#### Summer Ecology Research Assistant Opportunity

#### Dendroecology and fire disturbances on Hecate Island,

#### **Central Coast, British Columbia**

I am seeking a summer field assistant to help with my PhD research examining fire disturbances in coastal temperate rainforests on Hecate Island, in the Hakai-Luxvbalis protected area and at the Hakai Institute. This position has both field work and laboratory components. Field work includes spending much of the summer coring trees, digging soil pits and learning ecological methods at a remote research station. Laboratory work will be based out of the University of Victoria and include sanding tree cores, plant identification and data entry. The position has an anticipated start date of May 4th, and will run to August 14th 2015. Salary is in the range of \$1600/month.



#### Qualifications (you can still apply if you don't meet them all):

- Student in year 3 or 4 in Environmental Studies/Biology/Geography
- Previous lab and/or field experience, physically fit, comfortable in remote environments, okay with bugs
- Preference will be given to applicants who are familiar with BC plant and tree species identification skills, have boating experience, and are able to operate GPS/GIS equipment. Applicants should have completed their Wilderness First Aid training by the start of the field season
- · Boundless curiosity is a big plus
- High academic standing (minimum B+ average)

For more information, or to apply for the position, send your resumé and statement of interest to:

Kira Hoffman (khoff@uvic.ca)

#### Deadline for applications is February 6<sup>th</sup> 2015

# The importance of scale in ecology

Ecology, 73(6), 1992, pp. 1943–1967 © 1992 by the Ecological Society of America

#### THE PROBLEM OF PATTERN AND SCALE IN ECOLOGY

THE ROBERT H. MACARTHUR AWARD LECTURE Presented August 1989 Toronto, Ontario, Canada

by

SIMON A. LEVIN

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544-1003 USA, and Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853-2701 USA



Simon A. Levin MacArthur Award Recipient 'The problem of pattern and scale is
the central problem in
ecology, unifying
population biology
and ecosystems
science, and marrying
basic and applied
ecology'' – Levin 1992

# The importance of scale in ecology

"My thesis in this paper is that scaling issues are fundamental to all ecological investigations... The scale of an investigation may have profound effects on the patterns one finds." -Wiens 1989



### Spatial scaling in ecology

#### J. A. WIENS

Department of Biology and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado 80523, USA

'The only things that can be universal, in a sense, are scaling things'

(Mitchell Feigenbaum<sup>2</sup>)

#### Introduction

Acts in what Hutchinson (1965) has called the 'ecological theatre' are played out on various scales of space and time. To understand the drama, we must view it on the appropriate scale. Plant ecologists long ago recognized the importance of sampling scale in their descriptions of the dispersion or distribution of species (e.g. Greig-Smith, 1952). However, many ecologists have behaved as if patterns and the processes that produce them are insensitive to differences in scale and have designed their studies with little explicit attention to scale. Kareiva & Andersen (1988) surveyed nearly 100 field experiments in community ecology and found that half were conducted on plots no larger than 1m in diameter, despite considerable differences in the sizes and types of organisms studied.

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Figure 3. Increasing use of the concept of scale in ecology. Dotted lines bracket periods in which growth rate was exponential. (a) Articles with the term spatial scale in the text. (b) Articles with the word scale in the abstract. (c) Articles and books on hierarchy theory. (d) Articles and books that consider more than one space or time scale, whether or not the word scale is used. (e) Graphical expression of the concept of scale, as measured by publication of space-time diagrams with axes as shown.

# The importance of scale in ecology

Schneider 2001 The rise of the concept of scale in ecology *Bioscience* 

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Our Focus Today

I. What is scale?2. Why is scale important in ecology?

# What is scale?

- Spatial scale
- Temporal scale
- The temporal (or spatial) scale of a variable is the period (or distance) over which it is relatively unchanged –Steele 1991



Figure 4. First use of space-time diagrams in ecology (redrawn from Steele 1978). (a) Conceptual space-time diagram showing life span (days) versus patch size (kilometers) in phytoplankton (P), zooplankton (Z), and fish (F). Line shows mixing scales, measured as powerlaw relation of dispersion of dye ( $\delta$ , in km) with time (t, in days). (b) Instrumental space-time diagram showing space and time scales covered by various types of sampling programs.

# What is scale?

### A CONCEPTUAL FRAMEWORK FOR TEACHING ECOLOGY

|                      | Small                                      | Spatial Scale  | Large        |
|----------------------|--|--|--------------|
| Individuals          | Physiology & behaviour                     |  |              |
| Populations          | Local<br>population<br>dynamics            | Metapopulation<br>dynamics, dispersal, &<br>regional distributions                         | Geographic   |
| Species interactions | Competition, pr                            | etition, predation, mutualism, etc. globa  |              |
| Communities          | Local commu<br>dynamics & sp<br>coexistenc | nity Metacommunity dynamics,<br>ecies dispersal, & regional<br>e diversity and composition | biogeography |
| Ecosystems           | Fluxe                                      | es and stocks of energy and materials at   | all scales   |

#### Issues applicable everywhere:

**Drganizational Scale** 

- (1) Time: equilibrium vs. transient dynamics
- (2) *Methods*: theory, observation, experiment
- (3) Context dependency: organisms, habitats, environment

# Components of scale

- Scale refers to the **extent** relative to the **grain** of a variable indexed by time or space.
- Grain: the minimum resolvable area or time period; the size of the individual units of observation, the quadrats of a field ecologist or the sample units of a statistician
- Extent: the overall area (or time) of the study (ie. what we often think of imprecisely as scale)
- E & G define the upper and lower limits of resolution of a study, thus any inference about scaledependency is constrained by the E & G of investigation
   Fig. 1. The effects of





**Fig. 1.** The effects of changing the grain and extent of a study in a patchy landscape. As the extent of the study is increased (large squares), landscape elements that were not present in the original study area are encountered. As the grain of samples is correspondingly increased (small squares), small patches that initially could be differentiated are now included within samples and the differences among them are averaged out.

#### Wiens 1989; Steele 1991; Schneider 2001

### Which scale is relevant?

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FIG. 1. Relation of size to growth for plants (P), herbivores (H), invertebrate (I) and vertebrate (V). (a) From Sheldon *et al.* (1972) for pelagic marine ecosystems, (b) from Bonner (1965) using only the terrestrial species.

# Why is scale important?

- Unlike physics, ecology is scaledependent
- Ecological systems do not have a characteristic scale

here is no common currency for ecological interactions. For example, the consumption of a small fish by a larger one entails all the following characteristics: behavioral interplay during pursuit and capture, an instantaneous reduction of the prey population, greater reproductive potential for the predator, a flux of organic energy, and a transfer of mineral nutrients such as phosphorus and nitrogen. Thus the same event is viewed differently by behavioral, population, evolutionary, physiological, community, and ecosystem ecologists. Many ecological problems involve complexes of interactions that transcend the boundaries among traditional subdisciplines. Complex interactions arise when system components are linked by multiple types of pathways (e.g., predation, behavioral cues, and transfers of energy and nutrients) (Carpenter 1988a). Consequently, new combinations of approaches are often necessary.

### Consumer Control of Lake Productivity

Large-scale experimental manipulations reveal complex interactions among lake organisms

Stephen R. Carpenter and James F. Kitchell



Figure 3. Whole-lake experiments. Piscivore density (fish/hectare), planktivore density (fish/trap-hours), cladoceran length (mm), zooplankton biomass (g dry mass/m<sup>2</sup>), chlorophyll concentration (mg/m<sup>3</sup>), and areal primary production (mg C  $\cdot$  m<sup>-2</sup>  $\cdot$  d<sup>-1</sup>) versus time. To remove the effects of regional weather, we show the ratios of the experimental lake to an undisturbed reference system, Paul Lake. a. The summer seasons of 1984–1987 for the whole-lake experiment in Tuesday Lake. b. The summer stratified seasons of 1984–1987 for the whole-lake experiment in Peter Lake. Methods and detailed data appear elsewhere (Carpenter et al. 1987, Carpenter and Kitchell manuscript in preparation).

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Carpenter and Kitchell 1988 Bioscience

### Role of Scale and Environmental **Factors in Regulation of Community** Structure

1990 Trends in Ecology and Evolution

### Bruce A. Menge and Annette M. Olson

Pattern in ecological communities – the distribution, abundance and diversity of species – depends on a complex interplay between large- and local-scale processes. Large-scale variation in factors such as environmental stress, dispersal or productivity sets the stage for local-scale ecological processes such as predation or competition. Until recently, most research focused on local-scale explanations of community pattern. Current models attempt to integrate the role of individual large-scale factors with local-scale processes. This trend will continue, with increased effort to understand the specific means by which large-scale factors cause variation among communities.

Ecological communities vary in both space and time. Regardless of habitat, components of community structure exhibit consistent trends along environmental gradients.

Bruce Menge and Annette Olson are at the Dept of Zoology, Cordley Hall 3029, Oregon State University, Corvallis, OR 97331-2914, USA.

Specifically, patterns of species abundance and diversity, the size of food webs and the complexity of interactions among their components are often associated with gradients in elevation, water flow or salinity. Diversity, for instance, often varies within a site (local scale), among sites in a region (mesoscale). and among regions (global or geographic scale). A central issue in community ecology is to determine the various factors underlying spatial variation in community structure, and to place this knowledge into a predictive framework.

#### Scale and community variation

Both physical and biological factors cause differences within and among communities, and both operate on a range of spatial scales. For instance, predation, nutrients, dispersal or desiccation can vary over distances ranging from centimeters to thousands of kilometers. However, the relative importance of physical and biotic factors in regu-

lating community patterns appears to vary with spatial scale. On a local scale, physical and biotic factors interact to influence local patterns of community structure. Predation and competition, for example, can vary over a few meters depending both on interactions between these biotic factors and on direct and indirect effects of small-scale variation in environmental stress (e.g. solar input, flow forces, humidity). Larger spatial scales are associated with increases in the relative influence of variation in environmental or 'climatic' conditions (e.g. temperature), long-range dispersal vectors and nutrients. Such physical factors influence communities mostly indirectly, by modifying or regulating the importance of local-scale factors, but may also directly limit populations.

Development of a predictive theoretical framework of community structure will thus be hierarchical. with simpler local-scale models nested within more complex largerscale models. For instance, a model for community structure on an exposed rocky shore would emphasize physical disturbance, competition for space and predation as primary regulating processes. (Although factors such as temperature or nutrients undoubtedly vary on local scales, little evidence is available to suggest that these

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# The problem of scale

- Problems in ecology often exist at the scale of decades and large ecosystems
- 2) Most variables can only be measured directly in small areas, over short time periods
- 3) Patterns measured at small scales do not necessarily hold at larger scales, nor do processes prevailing at small scales necessarily prevail at larger scales.

Thus, pressing ecological problems cannot automatically be addressed by scaling locally measured variables directly to larger areas and longer times. Schneider 2001 The rise of the concept of scale in ecology *BioScience* 

• 'many ecologists...focus on their small scale questions amenable to experimental tests and remain oblivious to the larger scale process which may largely account for the patterns they study.'-Dayton and Tegner 1984

### The need for multiple scales of study

- Insightful research is likely to consider a range of scales.
- 'Ecologists should use all available tools to advance the analysis of communities and ecosystems at the scales of natural processes, management, and societal concern.'

**Table 1.** General characteristics of various attributes of ecological systems and investigations at fine and broad scales of study. 'Fine' and 'broad' are defined relative to the focus of a particular investigation, and will vary between studies.

|   | Scale  |                        |
|---|--|------------------------|
| Attribute   | Fine   | Broad                  |
| Number of variables important in correlations                   | many   | few                    |
| Rate of processes or system change                              | fast   | slow                   |
| Capacity of system to track short-term environmental variations | high   | low                    |
| Potential for system openness                                   | high   | low                    |
| Effects of individual movements on patterns                     | large  | small                  |
| Type of heterogeneity   | patch  | landscape<br>mosaic    |
| Factors influencing species' distribution                       | resource/habitat<br>distribution,<br>physiological<br>tolerances | barriers,<br>dispersal |
| Resolution of detail  | high   | low                    |
| Sampling adequacy (intensity)                                   | good   | poor                   |
| Effects of sampling error                                       | large  | small                  |
| Experimental manipulations                                      | possible   | difficult              |
| Replication   | possible   | difficult              |
| Empirical rigor   | high   | low                    |
| Potential for deriving generalizations                          | low  | high                   |
| Form of models  | mechanistic  | correlative            |
| Testability of hypotheses                                       | high   | low                    |
| Surveys   | quantitative   | qualitative            |
| Appropriate duration of study                                   | short  | long                   |

### Scale dependent results

- Conflicting results: container size (spatial scale) and experimental duration (temporal scale) can affect results;
- Aquatic ecologists (e.g. Carpenter, Schindler) advocate for whole lake experiments: 'Whole-lake experiments are feasible and can reveal fundamental mechanisms that regulate ecosystems' –Carpenter and Kitchell 1988
- 'Microcosms and non-manipulative studies have not yielded consistent results, and whole-lake experiments are rare' - Carpenter 1996

## Spatial scale-dependency in ecological processes

### **Spatial Distribution of Plankton in Enclosures of Three Sizes**

G. L. Stephenson, P. Hamilton, N. K. Kaushik, J. B. Robinson, and K. R. Solomon

Department of Environmental Biology, University of Guelph, Guelph, Ont. N1G 2W1

Stephenson, G. L., P. Hamilton, N. K. Kaushik, J. B. Robinson, and K. R. Solomon. 1984. Spatial distribution of plankton in enclosures of three sizes. Can. J. Fish. Aquat. Sci. 41: 1048–1054.

The horizontal distribution of plankton was studied in large (1000 m<sup>3</sup>, 16 m diameter, 5 m deep), medium (5 × 5 × 5 m deep) and small (2 × 2 × 5 m deep) enclosures in a 10.3-ha mesotrophic lake in southern Ontario. Zooplankton population estimates from samples collected along distance gradients in the small and medium enclosures varied slightly but no consistent patterned distribution was present. However, the large enclosures possessed a distinctive edge zone that extended about 1.0 m from the walls. On two of the three sampling times there were significantly more macrozooplankton and/or fewer microzooplankton in the edge zone. However, on no occasion were there fewer macroplankton or more microzooplankton in the edge zone. Although macrozooplankton, as a group, may be significantly more numerous in the edge zone ( $P \le 0.05$ ), individual species within this group exhibited both positive and negative responses. There was no defined edge zone in any enclosure with respect to phytoplankton density or biomass. Definition of the spatial distribution of organisms is essential to maximize precision of population estimates when using enclosure systems for ecotoxicological studies.



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FIG. 1. Sampling sites in the enclosures. (a) large corral (A, edge zone; B, middle zone; C, central zone); (b) medium corral; (c) small corral.

Stephenson et al. 1984 CJFAS

### Spatial and temporal scale-dependency in ecological processes

Table 1. Contrasting responses of phytoplankton species as a function of experimental time-scale. Species with increasing, decreasing, or unimodal responses to increased grazing in three-to five-day enclosure experiments are tabulated according to their response to whole-lake increases in grazer biomass lasting one to two years. Only those species with statistically unequivocal responses in both enclosure experiments and whole lake experiments are included (Bergquist 1985, Bergquist and Carpenter 1986, Carpenter et al. 1987, Elser et al. 1987, Elser and Carpenter 1988).

| Whole-lake response |          | Response in enclosur | re       |
|---------------------|----------|----------------------|----------|
|                     | Increase | Decrease             | Unimodal |
| Increase            | 2        | 20                   | 16       |
| Decrease            | 3        | 10                   | 9        |

- The differences in scale between the enclosure and whole-lake experiments cause them to measure different responses. Enclosure experiments reveal short-term regulation of the phytoplankton by fluctuations in biomass of the same zooplankton assemblage with which the algae coexist in the lake. In contrast, whole-lake experiments reveal processes that determine phytoplankton community structure over the long term under a broad range of food web structures, so the phytoplankton are exposed to zooplankton assemblages they have not encountered before. The distinction between enclosure and whole-lake responses is analogous to that between short-term processes that maintain community structure and long-term processes that establish community structure.'
- 'Extrapolation from short-term enclosure experiments to whole-lake dynamics can lead to major errors. On the other hand, certain small-scale experiments have revealed crucial information about regulatory processes and uncovered critical mechanisms that structure communities.'

### Scale and a key ecological question: What controls the distribution and abundance of organisms?



What controls the distribution of species? Four main processes (vertical axis) are believed to control the distribution of organisms; their relative importance changes with scale (horizontal axis). The thickness of the bar for a given factor at a given scale indicates how important that factor is at that scale. Ecologists began drawing such diagrams 25 years ago (16), but have only recently begun to perform empirical studies to test the suggested relationships. The question mark at intermediate scales of dispersal indicates that little data exist on this process at these scales. Climate is important for two scales, through two processes: microclimate (such as sun or shade) at small scales and biogeography at large scales. Most ecologists will disagree with some aspect of this figure, but it is the kind of complex, multifaceted, but testable hypothesis that ecology needs.

distribution and abundance of organisms.

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McGill 2010 Matters of Scale

### Macroecological signals of species interactions in the Danish avifauna

Nicholas J. Gotelli<sup>a,1</sup>, Gary R. Graves<sup>b</sup>, and Carsten Rahbek<sup>c</sup>

The role of intraspecific and interspecific interactions in structuring biotic communities at fine spatial scales is well documented, but the signature of species interactions at coarser spatial scales is unclear. We present evidence that species interactions may be a significant factor in mediating the regional assembly of the Danish avifauna. Because >95% of breeding species (n = 197) are migratory, we hypothesized that dispersal limitation would not be important and that breeding distributions would largely reflect resource availability and autecological habitat preferences. Instead, we detected a striking pattern of spatial segregation between ecologically similar species at two spatial scales with a suite of null models that factored in the spatial distribution of habitats in Denmark as well as population size and biomass of each species. Habitat utilization analyses indicated that community-wide patterns of spatial segregation could not be attributed to the patchy distribution of habitat or to gross differences in habitat utilization among ecologically similar species. We hypothesize that, when habitat patch size is limited, conspecific attraction in concert with interspecific territoriality may result in spatially segregated distributions of ecologically similar species at larger spatial scales. In the Danish avifauna, the effects of species interactions on community assembly appear pervasive and can be discerned at grain sizes up to four orders of magnitude larger than those of individual territories. These results suggest that species interactions should be incorporated into species distribution modeling algorithms designed to predict species occupancy patterns based on environmental variables.

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null models | assembly rules | interspecific territoriality | conspecific social attraction | allee affect



Fig. 1. Species richness of Danish breeding birds (*Left*) and spatial variation in habitat diversity (HD) (*Right*) of grid cells at a grain size of 5 km × 5 km (25 km<sup>2</sup>). The HD score is the product of relative grid cell area and the probability that two points randomly chosen within a grid cell represent different habitat types (54). The HD score was used to parameterize null models of random species colonization independently. Species richness ranged from 1 to 109 species per cell (16, 60). The best-fitting power function was 5 = 27.93681 (HD)<sup>0.1916</sup>,  $r^2 = 0.1171$ . See Fig. 51 for comparable figures at the 10-km × 10-km (100-km<sup>2</sup>) grain size.

# Scale dependencies: a way forward



**Fig. 1.** Species richness of Danish breeding birds (*Left*) and spatial variation in habitat diversity (HD) (*Right*) of grid cells at a grain size of 5 km  $\times$  5 km (25 km<sup>2</sup>). The HD score is the product of relative grid cell area and the probability that two points randomly chosen within a grid cell represent different habitat types (54). The HD score was used to parameterize null models of random species colonization independently. Species richness ranged from 1 to 109 species per cell (16, 60). The best-fitting power function was S = 27.93681(HD)<sup>0.1916</sup>,  $r^2 = 0.1171$ . See Fig. S1 for comparable figures at the 10-km  $\times$  10-km (100-km<sup>2</sup>) grain size.

- Which force(s) most important at a given scale?
- How? Collect more data on what controls species distribution and other variables (e.g. richness, productivity, and abundance) across scales

Gotelli, Graves, Rahbek 2010 PNAS McGill 2010 – Perspective piece

### Up Next: Discussions of Key Scale Papers

### http://uvic470ecology.weebly.com/

#### Week 2 (January 12-16th) - Ecological Aims and Approaches

M: Skills Tutorial 1 - Reading and critically evaluating papers: A major component of this course is reading, critiquing, and discussing the primary literature in the field of ecology. While you have probably already read many papers in the primary literature, it is likely that you could be doing so more effectively. We will discuss ways to achieve this in this tutorial, starting by reading the following two articles (you will have time to read these during the tutorial!):

- 1) Little, J and R. Parker (2010) How to read a scientific paper
- 2) Collins, L How to read a scientific article
- T: L The importance of scale in ecology
- W: D The importance of scale in ecology

Required reading:

- Levin (1992) 'The problem of pattern and scale in ecology' Ecology 73(6):1943-1967.
- McGill (2010) 'Matters of scale' Science 328: 575-576.
- F: D Microcosms in ecology

Required readings:

- Srivastava et al. (2004) 'Are natural microcosms useful model systems for ecology?' Trends in Ecology and Evolution (TREE) 19(7): 379-384.
- Carpenter (1996) 'Microcosm experiments have limited relevance for community and ecosystem ecology.' Ecology 77(3): 677-680.



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