## **Patterns of Species Richness Among Biomes**

Topics and approach What is biodiversity and why is it important? What are the major drivers of species richness? Habitat heterogeneity Disturbance Species energy theory Dynamic equilibrium hypothesis (interactions among disturbance and energy) [above covered in last lecture]

Resource ratio theory How does biodiversity influence ecosystem function? Biodiversity and ecosystem function hypothesis Integration of biodiversity theory

How might the drivers of species richness and hence levels of species richness differ among biomes?

Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252–254.

SET has received the strongest empirical support in explaining large scale gradients in species richness."

Kerr, J. T., and L. Packer. 1997.

We show that it apples to NA mammals only over in geographical areas where climate energy levels are low (AK and Canada).



Figure 2 A map of North America showing PET patterns (solid curves) in the north  $(mm yr^{-1})$  and topographical heterogeneity (dashed curves) in the south (metres). The PET contour at 1,000 mm yr^{-1} is in bold. North of this contour, PET is the best predictor of mammal richness, whereas heterogeneity predicts richness to the south.

#### PET – The amount of water that would evaporate from a saturated surface, an aspect of climatic energy availability.



**Figure 1** The relationship between PET and mammal species richness in North America. In areas where PET < 1,000 mm yr<sup>-1</sup>, PET explains 84% of the variance in mammal richness ( $F = 1,096, P \ll 0.0001$ ). South of this zone, however, PET is unrelated to mammal richness (F = 1.35, P = 0.248).

Kerr, J. T., and L. Packer. 1997.

In higher energy areas (US and southern Canada, topographic heterogeneity and local variation in energy are the best predictors.



**Figure 3** The contrasting relationships between mammal species richness and elevation variability, depending on PET levels (crosses when PET < 1,000 mm yr<sup>-1</sup>, and open circles when PET  $\ge$  1,000 mm yr<sup>-1</sup>). In combination with PET variability and coastal location, these factors explain 76.7% of the variability in mammal species richness patterns in high-energy regions of North America (*F* = 138.4, *P*  $\ll$  0.0001; mammal species richness = 43.3 + 0.00852 × topographical heterogeneity + 0.0354 PET variability – 9.60 coastal location). In regions where PET < 1,000 mm yr<sup>-1</sup>, elevation variability is a poor predictor of mammal richness (*F* = 20.12, *R*<sup>2</sup> = 0.0898, *P* < 0.0001).

#### Kerr, J. T., and L. Packer. 1997.

Table 1 Correlations between environmental factors and mammal species richness in regions in North America		
Environmental variable per quadrat <sup>6</sup>	Pearson correlation with MSR <sup>+</sup> in regions where $PET \ge 1,000 \text{ mm yr}^{-1}$	Pearson correlation with MSR‡ in regions where PET < 1,000 mm yr <sup>-1</sup>
Mean annual temperature (1) Mean PET (1) Mean actual evapotranspiration (1) Mean solar radiation (1) Mean precipitation (2) Elevation variability (3) Precipitation variability (3) PET variability (3) Annual temperature variability (4) Glaciation (5) Longitude Latitude Quadrat area Coastal location	- 0.392*** NS - 0.784*** 0.353*** - 0.522*** 0.808*** 0.344*** 0.615*** NS 0.698*** 0.335** 0.335** 0.194* - 0.176*	0.837*** 0.920*** 0.709*** 0.789*** 0.318*** 0.300*** 0.177* 0.542*** - 0.373*** NS - 0.150* - 0.806*** 0.238* - 0.571***
Peninsular location	- 0.215*	- 0.204**

The number after the environmental variable refers to the hypothesis that the variable tests (see Methods). Coastal and peninsular location and quadrat area are control variables; latitude and longitude provide spatial reference. MSR, mammal species richness; PET, potential evapotranspiration. \*P < 0.05; \*\*P < 0.005; \*\*P < 0.0001; NS, not significant. †n = 130.  $\ddagger n = 206$ .

In higher energy areas (US and southern Canada, topographic heterogeneity and local variation in energy are the best predictors.

Our results indicate that although there is no single determinant of large-scale variation in mammal species richness, there may be a hierarchical sequence of limiting factors.

Hawkins, B.A. et al. 2003.

Focusing on studies extending over 800 km, we found that measures of energy, water, or water– energy balance explain spatial variation in richness better than other climatic and non-climatic variables in 82 of 85 cases



FIG. 2. Relationships between potential evapotranspiration (PET) and species richness for terrestrial birds (a, c) and butterflies (b, d) in the Palearctic (a, b) and Nearctic (c, d). The vertical lines represent breakpoints identified by split-line regression at which the relationships shift from being positive to either negative (in the Palearctic) or null (in the Nearctic). The regressions were performed using JMP 4.0 (SAS Institute 2000).

Hawkins, B.A. et al. 2003.

Water variables usually represent the strongest predictors in the tropics, subtropics, and warm temperate zones, whereas energy variables (for animals) or water–energy variables (for plants) dominate in high latitudes.



FIG. 3. A hypothesis for the geographic distribution of the limits to the species richness of animals, based on the analysis of butterflies and birds (see Fig. 2). The bold lines represent the geographical distribution of the breakpoints above which potential evapotranspiration and species richness are not positively associated. Across all latitudes, animal richness is constrained by the interaction of energy and water, but north of these lines energy is hypothesized to represent the limiting component of the interaction, whereas south of these lines water is assumed to be the key limiting component (see Fig. 1).

Hawkins, B.A. et al. 2003.

We conclude that the interaction between water and energy, either directly or indirectly (via plant productivity), provides a strong explanation for globally extensive plant and animal diversity Gradients.

Davies, R. G., C. D. L. Orme, D. Storch, V. A. Olson, G. H. Thomas, S. G. Ross, T. Ding, P. C. Rasmussen, P. M. Bennett, I. P. F. Owens, T. M. Blackburn, and K. J. Gaston. 2007. Topography, energy and the global distribution of bird species richness. Proceedings of the Royal Society B 274:1189-1197.

Analyses presented here are based on a database of distribution maps for 9626 extant, recognized bird species globally.



Figure 1. Global maps of species richness

Davies et al. 2007.

topographical variability and temperature are identified as the most important global predictors of avian species richness in multipredictor models.

Topographical variability is most important in single-predictor models, followed by productive energy.

	all variables
	1°
predictor	F <sub>1,13851</sub>
elevation range	107.99
elevation range <sup>2</sup>	214.86 + + +
habitat diversity	85.04 + + +
habitat diversity <sup>2</sup>	
NDVI	68.10 + + +
NDVI <sup>2</sup>	4.08 -
temperature	208.24 + + +
temperature <sup>2</sup>	143.56
population density	4.79-
population density <sup>2</sup>	27.71 + + +
agricultural area	1.29
agricultural area <sup>2</sup>	1.66
ice covered/not	1.84
MDE	
MDE <sup>2</sup>	
AIC	24 521.0

Table 1. Best-fit global multi-predictor spatial GLS models of species richness.

### Davies et al. 2007.



A global perspective confirms the primary importance of mountain ranges in high-energy areas.

Adler et al. 2011. Productivity is a poor predictor of plant species richness. Science 333 1750-1753.

We conducted standardized sampling in 48 herbaceous-dominated plant communities on five continents.

We sampled plant species richness in standard 1-m2 quadrats located in blocks of 10 plots.



Fig. 1. Locations of the 48 Nutrient Network sites that provided data for this study. Numbers correspond to the "code" column in table S1. Colors and symbols represent the distinct biogeographic regions also shown in Fig. 3 (see Fig. 3 for key).

Adler et al. 2011.

We found no clear relationship between productivity and finescale (meters-2) richness within sites, within regions, or across the globe.



**Fig. 2.** Within-site relationships between productivity, measured as peak live biomass (dry weight) and species richness. The inset shows the frequencies of relationships that were nonsignificant (NS, thin dashed lines), positive or negative linear (thick dashed lines), and concave-up (+) or -down (-) (solid curves). Statistical results and separate figures for each of the 48 sites are available in table S2 and fig. S1, respectively. The marginal histograms show the frequency of species richness and peak live biomass across all sites.

#### Adler et al. 2011.

Fig. 3. Global relationship between mean productivity, measured as peak live biomass (dry weight), and mean species richness (meters<sup>-2</sup>) at each site. White dots indicate managed sites (burned regularly or grazed by domestic livestock) and crosses indicate sites of anthropogenic origin (pastures, old fields, and restored prairies). The solid curve shows the quadratic relationship between productivity and richness with all sites included: the dotted line shows the linear relationship that remains when the anthropogenic sites



are removed; and the dashed line shows the 0.95 quantile regression with all sites included. N. Am., North America.

Adler et al. 2011.

Criticisms

The study set up a straw-man hypothesis:

Although some studies have advocated multivariate approaches (3–5), much of the debate remains focused on evidence for a single, general relationship between productivity and richness.

This classic productivity-richness relationship (PRR) is humpshaped, with richness increasing at low to intermediate levels of productivity and decreasing at high productivity (6).

Nearly all studies point to multiple drivers and most point out that the shape of the relationship varies.

Adler et al. 2011.

Criticisms

The study set up a straw-man hypothesis:

The study quantified biomass rather than productivity.

We used the same protocol at all sites for estimating aboveground net primary production (ANPP) as peak–growing-season live biomass, an effective measure of ANPP in herbaceous vegetation (21), especially when consumption by herbivores is low.

The studies sampled a narrow range of the global gradient in biomass.

Each site sampled only 1 m 2 plots and had only 10 replicates.

The results actually showed several positive relationships

We found no clear relationship between productivity and fine-scale (meters-2) richness within sites, within regions, or across the globe.

#### Adler et al. 2011.

#### Criticisms

The study set up a straw-man hypothesis:

The study quantified biomass rather than productivity.

The studies sampled a narrow range of the global gradient in biomass.

Analyses within sites are very weak because of only 10 replicates of 1-m plots.



Adler et al. 2011.

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#### Criticisms

The study set up a straw-man hypothesis:

The study quantified biomass rather than productivity.

The studies sampled a narrow range of the global gradient in biomass.

Each site sampled only 1 m 2 plots and had only 10 replicates.

The results actually showed several positive relationships, esp at the global level.



#### Conclusions

Global patterns of species richness are strongly correlated measures of climate, primary productivity, water, and/or habitat heterogeneity.

The strength of each of these varies geographically, logically linked to which are the most limiting in a given location

The shape of the relationships may well vary from place to place predictably (e.g., species energy relationship flattens or decreases in more productive settings.

Cardinale et al. 2009

**Predictions:** 

(1) Ecosystems characterized by a greater total availability of resources should also have a greater number of species and summed biomass of those species.

(2) Ecosystems characterized by a greater imbalance in the supply of different resources should show lower levels of species richness and summed biomass.

(3) When resource availability and imbalance are held constant, summed biomass should increase as a function of species richness.

#### Cardinale et al. 2009

**Methods:** 

Examine patterns of covariation between algal species richness, algal biomass, and both the availability and imbalance of three potentially limiting resources (light, nitrogen and phosphorus) in an extensive data set for Norwegian lakes.



Figure 2 Map showing locations of Norwegian lakes. Data analysed in this paper originate from various monitoring programmes carried out in Norway between 1987 and 2000, and collectively comprises 2657 samples taken from 492 lakes. The data set contains information on algal biomass (chlorophyll- $a L^{-1}$ ), algal richness (no. species per lake) and three potentially limiting resources (nitrogen, phosphorus, and light).

Cardinale et al. 2009

**Results:** 

1. algal species richness and biomass both increased as a function of the total availability of resources.

2. Species richness and biomass both decreased as resources became increasingly imbalanced in their availability.

3. a significant direct effect of species richness on biomass that was positive.

But note that only 12% of the variation in species richness was explained by resource availability and ratio.

Some 51% of the variation in biomass was explained with resource availability having a stronger effect than species richness or ratio.



**Figure 5** Results of a Structural Equations Model (SEM) used to test whether covariance among variables measured in the Norwegian lakes data set could have been produced by the covariance matrix that is predicted from the multivariate hypothesis given in Fig. 1. The coefficients for each arrow give the standard deviation change in each downstream variable *Y* per unit standard deviation in each upstream variable *X*. Epsilons represent the error term for each 'downstream' variable, with the amount of variation explained by the model given by  $R^2$  values at top. Metrics of overall model fit suggest that the model cannot be rejected as a potential explanation of covariance in the data set ( $\chi^2 = 1.18$ , P = 0.28).

Cardinale et al. 2009

**Conclusions:** 

Predictions are supported but relationships are somewhat weak.

Primary production or abundance of plant species

My overall conclusions

SET, RRT, and BEF are not competing theories, but rather components of an integrated model of the interactions between abiotic factors, ecological productivity, and species richness.

Abiotic factors within an ecosystem ultimately set limits on population growth rates and species richness for both primary producers and consumers.



Global Gradient in Biotic Carrying Capacity

**Biotic Carrying Capacity of Ecosystems** 

Biotic carrying capacity - the limits on individual organisms, populations, communities, and rates of ecological processes set by resources and conditions within an ecosystem.



