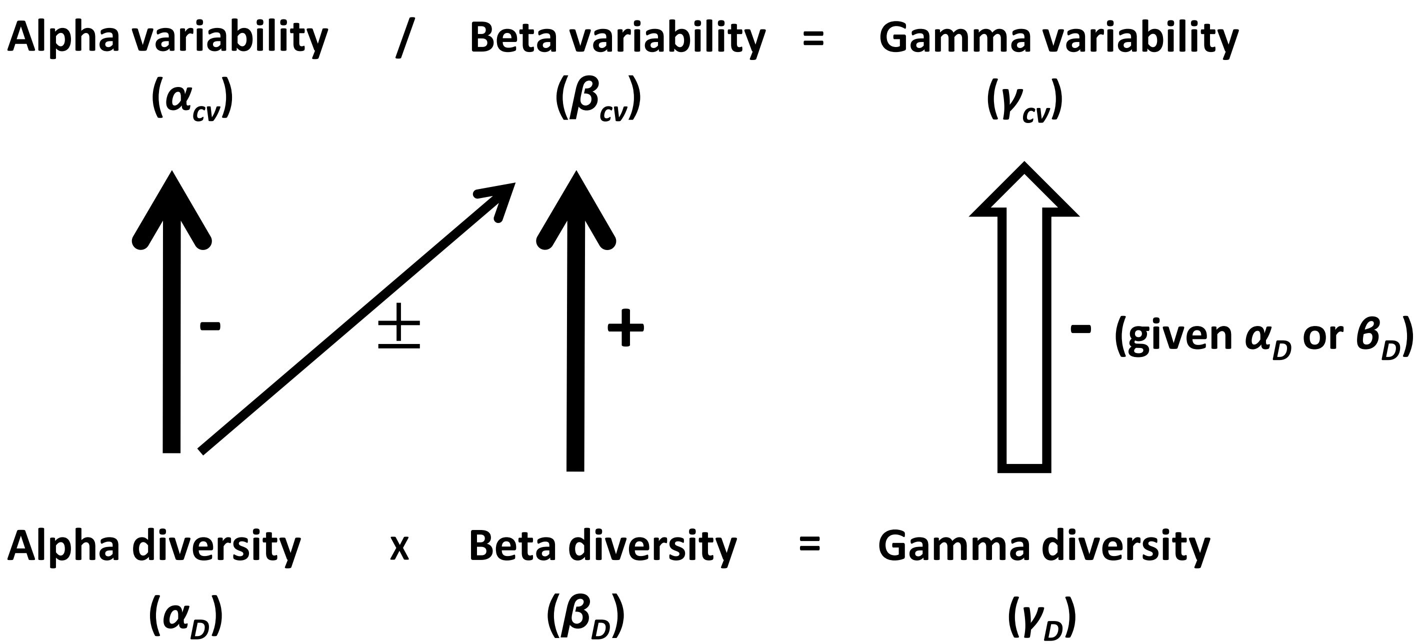
- species' intrinsic growth rate
- species unevenness
- species interactions
- demographic and environmental stochasticity
- dispersal

Species synchrony ($\varphi_{species}$)

- number of species
- species unevenness
- species interactions
- similarity in environmental response
- dispersal

Wang & Loreau, *Ecol. Lett.* 17: 891–901 (2014)

Ecosystem stability across scales: α, β and γ variability



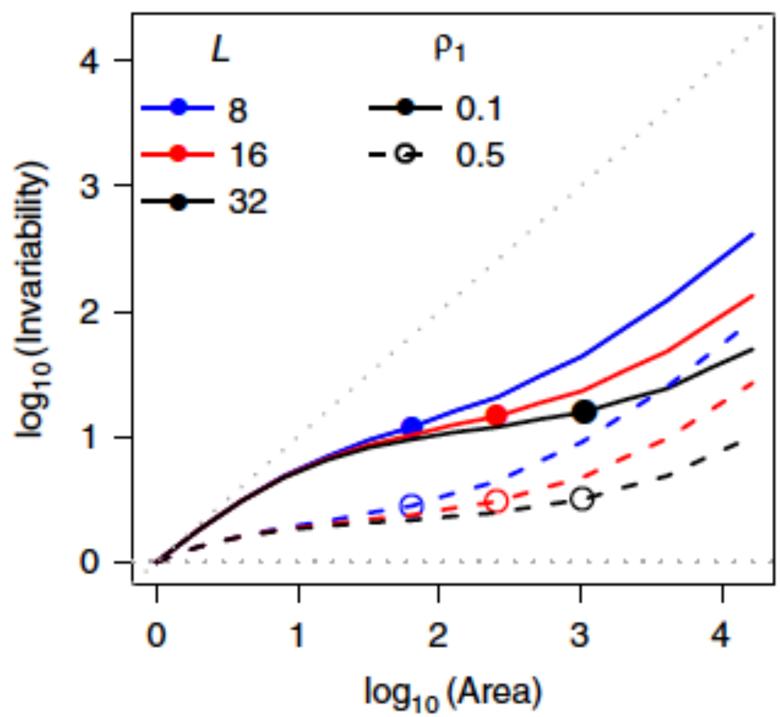
Biodiversity is important for ecosystem stability, not only through its local effects but also through β diversity, which enhances spatial asynchrony

Wang & Loreau, *Ecol. Lett.* 19: 510–518 (2016)

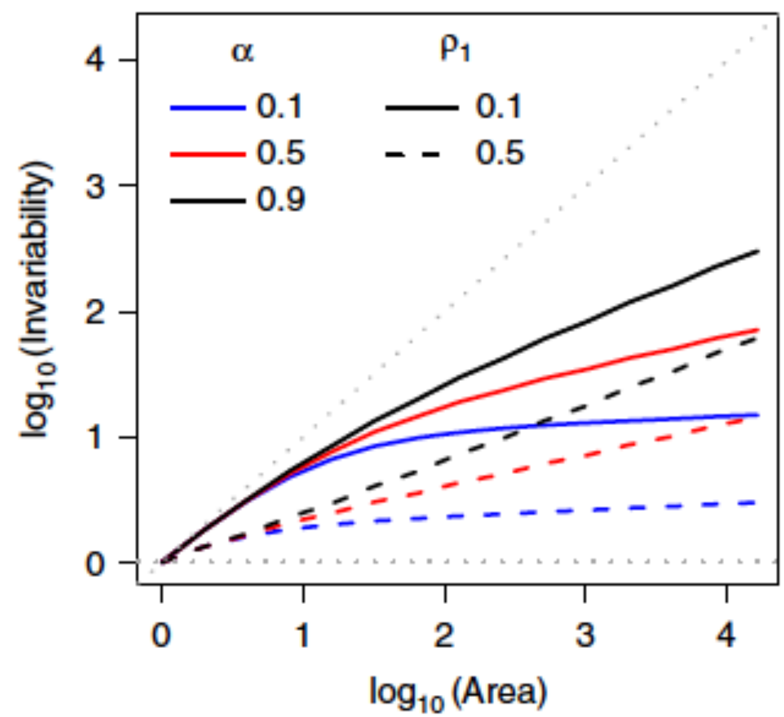
Ecological stability across scales: Invariability–Area Relationship (IAR)

$$Inv(A) = \frac{1}{CV^2(A)} = Inv(1)\left[\frac{A}{1+(A-1)\overline{\rho(A)}}\right]$$

Correlation ρ decays with distance exponentially

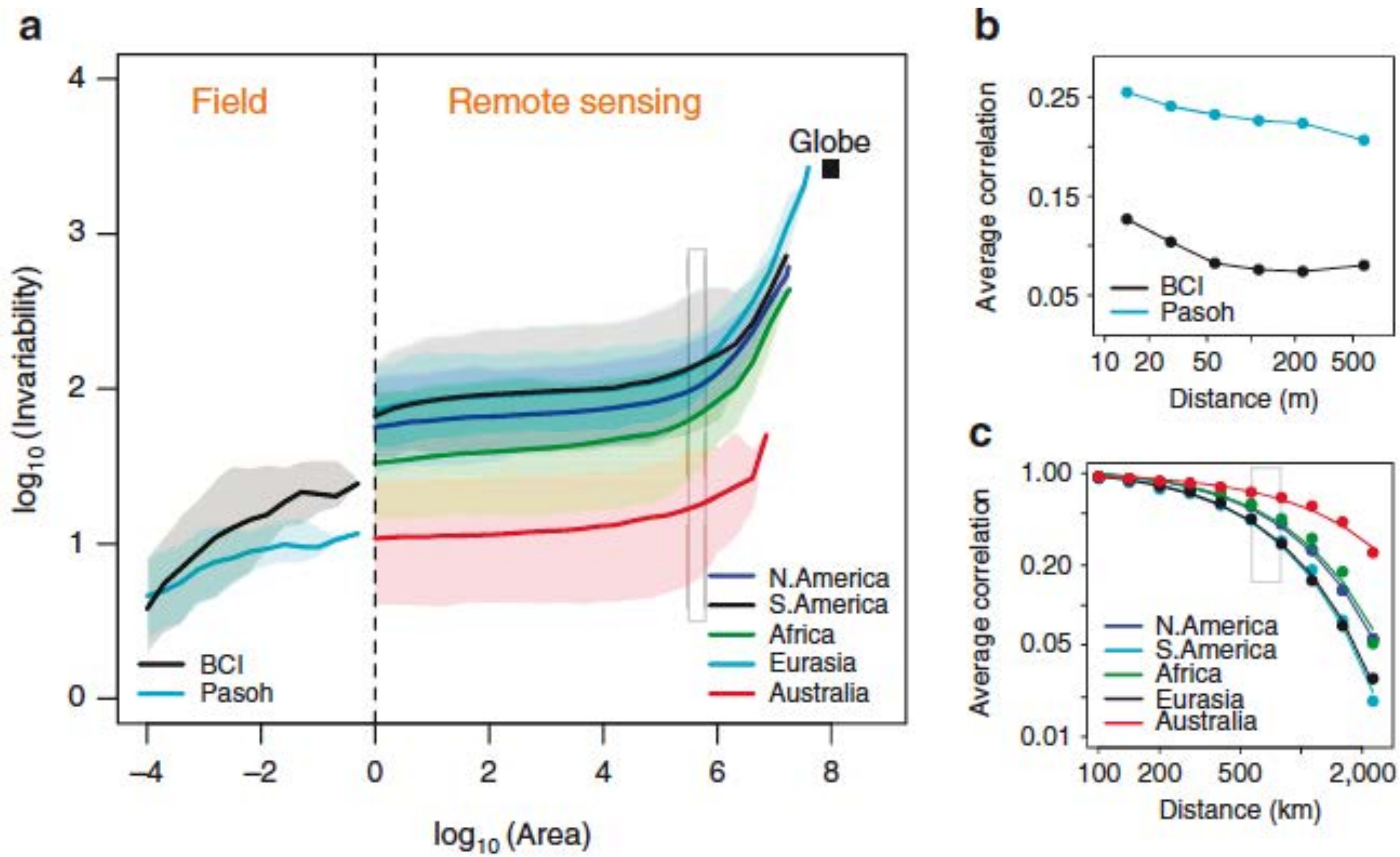


Correlation ρ decays with distance according to a power law



Wang et al., *Nat. Commun.* 8: 15211 (2017)

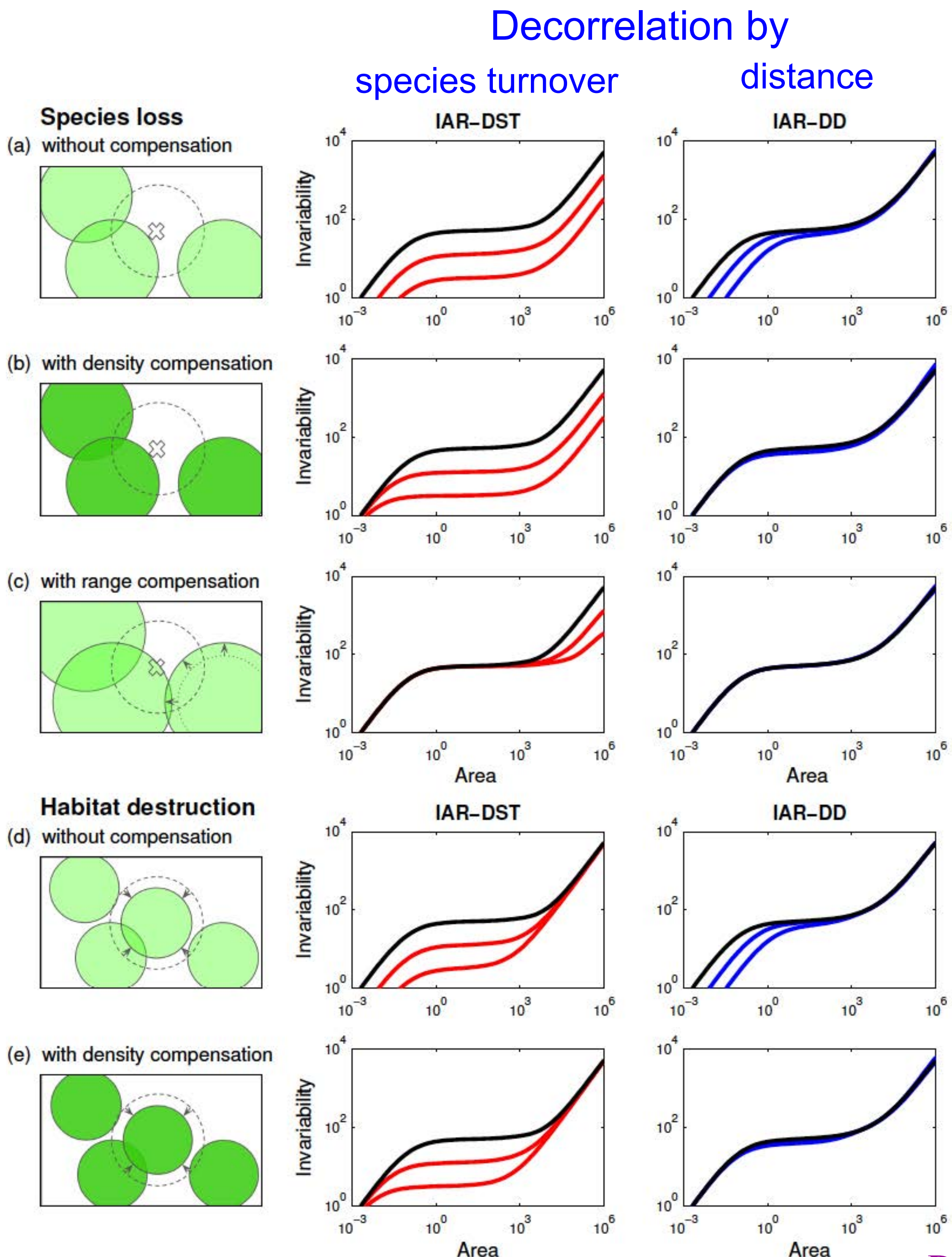
Ecosystem stability across scales: IAR of global primary productivity



IAR provides a powerful potential tool to predict the effects of global changes on the stability of ecosystem services

Wang et al., *Nat. Commun.* 8: 15211 (2017)

Ecosystem stability across scales: IAR

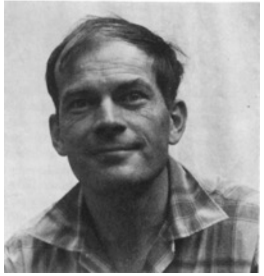


Delsol et al., *Global Ecol. Biogeogr.* 27: 439–449 (2018)

Diversity and stability of ecological systems: Who was right?

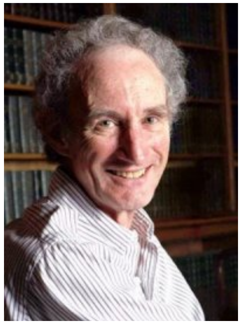
Charles Elton

Eugene Odum



Robert MacArthur

VS



Robert May

Diversity and stability of ecological systems: Some conclusions

- Classical ecological theory based on asymptotic resilience has been largely divorced from empirical data so far
- Invariability is a more flexible and empirically relevant measure of stability
- Invariability-based theory provides a completely new perspective on the old diversity–stability debate
- It predicts different diversity–stability relationships at the population and ecosystem levels that agree with empirical and experimental data

Diversity and stability of ecological systems: Some conclusions

- Invariability-based theory also provides a consistent framework for studying ecosystem stability across scales
- There is now strong theoretical and experimental evidence that biodiversity generally stabilises ecosystem properties at all scales, thereby playing an important role in the steady provision of ecosystem services

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Forest
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Shaopeng
Wang

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