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Restoring the Adaptive Capacity of Forest Ecosystems

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Enhancing maintenance of desired goods and services in the face of perturbations—i.e., enhancing the ecosystems capacity to adapt—is a key consideration for restoration efforts. Complexity science provides a scientific framework for understanding and studying ecosystems, which can facilitate restoration efforts that increase or restore adaptive capacity. Many characteristics of complex systems have been integrated into ecosystem ecology. However, unifying these concepts under complexity theory provides new insights into ecosystem behavior. Several cases highlight how this can be useful for restoration efforts. For example, including cross-scale hierarchies in the analysis provided a better understanding of variability in ecosystems—e.g., in terms of the diversity in boreal forests and in terms of natural regeneration dynamics. Another example shows how a "mechanistic view" of diversity of traits can help understand how restoration treatments influence selected ecosystem functions, and how restoration treatments can enhance or maintain these functions under changing climate conditions. I conclude by highlighting challenges that need to be overcome to enhance our ability to utilize concepts from complexity science, including addressing uncertainty and quantification of complexity and characteristics of complex systems.

KEYWORDS *adoptation, complex adaptive systems, uncertainty, cross-scale hierarchies*

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BACKGROUND

Future ecosystems will likely be exposed to environmental, ecological, and social conditions that are without an historical precedent (Puettmann, 2011). This raises questions about how to provide a scientific basis for restoration and management of these "no-analog systems" (Seastedt, Hobbs, & Suding, 2008). Also, it appears more and more obvious that historical conditions and experiences may augment our understanding of processes or interactions (Keane, Hessburg, Landres, & Swanson, 2009) but cannot provide an exact blueprint for future restoration activities, not even in parks and wilderness areas (Hobbs et al., 2009).

My collaborators and I initiated a review of the history and current practices of silviculture (Puettmann, Coates, & Messier, 2009) and concluded that the "efficiency paradigm" associated with the "agricultural model of forestry" may not be suitable for forest management activities on many ownerships in light of new challenges—such as limited budgets and staffing, social and political constraints, and other aspects of global change (Puettmann et al., 2009; Puettmann, 2011). As an alternative, we suggested that complexity science may provide a suitable scientific basis for forest management in these settings. The sustainable provision of goods and services in a variable and uncertain future can be ensured through maintaining ecosystem stability, through ecosystems that change in response to perturbations while still providing desired services (Puettmann, 2011) or, more likely, a combination of both (Figure 1). Stability and the associated principles of resistance and

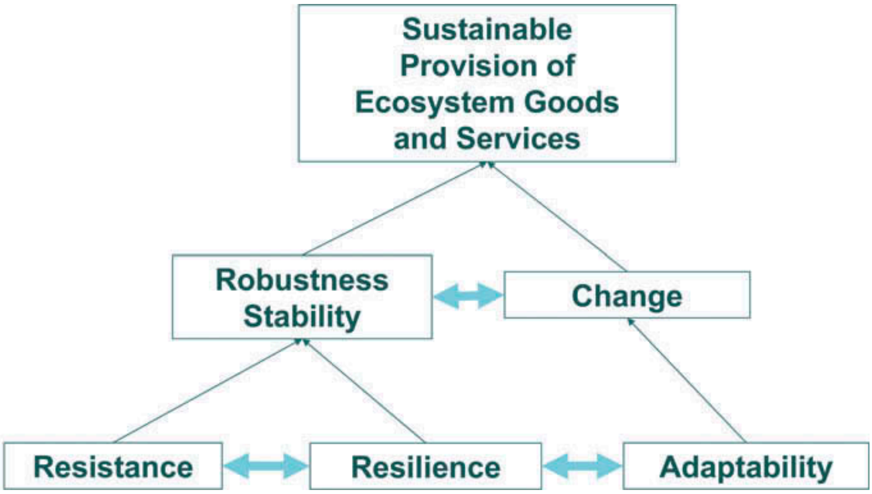

FIGURE 1 Diagram highlighting that the sustainable provision of ecosystem goods and services can be based on different concepts, such as stability/robustness and change. These concepts play out differently when developing restoration practices—such as a different emphasis on resistance, resilience, and adaptability.

resistances have received most of the attention to date (Landres, Morgan, & Swanson, 1999; Gunderson, Allen, & Holling, 2010), but we suggest much can be gained by placing an equal or higher emphasis on the adaptive capacity of ecosystems (Figure 1). As a visual example, Figure 2a highlights that ecosystems are defined by their structures (components, their arrangements, and interactions) and exist in a "fundamental niche" defined by environmental gradients (e.g., forest niches would be bordered by deserts and wetlands along a moisture gradient). A subset of structures and of the "fundamental niche" will supply the desired set of ecosystem goods and services (darker shade). This subset is defined by what is socially acceptable—i.e., driven by economic constraints, such as the value of selected goods and services; and political constraints, such as the Endangered Species Act. In response to perturbations, ecosystems will change their structure and move along the environmental gradient and may or may not fall outside the social acceptable limits. Emphasizing adaptive capacity in forest management means developing and implementing practices that increase the likelihood that ecosystem responses to perturbations stay within the socially acceptable range (Figure 2b)—i.e., that ecosystems sustainably provide desired goods and services. Our search for concepts and theories that help understand how ecosystems respond to perturbations led us to complexity science (Levin, 2005; Puettmann et al., 2009; Parrott & Meyer, 2012; Puettmann, Messier, & Coates, 2013), as forest ecosystems are prime examples of complex systems

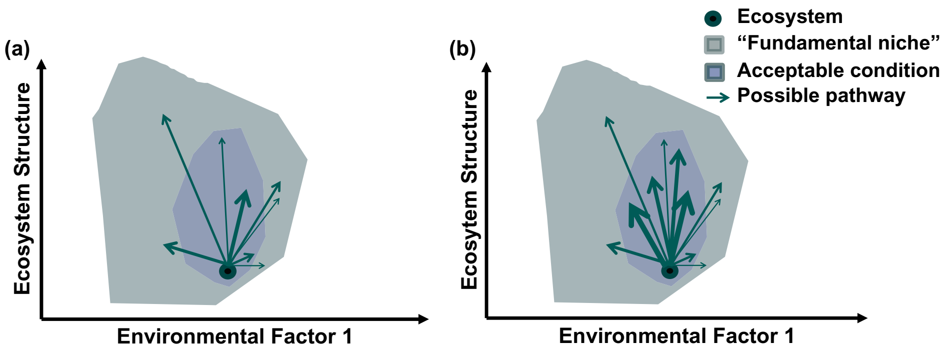

FIGURE 2 Diagram highlighting the concept of adaptive capacity (a). Ecosystems (dark circle) can operate within a range of environmental conditions and set of structures, similar to "fundamental niches" (light shade). Within these constraints, acceptable conditions (dark shade) are those in which desirable ecosystem goods and services are provided in a socially accepted manner. In response to perturbations, ecosystems will adapt and change, which likely means they will move along environmental and/or structural gradients. The length of the arrow is an indicator of the amount of change, while arrow thickness reflects the likelihood that this development path will be taken. (b) An ecosystem after restoration aimed at increasing adaptive capacity. Note, that both the number of pathways that stay within the acceptable conditions and the likelihood that these pathways are taken have increased due to restoration treatments.

(Levin 1999). However, considerable work remains before complexity science can be used to prescribe restoration and management activities on an operational basis (Messier, Puettmann, & Coates, 2013a).

This article provides a brief overview of recent activities my colleagues, students, and I have undertaken to investigate the potential for complexity science to provide a framework for forest restoration and management activities. First, I briefly introduce complex systems and why we think complexity science may be useful. Second, I highlight examples where viewing forests as complex systems provided new, worthwhile insights into ecosystems and how complexity science can be used to guide restoration and management activities. Next, I present examples, where we quantified impacts of forest management practices on adaptability of selected ecosystem functions in light of a changing climate. Finally, I highlight key challenges that need to be addressed before complex system theory can be widely applied as a scientific foundation for restoration and management activities.

COMPLEX SYSTEMS

Over the last century the ecosystem concept has grown in importance in the fields of ecology (Chapin & Matson, 2011) and natural resource management (Chapin, Kofinas, & Folke, 2009). Viewing forests as systems that are composed of more than trees but include innumerable physical and chemical, biotic and abiotic components, and their interactions, is a logical first step toward viewing forests as complex systems (Levin, 1999). Complexity science is a fairly recent development aimed at understanding the behavior of complex systems (Waldrop, 1992) that has received attention in a variety of disciplines, especially physics and economics (Delic & Dum, 2006) but less so in restoration and forestry (Puettmann et al., 2009). As stated by Puettmann (2011):

> Complex systems are more than just complicated, variable, or heterogeneous. Complex systems consist of a diversity of agents that interact across a variety of hierarchical scales, including organizational levels, time and spatial scales. These interactions include non-linear relationships and positive and negative feedback loops, which at higher scales lead to emergent properties (i.e., properties that cannot be predicted from information about the individual components). Important features of complex systems include the inherent dynamics—i.e., stable states or equilibriums are the exception, rather than the rule [Gunderson & Holling, 2002; Scheffer, 2009]. Another important feature is the bottom-up, decentralized control: the multitude of agents and interactions at low-level, local scales are the drivers of ecosystem behavior and are thus critical for the ecosystem's ability to self-organize (i.e., to adapt to changing conditions). This implies that ecosystem responses to perturbations are determined

> by the rules governing these local interactions. Consequently perturbations and management practices have to be viewed within the context of whether they can influence these rules and, if so, whether they increase or decrease the adaptability of ecosystems. (p. 324; more detail about forests as complex systems can be found in Levin, 1999; Parrott & Meyer, 2012; Puettmann et al., 2013; Parrott & Lange, 2013)

Viewing forests as complex systems is like looking at forests through a new "lens" that specifically focuses on nonlinearity, scale issues (including time, space, hierarchies), heterogeneity (including diversity and redundancy), and uncertainty (Levin et al., 2013) to better understand how ecosystems respond to perturbations. Information regarding ecosystem responses to these characteristics of complex systems will thus improve our understanding of how restoration activities impact an ecosystem's ability to respond to future changes (Puettmann et al., 2013).

OVERVIEW OF SELECTED ACTIVITIES AND OUTCOMES

Burton (2013) and Puettmann and Burton (2012) provide examples that demonstrate how viewing forests as complex systems can change the perception of ecosystems with resulting implications for restoration and management; focusing specifically on cross-scale hierarchical interactions. The traditional view of boreal forests as ecosystems with low species diversity (Hawkins et al., 2003) driven by large, infrequent fires has been used to justify widespread implementation of fairly simple, homogenizing management practice, such as large clear-cuts (Hunter, 1993). However, viewing ecosystems at multiple scales suggests that these forests are very diverse at smaller and larger (than species) hierarchical and organizational scales—e.g., at clone and provenance levels and through hybridizations of species (Burton, 2013). Similar arguments can be made for fire extent, severity, and frequency, as more detailed studies show high variability at various spatial and time scales (Bergeron, Harvey, Leduc, & Gauthier, 1999). Thus, complexity science highlights that historical perceptions of low-diversity boreal forests are due to applying these measures on a single organizational scale. Restoration activities will benefit if they are not bound by such perceptions, but account for multiple scales. Viewing forests as complex systems can also change perceptions of plant-plant and plant-animal interactions by suggesting that these interactions can be best understood when viewed as network components that interact across spatial and time scales as part of a meta-network (Simard, Martin, Vyse, & Larson, 2013). Such a viewpoint leads to different emphases. For example, sets of keystone species or processes other than those traditionally emphasized may deserve more attention in restoration activities, namely species or processes that link networks across scales.

These cases highlight how viewing forests through the lens of complexity science points out that our traditional view of forests or networks is—at least partially—an artifact of the reductionist viewpoint and can limit or hinder restoration and management activities. Similar assessments of temperate and tropical forests are provided by Haeussler, Canham, and Coates (2013) and Chazdon and Arroyo (2013), respectively.

Cornett and White (2013) and Messier, Puettmann, & Coates (2013b) explored in more detail how complexity science can be used as guidance for forest restoration and management activities, emphasizing practical and theoretical aspects, respectively. Rather than focusing on desirable stand or landscape structures or on past disturbance regimes, the authors suggest that restoration and maintenance of characteristics of complex systems should be restoration goals, as this likely increases the adaptive capacity of ecosystems to a variety of potential future stressors. Tying restoration and management practices directly to these characteristics allows for more concrete evaluations of interventions (see also discussion about measurements below). It provides more specific insights as to which aspects of complex systems are already accounted for with our current practices and how restoration and management practices may need to be modified to accommodate the remaining characteristics. Cornett and White (2013) highlight examples from the Lake States that show how their restoration activities can be viewed in terms of nested scales, self-organization, legacies, and adaptation. In contrast, Messier et al. (2013b) provide a conceptual overview of several silvicultural approaches and how they relate to specific characteristics of complex systems. A more detailed example of such an evaluation for close-to-nature forestry that can be helpful for restoration efforts is provided by Bauhus, Puettmann, and Kuehne (2013). The general conclusion appears to be that selected characteristics are already addressed in particular forestry operations, such as an emphasis on species and tree size diversity at small spatial scales, and on memory in close-to-nature forestry. In contrast, other aspects—such as uncertainty, self-organization, and adaptation—have received less attention. Furthermore, the emphasis of close-to-nature forestry on stability (in terms of stand structures and composition) appears to work counter to the goal to increase adaptive capacity of ecosystems (Bauhus et al., 2013; Messier et al., 2013b). The analysis also shows that practical experiences associated with selected management approaches will be quite helpful when starting to implement restoration treatments that are specifically designed to address selected characteristics of complex systems.

More detailed quantitative assessments of management practices in terms of their impact on adaptive capacity of ecosystems are in progress. For example, in experiments investigating the spatial scales of factors influencing tree regeneration (Dodson et al., in press), results support the notion that interactions across a variety of scales were important in understanding the sources of variability. Germination was mostly influenced by local, small-scale conditions, including understory vegetation. Sapling growth appeared to be more influenced by overstory trees at neighborhood scales. Species composition of tree regeneration was influenced by species makeup of overstories at larger, but within-stand scales. Lastly, the dominance of species—e.g., in our study sites, whether western hemlock or Douglas-fir was the dominant regenerating species—appeared to be a function of landscape characteristics, including climate and soils (Dodson et al., in press). Thus, emphasizing cross-scale interactions provided new insights into issues that were previously mostly assessed with studies that focused on statistical differences among treatments, but couldn't explain high within-treatment variability (Kuehne & Puettmann, 2008; Urgenson, Halpern, & Anderson, 2012). Using a similar approach, other efforts highlight how assessments of management practices in terms of ecological benefits and economic cost or income are directly influenced by spatial and time scales used in the assessments (Puettmann & Tappeiner, 2014). Switching scales—e.g., from the stand scale to individual trees—can lead to different results and thus suggest different restoration treatments. For example, replanting small patches with seedling mortality may be cost effective, if assessed at the stand scale. In contrast, at the scale of individual trees the additional costs of replanting may not be justified; especially if these younger, replanted seedlings have a competitive disadvantage compared to previously planted seedlings and thus are removed in precommercial or early thinning entries before they reach economic maturity (Puettmann & Tappeiner, 2014).

In a separate study, Neill and Puettmann (2013) applied the concepts of diversity and redundancy (as characteristics of complex systems) in investigating the capacity of ecosystems to provide a selected set of ecosystem goods and services in a changing climate. We used a trait-based approach, separating how thinning influences species with selected traits that are either characteristic of how plants respond to changes (response traits) or how plants contribute to ecosystem functions (effect traits; Elmqvist et al., 2003). This work is a first quantification of adaptive capacity in the context of forest management—i.e., how ecosystem functions will fair after perturbations and how management practices can influence this. The results suggest that thinning young, even-aged stands increases the probability that selected wildlife habitat features (e.g., production of berries and palatable foliage, insect pollination) are maintained under climate change conditions (e.g., increased temperature, droughts, and fires). The increase in adaptive capacity appears to be driven either by invading (but not necessarily exotic) species and by compensation of preexisting "minor" species (Neill & Puettmann, 2013). This analytical approach also allows for an economic assessment of the trade-offs in terms of stand density and growth with increasing adaptive capacity. Theoretical considerations (Levins, 1968) suggest a negative relationship between management to most efficiently achieve ownership

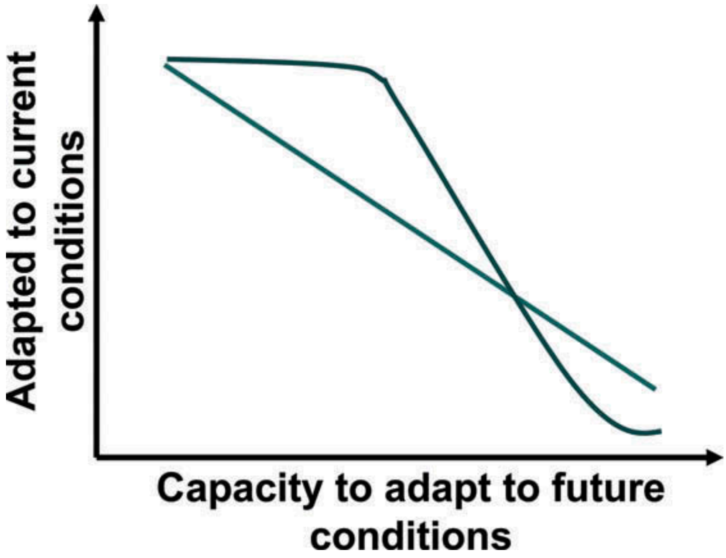

FIGURE 3 Conceptual relationship (linear and threshold) between ecosystems being adapted to current conditions (i.e., managed for efficient realization of ownership goals in a predictable biological and social environment) and the capacity of ecosystems to adapt to future conditions (i.e., the ability of ecosystems to respond to "surprises"). The exact relationship is likely to vary depending on variables and scales used in the analysis.

objectives assuming a highly predictable future (adapted to current conditions) and the ability of ecosystems to respond to "surprises" (capacity to adapt to future conditions; Figure 3). The exact relationship is not known and likely to vary with measures and scales. In conjunction with other investigations into trade-offs—e.g., among carbon storage and understory species diversity (Burton, Ares, Olson, & Puettmann, 2013)—such studies provide insights into how multiple objectives (including increasing adaptive capacity) can be addressed simultaneously (Ammer & Puettmann, 2009)—e.g., using the framework developed by Bradford and D'Amato (2012).

CHALLENGES

Numerous challenges have to be overcome to establish complexity science as a scientific basis that can replace or contribute to the efficiency paradigm as a basis for forest restoration and management activities (Messier et al., 2013a). For one, we acknowledge that restoration activities have to be viewed in a social-ecological context (Folke et al., 2002; Chapin et al., 2009; Levin et al., 2013), but until now our work has focused on ecosystems (reflecting our expertise). Large-scale implementation of managing forests as complex systems will only be possible if we can quantify the trade-offs in social, economic, and ecological terms that occur when shifting management focus from achieving current management objectives most efficiently to a focus that emphasizes the maintenance or increase of adaptive capacity (i.e., we need to populate Figure 3 with variables, units, and specific relationships for a variety of settings). A second challenge stems directly from our limited ability to deal with cross-scale interactions. For example, understanding how ecosystems adapt to changing conditions requires detailed knowledge about modifications that act at various organizational levels in ecosystems and—more importantly—how these levels interact (Table 1). Third, current approaches to quantify how close ecosystems are to tipping points using temporal (Scheffer et al., 2009) and spatial measures (Carpenter, 2013; Dai, Korolev, & Gore, 2013) need to be tested and modified to become operational for forest systems. Another major challenge for restoration is to more formally acknowledge and deal with the uncertainty inherent in complex systems. New approaches to planning, such as scenario analysis (Biggs, Carpenter, & Brock, 2009), appear to provide opportunities to address uncertainty in restoration efforts. The fifth and maybe most important point in linking complexity science to restoration is based on P. Drucker's quote, "What gets measured gets managed." While several measures have been suggested as an indicator of complexity (Parrott, 2010), providing a simple measure of adaptive capacity of ecosystems is challenging, maybe even impossible. As an alternative, we have proposed focusing quantification efforts on characteristics of complex systems rather than an individual complexity metrics. For example, heterogeneity can be quantified in various dimensions with some dimensions providing information about adaptive capacity. The work described above to assess how thinning impacts the likelihood that selected wildlife habitat features are maintained under climate change by Neill and Puettmann (2013) is a first attempt, and example,

TABLE 1 Examples of the Ability for Ecosystems Modification at Various Organizational Levels (Modified from Conrad, 1983)

Organizational level	Variable	Adaptability process
Ecosystem	Species composition	Migration, extinction, speciation
	Food web structure	Different routes and rates of energy and matter movement
Population	Number of organisms	Culturability—e.g., flexibility in reproduction rates, social structures, and relationships
	Spatial location of organisms	Social plasticity, movement
Organism	Number of organs, relative position of organisms	Developmental plasticity (e.g., leaf area, size, root/shoot ratio)
		Physiological plasticity, behavioral plasticity
Genome	DNA sequence	Gene pool diversity

The variables are examples of properties that can be measured and quantified. Adaptability processes are those mechanisms by which modifications may occur. It is important to note that these organizational levels are linked and any modification at one level is likely to influence other levels.

of how to quantify one aspect of adaptive capacity. This example also shows that embracing complexity science can provide new information from current data sets and provide a context for assessment of current theories. For example, complexity science stresses the importance of investigating the diversity-stability hypothesis at multiple spatial, temporal, and organizational scales, including their interactions; which has received limited attention so far. Just as highlighted above for the "reputation" of boreal forests, the new "lens" can provide an impulse to research programs that will be helpful when restoring and managing forests for a variable and uncertain future.

In summary, our work suggests that complexity science can provide a new scientific framework for forest restoration efforts. Viewing forests as complex systems has the potential to increase our understanding of how ecosystems respond to perturbations and provide the basis to develop and evaluate restoration tools that increase the adaptive capacity of ecosystems—i.e., allowing ecosystems to adapt to new conditions while at the same time providing desired ecosystem goods and services. However, major challenges remain before such concepts can be operationally implemented in restoration efforts—including the integration of social and economic aspects, development of tools that account for cross-scale interactions, managing uncertainty, and developing quantitative measures that can be used as management targets or benchmarks.

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