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

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Heading for a sixth mass extinction

How will biodiversity loss affect ecosystem functioning and human well-being?
### Effects of biodiversity on ecosystem services

<table>
<thead>
<tr>
<th>Category of service</th>
<th>Measure of service provision</th>
<th>SPU</th>
<th>Diversity level</th>
<th>Source</th>
<th>Study type</th>
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<th>Relationship</th>
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<td>Abundance of herbivorous pests (bottom-up effect of plant diversity)</td>
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</table>

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
Diversity and stability of ecological systems: An old debate

The new paradigm: Diversity and complexity beget instability

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:

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

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

How theoreticians see the world

$\text{Deviation from equilibrium } \propto e^{-\alpha t}$

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

How empiricists see the world

- Time
- Biomass
- Variability (inverse of stability)
- Mean

Graph showing biomass over time with variability and mean indicated.
Theoreticians and empiricists study different components of stability.

Measuring variability and invariability

The variance typically scales as the square of the mean:

\[ \text{Variance}(x) = \text{Mean}(x^2) - \text{Mean}^2(x) \]

\[ \sigma^2 = x^2 - \mu^2 \]

**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


Based on Tilman et al., *Science* 294: 843–845 (2001)
Species diversity also stabilises plant biomass production in grasslands


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

Population vs. ecosystem stability in grasslands

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

The insurance hypothesis

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

Predicting ecosystem stability from community composition and biodiversity

Mechanisms driving the stabilising effect of diversity

\( CV_{NT}^2 \approx \varphi_e \sum_e^2 + \frac{\sum_d^2}{N_T} + \lambda \frac{\sum_o^2}{n_x} \)

Environmental stochasticity  Demographic stochasticity  Observation error

Synchrony of species environmental responses  Mean total biomass  Simpson’s concentration index

Insurance hypothesis  Overyielding effect  Error reduction

Species diversity

Testing prediction against data from four long-term grassland experiments

Mechanisms driving the stabilising effect of diversity in grassland experiments

**Jena**
- Sp. richness
- Obs. CV
- R²=0.58

**Wageningen**
- Sp. richness
- Obs. CV
- R²=0.46

**Cedar Creek**
- Sp. richness
- Obs. CV
- R²=0.28

**Texas**
- Sp. richness
- Obs. CV
- R²=0.80

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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

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

Linking biodiversity, ecosystems and people: The scale mismatch

Ecological stability across scales: $\alpha$, $\beta$ and $\gamma$ variability

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

\[ \gamma_{cv} = \frac{\alpha_{cv}}{\beta_1} \]

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

\[ \alpha_{cv} = CV_{Species}^2 \cdot \varphi_{Species} \]

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

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

Species variability ($CV_{Species}^2$)

- 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

Ecosystem stability across scales: $\alpha$, $\beta$ and $\gamma$ variability

\[
\frac{\text{Alpha variability}}{(\alpha_{cv})} \quad / \quad \text{Beta variability} \quad = \quad \text{Gamma variability} \quad \frac{(\beta_{cv})}{(\gamma_{cv})}
\]

Alpha diversity $\times$ Beta diversity $= \text{Gamma diversity}$

\[
(\alpha_{D}) \quad x \quad (\beta_{D}) \quad = \quad (\gamma_{D})
\]

\textbf{Biodiversity is important for ecosystem stability, not only through its local effects but also through $\beta$ diversity, which enhances spatial asynchrony}

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

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

Correlation \( \rho \) decays with distance exponentially.

Correlation \( \rho \) 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

Decorrelation by species turnover distance

Ecosystem stability across scales: IAR

Diversity and stability of ecological systems: Who was right?

Charles Elton

Eugene Odum

VS

Robert May

Robert MacArthur
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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Bart Haegeman  
Forest Isbell  
Shaopeng Wang

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