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***Response to Bogaert, J. 2003. "Lack of agreement on fragmentation metrics blurs correspondence between fragmentation experiments and predicted effects"***

## Understanding Fragmentation: Getting closer to 42

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### INTRODUCTION

"There really is one?" "To Everything? To the great Question of Life, the Universe and Everything?"

"Yes"

"Tell us!"

"All right," said Deep Thought. "The answer to the Great Question..." "Is..." "Fourty-two."

"Fourty-two!"... "Is that all you've got to show for seven and a half million years?"

"I checked it quite thoroughly," said the computer, "and that quite definitely is the answer. I think the problem, to be quite honest with you, is that you've never actually known what the question is."... "So once you know what the question actually is, you'll know what the answer means."

This imaginary conversation, from *The Hitchhiker's Guide to the Galaxy* (Adams 1979) is fanciful, but we believe it comes close to encapsulating the nature of the arguments about the effects of fragmentation. Harrison and Bruna (1999, p. 225) suggested that while "the literature on fragmentation grows ever richer, ... we still lack a synthesis between general principles and consistent field evidence." Fragmentation experiments have addressed various hypotheses (see Debinski and Holt 2000), but as the questions change, so do the results. Haila (2002, p.321) suggested that "the effects of fragmentation vary across organisms, habitat types, and geographic

regions." In their excellent review of fragmentation experiment studies, Debinski and Holt (2000) noted that results were "entirely mixed". McGarigal and Cushman (2002) came to a similar conclusion. In an earlier paper, we (Bissonette and Storch 2002) concluded that the effects of fragmentation "can be understood as multicausal, exhibiting thresholds where they are unexpected; are characterized by time lags that may be unpredictable; are heavily influenced by the structural differences between the matrix and the patches...; and are heavily dependent on the temporal and spatial scales of observation. In addition, their dynamics are contingent on system history and therefore subject to unpredictable stochastic events." We wondered if the problem lies with mixing results from papers that asked fundamentally different questions regarding organism response to fragmentation. Our inability to "know what the question actually is" appears to blur our answers.

Bogaert (2003) responded to our "Insight" paper (Bissonette and Storch 2002) and correctly pointed out that we did not take into account the fact that the metrics used to assess fragmentation can and do introduce variability into results. We did not address measurement effect because it had been treated reasonably extensively in the literature, as Bogaert noted. Given the multitude of landscape metrics (Gustafson 1998) and their considerable overlap (Baskent and Jordan 1995, Tischendorf 2001) (but see Li and Reynolds 1994, McGarigal and Cushman 2002, Riitters et al. 1995), we instead concentrated on ecological phenomena that have not been treated widely but that certainly impact our understanding of the effects of fragmentation. We agree with Bogaert's (2003) suggestion that a good first approach is to "select the aspect of fragmentation that is of most concern to the *question* being investigated". This may involve the use of several relatively independent metrics (Li and Reynolds 1994, McGarigal and Cushman 2002, Riitters et al. 1995). This approach is probably more productive than the "shotgun method" of generating multiple metrics because we can and then trying to interpret them, except perhaps in a heuristic sense when we are exploring pattern and looking for reasonable hypotheses to test.

We do not agree with Bogaert's comment that "This issue (the 'metrics problem') should be clarified before a more complicated item, such as matching temporal and spatial domains (Wiens 1989, Bissonette 1997) is dealt with". A solution to the 'metrics problem' does not seem eminent and to wait for some enlightenment before addressing the ecological consequences of fragmentation does not seem reasonable. As we stated in our original paper: "... at some general level of explanation, ecologists may have predictive power regarding the effects of fragmentation, but complexity is likely to make prediction of specifics difficult or impossible" (Bissonette and Storch 2002). However, we argue that understanding fragmentation effects lies within what Loehle (1990, p. 123) has referred to as "the Medawar Zone", i.e., the "science of the soluble". We need only to marshal the necessary and sufficient explanatory variables to address the question. We do not think this will turn out to be a 'Question for God', sensu Ellner (2001).

## TEMPORAL COMPLEXITY

We argue that there are at least two areas that need to be addressed when studying fragmentation. First, fragmentation is about landscape pattern, which has at least two characteristics of importance; spatial arrangement and total amount of habitat (Schmiegelow and Mönkkönen 2002). Given that organisms need to move to access resources, one should expect different responses to spatial arrangement and amount of habitat from different species. Second, few have addressed how the timing of resource availability and quality may influence how we understand fragmentation effect. Understanding the effects of fragmentation on animal or plant populations involves at least two questions that might be phrased like this: 1) Does fragmentation influence resource abundance, availability, and quality across a landscape? and 2) If so, how do organisms respond to the resulting heterogeneity in space and time?

Although temporal complexity has been recognized as affecting both terrestrial and aquatic (Ward 1989) systems, few have addressed how time may influence fragmentation effects. In our 2002 paper, we mentioned three temporal aspects; specifically time lags, temporal scale, and system history. We did not address temporal variation in resource availability. This arguably most important aspect of time with regard to organism response to fragmentation is sadly neglected in the quest to understand fragmentation effects. All of the papers in the Debinski and Holt (2000) review appeared to involve some aspect of organism response to fragmentation, and spatial, but not temporal, analyses appeared to be the focus for evaluating organism response. Of the 51 research articles published in the journal *Landscape Ecology* in 2002, 34 (67%) addressed spatial issues only, while 17 (33%) treated both space and time. However, temporal variation was considered only between two ( $n = 10$ , 59%), or several points in time, with analyses typically compared over a series of years ( $n = 7$ , 41%). The *questions* addressed in these papers varied, but none addressed the timing of resource heterogeneity.

Organism response is mediated through the organism's basic needs including nutrients, water, cover, and mates. Satisfying these simple needs becomes complicated when resources are distributed heterogeneously in time and space. Not surprisingly, then, how organisms respond to resource heterogeneity is complex for us to understand. As Levin (1992) stated: "Prediction... require(s) the interfacing of phenomena that occur on very different scales of time ... (and) space... ." Because individuals need to move across space and over time in response to resource availability, we need to understand the how, when, where, and whys of that movement if we are to understand fragmentation effects. This is not only because individuals need to move across heterogeneous landscapes, but also because resource availability is discontinuous in time. To add to the points we raise in our earlier paper (Bissonette and Storch 2002), we argue that both pattern and dynamics of heterogeneity need to be addressed to better understand the effects of fragmentation.

## TEMPORAL EXPLICITNESS

The term spatial explicitness is common and we have become accustomed to thinking about spatial complications. For population biologists, the term implies spatially discontinuous populations, caused by the limitation of movements of individuals across a heterogeneous landscape. 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 (here we ignore the work on chaotic dynamics). The most common temporally explicit approach to ecology is to develop simulation models to explain spatial patterns observed in the field by temporal interactions between ecological processes such as disturbance and succession. For example, Wiegand et al. (1998) explored the impact of disturbances on spatio-temporal shrubland pattern evolution, Franklin and Tolonen (2000) modeled 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. As Johnson (2000a, p. 1697) suggested, temporal structure generally "exists when habitat dynamics are defined independently of population density." Thus, temporal variation of 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 interesting idea that species coexistence and metapopulation dynamics can be profoundly influenced by the temporal dynamic of habitat succession (Johnson 2000a,b).

The implication of the term "temporal explicitness" is that differences in individual performance (different rates of resource acquisition, hence 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. One reason why time has not been widely addressed explicitly in fragmentation studies is that we appear to have lacked a conceptual framework with which to address its effects. We have used fragmentation in a very limited spatial sense, and given token service to time. However, if we think of habitat fragmentation as a *discontinuity* in space and time, and thus, function (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.

## RESOURCES IN TIME

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 times 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 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. They can be absolute, as in ephemeral habitats such as ponds (Loman and Claesson 2003) and "rotting logs, dung, carrion, gravel bars in rivers, and forest openings" (Johnson 2000b). However, much of the temporal heterogeneity of resources is gradual, i.e., concerns variation in resource quality. We argue that the ecological reality of our studies is enhanced when we consider not only time of availability but also changing resource quality. These are the attributes that animals respond to. Simple organism needs are surprisingly complex to meet.

An important consequence of thinking of resources as not only spatially, but also temporally discontinuous is that quantitative descriptors can be measured. For example, temporal (as well as spatial) distribution and frequency 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. These are well-known metrics for assessing disturbances (White and Pickett 1985) and lend themselves to measuring resource discontinuities because disturbances themselves are discontinuous.

If we have a way to measure temporal differences in resource availability and quality, we then have a way to assess its influence on organism abundance, distribution, and response to habitat fragmentation. It is clear from the papers published on fragmentation effects and those reviewed by Debinski and Holt (2000), that spatial heterogeneity influences organism response. An additional question we need to ask is "what effect does temporal discontinuity of resources play in organism response to spatially fragmented habitats?" If we are able to conceptualize and quantify time *and* space effects, we will have gotten closer to the "42" of the fragmentation problem. We suggest as we did in our "Insight" paper (Bissonette and Storch 2002) that real world complexity is likely to make prediction difficult and inexact, but not impossible. By "getting closer to 42", i.e., accounting for temporal discontinuities in resource abundance, availability, and quality, we should have a better understanding of organism response to habitat fragmentation, and a closer approximation to the true state of nature.

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## RESPONSES TO THIS ARTICLE

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