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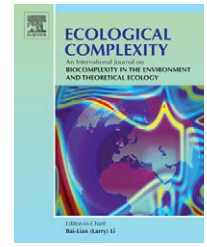

Review

Factors limiting our understanding of ecological scale

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ABSTRACT

Multi-scale studies ostensibly allow us to form generalizations regarding the importance of scale in understanding ecosystem function, and in the application of the same ecological principles across a series of spatial domains. Achieving such generalizations, however, requires consistency among multi-scale studies not only in across-scale sample design, but also in basic rationales used in the choice of observational scale, including both grain and extent. To examine the current state of this science, here we review 79 multi-scale wildlife-habitat studies published since 1993. We summarize rationales used in scale choice and also review key differences in scale-specific experimental design among studies. We found on average that 70% of the observational scales employed in wildlife-habitat research were chosen arbitrarily with no biological connection to the system of study, and with no consideration regarding domains of scale for either dependent or independent variables. Further, we found it common to change either both grain and extent, or the entire suite of independent variables across scales, making cross-scale extrapolations and generalizations impossible. We discuss these sampling limitations by clarifying the differences between multi-scale versus multi-design studies, including the distinction between spatial versus scalar observations, and how these may differ from the commonly cited "orders of resource selection". We conclude by reviewing both existing and suggested alternatives to reduce the arbitrary nature of observational-scale choice prevalent in today's literature.

Contents

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1. Introduction

Most ecologists now agree that scale is important when acquiring and interpreting ecological data. Scalar aspects of ecological observation and analysis have become common over the last two decades, and now figure prominently in prioritizing research objectives (Levin, 1992), designing organism-centered sampling methods (Wiens, 1989), and extrapolating process from observed patterns (Turner et al., 1989; Turner, 2005). These ideas have inspired a growing number of ''multi-scalar analyses'' intent on describing ecological phenomena at more than one observational scale. Unfortunately, increased interest in ecological scale has not resulted in new or innovative understanding of basic questions in scalar ecology. We still lack the ability to predict ecological phenomena across observational scales, which ultimately hinders our progress interpreting observed patterns into known mechanisms and processes. We argue that this inability stems from arbitrary and inconsistent cross-scale study design. To demonstrate this, we review and summarize a large sample of peer-reviewed literature that focuses on the application of scaling principles to wildlife-habitat models. We examine the rationale used by researchers to choose observational scales; evaluate the most commonly used approaches to multi-scale ecological studies; and from this, we summarize some limitations in scale research that require innovation and improvement.

Why use more than one observational scale? Most ecologists likely consider this question rhetorical, but approaches to and interpretations of multi-scale analyses suggest otherwise. The impetus for multi-scale studies should be twofold. First, the same ecological process might show different patterns if observed at different scales. If we study a system at an inappropriate scale, we may not detect its actual dynamics, but may instead identify patterns that are artifacts of scale (Wiens, 1989). The inability to distinguish emigration from mortality in many live-capture studies, for instance, is an artifact of trapping-grid scale. Second, not all aspects of an animal's biology can be observed using one observational scale. For example, different observational scales often are required to quantify local foraging movements versus natal dispersal movements. These are practical sampling reasons for using multiple observational scales, but there is also a fundamental theoretical reason that receives almost no attention: namely, the ability to *predict* patterns and processes across scales. Because ecological data are always limited, the ability to scale up or scale-down in our predictions is crucial, particularly in conservation and management of wide-ranging species. But, despite a growing number of scale-focused studies, empirical support for ecological scaling techniques remains elusive.

Why are we still largely unable to extrapolate across scales (Levin, 1992; Heuvelink, 1998; Peters and Herrick, 2004)? There are arguably several reasons, the most notable in the literature being the varied definitions of scale (e.g. Dungan et al., 2002), but perhaps the most elementary involve basic study design, and specifically the rationales used in choosing observational scales. Every scalar study must begin with the selection of a relevant scale, defined in ecological contexts as ''the spatial or temporal dimension of an object or process, characterized by both grain and extent'' (Turner et al., 1989; Gustafson, 1998; Dungan et al., 2002; also see Schneider, 2001). The constituents of grain and extent are the fundamentals of how we observe ecological systems; grain referring to the finest level of spatial resolution available in a data set, and extent to the physical size or duration of an ecological observation (Turner et al., 1989). Ideally, these both are selected based on relevant information regarding a species' biology, or grain of perception (Wiens, 1989), but often this is unknown and scalar references are arbitrary. With rare exception the number of scales employed is limited, meaning much weight rests upon rationales used in scale selection. Therefore, it is important to clarify rationales employed in selecting observational scales. If choices are largely arbitrary, published results may reflect scale artifacts and, by examining irrelevant or redundant scales of observation, may entirely miss true scalar processes. Patterns observed across scales will form the bases of hypotheses exploring underlying processes (Swihart et al., 2002), so an important distinction is whether these are derived from arbitrary/anthropocentric versus biological/organism-centered study designs. Similarly, it is worth examining whether cross-scalar experimental designs are consistent among studies. Both of these factors largely define our ability to produce scalar extrapolations and generalizations within the ''science of scale'' (Goodchild and Quattrochi, 1997).

2. Choice of observational scale

To quantify how observational scales have been chosen for study, we reviewed all multi-scale articles from a sample of journals that publish scalar studies: Landscape Ecology, Journal of Wildlife Management, and Journal of Applied Ecology. Our focus was on wildlife-habitat research: because study taxa are mobile and range over multiple scales, this field of study has produced more multi-scale studies than most, including the geographical sciences. It is from these studies that scalar insights will be generalized into the broader ecological literature. We used Web of Science to search for articles identifying ''spatial'' or ''scale'' in their abstract; then, we chose those claiming to have employed >1 observational scale. We analyzed each paper and determined the rationale for selecting the number and dimensions of each spatial scale. We considered choice of scale non-arbitrary if the authors provided a link between scale (grain or extent) and some aspect of the organism's biology (e.g. movement parameters, home range, dispersal area, foraging distance, etc.), even if cited from previous research. If authors chose a scale because they ''felt it to be representative...'' or ''considered it a good compromise...'' we scored these as arbitrary. We noted taxonomic class and field of study (population or community). In total, we reviewed 79 multi-scale wildlife-habitat studies published between 1993 and 2007. We summarized trends in choice of scale over time and among taxonomic and research sub-disciplines (i.e. population versus community ecology).