8-15-2006

Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S.

Lisa A. Schulte
Iowa State University, lschulte@iastate.edu

Robert J. Mitchell
Joseph W. Jones Ecological Research Center at Ichauway

Malcolm L. Hunter Jr.
University of Maine

Jerry F. Franklin
University of Washington

R. Kevin McIntyre
Joseph W. Jones Ecological Research Center at Ichauway

See next page for additional authors

Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S.

Abstract

While much has been written describing biodiversity, its global decline, and the need for action, the scientific underpinnings guiding conservation practice have received little attention. We surveyed 10 large-scale forest management plans in the U.S. to establish which ecological concepts are commonly used to guide forest biodiversity conservation and evaluate the relative importance of these concepts in processes related to forest stewardship. We then reviewed the scientific literature to assess the degree to which these concepts are founded in antecedent ecological theory, the extent to which they have been tested, and the limits of those tests. We found that the concepts of filters (fine, meso, and coarse), reserves, matrix management, hotspots, emulating natural disturbances, diversity begets diversity, patchworks, networks, and gradients are extensively employed in the forest planning efforts we surveyed. While most of these concepts received high utility scores, coarse filter was most commonly used, closely followed by matrix management and fine filter. A survey of the literature review suggests that all concepts have both direct and indirect relationships with foundational ecological theories, such as niches, natural selection, and island biogeography. All concepts also have some empirical support based on field tests and most have received some testing in an experimental framework. Yet, experimental tests of the concepts are far from comprehensive as, among other reasons: (1) many species are yet unknown, (2) many species are difficult to measure, (3) the occurrence of taxa that are often measured do not correspond well with the occurrence of those less frequently measured, and (4) although site conditions may be replicated, the historical and landscape contexts of each test are unique. Although we document wide use of these concepts, significant constraints hinder further incorporation into forest stewardship. Predominant among these is a lack of empirical support at the spatial and temporal scales over which forest management is implemented. Practical ways to advance conservation concepts include implementing effective, efficient monitoring protocols and establishing experimental tests in an operational context. Constructive bridges must be built between science and practitioner communities to realize these goals.

Keywords

conservation biology, forest planning, forest management, reserves, matrix management, operational experiments

Disciplines

Biodiversity | Forest Biology | Natural Resources Management and Policy

Comments

This article is from *Forest Ecology and Management* 232, no. 1–3 (2006): 1–11, doi:10.1016/j.foreco.2006.05.009.

Authors
Lisa A. Schulte, Robert J. Mitchell, Malcolm L. Hunter Jr., Jerry F. Franklin, R. Kevin McIntyre, and Brian J. Palik

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Forest Ecology and Management 232 (2006) 1–11

Forest Ecology and Management

www.elsevier.com/locate/foreco

Review

Evaluating the conceptual tools for forest biodiversity conservation and their implementation in the U.S.

Lisa A. Schulte [a,*], Robert J. Mitchell [b], Malcolm L. Hunter Jr. [c], Jerry F. Franklin [d], R. Kevin McIntyre [b], Brian J. Palik [e]

[a] *Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II, Ames, IA 50011-3221, USA*
[b] *Joseph W. Jones Ecological Research Center at Ichauway, Route 2, Box 2324, Newton, GA 39870-9651, USA*
[c] *Department of Wildlife Ecology, University of Maine, Orono, ME 04469-0001, USA*
[d] *College of Forest Resources, University of Washington, P.O. Box 352100, 228 Anderson Hall, Seattle, WA 98195-2100, USA*
[e] *U.S. Department of Agriculture Forest Service North Central Research Station, 1831 Highway 169 E., Grand Rapids, MN 55744-3399, USA*

Received 11 January 2006; received in revised form 5 April 2006; accepted 1 May 2006

Abstract

While much has been written describing biodiversity, its global decline, and the need for action, the scientific underpinnings guiding conservation practice have received little attention. We surveyed 10 large-scale forest management plans in the U.S. to establish which ecological concepts are commonly used to guide forest biodiversity conservation and evaluate the relative importance of these concepts in processes related to forest stewardship. We then reviewed the scientific literature to assess the degree to which these concepts are founded in antecedent ecological theory, the extent to which they have been tested, and the limits of those tests. We found that the concepts of filters (fine, meso, and coarse), reserves, matrix management, hotspots, emulating natural disturbances, diversity begets diversity, patchworks, networks, and gradients are extensively employed in the forest planning efforts we surveyed. While most of these concepts received high utility scores, coarse filter was most commonly used, closely followed by matrix management and fine filter. A survey of the literature review suggests that all concepts have both direct and indirect relationships with foundational ecological theories, such as niches, natural selection, and island biogeography. All concepts also have some empirical support based on field tests and most have received some testing in an experimental framework. Yet, experimental tests of the concepts are far from comprehensive as, among other reasons: (1) many species are yet unknown, (2) many species are difficult to measure, (3) the occurrence of taxa that are often measured do not correspond well with the occurrence of those less frequently measured, and (4) although site conditions may be replicated, the historical and landscape contexts of each test are unique. Although we document wide use of these concepts, significant constraints hinder further incorporation into forest stewardship. Predominant among these is a lack of empirical support at the spatial and temporal scales over which forest management is implemented. Practical ways to advance conservation concepts include implementing effective, efficient monitoring protocols and establishing experimental tests in an operational context. Constructive bridges must be built between science and practitioner communities to realize these goals.

Keywords: Conservation biology; Forest planning; Forest management; Reserves; Matrix management; Operational experiments

---

Contents

---

* Corresponding author. Tel.: +1 515 294 7339; fax: +1 515 294 2995.
E-mail address: lschulte@iastate.edu (L.A. Schulte).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2006.05.009

1. Introduction

Because forest planners and managers must often make decisions with less than complete information, assumptions founded on concepts are often substituted for empirical data as a basis for action. Although a growing body of literature is being developed to assist the transition between scientific theory and its application (Shrader-Frachette and McCoy, 1993; Noss and Cooperrider, 1994; Czech and Krausman, 2001; Lindenmayer and Franklin, 2002; Groves, 2003), substantial concern remains as to whether the conceptual basis for biodiversity conservation has received sufficient testing to be recommended for wide application (Simberloff, 1995, 2001). In particular, few efforts have specifically evaluated the practical utility and scientific support of the suite of conceptual tools available for biodiversity conservation (Doak and Mills, 1994; Prendergast et al., 1999). We begin to fill this knowledge gap by asking: what conservation concepts are commonly being used in forest management planning efforts? To what extent are they founded on ecological theory? What is the empirical support for these concepts? And, how can they be advanced in both strength and utility?

Several in-depth works have been published that address the development of scientific theory in ecology and conservation biology (Peters, 1999; Shrader-Frachette and McCoy, 1993; Pickett et al., 1994; Ford, 2000). Our goal is to evaluate scientific concepts that guide the conservation of forest biodiversity in forest planning and management settings. We achieve this goal by evaluating 10 large-scale forest management plans and through literature synthesis. Although a multitude of forest plans could be considered, we limited our analysis to those from the continental United States. The plans we reviewed represent a variety of geographic regions, ecological systems, scales, and organizations involved in forest stewardship. We then reviewed the literature to evaluate the degree to which these concepts are founded in antecedent scientific theory, the degree to which they have been tested, and the limits of those tests. Based on our analysis, we provide recommendations for how future efforts may enhance both conservation science and its practice.

2. Conservation concepts

Conservation concepts are important to forest scientists and managers in that they provide: (1) a scientific basis for predicting species response to conditions for which no data exist (e.g., locations, scales, management actions), including projecting to the future (Miller et al., 2004), (2) benchmarks for evaluating the outcome of management actions (MacNally et al., 2002), and (3) a creative framework for developing alternative management actions (Palik et al., 1997). We identified 11 concepts that we expected to have some relevance to forest planning and management, including reserves, matrix management, coarse filter, mesofilter, fine filter, hotspots, diversity begets diversity, emulating natural disturbances, patchworks, networks, and gradients. We chose not to include ecosystem management because of its breadth, which includes socioeconomic perspectives, and its overlap with several of the other concepts. We additionally solicited conservation practitioners for other relevant concepts through interviews; redundancy, population viability, and flagship species were mentioned by single practitioners. Though a standard conservation tool, we chose not to address population viability analysis because we considered it a component of the fine filter approach. Similarly, flagship species was not included because it is founded in social dimensions of natural resource management rather than ecological dimensions. For these reason and because most interviewed practitioners indicated that our list was comprehensive for the concepts they utilized, we did not expand our analysis beyond the 11 initial concepts.

Our definitions and descriptions for these concepts follow. We also provide key references that discuss the concepts more fully, although they are not necessarily the originators of the concepts:

- *Coarse filter*. Coarse filter assesses the conservation value of broad-scale ecosystems and landscapes throughout a bioregion (Noss, 1987; Hunter, 1991). The concept suggests that systematic protection of representative ecosystems should conserve the vast majority of species within that bioregion without the necessity of considering each species individually.
- *Mesofilter*. Mesofilter lies conceptually between coarse filter and fine filter; its core idea is that by protecting key habitat elements that have exceptional benefit to species but are too small to set aside in separate reserves, many species will be protected without the necessity of considering them individually (Hunter, 2005). Examples of the mesofilter concept in action include conserving logs and snags, riparian zones, vernal pools, seeps, rock outcrops, and hedgerows.
- *Fine filter*. Fine filter conservation deals with individual species directly that are assumed to be inadequately protected by coarse filter conservation, typically uncommon species or those jeopardized by over-exploitation (Noss, 1987). Species conservation is achieved by either protecting populations from over-harvest or other direct, negative impact, or by conserving their habitat.
- *Hotspots*. With hotspots, preservation is achieved by identifying and protecting locations of high species richness, especially of endemic species, that are threatened by human

development (Myers, 1988). Because of the criteria of high endemism, hotspots are frequently considered at global scales with regions such as the Caribbean, Madagascar, and New Zealand strongly considered, but the concept can be applied to finer scales.

- *Reserves*. Reserves are areas in which the primary management objective is to fully protect existing ecosystems and populations from direct human modification (Noss and Cooperrider, 1994). The reserve concept focuses on how to design and manage a system of reserves that will maintain native biota and natural ecosystem processes.
- *Matrix management*. Matrix-based conservation asserts that biodiversity and ecological function can be sustained in working landscapes, though attention must be given to maintaining habitat across the full range of spatial scales, from ‘‘logs to landscapes’’ (Lindenmayer and Franklin, 2002). Reserves are an important part of matrix management, but equal emphasis is placed on managing non-reserve areas in which reserves are embedded (the ‘‘matrix’’), by sustaining important ecosystem structures, processes, and patterns.
- *Diversity begets diversity*. This concept poses that a diversity of environmental conditions will provide habitat for a diverse array of species (Harris, 1984; Hunter, 1990); complex and heterogeneous environments are sought at all spatial scales. For example, a landscape covered by a mosaic of young forests and old forests, conifer forests and deciduous forests, is expected to provide habitat for far more species than any one of these would alone.
- *Emulating natural disturbances*. The fundamental idea behind this concept is that species have evolved adaptations to natural disturbance regimes, and will be better able to cope with human-induced disturbances if they closely resemble natural ones (Hunter, 1990; Landres et al., 1999). Designing forest management approaches to better resemble the outcomes of natural disturbances in terms of structure, composition, and spatial pattern is an example of emulating natural disturbances in practice (Perera et al., 2004).
- *Patchworks*. From the patchwork perspective, landscapes are arrangements of distinct, interacting patches (Forman, 1995). The concept suggests that the size and distribution of patches are strong predictors of biodiversity (i.e., patches can be optimally arranged for biodiversity conservation).
- *Networks*. Using networks, landscapes are viewed as at least partially consisting of highly interconnected linear features (Forman, 1995), and the network properties of connectivity and hierarchy are useful predictors of biodiversity. Networks are relevant when considering the movement of animals or materials, and have been particularly useful for understanding riverine and riparian systems.
- *Gradients*. This concept combines facets of patchworks and networks, though no discrete patch types need be assigned; rather, components are viewed as continuously varying in space, grading between absent and abundant (Gleason, 1926). Although the gradient concept is scaleless, it is most often applied at landscape scales or broader in the form of ecoregion classifications (e.g., Bailey, 1987), and it suggests that maintaining representative ecosystems along multi-dimensional ecological gradients will conserve biodiversity.

Depending on how they are used, these concepts can represent complements or alternatives to one another. Based on common underpinnings and application in forest planning and management, we grouped them as follows (Fig. 1):

- *Focal scale*. The filters describe the level of biological organization at which conservation action is focused.

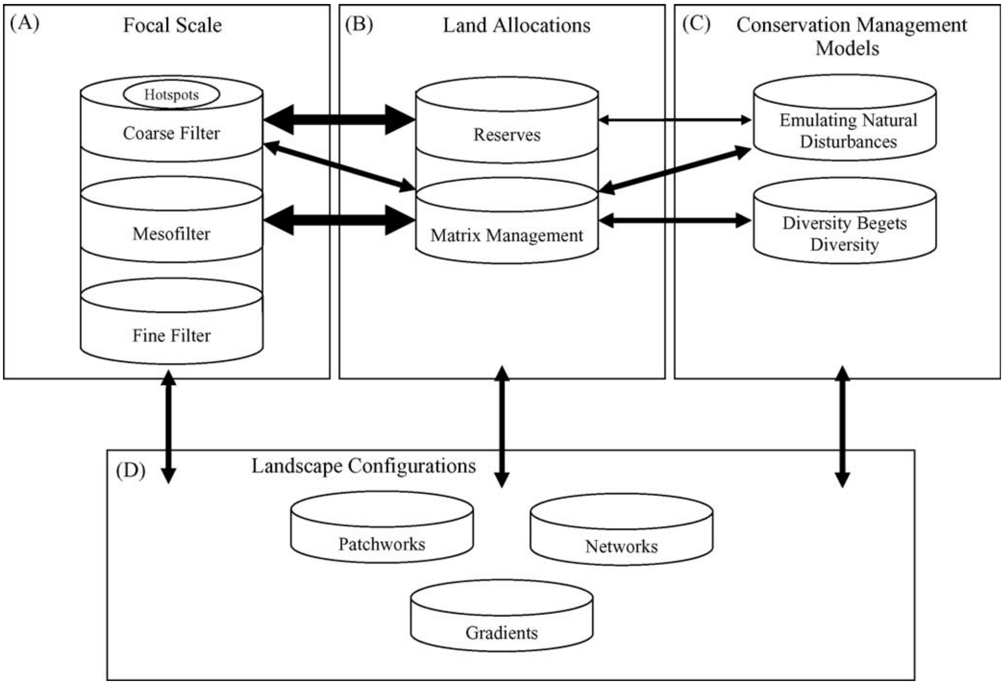

Fig. 1. Organizing framework relating conservation concepts; arrow thickness corresponds to the level of conceptual relatedness among concepts in different groups.

The selection and design of conservation areas can be based on ecosystems (coarse filters), ecosystem elements (mesofilters), species (fine filters), and/or areas of high species richness (hotspots). Hotspots is often seen as an alternative to coarse filter because it focuses on areas of high species richness rather than those that represent different ecosystems.

- *Land allocation*. Biodiversity conservation can be achieved through specific land allocations (reserves) and/or by managing for biodiversity throughout the landscape (matrix management). Reserve- and matrix-based approaches can be seen as alternatives if the forest management emphasis differs dramatically in and outside of reserves.
- *Conservation management*. Biodiversity management can be based on maximizing overall habitat diversity (diversity begets diversity) and/or by maintaining conditions based on natural models (emulating natural disturbances).
- *Landscape configurations*. Patchworks, networks, and gradients are fundamental constructs regarding the structure and function of landscapes and, consequently, basic concepts for approaching forest conservation over landscape scales (Lindenmayer and Franklin, 2002). Although conceptualized as alternatives, patchworks and networks can especially be used in combination to assess the extent and connectivity of habitat patches.

Note that some of these concepts can be construed as strategies or even goals under certain circumstances. Fundamentally, however, they each represent a set of ideas that can both inform management for biodiversity and be informed by science.

3. Conservation concepts in practice

The 10 forest management planning efforts we surveyed included three federal (Chequamegon-Nicolet National Forest, Northwest Forest Plan, Shawnee National Forest) and two state level plans (Florida Forever, Minnesota Sustainable Forest Resource Management Plan), as well as four from private organizations (Anderson-Tully Company, The Nature Conservancy [TNC] Blue Ridge, TNC St. John River, and the Greater Yellowstone Coalition) and one involving multiple planning entities (South Carolina ACE Basin; Supplementary Appendix A). All have a strong focus on forest management and together represent geographic locations across the United States, spatial scales, and organizations involved in forest stewardship. Our goal in choosing these plans was not to achieve replication but rather to survey the use of the conservation concepts across a range of forest types, socioeconomic settings, and conservation objectives.

We assessed use of the conservation concepts by reviewing written documents and conducting in-depth interviews of key practitioners associated with the plans. Interviewees included people involved in plan design and the initial phase of plan implementation. Between one and three people were interviewed independently per plan, depending on the extent of area covered by and the complexity of the plan. For example, one person was interviewed regarding TNC's Blue Ridge Plan, as one ownership and 15,000 ha were considered. In contrast, three people were interviewed regarding the Northwest Forest Plan given that the plan affected 19 National Forests, several federal agencies, and a total of 9.9 million ha (Supplementary Appendix A). We used a standardized set of 12 questions addressing the relative importance of conservation concepts in building the plans (Supplementary Appendix B). The interviews contained a combination of yes/no, rank, and open-ended questions. Although a combination of quantitative and qualitative data were collected, we used a qualitative analytical framework since the data were derived from a total of 16 interviews.

The case studies document that conservation concepts play a major role in current forest planning and management. Six of the 11 concepts were most frequently ranked as ‘‘highly considered’’ by survey participants and 10 of the 11 received at least ‘‘moderate consideration’’ (Table 1). Only the gradient approach received ‘‘little to no consideration’’, and was consistently listed as difficult to implement. The coarse filter strategy emerged as most useful when we asked interviewees to rank the importance of the concepts relative to each other (Table 2), and was cited as robust, cost-effective, and easy to implement. Matrix management and fine filter were close

Table 1
The extent of consideration given to each conservation concept in formulating forest conservation plans (1, highly considered and 5, little to no consideration)

Conservation plan	Coarse filter	Mesofilter	Fine filter	Hotspots	Reserves	Matrix management	Emulating natural disturbances	Diversity begets diversity	Patchworks	Networks	Gradients
ACE Basin[a]	1	5	3	5	3	2	4	1	4	3	3
Anderson-Tully	3	2	1	1	5	1	1	3	2	1	3
Blue Ridge	1	1	4	1	1	1	2	2	5	5	5
Chequamegon-Nicolet[a]	1	3	3	4	1	1	2	5	3	4	4
Florida Forever[a]	1	5	1	4	1	2	3	2	4	3	5
Greater Yellowstone	1	1	1	3	2	4	3	2	2	1	5
Minnesota SFRMP[a]	2	4	2	3	4	2	3	4	4	4	5
Northwest Forest[b]	1	1	1	4	1	1	3	4	2	3	4
Shawnee	1	1	1	1	2	1	2	4	1	1	1
St. John River	3	1	1	5	2	1	1	3	2	3	5

[a] As a summary, the value provided is the mean response of two interviewees rounded to the nearest whole number.

[b] As a summary, the value provided is the mean response of three interviewees rounded to the nearest whole number.

Table 2
Rank order of conservation concept in terms of extent considered in forest conservation plan (1, greatest consideration and 11, least considered)

Conservation plan	Coarse filter	Mesofilter	Fine filter	Hotspots	Reserves	Matrix management	Emulating natural disturbances	Diversity begets diversity	Patchworks	Networks	Gradients
ACE Basin[a]	4	11	7	10	5	3	9	1	8	2	6
Anderson-Tully	8	4	7	9	11	1	2	6	5	3	10
Blue Ridge	2	4	8	3	1	5	6	7	9	10	11
Chequamegon-Nicolet[a]	2	5	4	11	6	3	1	10	8	9	7
Florida Forever[a]	1	11	2	7	3	6	4	5	8	9	10
Greater Yellowstone	1	3	2	8	7	9	10	6	5	4	11
Minnesota SFRMP[a]	2	7	3	4	8	1	5	10	6	9	11
Northwest Forest[b]	1	5	3	11	2	4	9	10	7	6	8
Shawnee	1	3	2	5	9	4	6	10	7	8	11
St. John River	1	3	7	10	4	5	2	11	9	6	8

[a] As a summary, the value provided is the rank of the mean response of two interviewees.
[b] As a summary, the value provided is the rank of the mean response of three interviewees.

Table 3
Relationship between conservation concepts and scientific theories, mostly ecological (D, direct or relatively strong relationship; I, indirect or relatively week relationship; blank, little to no relationship)

Foundational theory	Reference	Coarse filter	Mesofilter	Fine filter	Hotspots	Reserve	Matrix management	Emulating natural disturbances	Diversity begets diversity	Patchwork	Network	Gradient
Niche	Hutchinson (1957)	D	D	D	D	D	D	D	D	D	D	D
Natural selection	Darwin (1859)	I	I	D	I	I	I	D	I	I	I	I
Community assembly	Diamond (1975b)	D	I		D		I	I	I	D	I	I
Productivity/ diversity	Huston (1994)				D			I				
Island biogeography	MacArthur and Wilson (1967)	D	I		I	D	I	D	I	D	D	
Metapopulation	Hanski and Gilpin (1991)			D		D				D	D	
Population regulation	Andrewartha and Birch (1954)			D		D						
Limiting factors	Liebig (1840)		I	D		D	I	D	I			
Disturbance	Pickett and White (1985)	D	I			D	I	D	D	D		D
Stability/ diversity	May (2001)				D			I	D			
Ecosystem development	Odum (1969)	I	I		D		I	I	D			
Succession	Clements (1916)	I	I	I			I	D	I	I		I
Continuum	Gleason (1926)		D				D		I			D
Boundary	Cadenasso et al. (2003)		I			D	I	D	I	D	D	D
Hierarchy	Allen and Starr (1982)	D	D	D							D	
Chaos	May (1976)	D	I				I	I	D	D		

seconds. Matrix management was seen by participants from government agencies as consistent with their mandate of multiple use—it provides the opportunity and the guidelines to manage for both timber and biodiversity conservation. As expected, the goals of the sponsoring organization heavily shape the planning process and content of the plan. Practitioners working for the National Forest System stated that their plans would have looked much different if conservation of biodiversity had been the primary goal, rather than one of many, often conflicting goals.

Conservation concepts were seen by practitioners as highly complementary, and were often used in combination to form conservation strategies (Fig. 1). For example, the three filters and the matrix approach were used together by the Chequamegon-Nicolet and Shawnee National Forests, Minnesota State Forests, and TNC St. John River. Initial biodiversity assessments were commonly performed using a coarse filter approach, a fine filter was later employed to determine remaining gaps, and this information was combined to design matrix management; mesofilters were a mainstay in applying conservation to the matrix. In comparison, the Northwest Forest Plan and Florida Forever were much more focused on reserves.

Emulating natural disturbances was listed as a dominant concept underlying the planning process for Anderson-Tully Company, Chequamegon-Nicolet National Forest, and TNC St. John River. Given the heavy influence of human activity on all remaining forests within these regions, a goal was to move ecosystems toward a composition, structure, and function more characteristic of the pre-Euro-American era, with strong attention to the scales over which these aspects were variable. Comparatively, diversity begets diversity received somewhat less support (Table 2), though it may be the most practical one in places where humans have changed the landscape so profoundly that it is difficult to know what the characteristics of a system driven purely by natural factors would be.

Although the reserves concept has been and will continue to be a mainstay for forest conservation programs, interviewees representing four plans noted that this concept became less important during plan development. Reserves were politically difficult to incorporate on the Chequamegon-Nicolet National Forest and Minnesota State Forests, and conceptual development of alternative approaches was also cited as a major reason for deemphasising reserves. The shift toward designing working forests that have ecological integrity (Hunter, 1990; Swanson and Franklin, 1992; Kohm and Franklin, 1997), especially through matrix management and emulating natural disturbances, was seen as a positive step by all practitioners; however, it was noted that lack of scientific support in some areas related to these concepts does make them difficult to incorporate, even if the basic ideas seem ecologically plausible.

Most individuals expressed satisfaction with the extent to which they were able to incorporate biodiversity conservation in forest planning, noting that the forest management plans of today look much different than those of a decade or more ago. A broader diversity of concepts available to draw upon, increasing scientific support, and greater awareness of conservation in both public agencies and private forest industry have allowed this transition. All practitioners, however, suggested that the concepts available were ample for their purposes in comparison to research proving their efficacy. Site-specific information on species response to management practices was seen as a particularly salient need.

4. Scientific foundations

We partially evaluated the scientific support for the 11 conservation concepts by tracing their intellectual foundations. We did not limit ourselves to consideration only of theories that have contemporary support. In fact, historical antecedents, including theories no longer in favor, were of particular interest, since an idea that is derived from long-established and tested theory may have more validity than an idea that has arisen *de novo* (Pickett et al., 1994). We identified 16 theories, primarily ecological, that most closely relate to the conservation concepts under consideration (Table 3). Although the list we identified is not comprehensive (e.g., we eliminated genetic drift because it was related to only a few of our concepts and systems theory because of its weak, generic relationships), it likely captures most of the theories with a strong relationship to forest biodiversity conservation. We also designated the relationship between each conservation concept and ecological theory as a ‘‘relatively strong relationship’’, ‘‘relatively weak relationship’’, or ‘‘little to no relationship’’ based on our knowledge and best judgment.

We found that all of the conservation concepts are tied to a large set of ecological theories in diverse ways (Table 3). For example, island biogeography has a strong and direct link to reserves (indeed, reserves is essentially applied island biogeography theory per Diamond, 1975a), while its relationship to matrix management is less direct (focusing on connectivity), and its relationship to fine filters is extremely weak (because fine filters are a species-centric concept whereas island biogeography focuses on communities). Metapopulation theory builds on the concept of habitat islands but is focused on specific species; hence, its direct relationship to both reserves and fine filters. As metapopulation theory predicts species persistence according to the extent and connectivity of habitat (Hanski and Gilpin, 1991), it is also directly related to patchworks and networks.

This analysis suggests that some ecological theories (e.g., niche, island biogeography, disturbance) have been more influential in the development of conservation concepts than others (Table 3). While an in-depth review of the intellectual parentage of each conservation concept is beyond the scope of this paper, it would be a worthwhile exercise for understanding the transfer of scientific theory to conservation practice and for teaching students about the scientific foundations of conservation. Shrader-Frachette and McCoy (1993) provide an example of such an analysis for island biogeography theory. Bestelmeyer et al. (2003) discuss species diversity theory as it relates to land management in general.

5. Empirical support

To further evaluate the extent of scientific support for the conservation concepts, we conducted a literature review using the Web of Science scientific literature search engine (Thomson, 2005). We generated a list of 1196 potentially related papers using the search terms ‘‘biodiversity’’ and ‘‘experiment*’’, and further supplemented this list with our knowledge of on-going studies. We concentrated on manipulative experiments because of the high level of rigor, in the form of control and inference, usually associated with this form of investigation (Eberhardt and Thomas, 1991; Ford, 2000). Because the concepts themselves are generalized and not stated as testable hypotheses, we articulated key researchable questions related to each of the concepts to evaluate the literature (Table 4). From the initially generated list, 83 papers involved empirical field tests that related to the conservation concepts we identified; of these, 44 specifically related to forest systems and 27 related to conservation in a managed forest context (Supplementary Appendix C). Many of the remaining 1113 papers included empirical field tests but did not bring any evidence to bear on key questions we articulated for each concept (Table 4); hence, for example, studies addressing the function of biodiversity, biodiversity diversity–productivity relationships, or biodiversity response to threats such as invasive species or climate change were not considered.

We found that all concepts considered have at least some empirical support, though in several cases the support has not been developed within an experimental framework (Table 4). Of all conservation concepts reviewed, reserves and networks have received the most rigorous and comprehensive attention, based on experimental testing and the number of taxa considered (Table 4). For example, an elegant test of corridors (i.e., networks) yielding much knowledge relevant to conservation is currently underway at the Savannah River Site National Environmental Research Park in South Carolina (Haddad et al., 2003). Haddad et al. (2003) hypothesize that networks increase species movement between habitat fragments. Their large-scale, replicated experiment contains patches, connected or not, of early successional habitat within a pine forest matrix. The movements of bird-dispersed plants, butterflies, and small mammals are measured as a response. Of the 83 papers with empirical data that we reviewed, 12% and 14% related respectively to reserves and networks (Supplementary Appendix C). Mesofilters and matrix management may soon acquire strong empirical underpinnings, especially in regard to the biodiversity implications of forest management practices, given the series of experiments recently implemented in Pacific Northwestern forests (Monserud, 2002; Supplementary Appendix C). Support for the fine filter approach comes from recent evaluations of species recovery plans (Boersma et al., 2001; Campbell et al., 2002).

Although we found that many sophisticated and elegant experiments are conceived, no existing tests comprehensively evaluate biodiversity conservation and few tests overall are executed at scales over which forest management is applied (Table 4; Supplementary Appendix C), especially landscape scales (but see Schmiegelow et al., 1997). Reasons for lack of comprehensive experimental tests relevant to forest management are multifold and include the following:

- Much of the biodiversity of the planet has yet to be described and/or is difficult to measure (e.g., bacteria, mycorrhizal fungi, arthropods, and the genetic level of biodiversity), and consequently it is almost always ignored (Nee, 2004).
- The occurrence of taxa that are often measured (e.g., plants, mammals, birds) do not correspond well with the occurrence of less frequently measured taxa (e.g., bacteria, arthropods, fungi; Andelman and Fagan, 2000; Noon et al., 2003). Furthermore, different organisms operate at different scales (e.g., what is a corridor for the rodent *Peromyscus polionotus* is not a corridor for the rodent *Sigmodon hispidus*; Haddad et al., 2003). Thus, congruence among taxa is lacking and tests are never inclusive of all organisms.
- The species richness and diversity measures that are often calculated incorporate just one goal of biodiversity conservation—sustaining a diverse array of species. Another key goal, sustaining rare species, is not always consistent in space and time with conserving the greatest species richness (Prendergast et al., 1993; Lennon et al., 2004).
- The historical and landscape context of a place will influence the outcome of any experimental test (Summerville and Crist, 2002; Foster et al., 2003; Luck and Daily, 2003); consequently, a test may only be applicable to the place in which it was conducted (Eberhardt and Thomas, 1991). Replicating by historical or landscape factors, or repeating the same experiment in many different places, would overcome this limitation, but such replication or repetition is difficult and rarely achieved.
- Replication, expense, social justification, long-term support, and carry-through by project participants are all logistical problems that constrain experimental tests (Walters and Holling, 1990). These limitations are great at the stand-level and magnified over landscapes.
- Lastly, multiple conservation concepts are used in concert by practitioners rather than as single approaches (see *Utility* section). Thus, a test of any one concept is not particularly helpful to forest management, but tests of multiple conservation concepts are subject to even greater logistical constraints.

Some of these limitations can be overcome with intervention analyses, descriptive studies, case studies, historical analysis, and/or computer modeling, but each of these methods of inquiry have its own sets of limitations (Eberhardt and Thomas, 1991; Shrader-Frachette and McCoy, 1993). All are constrained by our inability to comprehensively measure biodiversity and the lack of congruence among species.

6. Future directions

Overall, our assessment concurs with Simberloff (2001) in that, ‘‘A plethora of new concepts for managing production forests so as to preserve biodiversity have found their way into

Table 4
Key questions relating to conservation concepts and example studies that provide empirical support; where available, examples derived from forested ecosystems and experiments where multiple taxa were monitored

Concept	Key question, what level of biodiversity conservation can be achieved	Reference	Experimental	Taxonomic group(s)	Ecosystem type	Scale
Coarse filter	By protecting representative ecosystems?	MacNally et al. (2002)	No	Trees, insects and other invertebrates, reptiles, birds, mammals	Box-ironbark forest	Stand
Mesofilter	By creating/maintaining critical habitat elements within a managed matrix?	Monserud (2002)[a]	Yes	Fungi, lichens, bryophytes, vascular plants, invertebrates, fish, amphibians, birds, mammals	Coniferous temperate rainforest	Stand
Fine filter	On a species-by-species basis?	Boersma et al. (2001)	No	Plants, animals, ecosystems	Various	Various
Hotspots	By protecting areas of high species richness?	Raxworthy et al. (2003)	No	Reptiles	Tropical forest	Landscape
Reserves	By reserving forestland from timber extraction?	Bierregaard et al. (2001)[b]	Yes	Fungi, vascular plants, invertebrates, amphibians, reptiles, birds, mammals	Tropical forest	Stand
Matrix management	By reducing the disparity between managed and natural forests?	Monserud (2002)[a]	Yes	Fungi, lichens, bryophytes, vascular plants, invertebrates, fish, amphibians, birds, mammals	Coniferous temperate rainforest	Stand
Emulating natural disturbances	By employing silvicultural practices that emulate natural disturbances?	Waltz and Covington (2004)[b]	Yes	Plants, butterflies	Ponderosa pine forest	Stand
Diversity begets diversity	By maintaining a diversity of forest types and age classes on the landscape?	Sullivan et al. (2000)	No	Plants, small mammals	Douglas-fir and lodgepole pine forest	Stand
Patchworks	By maintaining natural patch sizes and shapes over landscapes?	Rothermel and Semlitsch (2002)	Yes	Amphibians	Forests and old fields	Edge
Networks	By maintaining habitat connectivity over landscapes?	Haddad et al. (2003)[b]	Yes	Plants, butterflies, small mammals	Southern pine forest	Landscape
Gradients	By maintaining natural gradients over landscapes?	Fischer et al. (2004)	No	Reptiles, plants, invertebrates	Grassland and woodlands	Stand to landscape

[a] Paper describes a set of on-going experimental studies testing this hypothesis.

[b] Experiment has produced several papers; see Supplementary material (Appendix C) for full list of queried citations.

management procedures without much testing to make them most effective''. Through this exercise we identified two key areas where the gap between scientific theory and its application may be spanned. First, instituting effective, efficient monitoring of existing forest management activities and implementing experiments in an operational forestry context would supply needed empirical data to support the conceptual foundations of conservation and fulfill the species- and site-specific data needs of practitioners. Yet, the forest planners and managers we interviewed noted that the social constraints they face are often larger than those imposed by lack of science. Thus, our second recommendation is to improve communication among stakeholders, scientists, and managers.

6.1. Recommendation 1: monitoring and operational experiments

Developing quantitative information on biodiversity and ecosystem process responses to human manipulations is a high priority (Palmer et al., 2005). Broad-scale testing of concepts could be achieved in connection with implementation of actual conservation plans. Indeed, the numerous, often large-scale conservation programs underway *should* be generating large amounts of data that *could* be used to test hypotheses according to the case study approach advocated by Shrader-Frachette and McCoy (1993). Such data and tests can be fed back into the decision-making process using an adaptive management framework. Unfortunately, monitoring programs that would provide data of necessary quantity and quality are uncommon and systematic evaluation of such data and feedback into modified management plans are nearly non-existent (Bawa and Menon, 1997; Boersma et al., 2001; Stokstad, 2005). Our interviewees indicated that monitoring programs are often written into forest plans, but break down during the implementation phase. Contributing factors included lack of sufficient and sustained funding, lack of institutional commitment, and technical challenges.

Although sophisticated experiments to test conservation concepts can be designed and have significant academic appeal, more practical tests of the various concepts could be carried out in connection with operational conservation programs. If well-designed, such operational experiments can produce robust data and generalizable results of the type needed to advance ecological theory and conservation practice, respectively (Walters and Holling, 1990). Such experiments are being initiated (e.g., Schmiegelow et al., 1997; Turner et al., 1997; Monserud, 2002; Haddad et al., 2003), but the level and spatial distribution of habitat features necessary to maintain species and processes is largely unknown and poses a serious limitation in developing ecologically based silvicultural prescriptions. For example, what are the implications for biodiversity of maintaining 5, 10, or 20 snags per hectare in a random or a clumped distribution? Two broad areas of research were identified by our interviewees: biotic response to (1) the retention of structural features in harvested stands and landscapes and (2) management actions intended to accelerate or maintain structural complexity.

6.2. Recommendation 2: communication and education

Forest planners and policy makers often need better delivery of existing information as much as new research. Several interviewees noted that the standard channels for distributing research results are not always accessible to managers and pointed out the need for simple, science-based tools that allow assessments of diverse management scenarios. Innovative approaches for continuing education on advances in forest conservation science and its application are sorely needed—delivery of information through journal articles is simply not sufficient (Prendergast et al., 1999; Nadkarni, 2004). Approaches should accommodate a range of practitioners' learning styles, from traditional mechanisms such as workshops, short courses, and demonstration sites to Internet delivery of training programs, interactive tools, and models (e.g., Gustafson, 1998; Hiers et al., 2003; Stoltman et al., 2004). Forest practitioners, especially individuals inclined to be ''early adopters'' and open to innovation, should be included in formulating strategies for information transfer.

More fundamental than technology transfer to practitioners and policy makers is the need to fully incorporate conservation science into undergraduate and graduate natural resources curricula. In recent years, natural resource and forestry programs at a number of major universities have been revised, or new majors developed, with a focus on conservation management; however, an Internet perusal of required courses for a number of these programs suggests that these majors may not always include conservation science in detail. Producing graduates capable of using conservation concepts to inform and guide forest biodiversity management should be a key goal of these programs.

7. Conclusions

The conservation concepts available to forest practitioners are much broader today than 10–15 years ago, and are being widely employed in forest planning and management. These concepts have limited but increasing scientific support, as assessed by our analysis of their theoretical foundations and empirical tests; however, needed information is often lacking at the spatial and temporal scales over which forest management is implemented. Conducting science in an operational forestry context, by both more effectively monitoring existing forest management actions and by implementing operational-scale experiments, would overcome several limitations to stand-to-landscape scale experimentation. Yet, barriers to interaction and knowledge transfer between the research and management communities must first be overcome to bring operational experiments to fruition. Both parties should find ample reward in building an effective bridge between science and its application.

Acknowledgments

We thank the following people who were interviewed with respect to conservation planning: Jim Furnish, Dennis Hardin, Craig Groves, Mike Miller, Jon Nelson, Linda Parker, Mark Robertson, Kurt Rusterholz, Mike Statten, Larry Stritch, Hilary Swain, Fred Swanson, and Barbara Vickery. We also thank Meredith Cornett, Diane Debinski, Jim Furnish, John Gordon, Craig Groves, Dennis Hardin, James MacMahon, Linda Parker, Fiona Schmiegelow, Mike Scott, Fred Swanson, and Bently Wigley for their contribution to a workshop on conservation biology and its practice held at the Joseph W. Jones Ecological Research Center. Input from reviews by Meredith Cornett, Diane Debinski, Ron Pulliam, Hal Salwasser, and Barbara Vickery is scattered liberally throughout this paper. This research was supported by the National Commission on Science for Sustainable Forestry.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2006.05.009.

References

Allen, T.F.H., Starr, T.B., 1982. Hierarchy: Perspectives for Ecological Complexity. University of Chicago Press, Chicago.

Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proc. Natl. Acad. Sci. 97, 5954–5959.

Andrewartha, H.G., Birch, L.C., 1954. The Distribution and Abundance of Animals. University of Chicago Press, Chicago, IL.

Bailey, R.G., 1987. Suggested hierarchy of criteria for multiscale ecosystem mapping. Urban Reg. Plan. 14, 313–319.

Bawa, K.S., Menon, S., 1997. Biodiversity monitoring: the missing ingredients. Trends Ecol. Evol. 12, 42.

Bestelmeyer, B.T., Miller, J.R., Wiens, J.A., 2003. Applying species diversity theory to land management. Ecol. Appl. 13, 1750–1761.

Bierregaard Jr., R.O., Gascon, C., Lovejoy, T.E., Mesquita, R.C.G., 2001. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, CT.

Boersma, P.D., Kareiva, P., Fagan, W.F., Clark, J.A., Hoekstra, J.M., 2001. How good are endangered species recovery plans? BioSci. 51, 643–649.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Jones, C.G., 2003. A framework for a theory of ecological boundaries. BioSci. 53, 750–758.

Campbell, S.P., Clark, J.A., Crampton, L.H., Guerry, A.D., Hatch, L.T., Hosseini, P.R., Lawler, J.J., O'Connor, R.J., 2002. An assessment of monitoring efforts in endangered species recovery plans. Ecol. Appl. 12, 674–681.

Clements, F.E., 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institution of Washington, Washington, DC.

Czech, B., Krausman, P.R., 2001. The Endangered Species Act: History Conservation Biology and Public Policy. Johns Hopkins University Press, Baltimore, MA.

Darwin, C., 1859. On the Origin of Species by Means of Natural Selection or the Preservation of Favored Races in the Struggle for Life. John Murray, London.

Diamond, J.M., 1975a. The island dilemma: lessons of modern biogeographical studies for the design of nature preserves. Biol. Cons. 7, 129–146.

Diamond, J., 1975b. Assembly of species communities. In: Cody, M.L., Diamond, J. (Eds.), Ecology and Evolution of Communities. Harvard Belknap Press of Harvard University Press, Cambridge, MA, p. 342.

Doak, D.F., Mills, L.S., 1994. A useful role for theory in conservation. Ecology 75, 615–626.

Eberhardt, L.L., Thomas, J.M., 1991. Designing environmental field studies. Ecol. Monog. 61, 53–73.

Fischer, J., Lindenmayer, D.B., Cowling, A., 2004. The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. J. Appl. Ecol. 41, 32–44.

Ford, E.D., 2000. Scientific Method for Ecological Research. Cambridge University Press, Cambridge.

Forman, R.T.T., 1995. Land Mosaics: The Ecology of Landscape and Regions. Cambridge University Press, Cambridge.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D., Knapp, A., 2003. The importance of land-use legacies to ecology and conservation. BioSci. 53, 77–88.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53, 7–26.

Groves, C.R., 2003. Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity. Island Press, Washington, DC.

Gustafson, E.J., 1998. Clustering timber harvests and the effect of dynamic forest management policy on forest fragmentation. Ecosystems 1, 484–492.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. Ecology 84, 609–615.

Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linnean Soc. 42, 3–16.

Harris, L.D., 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. The University of Chicago Press, Chicago, IL.

Hiers, J.K., Laine, S.C., Bachant, J.J., Furman, J.H., Greene, W.W., Compton, V., 2003. Simple spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Cons. Biol. 17, 1571–1578.

Hunter Jr., M.L., 1990. Wildlife, Forests and Forestry. Prentice Hall, Englewood Cliffs, NJ.

Hunter Jr., M.L., 1991. Coping with ignorance: the coarse filter strategy for maintaining biodiversity. In: Kohm, K.A. (Ed.), Balances on the Brink of Extinction: The Endangered Species Act and Lessons for the Future. Island Press, Washington, DC, p. 266.

Hunter Jr., M.L., 2005. A mesofilter conservation strategy to complement fine and coarse filters. Cons. Biol. 19, 1025–1029.

Huston, M.A., 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge.

Hutchinson, G.E., 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22, 415–422.

Kohm, K.A., Franklin, J.F., 1997. Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, DC.

Landres, P.B., Morgan, P., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9, 1179–1188.

Lennon, J.J., Koleff, P., Greenwood, J.J.D., Gaston, K.J., 2004. Contribution of rarity and commonness to patterns of species richness. Ecol. Lett. 7, 81–87.

Liebig, J., 1840. Chemistry in its Application to Agriculture and Physiology. Taylor and Walton, London, UK.

Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity. Island Press, Washington, DC.

Luck, G.W., Daily, G.C., 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. Ecol. Appl. 13, 235–247.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

MacNally, R., Bennett, A.F., Brown, G.W., Lumsden, L.F., Yen, A., Hinkley, S., Lillywhite, P., Ward, D.A., 2002. How well do ecosystem-based planning units represent different components of biodiversity? Ecol. Appl. 12, 900–912.

May, R.M., 1976. Simple mathematical models with very complicated dynamics. Nature 261, 459–467.

May, R.M., 2001. Stability and Complexity in Model Ecosystems, 3rd ed. Princeton University Press, Princeton, NJ.

Miller, J.R., Turner, M.G., Smithwick, E.A.H., Dent, C.L., Stanley, E.H., 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. BioSci. 54, 310–320.

Monserud, R.A., 2002. Large-scale management experiments in the moist maritime forests of the Pacific Northwest. Landsc. Urban Plan. 59, 159–180.

Myers, N., 1988. Threatened biota: hotspots in tropical forests. The Environmentalist 8, 178–208.

Nadkarni, N.M., 2004. Not preaching to the choir: communicating the importance of forest conservation to nontraditional audiences. Cons. Biol. 18, 602–606.

Nee, S., 2004. More than meets the eye—earth's real biodiversity is invisible, whether we like it or not. Nature 429, 804–805.

Noon, B.R., Murphy, D.D., Beissinger, S.R., Shaffer, M.L., DellaSala, D., 2003. Conservation planning for US National Forests: conducting comprehensive biodiversity assessments. BioSci. 53, 1217–1220.

Noss, R.F., 1987. From plant communities to landscapes in conservation inventories: a look at the nature conservancy (USA). Biol. Cons. 41, 11–37.

Noss, R.F., Cooperrider, A.Y., 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, DC.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Palik, B.J., Mitchell, R.J., Houseal, G., Pederson, N., 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Can. J. For. Res. 27, 1458–1464.

Palmer, M.A., Bernhardt, E.S., Chornesky, E.A., Collins, S.L., Dobson, A.P., Duke, C.S., Gold, B.D., Jacobson, R.B., Kingsland, S.E., Kranz, R.H., Mappin, M.J., Martinez, M.L., Micheli, F., Morse, J.L., Pace, M.L., Pascual, M., Palumbi, S.S., Reichman, O.J., Townsend, A.R., Turner, M.G., 2005. Ecological science and sustainability for the 21st century. Front. Ecol. Environ. 3, 4–11.

Perera, A.H., Buse, L.J., Weber, M.G., 2004. Emulating Natural Forest Landscape Disturbance: Concepts and Applications. Columbia University Press, New York, NY.

Peters, R.H., 1999. A Critique for Ecology. Cambridge University Press, Cambridge.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, FL.

Pickett, S.T.A., Kolasa, J., Jones, C.G., 1994. Ecological Understanding: The Nature of Theory and the Theory of Nature. Academic Press, San Diego, CA.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. Nature 365, 335–337.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., 1999. The gaps between theory and practice in selecting nature reserves. Cons. Biol. 13, 484–492.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426, 837–841.

Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Cons. Biol. 16, 1324–1332.

Schmiegelow, F.K.A., Machtans, C.S., Hannon, S.J., 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses. Ecology 78, 1914–1932.

Shrader-Frachette, K.S., McCoy, E.D., 1993. Method in Ecology: Strategies for Conservation. Cambridge University Press, Cambridge.

Simberloff, D., 1995. Habitat fragmentation and population extinction of birds. Ibis 137 (Suppl. 1), S105–S111.

Simberloff, D., 2001. Management of boreal forest biodiversity: a view from the outside. Scan. J. For. Res. Suppl. 3, 105–118.

Stokstad, E., 2005. Learning to adapt. Science 309, 688–690.

Stoltman, A.M., Radeloff, V.C., Mladenoff, D.J., 2004. Forest visualization for management and planning in Wisconsin. J. For. 102, 7–13.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F., 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest, southwest Canada. Ecol. Appl. 10, 1367–1383.

Summerville, K.S., Crist, T.O., 2002. Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. Ecol. Appl. 12, 820–835.

Swanson, F.J., Franklin, J.F., 1992. New forestry principles from ecosystem analysis of Pacific Northwest forests. Ecol. Appl. 2, 262–274.

Thomson, 2005. The Web of Science. The Thomson Corporation, Stamford, Connecticut Available from: http://portal17.isiknowledge.com/portal.cgi (accessed July 2005).

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monog. 67, 411–433.

Walters, C.J., Holling, C.S., 1990. Large-scale management experiments and learning by doing. Ecology 71, 2060–2068.

Waltz, A.E.M., Covington, W.W., 2004. Ecological restoration treatments increase butterfly richness and abundance: mechanisms of response. Rest. Ecol. 12, 85–96.