Monitoring of Biodiversity Indicators in Boreal Forests: A Need for Improved Focus

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Abstract—*The general principles of scale and coarse and fine filters have been widely accepted, but management agencies and industry are still grappling with the question of what to monitor to detect changes in forest biodiversity after forest management. Part of this problem can be attributed to the lack of focused questions for monitoring associated with an absence of null models and predicted effects, a certain level of disconnect between research and management, and recognition that, in the case of forest management, monitoring is research. Considerable research from the past decade has not been adequately synthesized to answer important questions, such as which species might be the best indicators of change, what is the importance, if any, of subtle changes in community structures, and causes of observed changes. A disproportionate research emphasis has been placed on community ecology, and mostly on a few groups of arthropods, amphibians, migratory songbirds, and small mammals, while other species, including soil organisms, lichens, bats, raptors, and larger mammals remain less well-known. Hence, our ability to deal with questions of persistence is limited, and demographic research on key species is urgently needed. Management agencies need to clearly articulate null models for monitoring, focus fine-scale monitoring on key species in key habitats and areas to answer clear questions, and have a protocol in place to adapt management strategies to changes observed. Finally, agencies must have some way to determine and define when a significant change has occurred and to predict persistence of species; this too should flow from a proper null model.*

Introduction

Effectiveness monitoring is the use of indicators to determine achievement of management goals and objectives, while validation monitoring is used to investigate the relationship between an action and an effect as a test of a hypothesis (Mulder and others 1999). These two types of monitoring with respect to forest management should not be considered different, and all biodiversity monitoring should examine objectives in light of expectation, or hypotheses. In other words, monitoring the effects of forest management should be considered a research problem. However, monitoring needs for management evaluation requires ecologists to conduct long-term research without the benefits of experimental manipulation. In this way, ecologists are caught in an experimental time-space warp.

Despite more than 20 years of research into the effects of boreal forest management on animal and plant communities, with few exceptions, management agencies are still uncertain of how to monitor effects (or effectiveness). The broad concepts of coarse and fine filters (Noss 1987, 1999, Hunter 1990), although somewhat modified from the original intent, are generally well accepted, as is the principle that forest management affects biodiversity at multiple scales. A large and varied number of criticisms have been made of the use of indicators to suggest change as a result of forest management (Steele and others 1984, Landres and others 1988, Prendergast and others 1993, Carignan and Villard 2002). Nevertheless, it is impossible to infer sustainability without monitoring something, and all authors agree that a set of indicators is needed (Landres and others 1988, McLaren and others 1998, Lindenmayer 1999, Carignan and Villard 2002).

However, difficulties arise in the development of details, particularly over what to monitor, how often to monitor, what sample sizes are needed, and ultimately how to decide whether or not a measured change is meaningful. In fact the latter issue is rarely considered in monitoring programs. These problems arise for several reasons including a lack of application of research results to management practice, uncertainty about the questions that a monitoring program should answer, and especially the lack of scientific rigor in application of a monitoring program to the problems at hand. There is a need for management agencies to develop clear questions before designing and undertaking monitoring programs. This paper suggests various means to correct some of the problems that have arisen, clouding the intent, design, and interpretation of results from monitoring programs. The paper does not address in a comprehensive manner the selection of indicators or the statistical considerations for designing a monitoring program. For specific discussions of ways to chose indicators, the reader is referred to: McLaren and others (1998), Noss (1999), and Carignan and Villard (2002), and for statistical and power considerations to Link and others (1994), Phillippi and others (1998), Gibbs and others (1998), Pollock and others (2002), Carlson and Schmiegelow (2002), and Rempel and Kushneriuk (2003).

A Need for the Improved Use of Available Research

The catalogue of research studies into the effects of boreal forest management on aspects of biodiversity during the past 20 or more years is impressive. A simple search on "biodiversity + boreal + forest management" in a single forestry-related library database, for 1980 to 2004, produced more than 300 published articles. However, much of the available research is in a published format that management agencies do not or rarely use. Academic researchers view the scientific community as their main "client," and so results are published in scientific journals that managers rarely read and using language that is difficult to read. As a result, much of this information remains obscure and unavailable to management agencies because of a lack of directed and meaningful syntheses, and the inability (or disinterest) of researchers to move their results into management practice. By "meaningful synthesis," I am referring to the need to use the published literature to develop predictive models of effects, which can lead to a strong set of indicators that can be monitored as a test of a hypothesis. Considerable information on which to base monitoring programs is available but remains non-influential, and as a result monitoring programs in boreal forests are somewhat mired in uncertainty.

As an example in boreal forests of Canada, researchers have keyed in on the importance of standing and fallen deadwood with certain characteristics that provides strong predictive capability for breeding by some species (Bonar 2000, Setterington and others 2000, Drapeau and others 2002, Steeger and Dulisse 2002). A synthesis of this information could be used to develop models leading to predictions of when certain species might begin to re-occur in managed forests, for example as was done by Bunnell and others (2002), leading to a hypothesis of effect. Models may also lead to predictions about thresholds of response to particular structures (fig. 1).

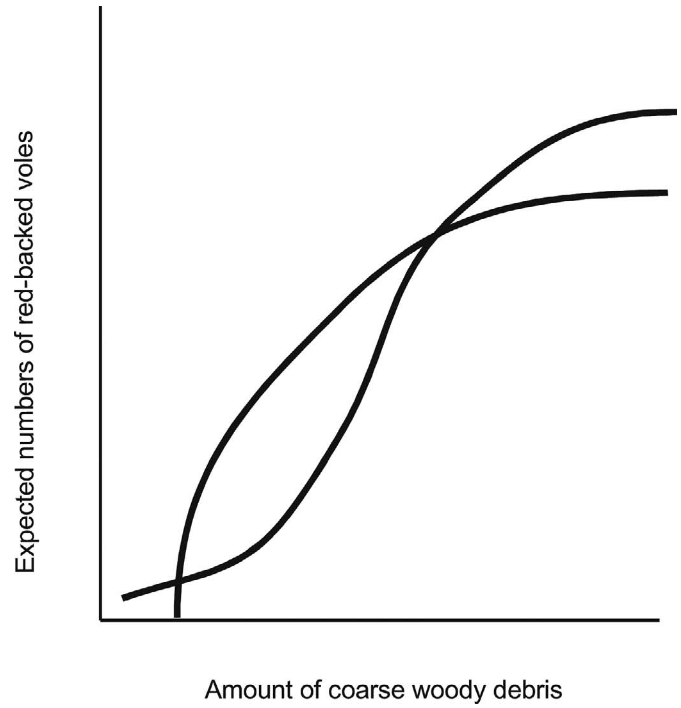

Figure 1. Possible thresholds and responses exist in response of species to structures and amounts of forest, and if properly modeled provides managers with testable hypotheses. In the illustrated case, two possible models suggest responses by red-backed voles (*Clethrionomys gapperi*) in mature boreal forests to the volume of coarse woody debris. Monitoring could be used as a test of the hypothesis that a certain volume of CWD is required for the voles to persist and to examine the suggested thresholds for population. These models are based on unpublished data for dry conifer (exponential) and lowland conifer (logistic) (I. Thompson, Can. For. Serv.).

However, little demographic information and few species-specific studies are available to enable assessment of persistence of species associated with dead wood structures. Nevertheless, models could be developed to predict responses.

Re-focusing Research

There has been excessive study of certain groups of organisms, especially carabid beetles, forest songbirds, and small mammals, yet on the other hand the cryptic and the more difficult-to-study organisms remain obscure as does species-specific information on demography. For example, certain groups of species that have proved to be useful indicators in Scandinavian boreal forests, have not been well-researched in the Canadian boreal forest. These include bryophytes, fungi, saproxylic beetles, and lichens (Esseen and others 1996, Jonsson and Jonsell 1999, Berglund and Jonsson 2001). As a result, even the broad effects of forest management on many potential indicators remain unknown. Other groups of species that remain poorly known in boreal forests include small carnivores, owls, raptors, cryptograms, and all soil organisms. Among the small carnivores, marten and lynx are reasonably well researched, but fisher, red fox, all three boreal weasel species, river otter, and mink have not been adequately studied to predict the effects of forest management.

For the commonly studied groups, researchers have most often decided to examine community-level questions. These studies invariably show a re-ordered abundance of species by forest management treatment, but provide limited information about the causal effects of forest management on species persistence and no information on the effects of such changes on ecosystem function. For example, a recent publication by Work and others (2004) concluded that the community composition of carabid beetles was dramatically different depending on stand origin (fire or logging) and by cover type. Their conclusion was that "…[the species] exist in different mixes and it is not clear that the persistence of all species would be assured [under different management regimes] on the managed landscape." This is the same as saying that they could draw no conclusions with respect to species persistence and so could not comment about the effects of forest management, other than to say that relative abundances had changed. The literature is replete with these kinds of studies, all indicating that differences in relative species abundance had occurred as a result of forest management, but which provided no information about important mechanistic relationships. Lindenmayer (1999) points out that such studies also reveal little about cumulative impacts in space or time. This kind of result has done little to inform management agencies and do not contribute to a monitoring program. However, what these community-based studies can provide is suggestions about species that may be affected and so lead researchers towards subsequent demographic and detailed habitat studies that may reveal causal links to the effects of forest management. Unfortunately, few such studies are available in boreal forests and modeling persistence is not possible for most species, although there are notable exceptions (marten [*Martes americana*], snowshoe hare [*Lepus americana*], and balsam fir [*Abies balsmifera*]). Schumaker and others (2004) developed habitat scenarios for suites of wildlife species but noted their inability to deal with the persistence issue owing to lack of information for most. We need to move past community studies and onto detailed examinations of habitats and demographics of individual species that are predicted to be affected negatively by forest management. Spatially explicit population models can be used to develop population-based predictions of effects that can be examined through monitoring.

What is the Correct Monitoring Question?

Forest management is a large-scale experiment in community ecology, hence monitoring requires research hypotheses that flow logically from this experiment. Logging in the Canadian boreal forest has a relatively young history, beginning in the 1940s, only becoming mechanized in the 1960s, followed by a rapid expansion in area in the 1970s in the east but not until the late 1980s in the west. There are no mechanically-logged second-growth forests that are old enough to compare to natural-origin old forests. Bearing this in mind, simulation modeling is the only tool to enable some perspective about the sustainability of forest management in the long term. However, we can examine younger forests that are comparable in age but were derived from natural and managed disturbances, while maintaining benchmark old forests to enable the longer-term modeling predictions to be tested.

For monitoring to contribute to our understanding of the effects of forest management, it must be viewed as a mensurative science experiment with testable hypotheses. Therefore, in designing a monitoring program, a key need is to formulate the correct questions. The main underlying question is not "how has abundance of species A or forest ecosystem X changed over time in response to a given practice?" Rather, the issue is "has a change occurred in response to a forest management practice that was unexpected and deleterious to the persistence of a population of a particular species?" (In Ontario, for example, the scale is set at the "forest management unit" [FMU, approximately 5000 km^2] because plans are developed at this scale and each plan has to demonstrate sustainability). In other words, "will the species or population continue to survive over the long-term in this forest?" In the ultimate sense, sustainable development is about the preservation of genetic diversity. Thinking at this level, that is, about what might cause the loss of genes from populations, should help to develop a monitoring program that will succeed. There is a need to monitor local populations (in other words, FMU-scale), not just species or elements at a regional scale.

There must be some a priori expectation (hypothesis) against which to measure effect and a means to identify an unacceptable level of impact. In the few instances where management agencies have followed a well-developed plan for a boreal biodiversity monitoring program (the Alberta Biomonitoring Program, Farr and others 1999), there is still no explicit means of determining when to declare that a problem exists. Monitoring programs need to consider observed changes measured under an appropriate null model, and in the light of changes to coarse filters that are also monitored. Null models provide a basis against which to determine that a significant negative effect has occurred. In the absence of a such a model, monitoring is nothing more than counting organisms and assessing trends in time (Krebs 1991, Nichols 1999), but cannot answer the question "when has a sufficient change occurred to warrant corrective management action?"

Appropriate null models are debatable and require considerable thought and various lines of evidence from research to develop properly. In recent years at coarse scales, forest management has moved away from sustained yield towards emphasizing planning that is "close to nature" or that "emulates natural disturbances," at scales from forest stands to large landscapes (Harris 1984, Hunter 1990, Attiwill 1994). In boreal forests, many authors have argued that "natural disturbance emulation" is the appropriate null model because these forests were mostly disturbance-driven, especially by fires (Harris 1984, Haila and others 1994, Bergeron and Harvey 1997). An important issue to understand, as a forest manager, is "will forest communities that result following harvesting converge with those forest communities that result following natural disturbances, and hence maintain associated biological diversity and all the same goods and services?" In other words, we need to know if it is possible to use forest systems while maintaining their ecological integrity, and ensuring their stability (age structure, species composition, structures, and processes) within known bounds (Thompson and Harestad 2004). A monitoring program is meant to suggest whether or not such bounds have been exceeded, and should be developed to test differences between natural and managed forests of similar types on similar sites and of similar ages, for a range of indicators across scales.

There is, of course, considerable debate about the ability of forest managers to emulate natural disturbances, and how appropriate the natural disturbance model may be is open to some question (Hunter 1993, Landres and others 1999, Reich and others 2001). It may be that past landscapes cannot really be true predictors of future landscapes, given that humans have altered even natural processes, for example through suppression of fires, climate change, and the introduction of exotic species. One could argue that an appropriate null model should be based on an expected landscape as designed by humans.

The ability to develop well-informed null models may be limited by knowledge; however, this limitation has been reduced in recent years with an accumulation of studies about boreal forests and their biodiversity. This work has flowed from well-funded research programs under the Canadian Model Forests Network, National Research Council's Sustainable Forest Management Network, Ontario's Living Legacy Trust, Manning Forest Products Research Trust, Fonds québécois de recherche sur la société et la culture, and British Columbia Forest Renewal Program. However, the problem of incorporating these results into monitoring programs remains problematic as noted above.

The Value of a Model-based Monitoring Program

Models can fulfill several roles in the development of a monitoring program including estimating required sample sizes, indicating power, suggesting sample distribution, but most importantly to develop predictions based on previous knowledge. The latter use provides managers with a means to assess success and the ability to estimate the probability of persistence of an indicator. In a more general sense, models also force managers and researchers to examine closely what they understand about causal links between forest management and effects on biodiversity, and lead ultimately to revised management strategies (Walters and Holling 1990) and more focused research.

An Example of Model-based Predictions for Monitoring

Thompson and others (2003) published a review of the impacts of intensive forest management that enabled them to develop predictive probabilistic models of effects on individual species. The species modeled were selected based on an expectation of detectable effects over time in second-growth boreal forest stands, as compared to natural-origin forests of the same age and type. The curves were developed based on published literature and expert opinion and provided testable null hypotheses of probabilistic effect. Relative population changes were modeled for several species based on forest change with harvesting on a 5000 km^2 landscape in boreal eastern Ontario, Canada. Cape May warbler (*Dendroica tigrina*) and Tennessee warbler (*Vermivora peregrina*) are illustrated in figure 2. Species for which predicted effects were distinguishable between treatments (natural vs. managed) at 40-50 years of age could be used as indicators of sustainable forest management, such as in the case of the two warbler species shown. The predicted population changes are hypotheses of effect and monitoring would permit testing against the model. A decline of 20 percent could be selected as severe and would occur for Tennessee warblers by year 48 on this particular landscape, if no post-harvest treatment was done.

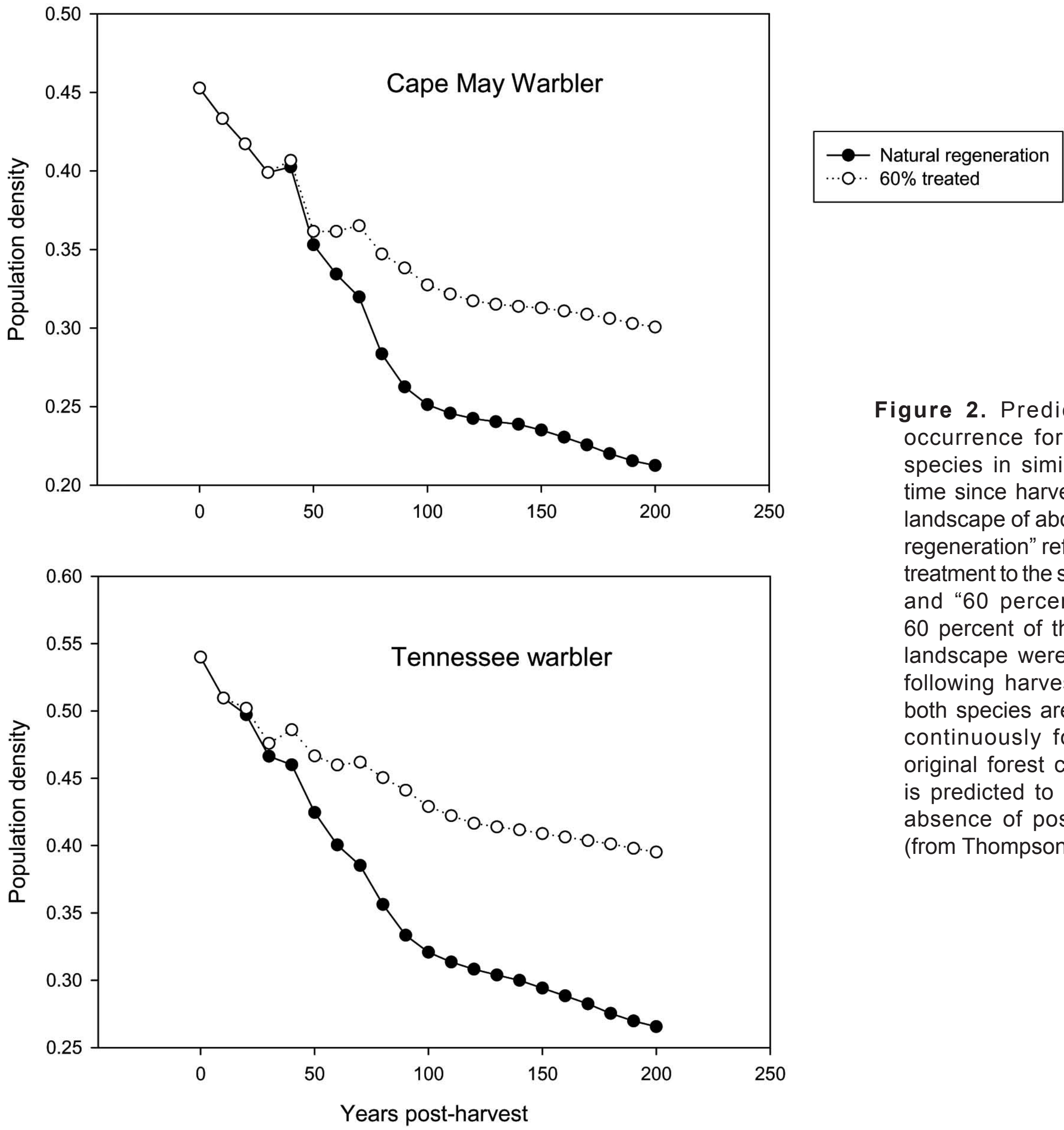

Figure 2. Predicted probability of occurrence for two boreal warbler species in similar forest types over time since harvest for a boreal forest landscape of about 5000 km^2. "Natural regeneration" refers to no post-harvest treatment to the stands post-harvesting, and "60 percent treated" refers to 60 percent of the stands on a given landscape were planted and tended following harvesting. Populations of both species are predicted to decline continuously following removal of original forest cover, but the decline is predicted to be precipitous in the absence of post-harvest treatment. (from Thompson and others 2003)

Some Additional Thoughts on Selecting Indicators

How to select species or elements to monitor is not the focus of this paper, and several excellent publications are available to help managers select indicators (see: Introduction). Nevertheless, some additional ideas to guide the selection of indicators would include: using existing community-based studies to implicate species of particular interest, choosing species for which modeling has suggested both stand and landscape effects (in other words, as predictor variables), including species that require specific forest structures known to change as a result of management, and selecting species that occur in rare or declining habitats (and monitoring the habitats themselves). Hansson (2001) called habitats in which there was a high probability of encountering "red-listed" species "key habitats" and suggested these areas required special consideration. Such areas have not been carefully identified in Canadian boreal forests. Although rare species present several sampling problems (for example, excessive zero plots, high variance, low power to detect change) (Link and others 1994), these species have a high probability of being among the first to become locally extinct, as a result of altered habitats or altered community-related processes, such as predation or competition. Hannon and others (2004) have suggested a protocol for identifying rare avian species in boreal forests. Locally rare species, especially where rarity is related to a rare habitat, warrant special consideration as indicators in a monitoring program. In the case of a rare indicator, concern over high variability among counts, or among years, could be offset by using several lines of evidence to determine change in population. For example, counts on snow transects, counts at scent posts, and camera traps might be used to provide three separate indices of a rare mammal species. Finally, to reiterate an earlier point, until the value as indicators of poorly studied groups of organisms is assessed (lichens, soil organisms, small carnivores), the available choices for indicators remains incomplete.

Conclusion

In the case of monitoring the effects of forest management, we need to be clear that monitoring is long-term research. A proper framework for monitoring programs that includes hypotheses, well thought-out models of effects, and clear objectives with respect to changes in numbers or amounts of indicators is needed for these programs to be effective. Simple arbitrary plans that declines will be detected are insufficient, as is the view that reporting numbers is somehow meaningful. A monitoring program should be seen and developed as a test of hypotheses relating to the experiment of sustainable forest management. Improved use of existing research can be made to develop testable hypotheses under a monitoring program, and future research should concentrate less on community ecology and more on key species and key habitats to understand causal links to the effects of forest management. Finally, in boreal forests considerable research is still needed on many poorly understood species so that indicators can be selected from the range of functional groups in these systems.

References

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63: 247-300.

Bergeron, Y., and B. Harvey. 1997. Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. Forest Ecology and Management 92: 235-242.

Berglund, H., and B. G. Jonsson. 2001. Predictability of plant and fungal species richness of old growth boreal forest islands. Journal of Vegetation Science 12: 857-866.

Bonar, R. L. 2000. Availability of pileated woodpecker cavities and use by other species. Journal of Wildlife Management 64: 52-59.

Bunnell, F. L., M. Boyland, and E. Wind. 2002. How should we spatially distribute dying and dead wood? In: W. F. Laudenslayer, P. J. Shea, C. P. Witherspoon, and T. E. Lisk, eds. Proceedings of the symposium on the ecology and management of dead wood in western forests. USDA Forest Service, General Technical Report PSW-GTR-181: 739-752.

Carignan, V., and M.-A. Villard. 2002. Selecting indicator species to monitor ecological integrity: a review. Environmental Monitoring and Assessment 78: 45-61.

Carlson, M., and F. Schmiegelow. 2003. Cost-effective sampling design applied to large-scale monitoring of boreal birds. Conservation Ecology 62: 11. Online at: http://www.consecol.org/vol6/iss2/art11

Drapeau, P., A. Nappi, J.-F. Giroux, A. Leduc, and J.-P. Savard. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. In: W. F.

Laudenslayer, P. J. Shea, C. P. Witherspoon, and T. E. Lisk, eds. Proceedings of the symposium on the ecology and management of dead wood in western forests. USDA Forest Service, General Technical Report PSW-GTR-181: 193-205.

Esseen, P.-A., K.-E. Renhorn, and R.B. Pettersson. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecological Applications 6: 228-238.

Farr, D., P. Lee, C. Shank, and B. Stelfox. 1999. Conceptual framework for monitoring forest biodiversity in Alberta. Online at: http://www.abmp.arc.ab.ca/Documents.htm

Gibbs, J. P., S. Droege, and P. Eagle. 1998. Monitoring populations of plants and animals. BioScience 48: 935-940.

Haila, Y., I. K. Hanski, J. Niemela, P. Punttila, S. Raivo, and H. Tukia. 1994. Forestry and the boreal fauna: matching management with natural forest dynamics. Annales Zoologica Fennici 31: 187-202.

Hannon, S. J., S. E. Cotterill, and F. K. A. Schmiegelow. 2004. Identifying rare species of songbirds in managed forests: application of an ecoregional template to a boreal mixedwood system. Forest Ecology and Management 191: 157-170.

Hansson, L. 2001. Key habitats in Swedish managed forests. Scandinavian Journal of Forest Research, Supplement 3: 52-61.

Harris, L. D. 1984. The fragmented forest, island biogeography theory and the preservation of biotic diversity. Chicago, IL: University of Chicago Press, Chicago.

Hunter, M. L. 1990. Wildlife, forests, and forestry. Englewood Cliffs, NJ: Prentice Hall. 370 p.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biological Conservation 65: 115-120.

Jonsson, B. G., and M. Jonsell. 1999. Exploring potential indicators in boreal forests. Biodiversity and Conservation 8: 1417-1433.

Krebs, C. J. 1991. The experimental paradigm and long-term population studies. Ibis, supplement 1: 3-8.

Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2: 316-328.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179-1188.

Link, W. A., R. J. Barker, and J. R. Sauer. 1994. Within-site variability in surveys of wildlife populations. Ecology 75: 1097-1108.

McLaren, M. A., I. D. Thompson, and J. A. Baker. 1998. Selection of vertebrate wildlife indicators for monitoring sustainable forest management in Ontario. Forestry Chronicle 74: 241-248.

Mulder, B. S., B. R. Noon, T. A. Spies, M. G. Raphael, C. J. Palmer, A. R. Olsen, G.H. Reeves, and H. H. Welsh. 1999. The strategy and design of the effectiveness monitoring program for the Northwest Forest Plan. USDA Forest Service, Pacific Northwest Forest Station, General Technical Report PNW-GTR-437. 138 p.

Nichols, J. D. 1999. Monitoring is not enough: on the need for a model-based approach to migratory bird management. In: Strategies for bird conservation: the Partners in Flight planning process. R. Bonney, D. N. Pashley, R.J. Cooper, and L. Nichols eds. Online at: http://birds.cornell.edu/pifcapemay/nichols.htm

Noss, R. F. 1987. From plant communities to landscapes in conservation inventories: a look at the Nature Conservancy (USA). Biological Conservation 41: 11-37.

Noss, R. F. 1999. Assessing and mentoring forest biodiversity: a suggested framework and indicators. Forest Ecology and Management 115: 135-146.

Phillippi, T. E., P. M. Dixon, and B. A. Taylor. 1998. Detecting trends in species composition. Ecological Applications 8: 300-308.

Pollock, K.H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L.L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics 13: 105-119.

Prendergast, J. R., R. M. Quinn, J. H. Lawton, B. Eversham, and D. H. Gibbons. 1993. Are species, the coincidence of diversity hotspots and conservation strategies? Nature 365: 335-337.

Reich, P. B., P. Bakken, D. Carleson, L. E. Frelich, S. K. Friedman, and D. F. Grigal. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology 82: 2731-2748.

Rempel, R. S., and R. S. Kushneriuk. 2003. The influence of sampling scheme and interpolation method on the power to detect spatial effects of forest birds in Ontario (Canada). Landscape Ecology 18: 741-757.

Schumaker, N. H., T. Ernst, D. White, J. Baker, and P. Haggerty. 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette Basin. Ecological Applications 14: 381-400.

Setterington, M. A., I. D. Thompson, and W. A. Montevecchi. 2000. Woodpecker abundance and habitat use in mature balsam fir forests in Newfoundland. Journal of Wildlife Management 64: 335-345.

Steeger, C., and J. Dulisse. 2002. Characteristics and dynamics of cavity nest trees in southern British Columbia. In: W. F. Laudenslayer, P. J. Shea, C. P. Witherspoon, and T. E. Lisk, eds. Proceedings of the symposium on the ecology and management of dead wood in western forests.

USDA Forest Service, General Technical Report PSW-GTR-181: 275-289.

Steele, B.B., R. L. Bayne, and C. V. Grant. 1984. Environmental monitoring using populations of birds and small mammals: analyses of sampling effort. Biological Conservation 39: 157-172.

Thompson, I. D., J. A. Baker, and M. Ter-Mikaelian. 2003. A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. Forest Ecology and Management 177: 441-469.

Thompson, I. D., and A. S. Harestad. 2004. The ecological and genetic basis for emulating natural disturbances in forest management: theory guiding practice. In: A. H. Perera, L.J. Buse, and M. G. Weber, eds., Emulating natural forest landscape disturbances: concepts and applications. New York, NY: Columbia University Press: 29-42.

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

Work, T. T., D. P. Shorthouse, J. R. Spence, W. J. A. Volney, and D. Langor. 2004. Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research 34: 417-430.