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The Complexities and Opportunities of Examining Scale in Ecology – With Application to Grassland Management

Skadi von Reis

ABSTRACT

Understanding the way in which biodiversity is created and maintained is the fundamental goal of applied ecology. In order to comprehend how diversity is distributed and isolate the factors contributing to diversity, multiple scales of study must be considered. Studies which base their conclusions on an isolated snapshot of an ecological system find their results challenged by considering both historical and spatial scales. The question of scale: its definition, the relevant scale at which biological processes produce observable patterns, the translation from small to large scales and the theoretical and technological complications scale presents, remain contentious issues in ecology. This review investigates the current definitions of scale, arguments over the importance of various scales, and the use of scalar components in research. Secondly, it looks at how careful consideration of scale gives rise to various limitations and complications of ecological studies. Finally, it addresses the difficulty of scaling up, from local to regional, through ecosystems. The question of scale is then applied to grassland management, a biome both vital to biodiversity and human use, in order to concretize theoretical arguments and provide direction to management. This review is conducted to generate a greater comprehension of scalar applications to future research, the contingency of current conclusions based on scalar limits will, and how this knowledge can be applied to aid management that engages all scales in order to preserve diversity.

INTRODUCTION

Biodiversity is the central focus of ecology and the ultimate objective of ecological management. The majority of species remain an untested pool for possible human utility; current society is functionally supported by less than 1% of all living species on earth (Wilson 1988). A world with reduced diversity faces a risk of losing key regeneration processes such as water filtration, stabilizing processes like river bank preservation, the production of goods, the function of improving our lives aesthetically and culturally, and finally the preservation of future use (Daily 2001). Although this anthropocentric value of biodiversity is criticized by deep ecologists, we must accept that it is ultimately human decisions that shape the future of biodiversity and these decisions will be based on species values to us: be it cultural or economic.

Biodiversity is complicated by the scale at which diversity is measured and the level at which diversity is created (Ricklefs 1987, Field et al 2008, Tylianakis et al. 2006, Gering and Crist 2002, Suding et al 2008). Some complications include choosing the correct scale at which diversity is shaped, the contingency of proper scales based on the model organism, the sheer technical difficulty of measuring both large and minute scales, and the translation of local to regional scales. The complexity arising from awareness of scales complicates the goal of cohesive of ecological theory. Scale is not only a vital consideration in building comprehensive ecological theory, but also understanding the scale at which diversity is created and manifested in ecosystems.

The grassland biome encompasses around 70% of all earth's surface and 61% of the surface in the United States (Fuhlendorf and Engle 2001) making it a vital terrain in which to study how diversity is created and maintained. Temperate grasslands are characterized by an absence of woody plants, dominance by floral and grass species, and rich, deep soils. Due to their inherent topography and fertility this biome in particular is the target of agricultural expansion as well as grazing pressure ("The world's biomes"). If biodiversity is the central concern within ecological health than the methods through which diversity is maintained is a central concern of management.

This review will address two major themes: it will focus on the issue of geographical scale and the complications resulting. It will then use grasslands as a model ecosystem to contextualize aforementioned issues of scale in hopes of informing awareness of scalar complexity in management. Questions prompting research include: What issues of scale arise in framing of ecological questions and measuring ecological phenomena? How can scalar studies contribute to the field? How does contemporary

grassland management use scalar dimensions and complicate questions of scale? This review is written in the context of the need to understand diversity processes, both how diversity is created and how it is maintained, for informed stewardship of landscapes.

CONSERVATION OF BIODIVERSITY

The importance of biodiversity

The essential dependency of human life on the diversity of non-human life is contradicted by the under-valuation and subsequent destruction of diversity which arises systemically from our society's capitalist based economy (Haneman in Wilson 1998). The loss of the mosaic of local agricultural and environmental relationships with the land is a result of the unifying process of westernization across the globe (Norgaard in Wilson 1988). The multi-faceted attacks on diversity arise from issues such as the imbalance of future costs and present benefits, biodiversity as a collective good with risks of loss spread collectively over society, as well as the increasing global specialization (Haneman in Wilson 1988). Ecological systems are unable to adapt as quickly as economical systems change, thereby pushing populations to unsustainable levels. Specifically, global expansion of agriculture combined with the rising agricultural and industrial pollutants, strengthens forces of extinction on species interacting with agricultural practices. These pressures arise at a time when the need for diversity amongst plants is essential due to expanding ranges of plant diseases (Norgaard in Wilson 1988).

Declines in biodiversity yield consequences beyond loss of ecosystem services. Within the grassland ecosystem, extensive studies by Tilman et al. (1996) shows that the diversity within ecosystems leads to a higher utilization of inputs such as nitrogen and sustains primary productivity in the long term. This supports the overarching concept that stability within ecosystems is derived from their inherent diversity (Tilman et al. 1996). Thus biodiversity loss threatens the stability and integrity of ecosystems.

We should keep in mind that the current biodiversity crisis discussed in biological fields is not limited to species loss but includes loss of heterogeneity in terms of knowledge of unique environments, cultural values and practices associated with knowledge, and the risk of forever losing the accumulated histories of our ancestor's successes and loss. Not only should our concern be linked to loss but also to future limitations, both biological and societal. Ecological diversity is inextricably linked to economic diversity, although the two operate at varying time scales. Ideologically

separating these two fields masks the future economic risk of present decline in ecological diversity (Norgaard in Wilson 1988). Although this review focuses on the specific case of grassland biodiversity it is situated amongst this global discussion of conserving the ability for a spectrum of life to exist on earth.

The conceptual limits of biodiversity conservation

Conservation, as it is discussed in many prominent ecological studies, is naively based on the division of human and non-human landscapes (Robbins 2004, Cronon 1995). This concept is mythological because in most cases, native or marginalized peoples were pushed off of the land prior to claiming the site as a “wilderness area”. Kay (1998) explains that the way in which society conceptualizes wilderness is as a state before the expansion of human populations, specifically Anglo-Saxons. An example in current literature is found in a prominent Ecology paper by Bjorndal and Bolten (2003). These researchers chose a target population size for marine turtles based upon population sizes cited by early American explorers, a choice that goes undefended during their paper.

Conservationists are constructing a mythical division of humans from natural systems and this binary discourse of conservation frames the way in which management of “natural” systems is legitimized (Robbins 2004). Research shows that ecosystems were greatly impacted by previously expansive native human populations (Kay 1998). Native Americans controlled ungulate populations, which since then have exploded across the landscape under “hands off” conservation initiatives (along with predator extirpation), thus causing a decline in encompassing fires so vital to grasslands. Thus, in discussing biodiversity and the management of grasslands later in this paper, it is important to reflect on the paradigmatic limits of the current conservation discourse and the importance of incorporating humans into future definitions of “diversity” and “conservation”.

SCALAR STUDIES IN ECOLOGY: DEFINITIONS, COMPLICATIONS AND USES

The complications of geographical scale and the contributions of Biogeography

“In retrospect, it became clear that a fascination with scale had underlain all these efforts; it is, I will argue, the fundamental conceptual problem in ecology, if not in all science.”

Simon A. Levin, MacArthur Award Recipient Lecture

Scale is important in understanding the ways in which diversity is created in ecosystems (Ricklefs 1987). Biogeography is a field of study which focuses on the whys and wheres of species distribution across the globe in the context of multiple scales of space and time. This field is useful in understanding the dynamic suite of species in particular locations in the context of historical and spatial relationships. Comprehension of factors behind patterns are only possible by observation at the proper scale and it is pattern which gives rise to information on species ranges, speciation, and succession (Levin 1992)—all important factors in the study of biogeography. Thus, scale is inextricably linked by pattern to the field of biogeography. Many of the publications covered in this review can be attributed to biogeographical studies, although this particular review focuses on scalar complications and contributions to all of ecology.

The Importance of Scale

Recent papers have identified many questions surrounding scale: What is the appropriate scale for studying animals versus plants (Huston 1999)? How do you combine the local and regional processes influencing species richness patterns (Gering and Crist 2002)? What is the appropriate scale to define a community in studies of community processes (Ricklefs 1987)? What is the relative strength of local vs. regional processes on diversity (Dauber et al. 2005)? This smattering of questions from studies of scale shows the importance of considering scale in all ecological questions, regardless of the focus of ones study.

How can scalar awareness challenge or convolute ecological study? Scalar dimensions challenge long-held theories utilized in ecological studies. For example, the random-walk model used to describe dispersers, larval ecology, and invasive species spread is over-simplistic because at different scales, different nodes or centers of dispersal will congregate. Thus, the backbone of the model will shift depending on the scale at which the organism is found (Levin 1992).

A second example of the importance of considering temporal scale in ecology is exemplified by Lindborg and Eriksson (2004). In their study of Swedish semi-natural grasslands they found that the historical connectivity of landscapes influenced the diversity found within patches today. Thus, observations that ecologists make about patterns in the temporally limited space of their studies overlook the historical impact of land-use on these patterns. Although not discussed further, the complication of temporal scale should be kept transparent in ecology.

It is important to keep these complications of temporal scale in mind when looking deeply into a body of literature. This review solely discusses modern day processes impacting diversity and refrains from the larger context of the previously mentioned evolutionary time-scale processes. Therefore in discussion of the factors associated with rangeland diversity, it is not that evolutionary timescales are being ignored but rather that their broad scope cannot be contained within this paper. As an aspiring ecologist, it is personally important to investigate this complexity before delving in to discussions of grassland diversity. Therefore, the study of scale is the central component of this review. Secondly, this discussion will be concretized by looking at management of diversity in the grassland biome.

The Complication of defining regional verses local

Despite the importance of scale in ecological studies, its definition and use remains hotly debated. What does the catch-all phrase of scale encompass? Scale is operationally defined dually in terms of extent and grain (O'Neill 1986). Extent is the entire area covered by the study whereas grain is the individual study unit, or the scale at which phenomena are measured. Thus, grain defines the lower limits of our understanding of processes whereas extent defines the upper limits. It is generalized that grain processes, or local processes are those that involve biotic interactions whereas regional processes, or extent processes, are determined by abiotic factors such as climate and other landscape factors (Fuhlendorf and Smeins 1996). Local processes include demographic differences, extinction history, rates of speciation (Schluter and Ricklefs 1993), predation and competition. However, these processes magnitudes and directions of influence on diversity vary (Huston 1999). All though the terms local and regional are deployed throughout these studies, they remain contested.

What constitutes the correct local scale? The scale must be one in which competitive interactions are meaningful, organisms must be correctly categorized into their functional group in the ecosystem to understand competition, and the state of the ecosystem should be of competitive equilibrium. Competition and predation are classically local scale processes studied extensively in ecological systems. An observable result of competition influencing the local ecosystem would be the regular spacing of species throughout the region as a result of niche division, whereas predation would be evident by the removal of predators and the subsequent change in ecosystem function (Ricklefs 1987). Habitat heterogeneity, disturbance, and change in

environmental conditions must be phenomena controlled for in determining local processes affects (Huston 1999), although whether this is actually feasible is another question.

Regional processes include evolutionary processes and geophysical phenomena such as climate. An example of a regional climatic process is the higher mutation rate in regions with higher temperatures contributing to greater diversity (Huston 1999). A thematic conflict in defining scales is the nominal valuation of what constitutes local versus regional scales. For example, in Gering and Crist (2002) they defined “transition states”, representing the change from local to regional, to represent their domains of scale. However, these transition states are ultimately defined by our conception of scales and the functional scale at which we are able to feasibly measure processes. Finally, it is difficult to conceptually understand the scale at which processes operate and scales at which they can be observed and recorded. In many cases, ecologists assume that local effects they observe are the result of local processes and regional patterns the result of regional processes. Unfortunately, this is a gross oversimplification of the relationship between cause and effect (Huston 1999).

Although complicated and relatively nominal, a division of regional versus local scales is possible but their relationship is less understood. Huston’s (1999) seminal paper discusses these complications. The main contest is the relative importance of local versus regional processes. For instance Huston (1999) poses the question: could it be that local processes are simply acting on a regional scale which influences the broadly held assumption that regional processes are more powerful?

The relative powers of the local and regional

Historically, ecological studies focused on local scales and a belief that local processes were the main constraints of both local and regional diversity was widespread throughout the scientific community. By focusing ecological studies on the local level, it was postulated that differences in regional diversity were caused simply by the difference in niche specialization (Ricklefs 1987). The theory arising from this stems from assumptions of niche saturation and the Theory of Island Biogeography.

If local diversity were constrained by local processes then a horizontal asymptote would be expected. If the species diversity curve continues to rise linearly in relation to regional diversity it indicates that local diversity is not constrained by saturation (Caley

and Schluter 1997) and is therefore dominated by regional processes. Locally unlimited patterns would indicate a lottery based pattern of local occupation, a disturbance-release due to competition, or randomized extinction and colonization processes. Examples of locally constrained ecosystems include those with limited dispersal and intense biotic interaction in constrained niche space (Caley and Schluter 1997) and examples of locally constrained systems are listed later in this review (Dauber et al. 2005, Davidowitz and Rosenzweig 1998).

In Caley and Schluter (1997), in which the authors analyzed an incredibly broad range of habitats in North America and Australia, there was a consistency in local diversity patterns as a function of regional diversity pools. The main difference was that local diversity slopes were of a flatter slope than a randomized linear line based on the regional pool. This effect can be attributed to beta diversity processes such as habitat heterogeneity and spatial species turnover, as evidenced by the larger slopes recorded in “local” areas sampled which took up a larger percentage of the total regional area. This study supports current work supporting the un-saturated state of local ecosystems and dependence on regional diversity processes.

There is growing evidence that local diversity is not constrained by local processes, thus deconstructing the concept of niche saturation. Rather, studies show an increase in local diversity with the introduction of novel species (Sax and Gaines 2008, Ricklefs 1987). This indicates the importance of considering both local and regional scales in ecological study. This can only be done by broadening our conceptualization of local community’s interactions with other scales and including biogeography explicitly within ecological studies (Ricklefs 1987). Nevertheless, it is indubitable that the impact of local versus regional processes on the overall patterns of diversity remains a contested issue.

Alpha, Beta, and Beyond

There is a wide range of interactions possible amongst local and regional processes, anywhere from absolute dependence of local diversity on the regional pool or complete absence of regional impacts on local scales (Caley and Schluter 1997). To comprehend the varying factors affecting diversity at different scales it is useful to uniformly define them. Alpha processes (α) are those processes acting within habitats such as competition, predation, or any other process that acts over a homogenous

habitat. Beta (β) processes are those that occur between habitats such as processes of dispersal and climate influences (MacArthur 1965).

In application, these processes become useful tools in which to measure where diversity is maintained at multiple scalar levels. Alpha diversity can be thought of as the diversity contained within a singular subplot whereas beta diversity refers to the variation of diversity amongst plots and across habitats due to regional processes, thus quantified by the proportion of all species in the plot which are not found in each sample unit across the region (Tylianakis 2006). Thus, alpha and beta do not specifically refer to size but rather to the distribution of diversity—alpha is diversity index to compare within plots holding habitat type steady whereas beta diversity is diversity between plots of different habitat types. Gamma (γ) diversity is a relatively recent term which refers to the combination of alpha and beta diversity. This measure is useful because gamma diversity at a small scale can then become alpha diversity when scaling up to larger extents (Tylianakis 2006).

Use of Scalar Studies

Different regions vary in their insular diversity. The high diversity in the tropics compared with temperate zones is a focus of many biogeographical studies. These studies use this discrepancy as an effective case study to determine which factor contributes most to diversity. Pianka (1966) was the first to outline the major theories: competition, evolutionary time, predation, productivity, climatic stability and spatial heterogeneity. Yet papers today are still investigating these forces (Davidowitz and Rosenzweig 1998, Jablonski et al. 2006).

Scale is used in studying the many theories of the latitudinal diversity hypothesis. To do this researchers calculate the diversity within a homogenous local (similar in their tested hypothesis) and compare this with diversity in a heterogeneous region. If local diversity is directly correlated with regional diversity than local processes have negligible effects on diversity. However, if local diversity can be limited by local processes, a result that is largely hinged on choosing the correct scale in which to measure this, then local diversity will not match up with regional diversity (Huston 1999). Scale remains a complicating factor in the study of the processes that shape diversity on latitudinal gradients. It would seem irrationally simple for all diversity processes such as climate or productivity, to impact diversity at different scales in the same way (Field et al 2008).

The relative forces of these controls on diversity remains inconclusive and studies continue to produce new findings.

Field et al. (2008) recently published a paper which took a massive amount of literature, 393 analyses in total, and examined the latitudinal diversity gradient in terms of species richness while explicitly incorporating scale, both extent and grain, in to their analysis. This study also included habitat medium, taxon, and habitat insularity. They analyzed both primacy, referring to the proportion of cases in which this factor contained the highest r^2 value, and the r^2 values as representative of the “force” of their independent variable. Climate was the most primary and most influential factor at large grain sizes although this variable is confounding with the primary productivity hypothesis, and is strongest in terrestrial non-insular systems. Oddly enough, they found similar results for species-richness correlations for both animal and plant species across taxons. At medium grains, biotic interactions were the most primal factor in influencing species-richness gradients, although these conclusions are limited by the difficulty of sampling at that level for biotic interactions. At smaller scales, their results become more convoluted and less conclusive on the most important factor correlating with diversity (Field et al. 2008). This recent publication reflects use of incorporating multiple scales into studying latitudinal diversity gradients in order to pinpoint the process that operates at a specific scale.

Application to the Latitudinal Diversity Gradient

Any overarching discussion of the ecological theory in relation to diversity will inevitably bring up the problem of scale. It is indisputable that the question of diversity is complicated by both temporal and geographical scale of analysis. For instance, Jablonski et al. (2006) examined the spread of mussel species across the Americas. Against the former notion that the tropics act solely as a source for new species they found that the tropics were both a cradle and a museum of older species which had since then radiated and evolved in temperate climes. As Marshall (2006) pointed out, further complexity arises in concluding whether regions (tropical or temperate) function as cradles or museums because conclusions hinge on the taxonomic and therefore temporal scale of analysis. If researchers had limited themselves to more recent temporal scales they would have concluded that mussels evolved in temperate climes and migrated to tropical regions, instead of simply returning to their origins, as exemplified by Jablonski et al. (2006).

Davidowitz and Rosenzweig (1998) compared the diversity of species in American Grasshoppers (*Acrididae*) at multiple scales in order to test the spatial heterogeneity hypothesis. This hypothesis states that the increased amount of habitat heterogeneity in tropical environments influences the higher diversity observed (Pianka 1966). They tested this according to Pianka's suggestion of choosing a model organism that crossed multiple latitudes and habitats, in this case American Grasshoppers. They then compared the diversity between a large multi-habitat area to the diversity within a singular habitat held constant across latitude, thus creating a test-group.

The slope of species diversity at these two scales was not significantly different and thus rejected the theory of spatial heterogeneity. However, this observation also means that within one habitat, spatial heterogeneity is emphatically important to determining grasshopper diversity (Davidowitz and Rosenzweig 1998). This study illustrates the functional use of scale, as well as the importance of relating multiple scales in order to investigate and understand larger ecological processes. For grasshoppers, it seems that local factors are the most important in determining their diversity. Scalar studies are extremely useful in picking apart questions related to the unsolved phenomena of the latitudinal diversity gradient.

PROBLEMS ARISING FROM THE STUDY OF SCALE

Problems of scale are foreseeable in a field that attempts to link landscape traits to local biological patterns, quantify the relationship of local to regional, and make conclusions on the various strengths of factors influencing diversity at both scales. In semi-arid perennial grasslands, spatial scale of observation greatly influences the understanding of ecosystem dynamics. Thus, inferences of equilibrium can be biased due to the grain and extent of analysis (Fuhlendorf and Smeins 1999), a troubling conclusion in the context of our understanding of these theories. But scale cannot be ignored. An understanding of the scalar component of ecosystem processes will aid in developing schemes for conserving biodiversity, especially managed agri-environment landscapes (Dauber et al 2005).

Theoretical and Technical Complications

Levin (1992) argues that correct definition of scale, local versus regional, is not a relevant issue because of the completely nominal definition. The tradeoff that scientists face in losing heterogeneity but gaining precision in terms of their model shows that the

process of 'choosing' scale is 'unnatural'. He argues that instead of focusing on appropriate scale, studies should address linking all scales present concurrently. This is because ecosystems are a gradient of scales, not a cross-section of an area at a particularly convenient scale to study and different species have extremely different scales of experience.

A practical complication of ecological studies is the difficulty of measuring certain factors at the appropriate scale due to the sheer limitation of human effort. Field et al. (2008) cites that the observed importance of biotic interactions at medium grains could be due to the fact that it is extraordinarily difficult to conduct this type of study at larger scales. Gering and Christ (2002) point out that different scales can be more or less effective when sampled, adding another complication of comparing richness across scales. In addition, humans inherently impose their own perceptual bias upon the landscape, thus choosing scales they are familiar or trained to (Levin 1992). Our traditionally held concept of scale is complicated by its condition as a nominal, biased, and technically limited cross section of a gradient based natural world.

Diversity measurements as dependent on the scale of analysis

A disturbing conclusion of many studies is the dependence of results on the scalar level of analysis. Recent studies attempted to measure diversity across various human land use schemes to gain a better understanding of the manner in which human activity impacts diversity. In Tylianakis et al. (2006) the researchers measured multiple scales of diversity, alpha, beta and gamma, at the different levels of subplots and plots amongst varying types of human land use in Ecuador. Their study organism was hymenoptera, or wasps and bees. They concluded that if they had measured diversity only at the subplot level they would have observed that diversity was the highest amongst pasture and rice fields. However, when they factored in the plot level diversity analyses they found that diversity did not differ amongst different types of land use. In this intensely managed agroforestry landscapes, they found that alpha subplot diversity actually increased, although beta subplot diversity decreased. Therefore, within plots diversity increased but between various habitats overall diversity decreased. This conclusion held across various land types and demonstrated how, when measured at the appropriate scale, diversity can increase between various habitat types in managed, human influenced ecosystems (Tylianakis et al. 2006). This example also illustrates the

difficulty of judging the appropriate scale in which to value diversity, a topic which remains up to human judgment.

Dauber et al. (2005) conducted a study on semi-agricultural land in Germany and addressed the main concern of measuring diversity at the same scale that diversity is produced. The challenge of diversity measurements is that a variety of processes occur at different scales and ecologists must match where processes occur with where they are measured. Ultimately the coupling of scales of measurement and operation will lead to the most efficient management schemes in cultivated land.

This study looked at five different taxa of macroarthropods, differing in habitat requirements and mobility, as model organisms to study how local patch heterogeneity affects diversity in comparison to landscape factors. Their findings include that these factors don't operate independently but synergistically-they found micro-habitat quality to be more influential than landscapes, although landscapes remain important to dispersal. Interestingly, this study contrasted with other studies conducted in the same region because it found that high dispersers, such as saphylinids were less or equally as affected by landscape level processes (Dauber et al. 2005).

This result is probably due to the smaller extent of this study than these previous studies. Dauber et al. (2005) shows the importance of small-scale influences which can be overlooked when larger landscape factors are under study. However, these findings differed between taxa, refuting the use of indicator taxa. Not only can the grain and extent of scale influence studies but also the study organism that is chosen biases ecologists generalizations if used as indicator taxa for a broad ecological theory (Dauber et al. 2003). A weakness of this paper is its conclusion that theory cannot be derived but rather that rules can only be applied to certain landscapes and organisms under study. This conclusion leads to the idea that general rules of ecology are impossible to derive, a disconcerting concept when general rules of diversity would aid in the conservation of diversity, especially in managed landscapes.

Lost in Translation: Scaling up from the Local to the Regional

The fundamental problem of scalar studies is linking the local to the regional, a process which requires determining which factors remain important at regional scales and what become 'noise'. Local processes are by nature more stochastic and regional processes are, at times, what scientists are interested in understanding (Levin 1992). The issues arising in studies of local-regional (LR) relationships are brought up by

Gering and Crist (2002). These authors criticize the oversimplification of assuming linear relationships between local and regional processes. The linearity of these relationships leads researchers to infer communities are non-interactive and regionally based. This inference is based on the assumption that saturation will occur in areas of interactive processes such as predation and competition (Cornell 1993).

They propose further digesting the LR relationship into alpha and beta processes to give a more accurate depiction of the influences on diversity. By distinguishing these two processes and using modern mathematical properties they were able to generate the relative strengths of alpha and beta processes across multiple scales. Their study looked at four spatial scales ranging from eco-region to the funnel in which the beetles fell, thus definitely fulfilling their aforementioned importance of not overlooking large or small scales. They concluded that regional richness greatly influenced values of local richness and also that these processes distinctly influence overall results at different scales. Thus, local interactions such as facilitation, sharing of resources and competition were not as evident at broad scales where beta processes such as immigration/extinction dynamics and dispersal were the main factors structuring communities.

Another interesting conclusion of their study was their finding of a non-interactive, linear relationship. This coincides with other insect-based studies which show that colonization is relatively random and population fluxes are relatively independent of local deterministic processes. Thus, local processes are not those limiting the richness observed in this study (Gering and Crist 2002). This contrasts with traditional niche-saturated models of ecosystems and thus restructures the way in which ecologists perceive the environment. The contribution of this model is that it allows researchers to incorporate processes acting at multiple scales. However, in comparison to previous studies showing the importance of local scales in insect diversity (Dauber et al. 2005) we are left once again unsure of the importance of various scales but confident in the importance of considering multiple scales of analyses.

Suding et al (2008), is a recent publication which addresses the scalar difficulty of connecting small scales with larger and proposes a mechanism for plants. How do you scale up community processes to the ecosystem level? This paper outlines the main problems of measuring across scales in context of formulating predications of environmental change, a hot topic in the subject of climate change. It provides a new framework for “translating” across scales by building a “response-and-effect” framework

which integrates how the ecosystem responds differently, in response and in effect, to changes in community. Change in community is thus calculated by the summation of abundance of species, while taking into account that certain 'response' species will translate the change into the community while others will be 'effect' species and transcribe that change into the larger community response. Thus individual responses are translated from functional groups to total ecosystem response (Suding et al. 2008).

Response traits are those affected by the change whereas effect traits are used in the prediction of the ecosystem outcome. Cumulatively it is the difference in how species with response traits change versus how species with effect traits change which will ultimately determine the outcome. For instance, a response trait like reproduction will not be an effect trait in a group of plants. Rather it is the effect traits of nutrient recycling which would be the trait most affecting the overall ecosystem response. Thus, a species can belong to a functional response group, but not a functional effect group.

By defining species as one and/or the other we can determine the net effect on a community. Along with this, abundance will clearly affect the outcome as well, given that even if the effect traits of certain species are greatly impacted, if their initial abundance is low than it would be of little importance. Within this framework the possibility of scaling change from individuals to the community is made more feasible. As this section has shown, scalar studies are also important in understanding how land-use impacts ecological communities (Ricklefs 1987), the latitudinal diversity gradient (Field et al. 2008, Davidowitz and Rosenzweig 1998), and how diversity changes and is shaped at varying scales (Dauber et al. 2005, Gering and Crist 2002). The following section will concretize the use and complexity of scalar studies within grassland ranges. In this biome, large scale spatial heterogeneity is the template which gives rise to the overall diversity of plant, ungulate and other supported species (Christiansen 1997).

GRASSLAND MANAGEMENT OF BIODIVERSITY

Background of Grassland and Ungulate Interaction

Grasslands are highly utilized by humans in order to raise agricultural products and ungulate populations. Over two-thirds of the world's land cover is utilizable "rangeland"-encompassing desert shrubland, annual and perennial grasslands, and coniferous forest. It is estimated that about 95% of nutritional needs of wild ruminants and 50-65% of domestic ruminant's nutrition is based off of rangeland use. Meat production is the primary human utilization from rangelands, although recreation, wildlife,

and water production are also essential contributions of this widespread biome (Holechek et al 2001). The greatest contributor to forage production amongst all types of rangelands is the grassland biome, dominated by the plant family Gramineae with Mollisol type soils characterized by high fertility and a 2m deep loam topsoil (Holechek et al 2001). The key role that grasslands play in productivity signifies the importance of understanding how to properly manage these highly utilized ecosystems.

Worldwide, grazers are the most important factor in disturbing grasslands, behind the process of fire, and powerfully shape dynamic changes in vegetation (Diaz et al. 2007). Much of rangeland management focuses around how to distribute grazing across the landscape in order to maximize productive output (Holechek et al 2001). Grazers of different types (digging mammals, lagomorphs, etc.) have ranging impacts on plant species due to their pattern and extent of grazing. However, large mammals consistently increase diversity of plants at appropriate densities via nutrient deposition, landscape level extent, and efficiency of seed dispersal (Olf and Ritchie 1998). Large mammal grazers will be the herbivore focused on in this review.

Initially, large mammal grazers choose consumption sites opportunistically based on the resources present such as water availability, minerals and nutrient content, with limitations based on slope and proximity to water source (Adler 2001). The other side to consider in management is the factors which influence the production and continuation of this incredibly geographically diverse grassland ecosystem include seasonal drought, grazing, and fire (Watkinson and Ormerod 2001). This review will focus on how grazing and fire interact to impact grassland diversity in the context of scalar complexity.

Goals of Rangeland Management

The goal of rangeland management in grasslands is to maximize plant diversity (Olf and Ritchie 1998) and the heterogeneity in the ecosystem through variation of grazing intensity, location and spatial dimensions, and occurrence in time (Fuhlendorf and Engle 2001). The recent review by Fuhlendorf and Engle (2001) which synthesizes their lifetime work in rangelands of North America proposes the goal of a shifting mosaic of grazing in a fixed space versus the traditional rotational based grazing management scheme. They propose using fire and fixed pasture spaces to create a heterogeneous patch system which shifts over time from the impact of fire events.

This theory of continuous grazing versus rotation based grazing is supported in other regions of the world as well. Sternberg et al. (2000) took a functional group

approach to study the impact of domestic cattle in the Mediterranean region. Functional grouping is placing plants in groups based off of their characteristics of responses to grazing. The researchers found annual precipitation was the most influential factor in determining the plant composition. By incorporating functional group analysis they could observe that tall grasses were succeeded by low lying legumes and less edible plants such as thistles under grazing regimes. There was an overall increase in species richness, especially amongst legumes, in continuously grazed patches verses seasonally grazed patches, regardless of the intensity of grazing. This can be attributed to the release of recessive plant species under intermediate disturbance regimes as a result of herbivory.

However, Sternberg et al. (2000) states that in addition to intensity of grazing impacting species heterogeneity, scale of observation is an important factor as well. Explicit in the understanding of these processes is addressing scalar dimensions. Many studies have examined how spatial heterogeneity varies amongst scales therefore indicating that ignorance of scale can lead to false conclusions based on the impact of ungulate grazing.

Background on the impact of domesticated and wild grazers

Ungulates can both reduce grassland diversity by under-grazing and allowing the succession of dominant woodland species or conversely, overgraze and degrade the plant biodiversity by only allowing the continuation of browsing tolerant species or nutrient poor grasses. Grazing can increase the nutrient content of grasslands by maintaining plants in early life stages, increase below ground nitrogen availability, and reduce non-growing portions of plants (Adler 2001). Yet, quantifying the impact of grazing is incredibly challenging to applied ecologists because one must not only factor in the species involved, but also timing and spatial heterogeneity (Watkinson and Ormerod 2001). This coordinated interaction of spatial and temporal scales is exemplified in the case study of the keystone role of bison discussed below.

The keystone role of bison

Bison play a keystone role in maintaining the diversity in North American grasslands. Bison were able to spread across the plains from the facilitation of other post-pleistocene ungulates which increased the spread of grasslands by prohibiting the succession of woody species. Although bison are contained within a range about five

percent of their original spread across North America, they are actively researched at the Konza TallGrass Prairie Long-Term Ecological Monitoring site in Kansas (Knapp et al. 1999). Research over the last twenty years at Konza is summarized by Knapp et al. (1999). In this paper they argue that, due to bison, there was an increase on the landscape scale of species diversity (23%), community heterogeneity (13%) and species richness (38%), indicating the keystone role of bison in tallgrass prairie habitat. The mechanisms by which bison increase heterogeneity are multiple and are discussed in detail below.

Bison create patches at small grains and larger grazing lawns in areas of about 400m² with boundaries apparent on large scales between grazed and ungrazed patches. The selective foraging by bison of dominant C4 grasses opens up space for less dominant, but highly diverse (>350 spp. at Konza alone) forbs to flourish. The change in primary productivity of grazed grasses is hinged on the time scale of observation. Within season, grazed grasses show a 53% rise in primary productivity but after two years this increase declines. Thus, only in highly dynamic systems, where bison are able to graze heavily for 1-2 seasons but then shift across the larger landscape, is maximum diversity attainable. Other ways in which bison influence the system is the more readily available form of nitrogen which they deposit through urine as well as their wallowing, or rolling, depressions in the land (3-5m deep) which can create microcosmic seasonal pools and create wetland like habitat. Cumulatively, bison can increase rates of nitrogen cycling, provide habitat heterogeneity, and increase primary productivity of the prairie system. However, this would only be possible if managers incorporated broader temporal and spatial landscapes.

The interaction of fire and grazing is particularly applicable to the discussion of scale. Historically, fires operated at much scales of thousands of hectares, much larger than the manner in which they are applied at Konza, and occurred at higher frequencies because grasslands were more contiguous. Due to fragmentation, managers must burn more frequently than what would “naturally” occur on these landscapes in the present day. By factoring in the scale at which these processes once acted, researchers can both observe how diversity is increased on landscape scales and provide managers with meaningful management benchmarks at appropriate historical scales.

Spatial Heterogeneity

Spatial heterogeneity is essential to the creation and continuation of biodiversity.

Heterogeneity offers a varied array of resources, making possible the coexistence of species which would normally not coexist in homogenous environments (Levin 1992). However, the conclusion of whether patches are heterogeneous or homogenous depends on the appropriate incorporation of multiple scalar dimensions (Adler 2001). In a study conducted in the Tonga Grassland Reserve in Kansas, the researchers investigated five treatments based off grazing and burning application. They found that those combinations which produced the greatest homogeneity at local scales within treatments, grazing and grazing+burned, produced the greatest amount of heterogeneity at regional scales. They conclude that this may be a function of more stochastic processes acting at regional scales such as immigration (Glenn et al. 1992). Had the researchers limited the extent of their study their conclusions would disregard the heterogeneity produced at regional scales.

Spatial heterogeneity is theoretically defined as the predictability of adjacent patches given information on a single studied patch. Spatial homogeneity is defined as randomized patch characteristics, not homogeneously similar but instead unconnected in relation to neighboring patches (Adler 2001). Although it seems antithetical to define homogeneity as randomized, it makes more sense to consider homogeneity a result of dominant local processes. Therefore, you would not be able to predict the next patch because other forces would be at work. A neighborhood of patches must be considered in order to comprehensively address ecological patterns.

Additional scalar complications and the niche saturation theory

Grassland biomes are host to many studies relating spatial scales of observation (Glenn et al. 1992). These studies conclusions indicate that results of the impact of grazers on species richness vary greatly with the spatial scale of analysis (Olf and Ritchie 1998). Olf and Ritchie (1998), in the vein of traditional island biogeography theory, state that biodiversity is increased by increasing species colonization or decreasing local species extinction.

The problem with this model is that it assumes niche saturation at local levels, a concept that hinges on the extinction of organisms with each additional related species colonization. This goes against current research showing the colonization does not necessarily mean extinction, especially in plant species (Sax and Gaines 2008). The model also assumes that the important scale to which we measure diversity is the local but as stated previously, this definition of what constitutes a local scale is both contested

and nominal (Levin 1992, Field et al. 2008, Gering and Crist 2002) and can be less important than regional scales (Gering and Crist 2002).

Weber et al. (1998) attempt to produce a model which can predict spatial heterogeneity changes on small scales across savannah landscapes for fifty years. The modeling problem they ran into is that plant interactions are inherently local due to their sessile life histories whereas the extent of ungulate impacts is much larger, thus creating a conundrum in terms of how to model the plant-animal interaction. This reflects back on the classic problem of how different species experience scale in different manners (Levin 1992). Weber et al. (1998) attempted to look at how the heterogeneity in both space and time created forage quality amongst plants. The model showed relatively widespread conclusions: that at high stocking levels, shrub cover increased and that the heterogenic mechanisms of grazing did not modify the impact of grazing at these high densities. Although their model was simply a beginning, the authors argued that models must explicitly take into account how carrying capacities are influenced by spatial aspects and the integration of spatial scales. Thus, this paper confirms that spatial aspects should not be ignored even though they present a difficulty to modeling.

Threshold analysis

Threshold analysis is a useful tool for understanding the transition between steady states of ecosystems and is widely used in management to distinguish what characteristics are necessary to favor preferred states. It is fundamentally based on the non-equilibrium paradigm of ecosystems (Briske et al 2006) and hinged upon the resilience of certain states of the ecosystem (van Nes and Scheffer 2005). A functional definition of an ecological threshold is a biotic or abiotic process which pushes the ecosystem over a spatial or temporal boundary which requires active management to return the ecosystem to its previous state. The specific threshold is a point in space or time where negative feedback mechanisms change to positive feedback mechanisms, thus requiring active management for returning to the previous state of the ecosystem (Briske et al. 2006). The recent application of this theory to grasslands has been limited to local scales but other papers suggest that local thresholds are inherently linked to broader scales, across ecological sites, which are often overlooked (van Nes and Scheffer 2005).

Ecosystems will not experience thresholds in a uniform manner across their bounds. Rather, the spatially dependent factors of spatial heterogeneity and dispersal

will significantly impact the manner an ecosystem crosses a threshold. In van Nes and Scheffer (2005) the researchers simulated a model based on three levels of spatial heterogeneity (none, linear based, and random) along with three levels of dispersal and a simulated random parameter which pushes the system to threshold levels. The study found that when heterogeneity was high and dispersal low the ecosystem shifts gradually, as opposed to catastrophic predictions of ecosystem change based on previous models.

Hysteresis, or the theory that ecosystems will change in a different manner forwards versus backwards, is also complicated by incorporating spatial heterogeneity and dispersal in the model. Hysteresis can be the ability of the system to exist in multiple states depending on the trajectory or path of change. In the study they found that forward moving processes, say prairie to woodland succession, occur synchronized on a large scale whereas backwards moving scales, say from woodland to prairie, can only occur at localized scales. Although variation in the scale of hysteresis would occur in differently in different systems the main conclusion of this paper is the explicit need to incorporate spatial aspects such as heterogeneity and dispersal in analysis of threshold responses as well as hysteresis theory.

CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

Grazing can be used as a tool for creating spatial heterogeneity at the scale desired (Adler 2001). In combination with fire, it can create a shifting mosaic of intense focal points for herbivory while leaving other areas unconsumed, similar to evolutionary grazing patterns, thus supporting a suite of species evolved to withstand varying pressures by grazers (Fuhlendorf and Smeins 2001). However, this type of management requires that we understand these processes, such as fire and grazing, which did not evolve at the same small scale with which they are deployed now, as a result of habitat fragmentation. Thus, managers must factor in historical scales and develop frequency of fire and grazing patterns based on these values (Knapp et al. 1999, Lindborg and Eriksson 2004). These measures will preserve spatial heterogeneity-an important feature of resilient and productive ecosystems (Levin 1992, Tilman et al. 1996).

Not only should scale be incorporated into the comprehension of complex ecological systems but it should also be utilized in the most current modeling techniques and made accessible to managers. This necessitates incorporating scalar components

into previous models of threshold analysis (van Nes and Scheffer 2005), into models which relate response and effect frameworks to greater ecological change (Suding et al. 2008), and also considering local saturation in linear models of local to regional relationships (Gering and Crist 2002).

The consideration of scale is vital to understanding the way in which diversity is both created and maintained in ecosystems. By utilizing such methods as division between alpha, beta, and gamma diversity on systems researchers can avoid overlooking key processes which might act on other scales than previously imagined. This review acknowledges the fundamental human, technological and theoretical, biases on interpretation of the relevant scales of experience for various species. This could be because processes which appear as patterns on larger scale could be functionally created at smaller scales, or vice versa.

Incorporating awareness and methodologies aforementioned in this paper should improve a holistic understanding of ecosystem function. However, this cannot be contained within biogeographical or spatial-specific studies but discussed more broadly in the field. By incorporating scale at this level the future generation of ecologists will be able to improve their studies comprehension of a natural world which knows no distinct boundaries of scale. As landscapes become fragmented from human land use we cannot rely on simplistic ignorance of one scale or the other-nor imagine that the boundary between these scales is fixed across time. Thoroughly understanding theories behind scale and how to incorporate spatial awareness into existing ecological models will build a stronger framework for comprehension of how diversity is maintained and created at various levels of the ecosystem.

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