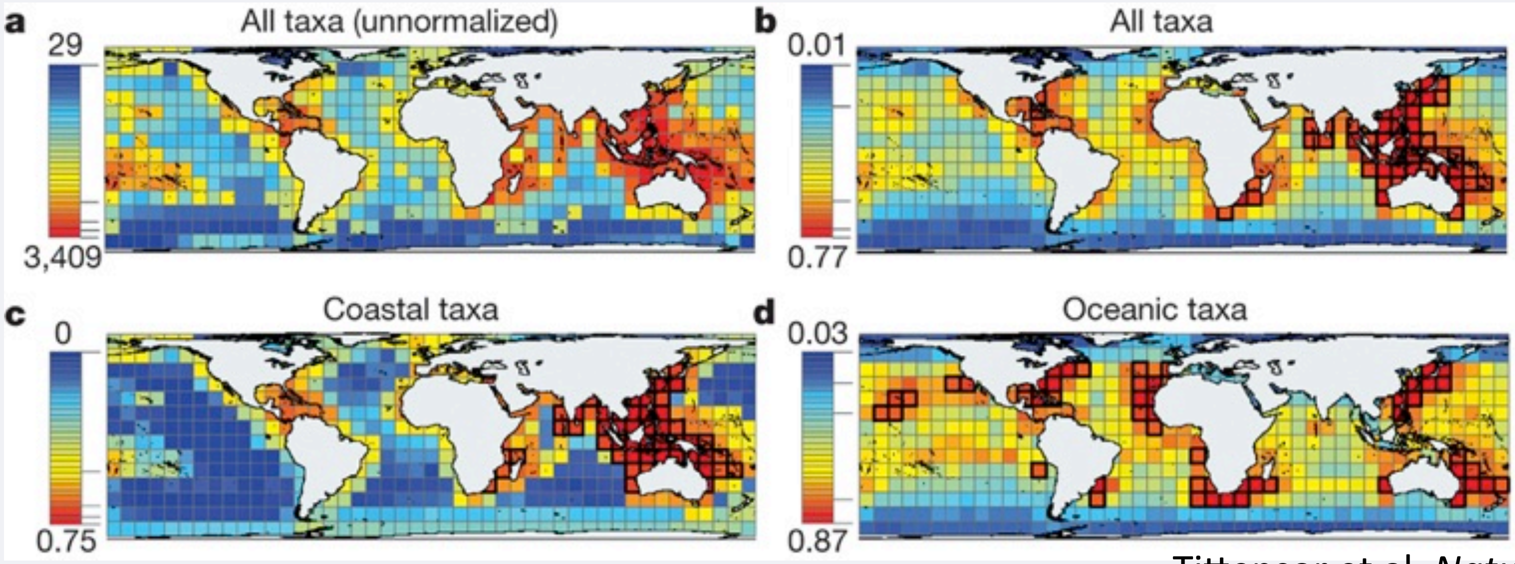
Week 9: Macroecology

Global species richness and hotspots across taxa.



Tittensor et al. *Nature* 2010

"The study of how species divide resources (energy) and space at large spatial scales with the goal to understand the assembly of continental biotas". –J. Brown

"An emergent research program in ecology that examines patterns and processes in ecological systems at large spatial and temporal scales. It acknowledges the complexity of ecological systems and the limitations of reductionistic approaches, emphasizing a statistical description of patterns in ensembles of multiple species. One of its goals is the identification of regularities that might eventually unveil the general principles underlying the structure and function of communities and ecosystems".-*P. Marquet, 2012, Princeton Guide to Ecology*

The Road to Macroecology…

Macroecology started in 1807 with the Alexander von Humboldt describing latitudinal distribution of biodiversity.

Initial 'macroecological' studies all had:

- Large spatial extent of patterns reported
- Statistical descriptions of species ensembles, including attributes: abundance, richness, geographic distribution, body mass
- Emphasis on emerging patterns rather than the component species

Macroecology provided a common framework for these patterns by recognizing the importance of, and the links among, ecological, evolutionary, and biogeographic processes and scales in the understanding of ecological phenomena.

The Road to Macroecology…

1) Recognizing role of regional factors in affecting local dynamics of populations & communities
   - Coupling between local and regional diversity: Robert Ricklefs
   - Metapopulation theory: Richard Levins, Ilkka Hanski

2) Great increases in development and/or availability of data, such as atlases on the distribution and abundance of taxa (e.g. Breeding Bird Survey) and the development of new technological tools to generate data on environmental variables at large spatial scales (e.g. satellite imagery, remote sensing, geographic information systems)

3) Growing recognition of limits to reductionistic*, microscopic approaches that had come to dominate ecology (E.g. trying to understand ecological communities from detailed knowledge of species interactions with manipulative experiments of short duration and limited spatial extent.

*Reductionism: Scientific approach by which understanding of complex systems can be obtained by reducing them to interactions among their constituent parts.

The Road to Macroecology…

Reductionism

Reductionistic Approaches

- Powerful for pair wise species interactions at a given locale
- Limitations: cannot deal appropriately with complex ecological systems:
  - Composed of networks of many species
  - Linked through direct and indirect paths of different strengths and degrees of nonlinearity
  - Subjected to processes at different temporal and spatial scales
- Highly variable with regard to relative importance of biotic interactions and their effect on local coexisting populations

"Ecology is a science of contingent generalizations, where future trends depend (much more than in the physical sciences) on past history and on the environmental and biological setting" – *Robert May, MarcArthur Award 1986*

"The answers to general ecological questions are rarely universal laws, like those of physics. Instead, the answers are conditional statements such as: for a community of species with properties A1 and A2 in habitat B and latitude C, limiting factors X2 and X5 are likely to predominate." -*Jared Diamond & Ted Case, Introduction to 'Community Ecology'*

Reductionism: Scientific approach by which understanding of complex systems can be obtained by reducing them to interactions among their constituent parts.

The Road to Macroecology…

Recall:

Are there general laws in ecology?

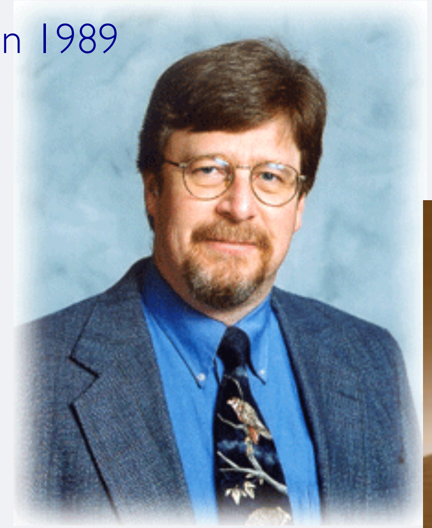
John H. Lawton

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177–192.

The dictionary definition of a law is: "Generalized formulation based on a series of events or processes observed to recur regularly under certain conditions; a widely observable tendency". I argue that ecology has numerous laws in this sense of the word, in the form of widespread, repeatable patterns in nature, but hardly any laws that are universally true. Typically, in other words, ecological patterns and the laws, rules and mechanisms that underpin them are contingent on the organisms involved, and their environment. This contingency is manageable at a relatively simple level of ecological organisation (for example the population dynamics of single and small numbers of species), and re-emerges also in a manageable form in large sets of species, over large spatial scales, or over long time periods, in the form of detail-free statistical patterns – recently called 'macroecology'. The contingency becomes overwhelmingly complicated at intermediate scales, characteristic of community ecology, where there are a large number of case histories, and very little other than weak, fuzzy generalisations. These arguments are illustrated by focusing on examples of typical studies in community ecology, and by way of contrast, on the macroecological relationship that emerges between local species richness and the size of the regional pool of species. The emergent pattern illustrated by local vs regional richness plots is extremely simple, despite the vast number of contingent processes and interactions involved in its generation. To discover general patterns, laws and rules in nature, ecology may need to pay less attention to the 'middle ground' of community ecology, relying less on reductionism and experimental manipulation, but increasing research efforts into macroecology.

Macroecology: Defining a new sub-field of ecology

Formally introduced by James H. Brown and Brian A. Maurer in 1989



Brown & Maurer Definition:

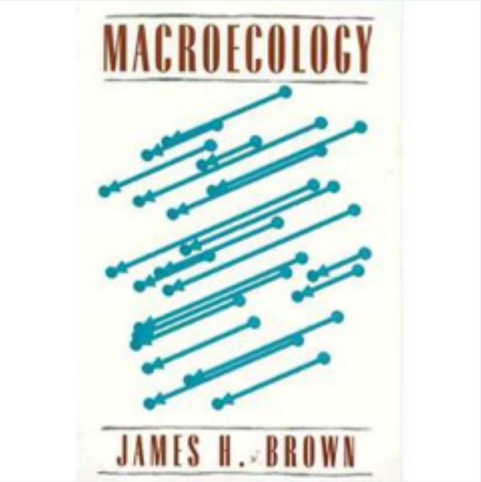
The study of how species divide resources (energy) and space at large spatial scales with the goal to understand the assembly of continental biotas.

- Expectation for high local variability to be cancelled out, therefore discovering general patterns and principles affecting ecological systems

Macroecology:

1) Study of biodiversity patterns and processes at large spatial and temporal scales, a sort of large-scale community ecology
2) Statistical mechanics where emphasis is on the statistical regularities that emerge from the study of ensembles or large collections of species, about which it tries to make fewest possible assumptions

**Focuses on the existence of statistical patterns in the structure of communities that may reflect or provide clues to the operation of general principles or natural laws*



Macroecological Patterns

I) Patterns in the Frequency Distribution of Ecological Attributes

Macroecologists concerned with shape of frequency distributions of traits like body size, abundance, and distribution *and* how these change across space and time

Questions?

- What determines the size of the largest and smallest species found in a given biota?
- Are there gaps in body size distributions?
- Why are most species of small to medium size?
- How does this distribution vary across time and/or from local to global scales?
- Do other taxa (e.g. trees, bacteria, birds) show similar distributions?

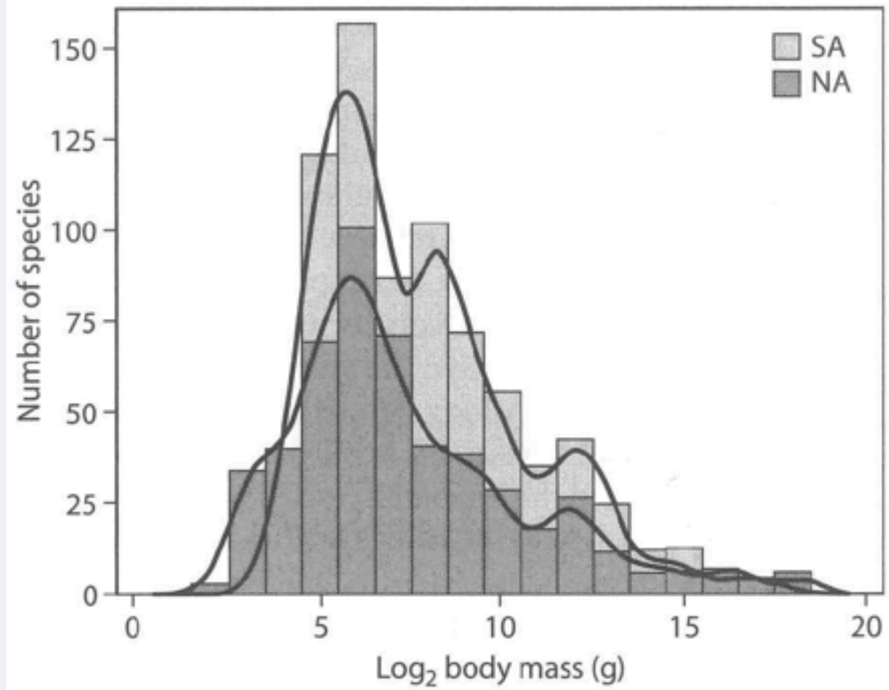


Figure 1. Body size distribution for North American (NA) and South American (SA) terrestrial mammals. The continuous lines represent the result of applying a kernel smoothing to reveal the complex structure of these distributions with lumps and gaps in body size. (After Marquet, Pablo A., and Hernán Cofré. 1999. Large temporal and spatial scales in the structure of mammalian assemblages in South America: A macroecological approach. Oikos 85: 299–309)

What Macroecologists do know…

- The area of landmass determines the size of the largest species that can evolve there and the shape of body size distribution is highly variable across space and taxon
- Body size distributions are affected by how speciation and extinction rates vary with body size & by how the strength and direction of these relationships are affected by environmental factors (temperature, area)

However, macroecologists do not yet have a general explanation for body size patterns

Macroecological Patterns

2) Patterns in the Covariation of Attributes

- Relationship between local and regional species richness
- Relationship between density and body mass:

Population density decreases with body size:

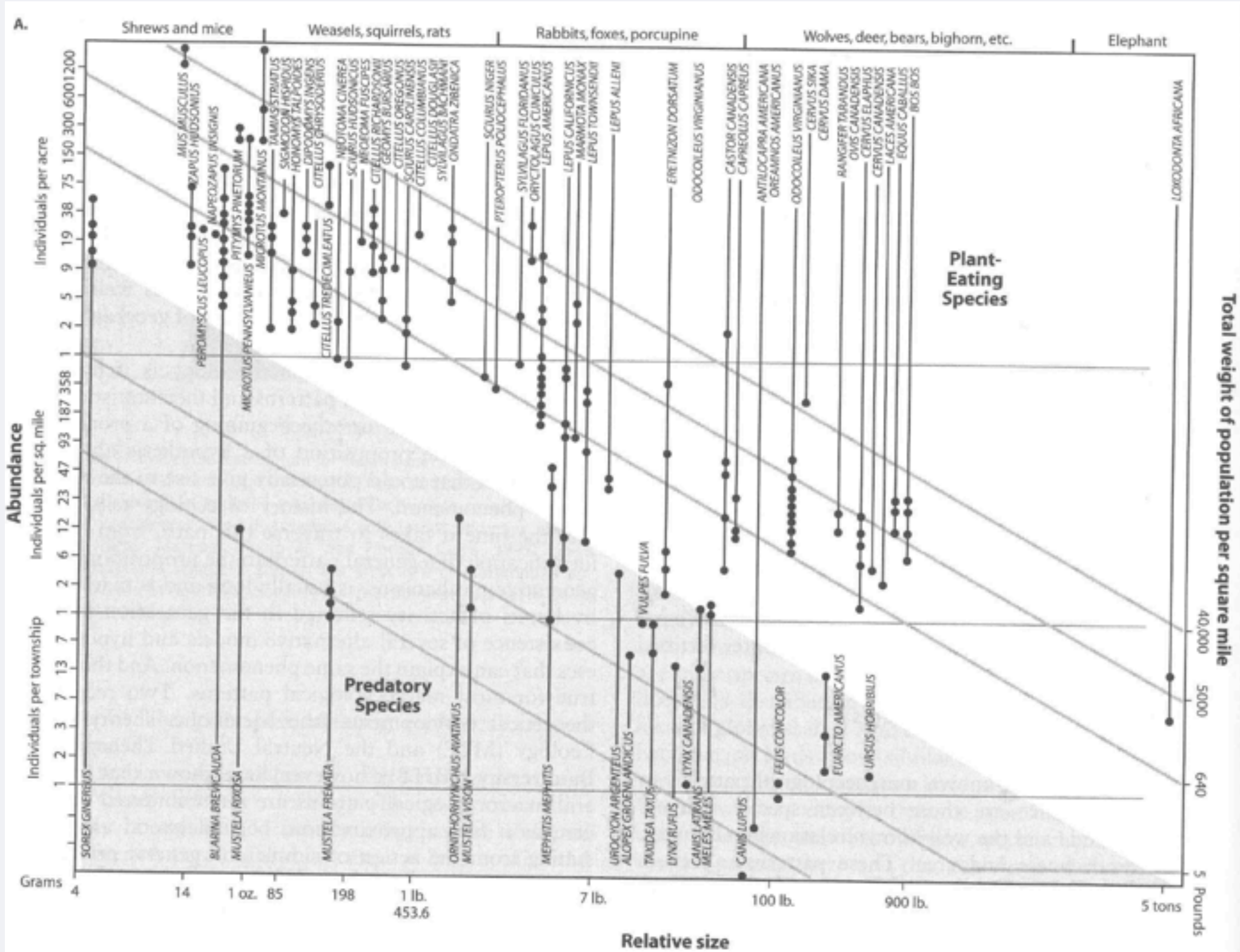


Figure 2. The relationship between population density and body size for (A) mammalian herbivore and carnivore species (from Mohr, Carl O. 1940. Comparative populations of game, fur and other mammals. American Midland Naturalist 24: 581–584) and for (B) 307 species of mammalian primary consumers. (From Damuth, J. 1981. Population density and body size in mammals. Nature 290: 699–700)

Fig. 2A Originally proposed by Carl O. Mohr in 1940. Did not pay attention to the biology of the relationship

Macroecological Patterns

2) Patterns in the Covariation of Attributes

- Relationship between local and regional species richness
- Relationship between density and body mass:

Population density decreases with body size

John Damuth (Figure 2B)

- Density reciprocally related to individual metabolic requirements → implying different species, regardless of size, tend to use similar amounts of energy within communities

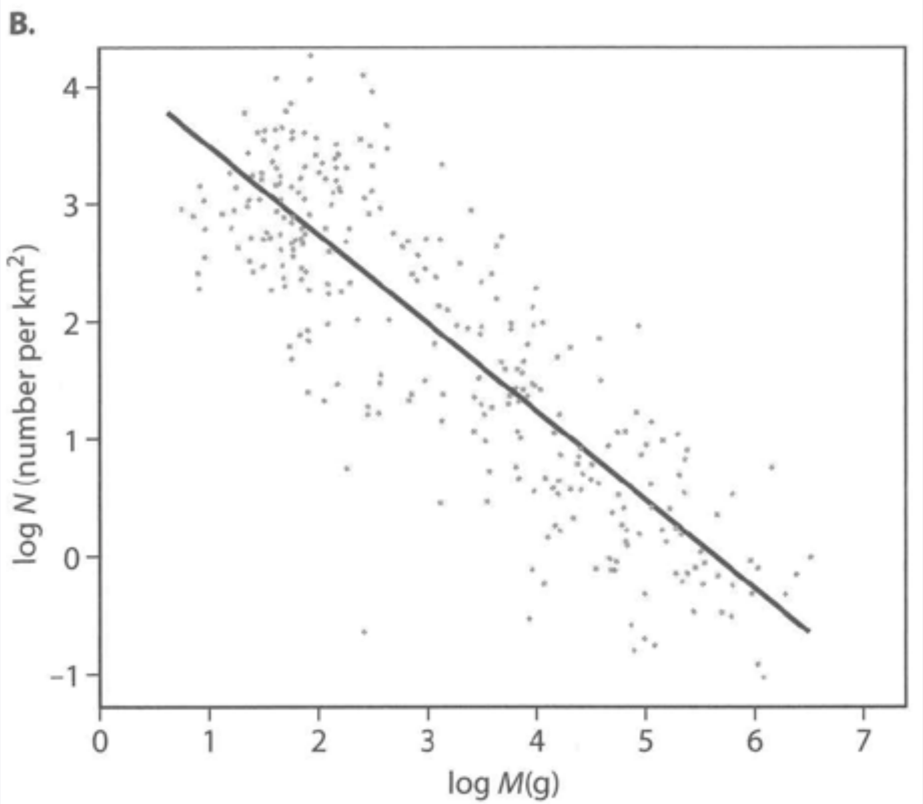


Figure 2. (*cont.*) Relationship between population density and body size for 307 species mammalian primary consumers (Damuth 1981)

Other traits that covary with individual size:

- Geographic range
- Home range area
- Population variability
- Lifespan

Macroecological Patterns

3) Patterns of Change in Attributes along Time or Space

Latitudinal pattern in species richness well documented in a great diversity of organisms and ecosystems (Fig. 3)

- Gradient should reflect latitudinal variation in rates of speciation and extinction.
- Many environmental factors affect these rates

Prevailing View

- Most species originated in tropical areas= *"cradle of diversity"*
- A large fraction remain there= *"museum of diversity"*

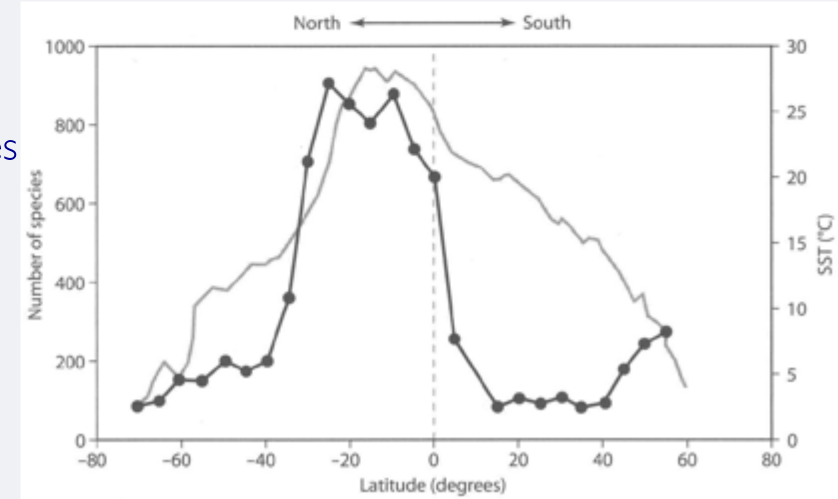


Figure 3. North–south view of the latitudinal diversity gradient of marine gastropod prosobranchs along the north- and southeastern Pacific shelves, from north Alaska to Cape Horn (gray line). Mean sea surface temperature (SST) along the continental margin is also shown (segmented line). (From Valdovinos, Claudio, Sergio A. Navarrete, and Pablo A. Marquet. 2003. Mollusk species diversity in the Southeastern Pacific: Why are there more species toward the south? Ecography 26: 139–144)

Bergmanns Rule: Tendency for individuals of a given species to increase in size toward the cooler areas of its geographic range

Copes Rule: tendency for lineages to increase their size over geological time

The Island Rule

- Gigantism: tendency for small species to evolve toward larger size in island
- Dwarfism: tendency for large species to evolve toward smaller size in islands

Macroecologists also consider the way population density changes across the geographic range of species, the temporal dynamics of the ranges, and geographic patterns in the size and shape of geographic ranges.

MACROECOLOGY is RICH in PATTERNS.

Macroecological Patterns

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REPORT

Cope's rule in the evolution of marine animals

Noel A. Heim[1,*], Matthew L. Knope[1,†], Ellen K. Schaal[1,‡], Steve C. Wang[2], Jonathan L. Payne[1]

+ Author Affiliations

+ Author Notes

*Corresponding author. E-mail: naheim@stanford.edu

ABSTRACT | EDITOR'S SUMMARY

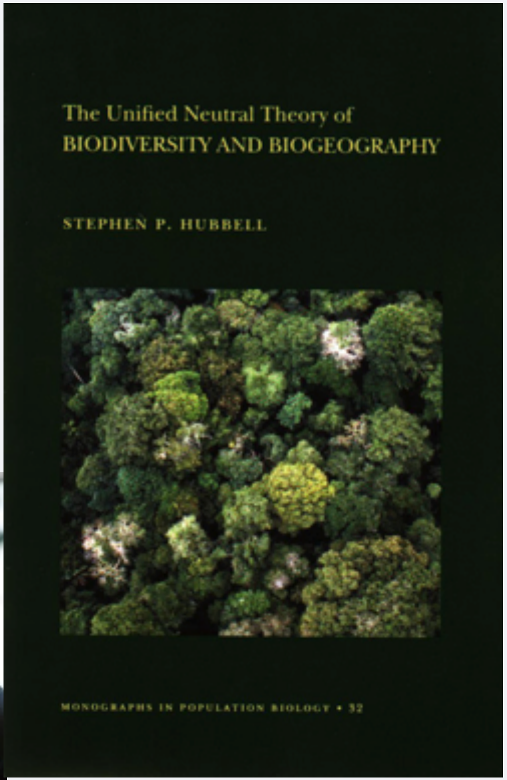
Cope's rule proposes that animal lineages evolve toward larger body size over time. To test this hypothesis across all marine animals, we compiled a data set of body sizes for 17,208 genera of marine animals spanning the past 542 million years. Mean biovolume across genera has increased by a factor of 150 since the Cambrian, whereas minimum biovolume has decreased by less than a factor of 10, and maximum biovolume has increased by more than a factor of 100,000. Neutral drift from a small initial value cannot explain this pattern. Instead, most of the size increase reflects differential diversification across classes, indicating that the pattern does not reflect a simple scaling-up of widespread and persistent selection for larger size within populations.

MACROECOLOGY is RICH in PATTERNS.

Neutral Macroecology

Hal Caswell (1976): developed a neutral theory in community ecology with the goal of understanding the role of biotic forces in affecting diversity regulation

- Assess importance of biotic factors by comparing empirical patterns against results of stochastic model that does not assume their existence
- Used stochastic models developed for population genetics under neutrality



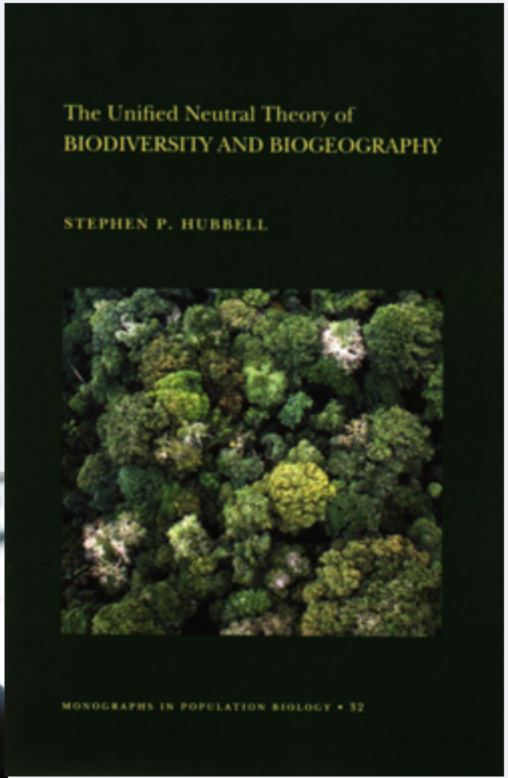
Stephen P. Hubbell (2001): Expanded on Caswell's work by developing the Unified Neutral Theory of Biodiversity and Biogeography (i.e. neutral macroecology)

- Generated several of the patterns usually studied by macroecologists, (species abundance and species-area relationships)
- Testable null hypotheses for macroecological patterns under assumption that individuals are equivalent (neutral) in terms of their vital rates of death, birth, migration, and the probability of becoming new species
- Builds on the idea of island biogeography (MacArthur and Wilson 1963)

Neutral Macroecology

Applies to trophically similar species:

- In local communities undergo random fluctuations in abundance (ecological drift) from stochastic birth/death/immigration rates
- Diversity is maintained in the local community by immigration from the metacommunity, where, in addition to death and birth, speciation occurs
- Community assembly results from stochastic immigration only (dispersal-assembled communities) instead of resulting from adaptive divergence in species niches (niche-assembled communities)
- Relative Species Abundance Distribution and the shape of Species-Area Relationship take different forms depending on the average rate of immigration and the biodiversity number



N.M. has become a null hypothesis for macroecological patterns due to its dynamic, individual based, quantitative and stochastic character as well as its ability to make predictions.

Metabolic Theory of Ecology (MTE)

- Simple framework to analyze role of energy flows from individuals to ecosystems
- Understand individual metabolism and consequences for population, community, and ecosystem dynamics

Kleiber's Rule: body size (M) is constrained by metabolic rate (B), the total rate of energy transformation by an organism

$$B = B_0 M^b,$$

B_0= normalization constant independent of body size
b=allometric or scaling exponent (~=3/4)

West, Enquist, Brown (1997)

- Mechanistic explanation for Kleiber's rule
- **Assumes**: natural selection has resulted in the optimization of biological distribution networks to minimize costs of transporting energy and materials within organisms
- *Geometric constraints on how energy flows*
- Provides an explanation for why most functional and structural characteristics of organisms relate to body size with scaling exponents multiple of ¼ and under which circumstances they might deviate from this theoretical expectation
- **'Universal Scaling Laws'** imply animal's properties are determined by their size
- This work lead to the MTE outlined by James H. Brown et al (2004)

Metabolic Theory of Ecology (MTE)

- Can be used to derive predictions on species abundance within communities:

$$N \propto \frac{R}{B}.$$

$$N \propto M^{-\frac{3}{4}}.$$

N=max number of individuals per unit area
R=rate of resource supply per unit area in the environment
B= individual metabolic rate
M=body size

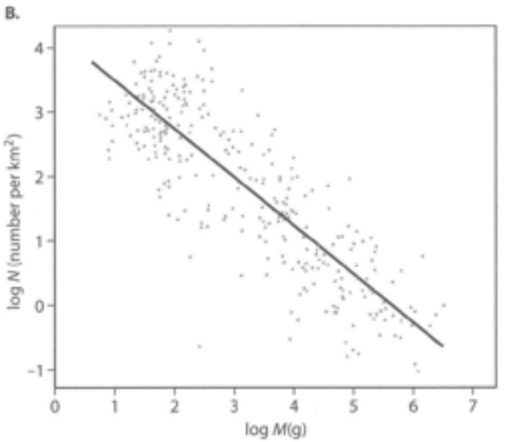


Figure 2. (cont.)

- John Damuth (1981): empirical relationship between abundance and body size usually yields exponents of approximately -¾
- Implies total energy flux by a population is independent of body size → species populations within communities are equivalent in the amount of energy they control (Energetic Equivalence Rule)
  *E.E. rule only works for species using the same resource
- To extend the theory to local communities with trophically dissimilar species one must consider
  - Species in different trophic positions usually differ in size
  - Efficiency of energy transfer between trophic levels is usually low (~10%)
- MTE then predicts that population density (N) across trophic levels should scale with mass (M^{-1}) and biomass (NxM) should be independent of body mass
- FW and marine communities across trophic levels have shown this prediction

Novel MTE contribution: characterizes combined effects of body size and temperature on metabolic rate:
Recent MTE studies: body size and temperature on nucleotide substitutions, speciation rates, latitudinal diversity gradient, ecosystem respiration, carbon cycle

The Future of Macroecology

- Needs more and better data on ecological systems and dynamics from local, regional, continental and global scales
- Needs to back up key empirical patterns with experiments and field studies

Two critical paths for the development of macroecology:

1) Link reductionistic ('microecological') approaches with macroecological patterns and explanations
2) Unify neutral macroecology and metabolic theory

The Future of Macroecology

The Macroecological Contribution to Global Change Solutions

Jeremy T. Kerr,[1]* Heather M. Kharouba,[1] David J. Currie[2]

2007 Science

Anthropogenic global changes threaten species and the ecosystem services upon which society depends. Effective solutions to this multifaceted crisis need scientific responses spanning disciplines and spatial scales. Macroecology develops broad-scale predictions of species' distributions and abundances, complementing the frequently local focus of global change biology. Macroecological discoveries rely particularly on correlative methods but have still proven effective in predicting global change impacts on species. However, global changes create pseudo-experimental opportunities to build stronger, mechanistic theories in macroecology that successfully predict multiple phenomena across spatial scales. Such macroecological perspectives will help address the biotic consequences of global change.

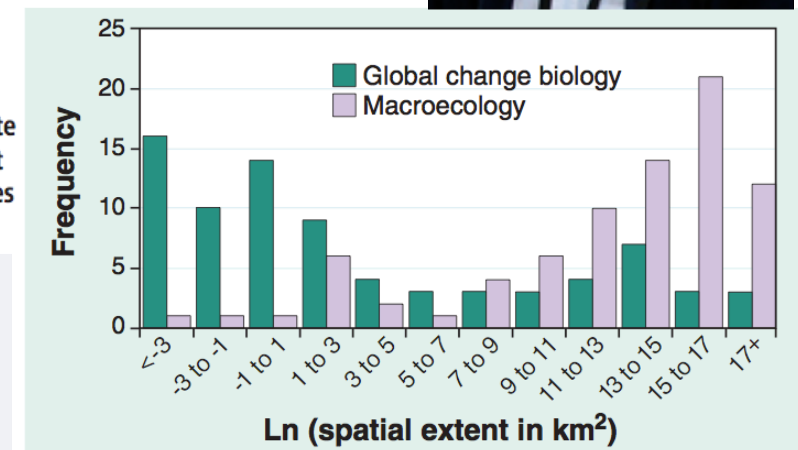


Fig. 1. The contrast in characteristic spatial scales of macroecology and global change biology is evident from this survey of recent publications in the two journals that address these disciplines most consistently: *Global Ecology and Biogeography* (GEB, which presents itself as the journal of macroecology) and *Global Change Biology* (GCB). We started with the most recent issue (December 2006 for GCB and January 2007 for GEB) and worked back until equal sample sizes of 79 studies for each journal were reached. Studies without an interpretable spatial extent (e.g., some meta-analyses) were omitted, but for all others, the spatial extents were recorded. Green bars represent results for global change biology and purple bars, for macroecology.

Macroecology aims to make quantitative predictions about abundance and distribution of species, over broad areas or over large numbers of species.

VS. Most 'global change' biology studies focus on small spatial areas with experimental techniques.

'Strong inference within highly controlled experimental settings [i.e. typically used in global change research] is purchased at the cost of clear broad-scale applicability'

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<u>*NEED for BETTER DATA:*</u>

Environmental characteristics can now be measured more spatially continuous through satellite and aerial remote sensing.

However, *biological data* is more localized.

Mismatch between sparse biological observations and spatially continuous remote-sensing data.

Niche models / Species distribution models can reduce this mismatch by using detailed environmental data to describe the species niche boundaries across a region into a spatially continuous prediction.

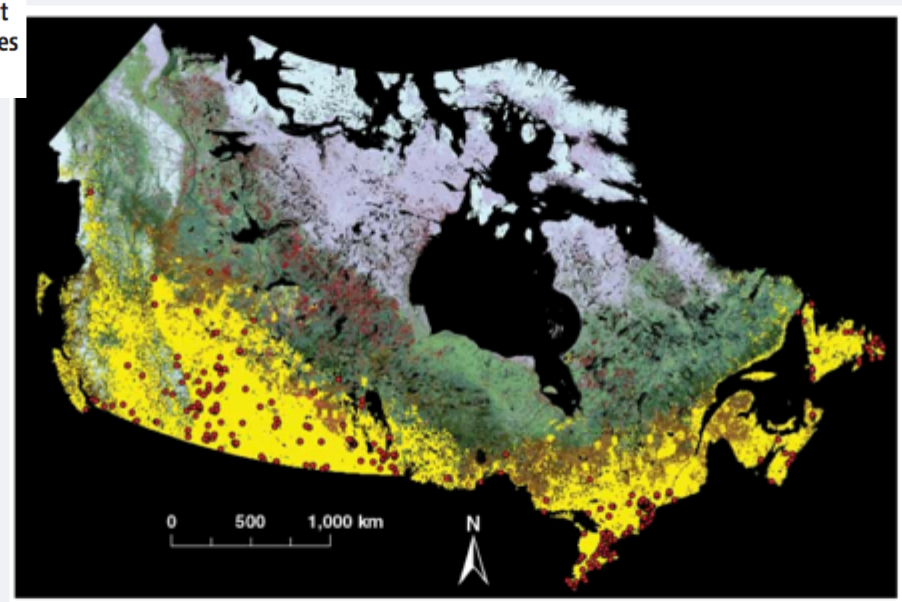

Fig. 3. Biological observations, if available, often include only a species name and a location where it was observed. Observation points across Canada for *Vanessa atalanta* (red admiral) are shown in red, derived from the Canadian National Collection (*59*). These are overlaid on a niche model (yellow) of its range derived with Maximum Entropy (*60*). Environmental data, such as the satellite-based land-use map (*61*) beneath the niche model, are capable of far greater spatial consistency than biological data, although they almost never achieve equally high local detail. Remote sensing is particularly useful for detecting rapid changes, as shown here, where recent forest fires beyond the northern frontiers of this butterfly species' range are in dark red.

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Macroecology must improve its capacity to demonstrate cause and effect.

Global change creates '<u>pseudo-experimental</u>' opportunities

What's Next:

Week 9 (March 9 - 13th) - Macroecology

M: Skills Tutorial 8 - Diversity indices in R

T: L - The macroecological approach and major patterns

W: D - Macroecology (foundation and a current example) - Led by Bryana and Hannah

Required Reading:

- *Classic: Brown & Maurer 1989 Macroecology: the division of food and space among species on continents. Science*
- *Recent: Trøjelsgaard & Olesen. 2012. Macroecology of pollination networks. Global Ecology and Biogeography.*

F: P - Future of macroecology - Led by Capri

Required Reading:

- *Beck et al. 2012. What's on the horizon for macroecology? Ecography.*

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