Temporal Dimensions of Landscape Ecology

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Wildlife Responses to Variable Resources

Edited by

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Contents

Part III. Temporally Focused Case Studies

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Introduction

Landscape ecology is about spatial heterogeneity; and when applied to animal population responses, it has often focused on the effects of large-scale habitat fragmentation. However, Haila (2002) has pointed out that fragmentation has been treated as a unitary phenomenon, whereas in reality, empirical work has shown a wide variety of direct and indirect effects. Haila (2002) refers to the unitary approach as the "schematic view" and credits its origins to the theory of island biogeography (McArthur and Wilson, 1967), where habitat fragments were compared to oceanic islands: homogeneous patches of habitat surrounded by an inhospitable matrix. He then suggested that the schematic view is limited in its ability to describe accurately the range of possible landscape configurations created by a variety of disturbances. The reality is that more than a simple binary classification of habitat and non-habitat exists. Earlier, McIntyre and Barrett (1992) recognized from their work in the northern tablelands of New South Wales that patchiness existed without a hostile matrix that presented barriers to movement by animal species. Indeed by 1999, McIntyre and Hobbs proposed a framework for conceptualizing the effects of human activities on landscapes. They visualized a synthesizing scheme that recognized a continuum of habitats (intact, variegated, fragmented, relictual) that depended on the degree of habitat modification and the amount of original habitat that remained. Manning et al. (2004) added reality to the concept of landscape heterogeneity and the idea of fragmentation with the suggestion that if two key concepts were brought together, namely: the presence of continua in nature; and the existence of species-specific perception and response (Umwelt), the resulting model would have major implications for understanding landscapes. They described two types of continua; spatial and environmental, and argued that recognition of individual species perception and response to the continua leads to the conclusion that different organisms perceive and respond differently to the environment in different ways. The essence of their argument is an organism-centered approach to landscape-animal relationships which coincides more closely with the physical reality of the landscape. A major point of the development of the idea of how we conceptualize habitat heterogeneity is that the continua-Umwelt model recognizes that landscapes change over time, while the fragmentation model (schematic view) reflects a "human-based perception of the landscape," and the present time (Manning et al., 2004, p. 626).

Ecologists have not been blind to time and temporal dynamics. For example, there is a large literature including studies of chronosequences (e.g., Bonet and Pausas, 2004), long-term climate change (e.g., Oliveira and Pillar, 2004); land-use history (Latty et al., 2004; Spooner and Lunt, 2004); fire histories (MacKenzie et al., 2004, Sanchez-Flores and Yool, 2004); long-term watershed studies (e.g., the work of Bormann and Likens (1979) and their students on the Hubbard Brook Watershed); and ecosystem effects of predator–prey dynamics (Ripple et al., 2001; Ripple and Beschta, 2004) that incorporate time as an important variable. Further, many species-specific books have reported on long-term studies of vertebrates and have been available for some time; e.g., Geist (1975), McCullough (1979), Clutton-Brock et al. (1982) and Berger (1986) to name a selected few. Fewer have addressed the idea of temporal discontinuities in resource availability, especially as it might influence animal population response (but see, e.g., Jaksic and Lima, 2003; Schmidt, 2003; Schmidt and Ostfeld, 2003; Stapp and Polis, 2003).

Time as a Discontinuity

Wildlife species live in heterogeneous landscapes. If heterogeneity is conceived as a discontinuity (Lord and Norton, 1990a,b), one can easily think about "patchiness" not only in space, but also in time and in process. For example, a fire regime, by definition, is a patchy distribution of fire events (processes) over time and over space. Likewise, resource availability and abundance change over time and space. Resource pulses occur as *episodic* events with long inter-pulse intervals. Ostfeld and Keesing (2000) placed the idea of pulsed resources into a community ecology perspective. Their argument was as follows: (1) In recent years, community ecology has begun to integrate the ideas of "top-down" and "bottom-up" control of animal populations; (2) This insight logically includes the idea of interaction strength, which may be direct or indirect; (3) *temporal fluctuations* (italics ours) in the strength of interactions among species have not been integrated into the "top-down/bottom-up" paradigm; (4) episodic resource pulses will change the balance between "top-down" and "bottom-up" interactions; and (5) integrating the impacts of the pulsed nature of resource availability into the argument begins to address the "top-down/bottom-up" paradigm more effectively, but requires the incorporation of the ideas of time delays and animal mobility to understand community dynamics more fully.

As landscape ecologists working primarily with wildlife species, we identified a logical extension of this most heuristic idea. Could all resources be considered, in some sense, to be pulsed or discontinuous? What would be the population consequences if this were so? How might ecologists identify and measure these effects?

We looked at two journals, Landscape Ecology and the Journal of Wildlife Management (JWM). In some sense, these journals represent two complimentary but very different outlets. Landscape Ecology publishes papers that address issues of space and time explicitly, while the Journal of Wildlife Management primarily publishes species focused papers aimed at managers and conservationists. We found that in the first 2006 issue of the Journal of Wildlife Management (Vol. 70, No.1) for example, 6 of 34 papers mentioned spatial aspects overtly, 4 mentioned temporal effects, and 2 papers considered both; 23 papers (67.7%) did not address either spatial or temporal issues directly. However, one paper did mentioned temporal change in relation to species ecology. We then looked at the January 2006 issue of Landscape Ecology (Vol. 21, No.1). Of 10 articles published, 6 (60.0%) addressed spatial issues primarily, and 4 (40.0%) addressed both space and time. But the key was *how* time was addressed; temporal analyses were treated either as a single time step, i.e., the time duration between two calendar dates, or as a repetitive time step variable, typically from year to year. Only one paper in JWM addressed the timing of resource availability and its acquisition overtly.

We realize that the idea of pulsed resources has been addressed for over 30 years by botanists and plant ecologists who have studied nutrient availability. Indeed, in the October 2004 issue of Oecologia, many papers were published under the general heading “Pulse Events and Arid Ecosystems.” Many addressed directly or indirectly the “two-layer” or “pulse-reserve” hypotheses (Ogle and Reynolds, 2004) that examined the relationship between rainfall and plant productivity. Additionally, the idea of patch dynamics dates to at least the late 1970s, and in the mid-1980s, Pickett and White (1984) addressed temporal issues when they linked the ideas of disturbance regimes and patch dynamics. Patch dynamics imply ecological systems with relatively discrete spatial patterns, characterized by a relationship between patches and matrix generated by disturbance (Turner et al., 2001). Of course, resources can be found in patches, or not, or may be synonymous with a patch, or not, but the key element of interest for this book is a focus on the temporal, pulsed nature of the resources themselves, not disturbance-generated patches. There is also a vast literature on population cycles and the temporal factors that might cause them.

For the wildlife manager or land use planner, basic animal needs are simple. Animals need food, water, cover for shelter and from predation, and access to mates. Were the world homogeneous, satisfying these needs would be relatively simple for organisms. Complications arise when spatial heterogeneity is introduced across the landscape. Anthropogenic impacts that change spatial heterogeneity rapidly over time present a real complication and one many ecologists have been trying to understand. We argue that an approach that addresses only spatial complications may be addressing only part of the relevant dynamics. Resource availability and quality are not distributed homogeneously over *time*. For primary consumers in temperate environments, plants ‘green up’ in the spring, and over the growing period the quality of nutrient content changes. At the same time, where plant resources are found is influenced by the disturbance regimes imposed on the system and by the patterned landscape. The same argument can be made for secondary consumers. Prey availability is pulsed and discontinuous. Prey are often most vulnerable during the egg and fledgling stages, and for a few days right after birth.

Additionally, prey energy value changes with growth. We argue that understanding this idea and incorporating the temporal discontinuities of resource availability into our studies is critical if we are to make progress in both theory and practice. The ideas embodied in this book are an attempt to bring together papers that address the idea of temporal explicitness of resource availability and quality. We hope to bring a focus to the neglected temporal issues so important to understanding species and community responses.

The Structure of This Book

This book is divided into three sections: (a) Relevant Temporal Theory (Chapters 1–5), (b) Statistics of Time (Chapters 6 and 7), and (c) Temporally Focused Case Studies (Chapters 8–14). In the first chapter of section 1, Relevant Temporal Theory, Bissonette makes the argument that an enhanced understanding of animal response to resource availability may be possible if two elements are added to the standard, single currency quantity approach. The first element relates to measuring resource *quality* and requires adding an additional currency to our ecological ledger book. The second element incorporates the idea of temporal discontinuity in resource quantity and quality. Bissonette suggests that a broader incorporation of these two elements into wildlife ecology will enhance our understanding of animal response to resource availability at both small and larger spatial extents. In the second chapter, Ostfeld and Keesing argue that pulses of resources are major bottom-up drivers in ecological systems, leading to a suite of responses by consumers that interact with those resources either directly or indirectly. Given that the ability to predict system-wide consequences is still somewhat limited, they describe several axes of variation for resources and consumers that will influence the responses of ecological systems to pulsed resources. In Chapter 3, With argues that most landscapes bear the imprint of past human land use (legacy effects) that in some cases date back centuries or even millennia, even after the landscape seemingly has been restored to its natural pre-settlement state. She explains that as a result, current species distributions may thus better reflect historical than contemporary landscape configurations, owing to the lagged response of species to landscape change. With illustrates these “ghosts of landscapes past” with several case studies. In Chapter 4, Grimm and his colleagues use individual-based models that incorporate adaptive behavior to understand animal response. They explain that the adaptive responses of individuals to short-term environmental conditions give rise to population- and community-level phenomena. They provide a rationale for the framework and provide case examples to illustrate the concepts. In Chapter 5, the last of section 1, Gunderson and his colleagues concentrate on the scaling axis of time, and describe cycles in temporal patterns in the Everglades ecosystem. They relate the temporal frequencies of ecosystem structuring processes to the interaction of animals with their environment, and describe how spatial and temporal turnover and variability in animal communities relate to variation in the availability of resources in time and space. They posit that discontinuous distributions of key structuring variables in time should be manifest as a few resonant frequencies in temporal processes and test their ideas with time series data of rainfall, evaporation, water-flow, air temperature, sea level, and fire history. In section 2, *Statistics of Time,* Gutzwiller and Riffell address in Chapter 6 the issue of measuring temporal variation in animal responses to landscape conditions. They suggest that several statistical modeling approaches are appropriate for explicitly incorporating time into analyses of animal–landscape relations, but landscape ecologists have not commonly used them. They explain that the analytical assessment of temporal variation may involve independent or dependent data. If independent data are used, interaction effects involving time and landscape metrics can be estimated using cross-product terms. With dependent or repeated measures data, Gutzwiller and Riffell explain that the analytical assessment of temporal variation may involve up to three dimensions. They provide a clearly explained approach for the analysis of larger scale temporal data. In Chapter 7, Cushman and McGarigal develop and demonstrate for the reader a flexible multivariate approach to analyze landscape pattern trajectories over time. They combine a habitat suitability model for marten, metrics from FRAGSTATS, and a multi-temporal principle components analysis to define a parsimonious suite of independent landscape gradients and to project changes in marten habitat as a series of trajectories in space. Section 3, Temporally Focused Case Studies, contains 7 chapters. In Chapter 8, Storch illustrates limitations of conventional habitat assessments caused by smaller-scale temporal variation in rainfall patterns that may lead to inappropriate management action, using case examples of Capercaillie *Tetrao urogallus* in the German Alps. The examples show that standard "snapshot" habitat assessments ignore temporal variation and may have major consequences for species-habitat relationships and population dynamics, and thus, for management and conservation planning. In Chapter 9, Mooij, Martin, Kitchens, and DeAngelis explore the viability of the Florida snail kite *Rostrhamus sociabilis plumbeus* population under different spatially and temporally explicit seasonal drought regimes in its wetland habitat. The Florida snail kite is an endangered raptor that occurs as an isolated population of about 2000 birds in the wetlands of southern and central Florida. To explore the interplay between the timing and spatial synchronization of water resource availability, Mooij and his colleagues used an individual-based snail kite simulation approach that modeled kite behavioral responses. Because of its weekly time resolution, the model discriminated relatively subtle temporal variations in hydrological patterns. Their results revealed the complexity of the effects of temporal variation in water levels on snail kite population dynamics. Specifically, they found that management decisions should not be based on annual mean water levels alone, but must consider intra-annual variability. In Chapter 10, Reynolds and Mitchell argue strongly that the spatiotemporal resolution of observations should match the level of the ecological process under study if reliable insights are to be gained. They present a concept of designing ecological studies that integrates three axes: temporal resolution of the study, spatial resolution of the study, and the resolution of the ecological process addressed. To buttress their arguments, Reynolds and Mitchell provide two examples from their long-term research on black bears

Ursus americanus. They show that the temporal scales at which different vital rates are manifested in a bear population may differ, and affects the way disturbances (e.g., clearcuts, roads) affect habitat quality. In Chapter 11, Felix, Linden, and Campa argue that land-cover databases can be used to understand wildlife-habitat relationships but do not identify vegetation structure, temporally explicit vegetation trends, successional dynamics, or vegetation types on distinctive soils that may have different wildlife values. They suggest that the use of ecological classification systems, where ecosystems are classified and mapped according to specific biotic and abiotic properties, can facilitate assessment of distributions and movements of wildlife populations based on spatial and temporal identification of resources necessary for survival. They use a habitat-type classification system, which is a specific type of ecological classification system, as a basis to predict vegetation development and successional change. They discuss three case studies from Michigan to demonstrate how to build and apply models to assess temporal changes in forest wildlife habitat. One case study determined the potential of habitat types to provide white-tailed deer *Odocoileus virginianus* habitat, a second characterized how structure and composition of aspen *Populus* spp. changes throughout succession in different habitat types, and a third case used GIS to analyze differences in land use and land cover over the last century and model changes in the location and suitability of habitat for the threatened Canada lynx *Lynx canadensis* in the Upper Peninsula of Michigan. In Chapter 12, Lewis explains how the historically common but now endangered Gouldian finch *Erythrura gouldiae* of Australia has suffered dramatic reductions in population numbers during the last 40 years. Possible causative scenarios, including (a) increased commercial livestock grazing, (b) commercial trapping, and (c) parasite infections, have had limited success in explaining the continued decline in the number and size of Gouldian finch populations. Unlike other Australian finches, the Gouldian finch is solely granivorous and relies upon native grass species for survival. In this chapter, Lewis presents experimental evidence to show that different patterns of seed production are dependent upon fire periodicity and the intensity of burning, and that in breeding seasons following periods of reduced fire intensity and therefore higher seed production, there is about a 30% increase in reproductive success and increased survival of adult Gouldian finches. Lewis argues that understanding the temporal patterning and spatial distribution of resources across the landscape provides valuable perspectives on how to manage landscapes for declining species such as the Gouldian finch. In Chapter 13, Drever and Martin argue that in the mixed forests of interior British Columbia, Canada, temporal trends may have more dramatic effects than spatial patterns on species responses. Time and space interact and the drivers of temporal change differ spatially for short and long distant migrant species that respond to ecological conditions at a continental scale extent compared to resident species where temporal trends are driven by climate change and forest management conditions at a landscape or regional scale extent. The authors conducted a study that involved multi-annual responses of cavity nesters to an ongoing major outbreak of mountain pine beetle (*Dendroctonus ponderosae*) and other bark beetles and forest insects in British Columbia that resulted in large-scale increases in the availability of dead and dying trees. In addition to the annual variation in phenology, breeding density, and reproductive success, unexpected and dramatic directional temporal changes occurred. Drever and Martin were able to fit a linear trend model to 100 species observed during point counts, of which 21 showed a significant decline in abundance over the study period, 21 showed an increase in abundance, and 58 showed no trend. These concurrent declines and increases in abundance mean that community-level measures such as species richness and abundance within cavity-nesting guild did not change following the outbreak, indicating that community structure, per se, has remained stable during the large increase in resource availability. These results suggest that species' responses to the availability of resources may thus also depend on the current status of competitors, predators, and facilitators. In Chapter 14, MacLeod, Parish, and Robinson used an introduced bird species, the yellowhammer *Emberiza citrinella* L. in New Zealand as a model to test predictions based on the niche opportunities hypothesis. They tested the prediction that the success of yellowhammers in New Zealand can be explained by differences in temporal variation in availability of better quality food resources in its introduced range compared to its native range; specifically that (a) winter seed resources were more abundant; and (b) there was less temporal variation in resource availability during the breeding season in New Zealand. They found that Yellowhammer breeding territory densities were over three times higher in New Zealand (0.40 territories per ha) than in comparable British farmland (0.12 territories per ha), however, they also found that niche availability and quality, as indexed and measured by habitat availability and invertebrate densities, could not explain the higher density of yellowhammers in New Zealand.

Objectives

In this volume, we have compiled 14 papers that cover a wide range of topics and approaches, but all address the issue of time in landscape ecology research. If successful, these chapters may provide a prolegomenon of a conceptual framework for a spatially *and* temporally explicit landscape ecology. Our overall objective was to illustrate that time and temporal variation have in large part been a neglected dimension in landscape ecology. Animal response to *spatial* heterogeneity is complicated enough to understand; to include temporal heterogeneity explicitly in our thinking and research will certainly not make the work of landscape ecologists any easier. It should however make the science more realistic and result in better and more reliable management recommendations. If the book succeeds in stimulating thought and discussion, we will be satisfied.

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I

Relevant Temporal Theory

1

Resource Acquisition and Animal Response in Dynamic Landscapes

Keeping the Books

JOHN A. BISSONETTE

Abstract. Quantification in ecology has been the *sine qua non* that has differentiated rigorous science from something less. It is how we have "kept the books." Quantifying the quantifiable to account for population response to resource availability usually has meant that the *quantity* of some resource (e.g., for herbivores, plant biomass, or areal coverage of the plant community or habitat) has been assumed to have some causal effect on some quantitative measure of animal response (e.g., the number or organisms surviving and recruited into the population). As scale effects have been recognized as important, landscape ecologists have followed a similar methodology and have assumed that the habitat area coverage (*quantity*) bears some relation to population and species performance and health. The explanatory power of the spatial amount of habitat elements seems inconsistent, and available metrics to assess the effects of spatial arrangement are problematic. Further, organisms respond to the quality of their food resource. In this chapter, I make the argument that an enhanced understanding of animal response to resource availability may be possible if two elements are added to the standard, single currency quantity approach. The first relates to measuring resource *quality* and requires adding an additional currency to our ecological ledger book. The second element incorporates the idea of temporal discontinuity in resource quantity and quality. I suggest that consideration and a broader incorporation of these two elements into wildlife ecology will enhance our understanding of animal response to resource availability at both small and larger spatial extents.

1.1. Introduction

If habitats can possess a spatial structure relevant to ecology, is it possible that the temporal structure of habitats is also potentially important? Johnson (2000a)

Animal populations, in particular, have often been considered limited by resource *quantity*, but not by the chemical composition of the resource.... Resource *quantity* limitation is a single currency approach.... (italics added) Moe et al. (2005)

ac·count·ing: Pronunciation: (ᵊˈkaᵘntᶦᵑ) &-kaun-ti[ng], Function: *noun,* 1 : the system of recording and summarizing business and financial transactions and analyzing, verifying, and reporting the results; *also* : the principles and procedures of accounting, 2 a : work done in accounting or by accountants b : an instance of applied accounting or of the settling or presenting of accounts.

cur·ren·cy: Pronunciation: (ˈk^rᵊnsᶦ) ˈk&r-&n(t)-sE, ˈk&-r&n(t)-, Function: *noun*, Inflected Form(s): *plural* –cies; 1 a : circulation as a medium of exchange b : general use, acceptance, or prevalence c : the quality or state of being current: currentness. 2 a : something (as coins, treasury notes, and banknotes) that is in circulation as a medium of exchange b : paper money in circulation c : a common article for bartering d : a medium of verbal or intellectual expression (Merriam-Webster Online Dictionary, www.m-w.com).

Accounting in ecology is accomplished by recording and summarizing data (explanatory and response variable interactions) and by analyzing, verifying, and reporting results. Perhaps insufficiently appreciated is the idea that ecologists use different currencies and accounting to understand ecology, and the differences matter. The term "observation set" (O'Neill et al., 1986) has been used to define and delimit different approaches to science and includes the phenomena of intellectual interest, the nature of the measurements taken (i.e., the currencies), and the statistical and analytical techniques (the accounting) used to derive conclusions (Bissonette, 1997). For example, geneticists, population ecologists, and ecosystem scientists all use different measurements (e.g., gene frequencies, number of animals, or nutrient cycling and energy flow, respectively) to account for the interactions they observe. Quantities of some variable most often represent the currency measured. Given the different observation sets used, accounting in ecology involves ledger books that have fundamentally different currencies that measure "quantity" and often are difficult to reconcile. Quantifying the essentially qualitative nature of nature is arguably more difficult and done less often. However, for behavioral, population, community, and landscape ecologists with an interest in animal response to resource availability, new theoretical developments suggest that single currency approaches, i.e., consumer response to the *quantity* of resources can be informed by addressing temporal differences in resource *quality* as well as quantity. Indeed, net trophic transfer of energy and biomass (both often represented by carbon, C), is often limited by the availability of other key elements such as nitrogen (N), phosphorous (P), and trace elements (Moe et al., 2005). The primary objective of this chapter is to address the idea of basic organisms needs and how spatial and temporal heterogeneity complicate our ecological accounting. To do that, I: (a) examine the idea of temporal explicitness in resource availability (quantity) and quality; (b) discuss the different ways that we keep the books; (c) briefly describe two simple but sometimes neglected distinctions relevant to our understanding of the effects of special complexity, viz., the components of pattern and the differences between fragmentation and habitat loss; (d) suggest that the fragmentation model of conceptualizing landscapes is but one possible way of thinking about heterogeneity and may hinder our accounting and hence our understanding of the effects of varying temporal and spatial variation in resource availability on animal response; and (e) attempt to address the problems inherent in single currency approaches by reference to ecological stoichiometry. Throughout, I place these ideas in the context of temporal explicitness.

1.2. Basic Organism Needs Get Complicated

Basic vertebrate organism needs are surprisingly simple to list. Minimal resource needs include access to food, free or metabolic water, cover from predators and perhaps inclement weather, and to mates, all at variable rates that influence fitness. However, resource acquisition is complicated when resources are distributed heterogeneously. One might get the impression from the current voluminous literature in landscape and population ecology that the complexity stemmed primarily from spatial complications. Indeed, much is promised by an understanding of the effects of spatial scale on animal population response. At one time, panmictic mixing and homogeneous landscapes were common assumptions used in population dynamics (Fisher, 1930) before the broad acceptance that habitat heterogeneity had causal effects and that appropriate scaling of our accounting metrics was essential for a more complete understanding of animal and population response (Wiens, 1989). For ecologists, scale effects or scale complications mean, among other things, that discrete populations exist with different vital rates, i.e., averaging statistics for populations cannot be used as they were traditionally when panmixis was assumed (Ritchie, 1997). The reason is that animal movement in naturally heterogeneous landscapes is often hindered (Merriam, 1998) and panmixis is not commonly possible. Panmixis is probably always a simplifying assumption given mate competition, social hierarchies, as well as individual variation in vagility. Regardless, how organisms fulfil their resource acquisition needs is complicated and often difficult for them to do because individuals need to move across potentially dangerous heterogeneous landscapes in response to temporally discontinuous resource availability. It is not surprising that our ecological accounting is similarly difficult. Both pattern, as well as the dynamics of heterogeneity, need to be accounted for to better understand organism and species responses in space and time.

1.3. Temporal Discontinuities

Temporal resource discontinuities can be regular or pulsed (Ostfeld and Keesing, 2000) or occur stochastically at irregular intervals. They may occur at temporal scales spanning from time of day (e.g., activity patterns, and thus availability of prey), to seasons (primary production) and years (mass seeding events), to decades and even centuries (succession of some desert and forest ecosystems). Temporal resource discontinuities are caused by factors such as seasonality (Norrdahl et al., 2002), phenological events (Kelly, 1994), trophic relationships (Khan and Ghaleb, 2003), or disturbances (White and Pickett, 1985). They can include ephemeral habitats such as ponds (Loman and Claesson, 2003) and "rotting logs, dung, carrion, gravel bars in rivers, and forest openings" (Johnson, 2000b). One of the most obvious discontinuities in resource availability in time is the fruiting of plants. The availability of acorns is a good example of a resource that exhibits strong temporal discontinuities (Abrahamson and Layne, 2003). Wolff (1996) found that rodent densities were positively correlated with oak mast production over a period of 14 years. However, much temporal heterogeneity of resources is gradual; i.e., it concerns variation in resource quality. In this ecological sense, all resources may be considered pulsed or discontinuous to some degree (see Ostfeld and Keesing, Chapter 2, this volume). Most resources appear seasonally in temperate and tropical environments. Additionally, resource quality changes over time as well as over spatial gradients. There is a voluminous literature on the response of species to environment resource gradients. These were largely a result of two papers by Tilman (1980, 1982) who proposed what has come to be known as the resource-ratio theory. The theory essentially describes interactions of competing species through their use and effect on shared resources, and had its antecedents in work by MacArthur (1972), Maguire (1973), and others. Miller et al. (2005) summarized the use of the theory by ecologists, and I will not address that issue here, except to suggest that the idea of "use and effect" would appear to be a multiple currency or bivalent approach at the producer-herbivore trophic interface.

1.4. Temporal Explicitness

The term *spatial explicitness* is common and we have become accustomed to thinking about spatial complications. For population ecologists, the term implies among other things, spatially discontinuous populations, inhibited movement of individuals across heterogeneous landscapes, and processes whose effects are understood only if viewed at the appropriate spatial resolution and extent (Addicott et al., 1987). As a result, vital statistics—viz., birth, death, survivorship, recruitment, and genetic composition may vary in space, and thus, cannot simply be averaged across populations (Ritchie, 1997). Temporal explicitness has been treated far less extensively in those studies that relate animal response to resource availability.

A common temporally explicit approach in ecology is to develop simulation models to explain observed spatial pattern differences caused by ecological processes such as disturbance and succession. For example, Wiegand et al. (1998) explored the impact of disturbances on spatio-temporal shrub land pattern evolution, Franklin and Tolonen (2000) modelled the temporal relationship between fire and vegetation using pollen and charcoal data, and Tian et al. (2002) simulated the spatial and temporal effects of microbial contaminants on grazed farmlands. Because most studies are of relatively short duration, often on the scale of a few years, a space for time substitution is most often used (Hargrove and Pickering, 1992) where landscapes are replicated in space rather than time. The powerful effects of unique historical events on subsequent dynamics, e.g., violent disturbances, are often muted or ignored and lost. System history disappears. Almost... (see With, Chapter 3, this volume). Johnson (2000a, p. 1697) suggested that temporal structure generally "exists when habitat dynamics are defined independently of population density." Thus, temporal variation of processes in landscapes has important implications for metapopulation studies (Holyoak and Ray, 1999). Johnson (2000b, p. 67) considered that "species in successional landscapes may represent the most appropriate examples of classical metapopulations" and explored the idea that species coexistence and metapopulation dynamics can be influenced profoundly by the temporal dynamic of habitat succession (Johnson, 2000a,b). Clearly a major problem lies with the observation that landscapes are changing more rapidly than slower changing animal populations can accommodate (With, Chapter 3, this volume).

The implication of the term "temporal explicitness" is that differences in individual performance (different rates of resource acquisition, and hence presumably fitness) and in vital rates of populations can be caused generally by temporal discontinuities, and specifically, in the present context, by temporal differences in both resource availability and quality. The apparent novelty and general lack of appreciation of this idea points to the problem. There are at least two reasons why temporal dynamics have not been widely addressed explicitly in fragmentation studies of animal response. First, we appear to have lacked a generally accepted conceptual and methodological framework with which to address its effects. Second, the single-currency approach may have limited our ability to measure the important effects of resource quality that vary through time.

One reason that time has not often been addressed explicitly may be because the concept of fragmentation has most often been conceived in a very limited spatial sense. If we think of habitat fragmentation as a *discontinuity* in space and time, and thus in function and process (Lord and Norton, 1990), we then can find a way to address the complexities of time as a variable influencing organism response to habitat fragmentation, and hence to resource availability. For example, a fire regime is a discontinuous process in time. Disturbance regimes are by definition discontinuous. Hurricanes, tornados, and severe weather events occur in some sense predictably, but are discontinuous in time. An important consequence of thinking of resources as not only spatially, but also temporally discontinuous is that quantitative descriptors can be measured using metrics borrowed from disturbance theory. In other words, the currency we have available for ecological accounting is expanded. For example, temporal (as well as spatial) distribution of resources, predictability in the timing that resources are available, differences in amount and quality, and possible concurrent interactions of the availability, quality, and timing of other resources i.e., synergisms, can be measured (See Ostfeld and Keesing, Chapter 2, this volume). Disturbance metrics (White and Pickett, 1985) are well known and lend themselves to measuring resource discontinuities because disturbances themselves are discontinuous. When we are able to consider temporal discontinuities in resource availability (quantity) and resource quality, our understanding of ecological reality is enhanced, because these are the attributes to which animals respond.

1.5. Two Important Distinctions

Words have specific meanings and when we blur definitions, the result is more often than not confusion. I make two important distinctions here. First, landscape pattern has at least two distinct characteristics of importance to those who study fragmentation effects and species response: composition (sometimes given as total amount of habitat (Schiemegelow and Mönkkönen, 2002) and spatial arrangement (Turner, 1989). Both influence and constrain animal response. The colloquial expression might be stated as, "what habitats are present (composition) and where are they (arrangement)?" Given that most organisms need to move to access resources (Merriam, 1998), one should expect different responses from different species to these two characteristics. It is of little consolation that many (but not all) metrics used to quantify landscape heterogeneity confound the effects of composition and arrangement (Gustafson, 1998; Li and Wu, 2004; Neel et al., 2004), i.e., they measure multiple components of spatial pattern and often are correlated, making causal interpretation difficult. Li and Reynolds (1995), Riiters et al. (1995), McGarigal and McComb (1995), and Jaeger (2000), using different methodological approaches, have provided assessments of which landscape metrics appear to be most useful. A priori and clear thinking about species natural history requirements as well as about the processes suspected to be operating, coupled with reasonable hypotheses about pattern composition and arrangement effects would seem to be necessary initial steps in any ecological accounting of species response to fragmentation and resource-related effects.

Second, it is possible that when we think about fragmentation as a process, we make assumptions that seem reasonable but may not hold. Fahrig (2003) provided insight into one of the reasons that fragmentation studies often produce mixed or counter-intuitive results. She suggested that many studies have not differentiated between "fragmentation per se," i.e., the breaking apart of habitat, and habitat loss. The two are not the same, although both are part of the *processes* that occur when landscapes change over time. See Cushman and McGarigal (this volume) for examples of an analysis that distinguishes between the two. When fragmentation is viewed as a process, four effects are implied: (1) a reduction in habitat amount; (2) an increase in the number of habitat patches; (3) a decrease in mean patch size; and (4) an increase in patch isolation. These effects appear logical because we make the tacit assumption that the starting point is an unfragmented landscape. If we relax that assumption, then it is easier to understand that different scenarios may result. Fahrig (2003) provided five possible scenarios where one or more of the expectations were not met, suggesting strongly that we should keep these differences in mind in both the studies we design and the analyses we use. To do otherwise is unhelpful, as Debinski and Holt's (2000) review of 21 experimental fragmentation studies clearly suggests. An additional component relates to the idea that the concept of "habitat" is species-centered and not an arbitrary decision on the part of the observer. This leads to an overt consideration of when "habitat" is really habitat. Additionally, how we conceive "landscape" as a working construct is germane here.

The concept of landscape fragmentation has often been used as if it were a "unitary phenomenon" (Haila, 2002, page 322); the schematic view has its origins in Island Biogeographic theory (MacArthur and Wilson, 1967). However, when translated to terrestrial systems, some of the early assumptions remained: (1) habitat islands were the result of disturbance and breaking apart of once contiguous habitat;

(2) were isolated from one another by an essentially inhospitable matrix that was hostile to a majority of organisms (Haila, 2002); and (3) movement of biota often depended on corridors or long-distance dispersal movement to move between patches (Saunders et al., 1991; McIntyre and Barrett, 1992). This schematic view led to the description of landscapes in terms of patches (usually homogeneous), corridors (usually linear), and matrix (the most connected part of the landscape (Forman, 1995; McIntyre and Hobbs, 1999). Of course, depending upon the degree of disturbance, the matrix can be original habitat or the disturbed area. Observations in Australia in the early 1990s led McIntyre and Barrett (1992) to suggest that the schematic view of landscape did not apply to systems heavily modified by agriculture. They observed that the "intervening areas" were modified versions of the original habitat and were not totally inhospitable to movement; animals moved through these areas. This was a significant finding and implied that habitat modification may result in more than just a binary option of "habitat" vs. "non-habitat" (McIntyre and Hobbs, 1999). A significant conceptual advancement, and one that modifies a significant assumption of the schematic view, is that disturbed habitat is not always inhospitable. McIntyre and Hobbs (1999) presented a modified version of the schematic view where various levels of habitat modification were represented on a continuum of habitat destruction while at the same time considering spatial arrangement, resulting in landscapes ranging from intact ($<10\%$ modified, connectivity high), to relictual ($<10\%$ intact habitat, no connectivity). The schematic view of landscape fragmentation had its "assumption descendants" in the "community-unit theory" (Manning et al., 2006), which holds that plant communities were "homogeneous, discrete, and recognizable units" (Austin, 1985, p. 39). Viewing landscape patches as "habitat" for animals homogenizes them into discrete and recognizable units. The relevant question is: do animals recognize habitat patches in the same manner that we do, i.e., according to the schematic view? Manning et al. (2004) suggested viewing landscapes as evidencing both environmental and spatial continua, i.e., gradients. Indeed, Lindenmayer et al. (2002) found strong gradients in bird assemblages in eucalypt and pine forests in Australia that were governed by a combination of landscape context, and remnant patch size and shape. Manning et al. (2004) suggested that environmental continua occur in abstract ecological space while spatial continua or gradients occur in geographical space. Their concept of "Umwelt" incorporates species response and perception into both environmental and geographical gradients, hence is a significant departure from the schematic or fragmentation model. Finally, Fischer and Lindenmayer (2006) proposed a process based conceptual "continuum" model that provides for individual species response to gradual changes in spatially distributed ecological variables such as food and shelter. It seems to me that the schematic fragmentation model allows assessment of the effects of pattern, while the continuum model (Fischer and Lindenmayer, 2006) may allow linking animal response to ecological processes. The continuum model will be especially valuable if temporal discontinuities in resources can be taken into consideration.

Attention to spatial distinctions is necessary but not sufficient. Note that we essentially are measuring some *quantity* rather than *quality* effect as the explanatory variable. This has been referred to in a general sense as a single currency approach (Moe et al., 2005), where the clear implication is that "currency" refers to either quantitative or qualitative effects, but not both. Regardless, if the objective is to learn how species respond to changing landscapes and hence changing resource availability (quantity) and quality, attention to spatial details gets us only part way there. Attention to temporal effects as well as consideration of the qualitative differences in resources is necessary.

1.6. Resource Quality: Keeping the Books

So then, how might we improve our keeping of the books in ecology? Keeping the books, i.e., accounting in ecology, implies that we are capturing the essence of the interactions so that understanding is enhanced. Specifically, it implies that our observations are buttressed by a conceptual understanding that makes sense. Put another way, the assumption is that the variables we measure, i.e. the currencies, are appropriate and up to the task. Studies of habitat fragmentation that have addressed animal responses to resources availability have used almost exclusively the currency of *quantity* of resource as the explanatory variable. Indeed, many habitat use/preference studies appear to be based on the hypothesis that the *amount* of habitat is more or less directly causally related to response variables such as animal density, growth, reproduction, survivorship, and birth and death rates. Additionally, even though habitat types themselves are often assumed to represent areas of different resource quality, the connection is not at all direct, and begs again the question of when "habitat," arbitrarily defined, is really habitat. In habitat selection studies, habitat quality is inferred by assessing individual performance or by some measure of population performance (Morrison, 2001), rather than by a more direct measure of quality as the explanatory variable.

At larger spatial scales, studies using GIS have used time step analyses of landscape changes that elucidate differences in habitat *composition* and *spatial arrangement* over time to explain, for example, changes in biodiversity. Indeed, a large proportion of habitat fragmentation studies have used landscape composition variables (i.e., how much) to imply or show changes in population abundance or biodiversity (number of species). The literature suggests that ecologists most often simply use quantity over some specific time period as the explanatory variable to explain animal response. However, most ecologists would agree that trophic transfer of energy and biomass can be limited by key elements (Liebig's law of the minimum; but see Muller et al., 2001, for a discussion on multiple and simultaneous limiting factors). For herbivores, nitrogen (N) and phosphorous (P) have been the elements usually measured, although other trace elements have been implicated (White, 1993). Moe et al. (2005) used the convention of referring to carbon (C) as representing energy and biomass, and phosphorous (P) and nitrogen (N) and other elements as nutrients. The idea of limiting resources over a longer time constant can be extended to animal populations. For example, population growth may be limited by the minimum amount of resources available to that population at the time of year of greatest scarcity and not by the total amount of resources available throughout the year. The clear implication is that the single currency of *quantity* of resource that ecologists have used to understand animal response may not be adequate to reflect what ecologists inherently suspect: i.e., dynamic changes in resource quality across heterogeneous landscapes are important determinants of population performance. This begs a need for an appropriate currency with which to measure quality effects.

1.6.1. Ecological Stoichiometry: Another Currency

Ecological stoichiometry, an emerging branch of ecology (Sterner and Elser, 2002; Anderson et al., 2004) has been variously described as "the study of the balance of energy and multiple chemical elements in ecological interactions" (Hessen and Elser, 2005, p. 3), "the study of the balance of elements in ecological processes" (Moe et al., 2005, p. 29), "the study of the balance of energy and materials in living systems" (Kay et al., 2005, p. 6), and "dealing with the balance of energy and chemical elements in ecological interactions and especially in trophic relationships" (Anderson et al., 2004, p. 884). The field developed primarily from pelagic, freshwater studies (Hessen and Elser, 2005). One field of concentration has explored how an imbalance of elements and energy can place strong constraints on individual organism growth and reproduction (Bruning, 1991; Sterner and Schultz, 1998; Aerts and Chapin, 2000). Another approach (Kay et al., 2005) has examined stoichiometry in an evolutionary context across multiple scales, exploring the reciprocal interactions between evolutionary processes and the elemental composition of organisms and their resources, and relating elemental ratios in organisms to phenotypic and genetic variation upon which selection can act. Yet another approach has expanded the ideas of a stoichiometric approach to biogeochemical cycles to address the sustainable acquisition of ecosystem services (Ptacnik et al., 2005). Schade et al. (2005) have provided a conceptual framework for thinking about ecosystem stoichiometry. Importantly for this book, ecological stoichiometry has implications for understanding temporal explicitness in resource quality and its influence on terrestrial populations in fragmented landscapes.

Ecological stoichiometry is well established in aquatic ecology but not yet in terrestrial ecology. Two recent papers on stoichiometry (Anderson et al., 2004, Moe et al., 2005) argue persuasively that ecologists interested in animal population response to resource availability need to consider the currency with which they examine plant-animal interactions. They argue that ecological stoichiometry provides a multiple currency approach to understand the effects of resource *quality*. By multiple currency, they mean that rather than "abstracting populations as aggregations of individuals or biomass," organisms are represented by carbon (C), phosphorous (P), and other trace elements that allow "key feedbacks, such as consumer-driven nutrient recycling" processes (Anderson et al., 2004 p. 884). The argument is that both food quantity and quality can be incorporated into a single framework. The concept of "currency" here has two related parts: one meaning refers to the difference between the effects, or explanatory variables, being measured, viz., quality versus quantity; the other meaning refers to the metrics used. The term “multiple currency,” therefore, can be interpreted to refer to measuring not only *quantitative* but also *qualitative* aspects of the resource using *quantitative* metrics. The message is that measuring only quantity is insufficient; quantification of the qualitative aspects of the resource base is needed. Owen-Smith (2005, p. 613) reinforced this idea when he stated, “the numerical approach to population dynamics is seductive, but potentially misleading through overlooking the material basis for changes in N.” These papers suggest a conceptual basis for some of the observations that ecologists have made concerning plant quality and its importance to herbivore response. An understanding of ecological stoichiometry can be gleaned from these papers as well as from other papers from a workshop called “Woodstoich 2004” sponsored by the Center for Advanced Study at the Norwegian Academy of Sciences and Letters and published in 2005 in volume 109 of Oikos. An additional group of papers appeared in volume 85(5) of Ecology 2004 as a Special Feature edited by D.O. Hessen and called Stoichimetric Ecology.

Box 1.1. What is stoichiometry?

Stoichiometry is the accounting, or math, behind chemistry. Traditional textbooks in chemistry explain that stoichiometry is used to calculate masses, moles, and percents within a chemical equation. While it is beyond the purpose of this chapter to delve into this in detail (readers are encouraged to look at a basic chemistry textbook for a full explanation) the following is given to provide background to understand the developing field of ecological stoichiometry. The balanced chemical equation $8\mathrm{Al} + 3\mathrm{Fe_3O_4} \rightarrow 4\mathrm{Al_2O_3} + 9\ \mathrm{Fe}$ contains aluminium (Al), iron (Fe), and oxygen (O). The numbers 8, 3, 4, and 9 are coefficients that show the relative amounts (molecules or moles) of each substance present, and can represent either the relative number of molecules, or the relative number of moles. A mole is equal to Avogadro’s number (6.023×10^{23}) of molecules. A mole is simply a term to denote an amount. For example, if have a half dozen apples, you have six of them. If you have a mole of apples, you have 6.023×10^{23} apples. If no coefficient is shown, a one (1) is assumed. Given the equation above, we can tell the number of moles of reactants and products. Hence we have an accounting system to work with chemical formulas. Ecological stoichiometry is extending this basic accounting system to ecological systems. Essentially, the accounting considers both the quantitative as well as the qualitative relationships involved; here the quantity and quality of the resource base are considered important and incorporated into analysis of their influence on heterotroph population response (UNC Chapel Hill Chemistry Fundamental Program 2006).

1.6.2. Resource Quality and Population Response

Anderson et al. (2004, p. 884) have argued that “population dynamics theory forms the quantitative core from which most ecologists have developed their intuition about how species interactions, heterogeneity, and biodiversity play out in time." They show that by using stoichiometric models to examine trophic interface dynamics, one derives qualitatively different predictions (sec. 1.6.3) about the resulting dynamics. A fundamental principle of ecological stoichiometry is that "the requirements of multiple elements vary within and among species, and can cause mismatches between demand and supply at ecological interfaces" (Moe et al., 2005). What this means for herbivores is that plant quality varies over time and space and the conversion of plant biomass into herbivore biomass is often constrained by plant quality and not necessarily plant quantity. The other side of the coin (Anderson et al., 2004) suggests that nutrient cycling back across the trophic interface, e.g., by excretion and elimination, will also be constrained by herbivore nutrient needs relative to what is needed, with the surplus being recycled back. Examining stoichiometric imbalance between carnivores and their prey may be less fruitful because the stoichiometric imbalance in nutrients between food (prey) and consumer (predator) is less for carnivores; the prey themselves are heterotrophs. Hence, the physiological variation between D:N:P ratios is "typically an order of magnitude less" between predator and prey (heterotrophs) than what is encountered between autotrophs (food) and consumer (heterotroph) (Anderson et al., 2004, p. 885). This suggests that predator heterotrophs may be seldomly limited by food quality. More work is evidently needed in this area.

Stoichiometric theory has formalized these constraints (Anderson et al., 2004) by what is known as the threshold elemental ratio (TER). This is the carbon: element threshold where the resource limitation shifts from carbon (C) to nutrient (P, N), that is, where the quality of the plant resource makes a difference. With plant C:element ratios <1, plant quality is always adequate for the herbivore and a single currency approach based on quantity of food will not deviate significantly from a stoichiometrical approach (Urabe and Watanabe, 1992; Urabe and Sterner, 1996). In these cases, ecologists have correctly used quantity to reflect herbivore response. It is when TER ratios >1 that a stoichiometric model approach can be illuminating.

1.6.3. Different Predictions

Perhaps the fundamental key for population ecologists is that because stoichiometric models incorporate *both* food quantity (which ecologists usually measure) and quality, which is inferred but much less frequently incorporated into the measurements, there may appear empirical phenomena that cannot be predicted by single currency models. Examples from laboratory experiments include the observations of a (1) positive density dependence and a shift in the nature of the interaction from competition to facilitation (Sommer, 1992), similar to the Allee effect; (2) coexistence of more than one predator on a single prey item in contrast to predictions based on the single (quantity)-currency theory (Grover, 2003; Hall, 2004; Hall et al., 2005); and (3) the diversity enhancing effects on herbivores of poor food quality (Anderson et al., 2004). Although these results come primarily from aquatic system experiments, terrestrial ecologists may find that