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Implications of scale in the study of fragmentation and it effects

Abstract: Recognition of the importance of scale in ecology has undergone a revolution in the last decade. I assess the importance of scale in pattern measurement, ecosystem functions and fragmentation. The measurement of fragmentation will differ with scale. In order to understand the effects of fragmentation it is necessary to understand how species perceive fragmentation at different scales. New models in complex adaptive systems theory may help ecologists to integrate different scales of pattern and process and improve predictive models.

Keywords: scale analysis, scale variance, fragmentation ecology.

Introduction

“Different patterns emerge at different scales of investigation of virtually any aspect of any ecological system” – (Wiens 1989, pp. 386).

Recognition of the importance of scale in ecology has undergone a revolution in the last decade. Scale is not just a ‘new ecological buzzword’ but the primary focus of research called for by Wiens (1989) and modern ecological studies no longer tacitly imply the 1m^2 quadrat is an intrinsic property of nature.

Attempts are now being made to explicitly design experiments on an appropriate *ecological* scale (Johnson et al. 2001; Vos et al. 2001). Increasing numbers of experiments are being designed to investigate the same aspect of the study ecosystem at multiple scales to quantify differences in pattern with scale (Syms 1999).

However ecology is still primarily concerned with describing what things look like rather than explaining and understanding patterns (Baskerville 1997). Little is known about how ecosystems function, and even less about the consequences of anthropogenic global change. Ecologists need first to understand how ecosystems function at multiple scales and then ecologists can predict the consequences of anthropogenic change.

The aim of this paper is to discuss the shortcomings of ecological research that doesn’t explicitly deal with the elements of scale within the subject ecosystem and within the methodology of the study. I discuss the need to understand an ecosystems individual components and processes in order to appreciate the scale they operate on, followed by a discussion of the way ecosystem processes interact, within and between different levels of the scale hierarchy, to form the patterns that ecologists observe. I then discuss how understanding of scales of process, pattern and measurement apply to fragmentation and its effects and new models that may help to integrate ecological knowledge at different scales.

Patterns and process in ecology

Scale and the nature of patterns

The human experience is one of observing and responding to pattern and it is worthwhile explicitly considering the nature of patterns. The Nazca lines are a set of giant figures engraved in the surface of the Peruvian desert. On the surface these figures appear as straight paths on the desert floor. The paths only form an image, a recognizable pattern, when observed at a much greater scale, such as from the air. However, although the Nazca lines are statistically significant only on a large-scale, etching of paths in the desert-floor (assuming support for the human origin hypothesis) that caused the pattern occurs only on the much smaller human scale. However, geological processes operating over millions of years formed the rock on the desert floor used to create the Nazca figures. The observed pattern is the result of several processes that have vastly different origins and scales in space and time.

In the natural world pattern may also emerge at a different scale from the processes causing the pattern and may be the combination of multiple processes of natural and human origin, operating at different spatial and temporal scales (Wiens 1989).

Scale variance of patterns

Ecological research has demonstrated that different processes dominate measurement of the same pattern at different spatial and temporal scales (Wiens 1989). Although interesting in its own right, this scale variance makes it difficult to predict how processes will interact across scales, or how ecological understanding at one scale can be transformed to be applied at another scale (Peterson et al. 1997).

Studies of small mammal fauna of Valdivian temperate rainforests in southern Chile found that the numerically dominant species co-occurred with other species more frequently than expected by chance when measured at local scales (Kelt et al. 1999). At slighter larger scales species show a negative correlation indicating apparent competition. At regional scales it is anticipated that species assemblages would relate positively once more because of similar inter-species adaptation to bio-climatic zones. Similar scale variance in species-species interaction was also found by Sherry & Holmes (1988) between Least flycatchers (*Empidonax minimus*) and American redstart (*Setophaga ruticilla*) bird species in hardwood forests in the United States (read in Wiens 1989).

This scale variance can be broadly generalised by stating that geophysical and habitat dependencies dominate at large scales while interactions between biota dominate at small scales. This observation is limited to short time-scales and it is likely the ‘space-for-time’ analysis (Burke et al. 1997) would show increasing importance of local processes such as competition as timescales increase.

Scale measurement variation

Two properties, the *grain* and the *extent* define the scale of measurement (Wiens 1989). The grain reflects the smallest unit that can be measured directly and the extent the largest.

In the field of remote sensing the extent is represented by the total area covered by the satellite image and the area covered by a single pixel. It is not possible to observe patterns or processes below a single pixel or beyond the extent of the image. Multiple images of the same area at different time periods is often used to measure large-scale processes such as fragmentation (Chatelain et al. 1996; Riitters & Wickham 2000) but extrapolating analysis beyond the temporal extent of the data relies on the precarious assumption that processes are linear over time.

The choice of grain and extent is crucial to any ecological experiment and it is always true that reducing the grain size and increasing the extent of a study will improve the ability to detect pattern. However, for logistical and practicality reasons ecologists must usually choose between a broad-scale study with large grain size or a smaller extent at finer resolution (Wiens 1989).

Hierarchies of scale

Small-scale processes feedback to large-scale processes and large-scale processes feedback to small-scale processes.

The biosphere is a grand-scale example of feedback between different levels in the scale hierarchy. Small-scale biota produces and consumes oxygen and carbon dioxide that in turn regulates the growth of small-scale biota. It is interaction between processes operating at different scales that cause the non-linearties observed in scale variance.

Fragmentation and its effects

Scale and fragmentation theory

Lord & Norton (1990) define fragmentation as simply, "the disruption of continuity" in ecosystems, and traditional geographical fragmentation, the human-induced division of forests into habitat islands, as a special case.

Fragmentation occurs at different spatial scales, though 'scale' terminology in the literature is sometimes imprecise. Dale et al. (1994) use scale of fragmentation to refer to the spatial extent of fragmentation. Lord & Norton (1990) use scale to mean the 'grain size' or size of the landscape elements.

The use of the term scale is also associated with spatial arrangement attributes such as habitat quality, differences in patch shape and size, and variation in isolation among patches (Keitt et al. 1997). Ecologists quantify these spatial patterns at landscape level with indices such as fragment size (Vos et al. 2001). However to fully quantify fragmentation it is necessary to measure at a much smaller level than landscape indices provide (Keitt et al. 1997).

In the special case of anthropogenic fragmentation ecologists are able to observe the primary mechanisms causing fragmentation, logging, road building and human migration and urbanization.

However though it is often easy to describe the causal mechanisms and measure the pattern of fragmentation it can be very difficult to assess the effects. The questions being asked of ecologists are these. How much fragmentation is occurring in the environment? What will be the effects on organisms in newly fragmented habitat?

How fragmented is the environment?

To assess the amount (sometimes confusingly referred to as the scale!) of fragmentation ecologists need to consider what scale to measure fragmentation on. In a study of forest fragmentation based on 1km^2 land cover maps (Riitters & Wickham 2000) enlarged the grain size used to classify forest areas into interior, perforated or edge and observed that more fragmentation appeared to be detected and interior forest decreased. Also, as increasingly fine recognition of forest types was added to the analysis, fragmentation also appeared to increase (Riitters & Wickham 2000).

Percolation theory is used to examine the scale relationship for dispersal between patches (Keitt et al. 1997). Habitat patches are 'connected' if the minimum distance between patches is below a threshold distance. Habitat patches in a large, 1.5 x 10^6 km^2 region of the south-western United States were mapped by Keitt (1997) and the connectivity of the landscape examined with threshold distances between 10 km and 100 km. It was found that, at a critical distance of between 40-45km, the regional connectivity transitioned between disconnected and connected phases. Furthermore some, otherwise insignificant, habitat patches were found to be critical to the regional connectivity.

What will the effects of fragmentation on biota?

The ramifications of connectivity analysis for biota is that species that have dispersal distances well below the critical distance of connectivity will not be effected by removal of sensitive patches as they will already perceive the landscape as disconnected. Likewise species with dispersal ranges well above the critical distance will be insensitive to further defragmentation. However, in the south-western United States, Mexican Spotted owls which are known to occasionally travel more than 45km may be crucially effected by the removal of sensitive connecting habitat patches (Keitt et al. 1997).

Similar connectivity and sensitivity analysis may apply to different scales. Bees of medium body size can regularly fly 1-2 km from nest site to a forage patch (Cane 2001). Fragmentation will have a larger effect on bees when the critical threshold of the landscape fragmentation is in the related dispersal distance for this species. In the situation of bees fragmentation may also be crucial because the supply an important ecosystem service, pollination (Cane 2001).

Many species are thought to exist in metapopulations, homogenous local patches loosely connected throughout a heterogeneous landscape. The importance of connectivity between habitat fragments is that some species are thought to rely on the ‘rescue effect’ between patches to ensure the long-term survival of local populations (May 1994). Work modelling meta-populations of predators and prey have demonstrated that, in theory, predator species need connected areas many times the area they would range in their lifetimes to survive perpetually (May 1994).

The effect fragmentation will vary from species to species and from scale to scale (Keitt et al. 1997; Wiens 1989) and it is usually necessary to examine each case individually. Ecologists often categorize similar species into functional groups based on factors such as diet or morphology. However, functional groups may vary depending on the scale of analysis (Andersen 1997). Consumers that use sparse or clumped resources are likely to operate on larger spatial ranges (Wiens 1989). Migratory species such as birds or Serengeti mammals will perceive the environment differently from sedentary species (May 1994). Specialists are more affected by small-scale fragmentation than generalists (Lord & Norton 1990).

The rate of extinction of mammals in six Tanzanian parks over the last 35-83 years is significantly and inversely related to park area, suggesting that increasing insularisation of the parks has been an important contributory factor in large mammal extinctions (Newmark 1996).

Indirect effects such as the effects of fragmentation on food sources can alter species response. The bird guild that follows army-ant colony eating insects stirred up by the migrants was found to disappear rapidly in newly formed (1-10 hectare) Amazonian forest fragments (Lovejoy et al. 1984). Army-ant followers disappeared even in fragments as large as 100 hectares. General insectivores disappeared from fragments much more slowly.

Overall, the way in which fragmentation affects a species can vary considerably between even quite similar species. Detailed ecological knowledge of the scale dependency and interactions of individual species are needed to accurately predict effects.

The scale dichotomy in fragmentation ecology

Ecological research must range from the natural history and behaviour of a single species to regional experiments (Peterson et al. 1997). However, ecologists are still struggling to reconcile the dichotomy between large-scale observations of landscape pattern and fragmentation and small, species-scale measurements.

Remote sensing is the only feasible way to map ecosystem fragmentation at regional and global scales (Foody et al. 1997) but there is a lower scale limit. Some fine-grained fragmentation is beneath the resolving power of these instruments and most ecosystem properties and functions cannot be resolved. Additionally there is a spatiotemporal trade-off forcing researchers to choose between fine-scale or frequent measurements (Foody et al. 1997).

So small-scale experiments and species-specific research remain crucial to our understanding of biological processes at management scales (Peterson et al. 1997). However, there is an upper scale limit to our ability to measure ecosystem function by traditional sampling methods. The largest scale forest inventories completed in neo-tropical rainforests are between 1-3 hectares in size. At this scale the indices of similarity (Sorenson's index) ranges from 0.16 to 0.21 (Campbell 1994), showing there is very little similarity between adjacent rainforest plots. This either means that there is no pattern to tree species distribution in tropical rainforests or that observations are below the scale of pattern expression, the equivalent of trying to understand the Nazca figures from a few $1m^2$ quadrats on the ground.

As most ecological patterns and processes are scale-dependent to some degree and observations made at one scale may not be applied directly to other scales (Andersen 1997; Peterson et al. 1997; Wiens 1989). Ecologists must be certain they understand how fragmentation effects vary with scale before attempting to generalize probable impacts (Andersen 1997).

Some hope for reconciling these spatial scales contradictions may lie in modelling of complex adaptive ecosystems using individual-based algorithms (Railsback 2001) and cellular automata (Gassmann et al. 2000). This involves using small-scale, species focused ecological experiments and large-scale remote-sensed landscape information to populate computer models attempting to reproduce and predict some of the larger-scale emergent properties of ecosystems (Ranson et al. 2001).

Conclusion

As much as possible ecologists need to increase the extent and decrease the grain size of experiments. This is theoretically, though not logistically, the simplest way to overcome scale difficulties.

Measuring at multiple scales is allows the scale variance of patterns to be explicitly quantified. Phase transition at different scales can reveal critical point in many areas of ecology, as seen by fragmentation examples. Management should be aware that decisions may have greater effects at critical scales.

Ecology needs to expand to include the large without abandoning the small. Another way to say this is that ecology needs to include the small without abandoning the large! New methods such as complex adaptive system theory may help to find ways to overcome scale variance of experimental results.

Most importantly ecologists need to recognize scale theory affects every aspect of ecology and deal with scale explicitly in their experiments.

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