Scale, the Dynamic Stability of Forest Ecosystems, and the Persistence of Biodiversity

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1 Introduction

Even as ecologists documented the importance of disturbance and non-equilibrium in vegetation dynamics, they began to ask whether the dramatic changes at the local, patch scale, would contribute to an equilibrium at larger spatial scales. Heinselman (1973) hypothesized a 'shifting mosaic' for the dynamics of boreal forests in which the spatial location of recent burns and stands of various successional ages would shift, but each would continue to be present within the larger landscape at some relatively constant frequency. The 'mosaic-cycle concept of ecosystems' (Remmert 1991) also conjectured that an overall dynamic equilibrium would be maintained in spite of local dynamic changes. Recent studies of disturbance focused on functional resilience, biodiversity and landscape equilibrium (e.g. Romme 1982, Turner et al.1993, Peterson et al. 1998, Engelmark et al. 1999, Frehlich and Reich 1999, White et al. 1999, Walker et al. 1999, White and Jentsch 2001).

We define function as the product of an ecological unit (e.g. an organism, a successional sere) and an ecological process (e.g. photosynthesis, nitrogen fixation). Thus, functional stability and diversity results from the stability and diversity of units combined with processes.

In this paper we explore the relation between disturbance pattern and the stability of forest dynamics by addressing two questions: 1) Which are appropriate scales for analyzing the interrelations between disturbance pattern and forest dynamics? 2) How does disturbance pattern in space and time influence biodiversity, functional resilience and landscape equilibrium in boreal forests? We hypothesize, that stability of forest dynamics is a scale-dependent product of disturbance pattern and ecological complexity. We apply stability concepts at the multi-patch scale and ask, whether dynamic pattern with disturbance being part of it can itself be resilient.

2 Conceptual Issues: Disturbance, Stability, and Biodiversity

We define disturbance as a discrete event in time relative to the life span of an ecological unit like an individual tree or a particular succes-

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sional community (see Pickett and White 1985, White and Jentsch 2001). Disturbances create patches in space and time. Spatio-temporal patch dimensions are determined by the patch-specific disturbance responsible for the patch-creation. This is the ‘patch scale’ – relative to the particular dimensions of a certain type of disturbance. A disturbance regime is the sum of all disturbances over space and time affecting an ecological system at the multi-patch scale. This scale comprises various patches, some being disturbed, others temporarily undisturbed, and all being further differentiated by environmental factors such as edaphic variation. Being determined by disturbance, these patterns of patches are non-random. At the multi-patch scale we can analyze pattern dynamics, questions of stability or change, and persistence of biotic diversity.

Stability has been divided into three concepts: constancy, resistence and resilience (e.g. Connell and Sousa 1983, Remmert 1989, Harrison 1997, review in Grimm and Wissel 1997). These terms are usually applied to some trait or property, that is measured in a system, e.g. structure, biomass, productivity, or species diversity. ‘Constancy’ is associated with persistence of a particular reference state or reference dynamic. Since disturbances are ubiquitious in boreal forests, this case is rare. ‘Resistance’ characterizes an ecological system staying essentially unchanged in the presence of disturbance. And ‘resilience’ is the ability to return to a reference state after a temporary disturbance. Since disturbance can maintain a dynamic pattern, a change in this pattern is not due to the mere presence of disturbance, but to a shift in the amount of disturbance. At the multi-patch scale, we average properties across disturbed and undisturbed patches. Here, resilience is the ability of a dynamic pattern to reform after displacement without loss of parts – parts being ecological units and ecological processes. The interrelation of units and processes determines ecological functions. Functional resilience therefore implies qualitative persistence of functions at the multipatch scale despite change of function at the patch scale.

This suggests that disturbance affects biodiversity in many ways. It has influence on the number of ecological units and the contrast between them. It affects also ecological processes and interactions. At the multi-patch scale, disturbance has an effect on spatial organization, on speed and periodicity of temporal development and on ecological functioning. Ecological complexity integrates all units and functions of an ecological system. The multi-patch aggregation is necessarily more complex than a single patch unit.

3 The Patch and Multi-Patch Scale in Boreal Forests

While the location and the final shape of a particular patch is modified by stochastic phenomena, once a disturbance has occurred, the resulting patterns of forest structure and composition are non-random. They emerge at various spatial and temporal scales as a product of site conditions (e.g. nutrient availability), ecological processes (e.g. disturbance) and ecological units (e.g. functional groups). When assessing the impact of disturbance on forest dynamics and biodiversity, we must choose the appropriate scale for analysis (Fig. 1).

Patterns emerge at a certain temporal scale, below which variability is noise and above which it is background. Perception of spatial pattern is dependent on a particular scale and resolution of observation. Nevertheless, disturbances are highly variable in kind, cause and effect, they act across spatial and functional scales, and influence landscape composition and structure long after their brief duration of occurrence. They produce mosaics of patches being disturbed and undisturbed. These patches dynamically interact. Shugart’s 1:50 rule suggested that, when the size of a landscape surpasses 50 times the size of an average patch, the biomass throughout a landscape is in dynamic equilibrium (Shugart 1984). This finding assumes that disturbances in patches are controlled by feedback between the ecosystem state and the susceptibility to disturbances within patches. Patch sizes, the duration of their existence and their interactions may vary with stand structure and type of disturbance. In order to describe the impact of disturbances on forest dynamics, we need to focus on two relative scales: the patch scale and the multi-patch scale (Fig. 2).

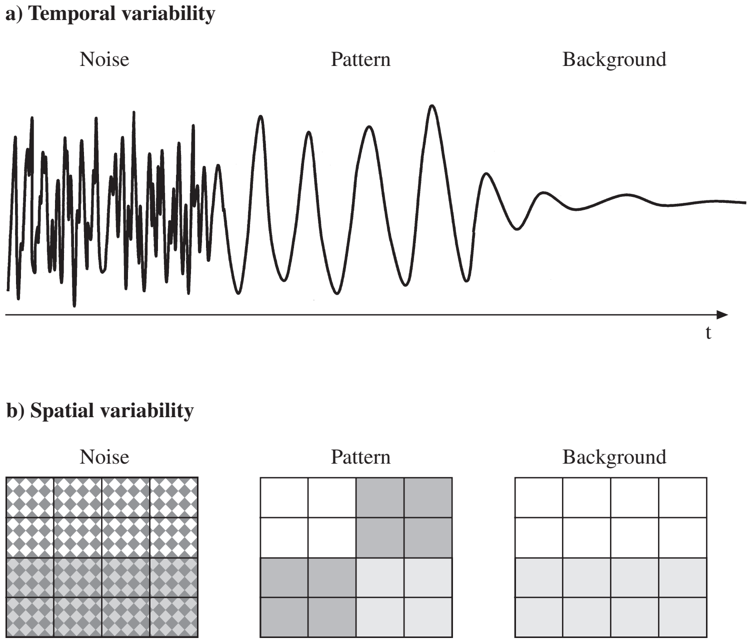

Fig. 1. Pattern emergence depends on scale and resolution. a) Temporal variability: frequency pattern emerges at a certain temporal scale, below which it is noise and above which it is background (e.g. climate change). b) Spatial variability: spatial pattern emerges at a certain spatial scale and resolution, below which it is diffuse (noise) and above which it is not differentiating either (e.g. environmental background).

At the patch scale, e.g. in an actual clearcut or burned area, disturbance may destroy biomass, homogenize plant species composition and disorganize established patterns of growth and competition. A plant community may be entirely burned, with only few species re-establishing in a stand characterized by little competitive interaction. Nevertheless, other units like microbes and other processes like mineralization or insect colonization may become more important. The patch scale does not include all relevant processes to support biodiversity. Properties within a patch depend on properties of the surrounding patches, because patches are connected by dispersal and other interactions in space and time.

At the multi-patch scale we deal with aggregates of disturbed and undisturbed patches. Here, we are interested in patch interactions, overall biodiversity, and functional resilience as defined before. Whether regarding the structure of old growth forests or the process of nitrogen fixation, a forest landscape could only be considered to be resilient in face of disturbance, if averaged across all patches. This multi-patch scale is the appropriate scale to examine the influence of disturbances on species richness, or the stability of forest dynamics. At the multi-patch scale disturbance may serve as a constituent factor for reorganizing system structure, for driving and stabilizing pattern dynamics within a certain range of variation. A landscape may consist of numerous successional communities and stand structures characterized by a range of functional interactions across various scales.

Numerous disturbances – e.g. fire, logging, insect pests, windthrows, tornados, digging animals, herbivory, forest harvesting - operate on various scales in boreal forests. Stand composition, patch size and structure vary tremendously, and this variability maintains biodiversity. To

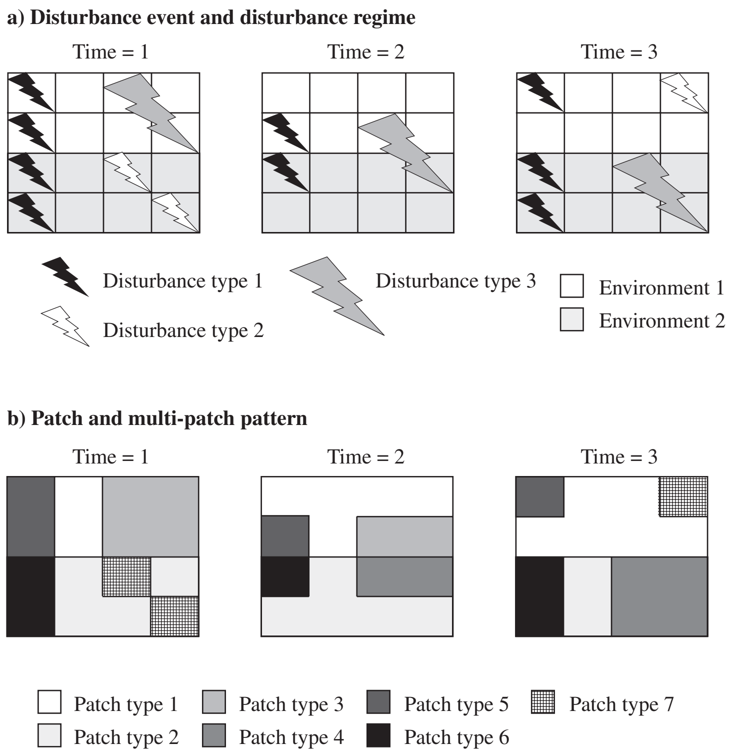

Fig. 2. Patch Scale and Multi-patch Scale. The spatial and temporal organization of an ecological system is a scale-dependent product of disturbance pattern and environmental background. a) Pattern of disturbances with various magnitudes in space and time. Dimensions of patches are determined by the spatio-temporal dimensions of disturbances. b) Aggregation pattern of disturbed and undisturbed patches at the multi-patch scale. Note, that disturbance type 3 does not lead to patch differentiation, although there is variance in environmental background. No closed cycle is shown here: There are also patches that remain temporarily undisturbed. Effects on patch pattern, that are out of proportion of the short duration of disturbance events are not shown either.

understand this variation in disturbances and responses, we need to measure species composition, degree of heterogeneity, resource availability and the legacy of the pre-disturbance ecosystem within individual patches. We also need to describe the site quality relative to landscape trajectory. At the multi-patch scale, we can focus within or between patches, whether large, infrequent disturbances show similar effects on vegetation dynamics compared to those that are small and frequent. We can assess how disturbances affect forest ecosystems and landscapes, whether resilience of pattern occurs, so that dynamic equilibrium is maintained despite or due to disturbance.

A key question associated with stability of forest dynamics is, whether disturbances produce a dynamic equilibrium at larger scales (White et al. 1999). One sort of equilibrium is the qualitative equilibrium which suggests that even though patches and their species fluctuate in abundance, they go on persisting. The implication is that the mutiple-patch aggregation within an ecological system 'works' in the sense that the next

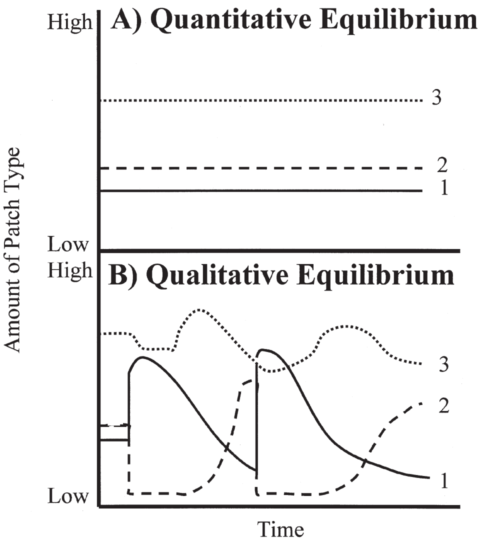

Fig. 3. Quantitative and Qualitative Equilibrium. The proportions of three patch types (1, 2 and 3) across a hypothetical ecological system (multi-patch aggregation) are shown through time. A. Quantitative equilibrium: proportions remain constant. B. Qualitative Equilibrium: the three patches fluctuate in abundance but all persist through time. They are not lost from the system at any time - conditions of resilience are met. (White et al. 2000).

disturbance patch occurs within the reach of the dispersal of early successional species of the older patches. The new patches must fall near enough in time and space so that species hop about but don't go extinct. Under this equilibrium there is bounded variation: no patch or species or successional state or ecological function become extinct on an ecological system, but they can fluctuate in abundance. By contrast, quantitative, shifting-mosaic, or steady-state equilibrium is more stringent in that variance must be small and average values of parameters of interest more or less constant when measured at the appropriate scale (Fig. 3). As Romme et al. (1998) argued, quantitative equilibrium is rare, especially for ecosystems affected by large, infrequent disturbances.

The patch and multi-patch scale approach provides an operational method for searching for generality in theory of disturbance and ecosystem dynamics (White and Jentsch 2001). Turner et al. (1993) proposed the concept of landscape equilibrium caused by various kinds of disturbance regimes. They predicted both the presence and absence of equilibrium and variance in ecosystem states as a function of two ratios: the ratio of the disturbed area to the landscape area and the ratio of the disturbance frequency to the time needed for successional recovery. The smaller the patch relative to the landscape size and the lower the disturbance frequency relative to the recovery time, the greater the chance for dynamic equilibrium in all patches. Shugart (1984) found, that the distribution of patches is generally more stable and that overall habitat diversity is higher for high ratios of landscape area to patch size. Examining stability and equilibrium as functions of the patch to multi-patch ratio allows the comparison of forests with diverse disturbance types and patch sizes.

4 Disturbance, Biodiversity and Resilience at the Multi-Patch Scale

Disturbance is essential for the dynamics of boreal forests at larger scales. It is an ubiquitious driving force for vegetation dynamics at all levels of biological organization, and plays a crucial role in maintaining biotic diversity (e.g. Darwin 1859, Connell 1978, Sousa 1984, Pickett and White 1985, Tilman 1996). At the multi-patch scale, disturbance impacts biodiversity and forests dynamics: it increases species richness, it is a primary cause of spatial heterogeneity, it enhances temporal rhythm of stand replacement, and it contributes to ecological processes, functions and interactions (e.g. Platt 1975, Loucks et al. 1985, Collins and Glenn 1988). Biodiversity, in turn, influences the stability of dynamic pattern and ecological resilience, ensuring persistence of functions in the presence of disturbance.

4.1 Disturbance Increases Diversity (e.g. Species) at the Multi-Patch Scale

Disturbance regime is a major shaping force for forest composition. It acts as evolutionary force, causing adaptations in the biota exposed to it. Disturbance-dependent species and successional stages have evolved, persist and add to overall species diversity within a multi-patch aggregation. But, species diversity may decrease after disturbance at the patch-scale. According to the oversimplified Intermediate Disturbance Hypothesis, intermediate degrees of disturbance produce maximum species diversity – this is true for grasslands sites of intermediate productivity. However, at high population-growth rates, diversity peaks at high disturbance rates and, at low population-growth rates, diversity is highest at low disturbance rates. As Hubbel et al. (1999) note for tropical forests, there is no relationship between gap-disturbance regimes and tree-species richness. In this example, there is only structural pattern affected by disturbance (gaps being created). Still, this may cause functional diversity, e.g. patches of higher productivity important to other organisms. Other environmental conditions or disturbance types may nevertheless cause local change in composition of ecological units. The topic of niche partitioning in forest gaps is an area of active research (Busing and White 1997; Brokaw and Busing 2000), with most investigators finding no evidence or weak evidence for gap partitioning in relatively small gaps. However, they find more evidence of specialization as the gap size increases and conditions within the gap contrast more with those in the forest matrix.

4.2 Disturbance Contributes to Pattern and Structural Diversity in Space and Time

Disturbance produces heterogenous environments and drives a grand variety of successional pathways, often resulting in cross-scale system dynamics: The biotic legacies that remain after disturbance vary in quality and quantity, leading to a range of regeneration patterns like fine scale gap dynamics, patch dynamics or regeneration succession (Van der Maarel 1996). Site productivity and resource availability control the rate of return to pre-disturbance conditions on a patch. For example, the effect of a large blowdown varies on a gradient between productive and unproductive forests. At productive sites, colonization and growth are rapid, so the canopy closure is achieved relatively quickly compared with closure at an unproductive site. Establishment and development on the unproductive site may take longer, resulting in a less evenly aged stand. Thus, disturbance creates patchiness in the forest canopy with patch origins being diverse and patch persistence ranging widely. It produces spatial and temporal heterogeneity in forest structure and adds to the process of pattern dynamics at the multi-patch scale. Pattern diversity in turn is a major cause for species diversity. Disturbance also locally removes inertia present in forest ecosystems, which are naturally dominated by long-lived, slow-acting organisms. So, due to disturbance, successional pathways are continuously altered in composition, velocity and trajectory, when exposed to varying environmental conditions like global warming or species invasion. As specific disturbance patterns are responsible for patch size and life span of patches, they influence the contrasts between neighbouring patches (heterogeneity within the multi-patch aggregation) and therewith the stability of patch dynamics at the multi-patch scale.

4.3 Disturbance Contributes to Diversity of Ecological Processes, Functions and Interactions

Within a multi-patch aggregation, each patch – disturbed or undisturbed – consist of a variety of species, that carry functional traits, so that each patch is characterized by a particular potential of ecological functions. Disturbance can contribute to the diversity of interactions within- and between patches, to recruitment and competition, particularly seedling establishment, and to local imbalances of resource availability regarding e.g. light and nutrients. Of course, species or patch diversity does not inevitably enhance functional stability, because there may be redundancy in functions. Still, many scientists propose an increase in functions (nonlinear), when particular species are added to a system (MacArthur 1955, Holling 1973, Main 1982, Lawton 1994, Naeem and Li 1997). Apparently redundant species may operate at different spatial and temporal scales, thereby reinforcing function across scales (Ehrlich and Ehrlich 1981, Peterson et al. 1998).

At the multi-patch scale, the interplay between disturbance-adapted/dependent and non-adapted species or between structural and functional traits of dominant and minor species is particularly interesting. When dominant species are primarily the ones affected by disturbances, other species may increase after disturbance, even if their functional traits are similar to the previous dominants. This has been expressed by the Resilience-Hypothesis (Walker et al. 1999): Dominant and minor species within same functional groups still differ in their capabilities to respond to disturbance. They may switch in abundance under changing environmental conditions. Redundancy is important in ensuring persistence in ecosystem function at the multi-patch scale under changing environmental conditions or in face of disturbance. The degree of stability in boreal forest dynamics also depends on the kind of species present. This is a somewhat circular relationship: Disturbance increases species diversity producing redundancy in functions, and in turn functional redundancy ensures the persistence of functions in response to disturbance. At the multi-patch scale, disturbance may periodically change the proportions of various patches present and therewith reduce the abundance of some species and functional groups. However, as long as the diversity of functions is maintained qualitatively, resilience is possible and functional stability is ensured.

5 Conclusion

Important forest properties at the multi-patch scale, like biodiversity, functional resilience and structural pattern, are sensitive to the overall disturbance regime. The major challenge assessing stability of forest dynamics and persistence of biodiversity in boreal forests is to figure out the multi-patch scale of a particular forest being exposed to particular disturbances.

Natural dynamics of boreal forest are superimposed by human disturbance, and there are limits to resilience. So, an important question for society at large is, whether or not human influence destabilizes the dynamic pattern. If the degree of disturbance surpasses the balance maintained at the multi-patch scale, e.g. intensive logging or rapid increase in temperature, the system will qualitatively change. When will parts be lost or dispersal distances be too far for species to ensure their former roles and functions?

The multi-patch scale approach offers an operational method to tackle these questions. In essence, we propose to measure absolute and relative conditions (space, environmental characteristics, resource availability, biotic inventory, functional types) at the patch scale, and to consider aggregate effects and dynamics at the multi-patch scale.

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