# BIODIVERSITY AND LAND MANAGEMENT: FROM CONCEPT TO PRACTICE

by

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**Abstract**

The Canadian government is committed to conserving biodiversity. This thesis asks which landscape patterns will best conserve biodiversity in managed forests in British Columbia. First, I define an appropriate measurement of biodiversity; then, I develop a decision support tool to assess the impacts of planned management on biodiversity, illustrated with a case study; and finally, I provide options for the amount and pattern of old forest to preserve.

Biodiversity can be measured at gene, species and ecosystem levels. Ecosystems provide the best measurement for forest managers. Ecosystems are a comprehensive measurement over large temporal and spatial scales, they develop predictably over time, and they are directly linked to the land. A coarse ecosystem approach must be accompanied by attention to certain species. Research must address the relationship between biodiversity and ecosystems and must help establish goals for management.

I develop decision support software (SIMFOR) which simulates effects of forest management and stand development in 5,000 to 50,000 ha forests, calculates landscape composition and ecosystem pattern and predicts habitat distributions for selected species. In a case study, the low-profit management plan better conserves biodiversity, generating more old forest, larger patches and less edge habitat than the high-profit plan.

I explore the general relationship between animal spatial requirements (home range, dispersal, and viable population size) and landscape pattern (patch size and abundance) using a scale-independent model. Home range size limits landscape suitability when patch size is smaller than home range size, and dispersal limits suitability when patch size exceeds 10 times home range size. Decreasing habitat abundance increases inter-patch distance, limiting dispersal. Landscape connectivity reflects threshold effects which depend on habitat abundance. First, landscapes are either mostly connected or mostly unconnected by dispersal, suggesting that population decline may occur without warning. Second, small habitat patches merge to form large contiguous areas at approximately 40% habitat abundance (given the assumptions used in the model). When

habitat abundance is less than 40%, large patches or mixed patch sizes are good management options. When habitat abundance exceeds 40%, patch size is less important.

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# Chapter 1.

## General Introduction

"...natural resources are not given to us by our fathers but are loaned to us by our children"

Harris, L.D. 1984

As the global population increases (now 5.3 billion and projected to be 8.5 billion by 2025; WRI 1992, p 76) and the negative impacts of resource use by the human species become more common (Ludwig et al. 1993), humanity struggles to understand its relationship with nature. The wide media coverage received by the Bruntland Report, which links sustainable economies and ecological integrity (WCED 1987), represents a milestone of public awareness. Controversial development issues now receive international attention (e.g., clearcut logging of temperate rainforest in Clayoquot Sound, British Columbia, has fueled international pressure for "clearcut free" products; CPPA 1994). Such controversies reflect disparities in the allocation of the costs and benefits of development (Hardin 1985) and the differing values of our diverse society.

Terms such as sustainable development, ecosystem health and biodiversity have become popular in public, political and scientific arenas, but they are difficult to measure and are rarely defined explicitly (Berry 1993). Without clear operational definitions, the meaning of these terms cannot be readily translated into management practice. Thus, these terms may be used to express lofty goals without committing to explicit action. An operational definition of biodiversity, however, is emerging (Noss 1990, Solbrig 1992). In this thesis, I focus on the concept of biodiversity in relation to forest management in British Columbia.

"Biodiversity" is the variety of life and its interactions (see Chapter 2). Species, which may number from 5 million to 30 million worldwide (Wilson 1988a), are often used as the basic measure of biodiversity. Biodiversity provides many benefits (Bunnell 1990, Burton et al. 1992) including free ecosystem services which are not easily replaced by technology (Ehrlich and Mooney 1983). Canada has made an explicit commitment to maintain biodiversity by signing and ratifying "The Convention on Biological Diversity" (UNEP 1992), a commitment which has been endorsed by British Columbia (BCMOF 1993).

There is ample evidence that species are disappearing at a rapid rate (Scudder 1993). At a general level, the cause is easily understood: relative to other species, humans are better competitors for resources. Humans directly use or indirectly influence approximately 40% of potential terrestrial net primary production (the portion of solar energy bound to organic

molecules during photosynthesis; Vitousek et al. 1986). Humans compete for habitat by converting natural lands to agricultural, urban and industrial use. Such alteration of habitat is likely the primary factor reducing biodiversity (Ehrlich 1988). Conversion of forested land to alternative uses is particularly problematic, because the majority of wildlife species are forest dwelling (Bunnell and Kremsater 1990, WRI 1992). Out of 61 countries, 49 have lost more than half and 24 have lost more than three quarters of their forest habitat since pre-agricultural times (WRI 1990, Table 20.4). Forests over the globe decreased by about two percent over the last decade, but tropical forests decreased by nine percent between 1980 and 1990 (WRI 1992, Table 8.2). The loss of tropical forest is of particular concern because they harbor more than 50% of the world's species (Wilson 1988a).

About 30% of the global land base is presently covered with forests (approximately half tropical and half temperate or boreal; WRI 1992, Table 19.1). British Columbia has one percent of global forest land. In the temperate region, rainforests were never extensive (0.2% of the global land base; p. 131, WRI 1992). Today they have been reduced to 44% of their original area, remaining mostly along the Pacific coast of North America (Weigand et al. 1992). British Columbia has approximately one quarter of the remaining global temperate rainforest (Weigand et al. 1992, BCMOF 1994a).

In addition to agricultural or urban development, commercial forestry modifies forest land and its ability to support a given species (Hunter 1990). Fibre production is less intensive but more extensive than conversion of forest land to alternative uses. In British Columbia, approximately 500 ha are harvested each day (0.8 % of the productive, accessible forest area per year); approximately 32% of this harvest comes from coastal regions, comprised largely of temperate rain forest (BCMOF, 1994a). In British Columbia, extensive forestry practices may have the largest impacts on biodiversity.

Given global losses of species, the high proportion of the world's temperate rainforest remaining in British Columbia and the uncertain impacts of extensive forest operations, it is appropriate to examine the relationship between forest management and biodiversity in British

Columbia. In this thesis, I address the broad question of how to incorporate biodiversity into forest management practice in British Columbia. Chapter 2 reviews biodiversity in relation to land management and suggests components of an operational definition of biodiversity. The relationship between landscape pattern and animal survival emerges as an important, but poorly understood, link between forestry and biodiversity. Chapter 3 uses simulation to examine the relationship between landscape pattern and animal mobility. Appendix 1 clarifies the relationship between the variables (habitat abundance, patch size and inter-patch distance) which determine landscape pattern. To link research with management, Chapter 4 presents decision support software which includes some of the important variables identified in Chapter 3 and which calculates indices of biodiversity to aid land use planning. Chapter 4 also describes the results of a case study, demonstrating the application of the decision support software.

# Chapter 2.

## "Biodiversity" and its Implications for Land Management

"It is one of the maxims of civil law that definitions are hazardous. Things modified by human understandings, subject to varieties of complication, and changeable as experience advances knowledge, or accident influences caprice, are scarcely to be included in any standing form of expression, because they are always suffering some alteration of their state."

Samuel Johnson, The Rambler, 28 May 1751, cited in Endler 1986

## Introduction

Conservation of biodiversity is an explicit goal of the Canadian government (Convention on Biological Diversity; UNEP 1992)—but what is biodiversity and how do we conserve it? Biodiversity has been addressed in the conservation and forestry literature (e.g., Noss 1990, Bunnell and Kremsater 1990), but confusion caused by varied interpretations and measurements of biodiversity still hinders conservation (see below). Existing agencies (e.g., responsible for wildlife management or forest management) have been charged with the relatively new goal of biodiversity conservation. Approaches to conservation of biodiversity seem to reflect the talent and bias of these agencies.

In forest management, approaches to the conservation of biodiversity have considered species and their habitat. Conservation plans based on detailed analysis of life history traits have been developed for high profile species (Thomas et al. 1990). Habitat models which do not consider spatial relationships have been used to assess impacts of proposed forest plans (Bonar et al. 1990). Recently, spatially-explicit habitat models have been used as part of a general approach for assessing impacts of forestry on vertebrate diversity (Daust and Bunnell 1992, Hansen et al. 1993).

Impacts of forestry on important habitat features have been considered at both the stand scale and landscape scale (Franklin 1986, Bunnell and Kremsater 1990). In the stand, the reduced amounts of snags and downed wood associated with forestry influence species distributions. On the landscape, the distribution of seral stages and the size and arrangement of patches influence species distributions. A comprehensive ecosystem-based approach for measuring biodiversity in managed forests has not yet been described.

In this chapter, I examine various interpretations of biodiversity, including formal definitions and common connotations, to demonstrate that biodiversity is a broad concept which is not directly measurable. I then describe possible measurements of biodiversity at gene, species and ecosystem levels and evaluate these measurements in the context of conservation of biodiversity in managed forests in British Columbia. Finally, I propose that biodiversity should be

measured at the level of ecosystems and I describe an ecosystem-based approach to forest management.

**Defining biodiversity**

"Biodiversity" was introduced by W.G. Rosen in 1986 (Wilson 1988b). Biodiversity has since been defined more formally by various government agencies (Table 2.1).

Biodiversity is a broad concept and is not directly measurable. Its essential components are (1) "variety", (2) "all life" and (3) "linking processes". By stressing all life and relationships between living organisms, biodiversity emphasizes complexity and concept rather than measurement. Biodiversity is a global concept because it considers all life. Biodiversity can be perceived at various levels of organization including genes, species and ecosystems. Each level provides a different picture of the same phenomenon.

"Biodiversity" carries several value-laden connotations:

1. Biodiversity is threatened. The current rate of global species extinction is estimated as 1,000 to 10,000 times that of the background rate before human intervention (Wilson 1988a). Current extinction results mainly from habitat loss (Ehrlich 1988). Lewin (1986) projects (using estimates from the Food and Agriculture Organization and United Nations Environmental Program) that tropical forests will be completely destroyed by 2135 if current trends continue, leading to extinction of half the species on earth (Scudder, 1993). Losses are not quickly recouped: recovery from mass extinction takes about 5 million years (Scudder 1993).
2. Biodiversity is a resource. Burton et al. (1992) summarize several economic values of biodiversity, including the use of species by subsistence societies, the use of wild populations to improve commercial crops and the use of species for pharmaceuticals. Based on potential

Table 2.1. Definitions of biodiversity.

| Source | Definition of biodiversity |
|---|---|
| United Nations (UNEP 1992, pp. 1.) | "Biological diversity means the variety among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." |
| United States Government (U.S. Congress 1987, pp. 3.) | "biodiversity is the variety and variability among living organisms and the ecological complexes in which they occur" |
| Canadian Government (FPTBWG 1994, pp. 2.) | "..is the term describing the variety of life on earth... It refers to all animals, plants and micro-organisms in terrestrial, freshwater and marine environments. It includes three levels: species, ecosystem and genetic diversity. It emphasizes the complex relationships among all living things on earth." |
| Canadian Forestry (CFS 1994, pp. 19,20.) | ...comes from the latin words *bio*, meaning life and *versitas*, meaning variety... Biological diversity occurs at four different levels Genetic diversity describes the range of genetic traits found within a species and among different species... Species diversity refers to the range of plant, animal and microorganism species on Earth... Ecosystem diversity describes the variety of natural systems found within a region... Landscape diversity describes the broad linkages between and among ecosystems within a landscape type..." |
| British Columbia Forestry (BCMOF 1994b, pp. 173.) | "The diversity of plants, animals, and other living organisms in all their forms and levels of organization, including genes, species, ecosystems, and the evolutionary and functional processes that link them." |

pharmaceutical value alone, the average value of a single plant species in the United States is US$ 203 million (Farnsworth and Soejarto 1985).

3. Biodiversity has moral value. Some people believe that species have intrinsic value. Species may also be of moral value to humans by influencing value systems (Norton 1987, 1988).
4. Biodiversity represents our biotic environment. Ultimately, humans depend on other forms of life for survival. While the loss of a few species may not threaten our environment, the loss of many species can lead to desertification or reduced ecosystem productivity (Ehrlich and Mooney 1983, Naeem et al. 1994). The importance of each lost species to human welfare is unpredictable, but some species play key roles in ecosystem functioning (Terbough 1986).

The encompassing nature of biodiversity is appealing to conservationists, but the narrow definition of biodiversity used by some scientists confuses discussion. Biodiversity, perhaps more because of its connotations than its definition, has become a central concept in conservation. Biodiversity can easily be confused with measurements of species diversity. The terms "biodiversity" and "species diversity" are sometimes used synonymously (e.g., A.R.E. Sinclair, Jan. 27, 1994). Noss and Harris (1986) note the undue emphasis on "species diversity" in conservation. Pielou (1992) notes a case where diversity indices are used to draw inappropriate conclusions about impacts of forestry on biodiversity. Species diversity is one of several possible measurements of biodiversity.

**Possible measurements of biodiversity**

Biodiversity can be divided into multiple levels of organization including genes, species and ecosystems (Table 2.1, Noss 1990). Each level has costs and benefits for measurement.

Genes are distinct, identifiable units which capture more variation than other levels and hence have the potential to describe biodiversity more precisely. In practice, the quantity of genetic information is overwhelming. Thus, genetics does not provide a practical means of

examining biodiversity at a large scale (Antonovics 1985). Genetic techniques may be of greatest value in assisting research related to biodiversity, for example, by establishing relatedness.

Species are relatively distinct, easily identified units (Bunnell and Williams 1980, Orians 1993): obvious genetic diversity exists between species and less obvious genetic diversity exists within species. Populations represent some of the genetic diversity within species. If species are to be used as surrogates for biodiversity, Bunnell and Kremsater (1990) have suggested that maintaining viable populations (viability is related to population size; Remmert 1994), across their natural range will maintain genetic diversity within species. Using species as a measurement of biodiversity carries costs. Measuring species distributions is an overwhelming task. Even large samples will miss many species and will be biased towards visible species. Furthermore, species distributions are ephemeral.

Rather than examining many species, selected species which are sensitive to environmental impacts or indicative of a larger group of species may be measured. This approach is feasible but depends on the assumed sensitivity or linkage to other species.

Ecosystems are communities of organisms interacting together and with their physical environment (Tansley 1935). A benefit of using ecosystems is their broad focus. Ecosystems include many species. They are less numerous than genes or species, thus they are feasible to monitor. Ecosystems may better represent the processes and linkages responsible for maintaining biodiversity. Unfortunately, ecosystems are often indistinct and difficult to classify (Orians 1993). Ecosystem boundaries depend on the location of species on the landscape. Species locations are influenced by three factors: interaction with the abiotic environment (including soil moisture and nutrient conditions and climate), interaction with other species (including competition, predation and symbiosis), and chance (Diamond 1975). Chance events, such as dispersal and disturbance, limit our ability to predict species distributions accurately. As a result, different vegetation can be observed under similar abiotic conditions. Ecosystems may exist in different stable states (Kimmins 1987). Because different species use different spatial scales (Holling 1992), precise delineation of communities (and hence ecosystems) at any one scale is impossible. Despite these

limitations and ongoing theoretical arguments about the existence of ecosystems, British Columbia has a well-accepted Biogeoclimatic Ecosystem Classification System (BEC) which classifies forest land based on soil conditions and plant distributions (Pojar et al. 1987). For practical application, the lack of clear ecosystem boundaries does not seem to be a problem.

In summary, tradeoffs exist between the degree to which measurements capture variation and the degree to which they represent breadth. Genes and species describe variation precisely, but they are too numerous to be measured over large areas. Focusing on a selected species omits variation associated with other species. Ecosystems are less numerous and provide a broader picture, but they are less precise. In British Columbia, the BEC provides the necessary basis for ecosystem-level measurements. No single level both precisely characterizes biodiversity and is easily measured, suggesting that a single comprehensive measurement of biodiversity does not exist.

**Assessing measurements of biodiversity for forestry**

Rather than searching for one definitive measurement, it is better to select a measurement which is appropriate in a given context. Important considerations in the context of conservation efforts in managed forests include dealing with (1) large spatial scales, (2) large temporal scales and (3) uncertainty:

1. Large spatial scales are important because the number of species increases with the size of the area examined. At a global scale, species differ between continents. At a continental scale, species diversity follows climatic conditions (MacArthur 1975). Within a continent, the number of species increase as area increases (Preston 1962). This latter increase results partly due to chance, partly due to increased variation in habitat and partly due to the large area requirements of some species.

   Spatial scale is also important because the effects of management accumulate with area and cannot be properly assessed at small scales. For example, while dispersed clearcuts

in one watershed had relatively little influence on runoff, the overall impact of harvesting several watersheds was significant (Grant and Swansen 1991). Similarly, cumulative effects of forest fragmentation on wildlife are seen at large scales (Angelstam 1992). In many cases, ecosystem disturbance which destroys habitat at small scales maintains habitat diversity at larger scales. Measurements of biodiversity should be sensitive to cumulative effects of management and natural disturbance.

2. Large temporal scales are important. Evolution through natural selection is a slow process. Life has existed on earth for at least 3.5 billion years. "Recovery" from mass extinction takes about 5 million years (Scudder 1993). Homo sapiens has existed on this planet for nearly one million years. Considering the benefits of biodiversity to humans alone or the moral value of biodiversity, extinction of a species now or 100 years from now makes little difference in an evolutionary sense. Projecting impacts for short periods (e.g., 20 years) is not sufficient. Unfortunately, predictive power decreases as the time frame increases. General conditions should still be predictable, however, over sufficiently large areas. Plans made today may be reversible, but successful conservation certainly grows more difficult and costly with the elimination of options. Measurements of biodiversity must be predictable. Precise, detailed measurements of biodiversity are less predictable than broader measurements, minimizing the benefits of precision.

3. Uncertainty is an important component of conservation efforts because impacts must be predicted over long periods and for many species. Life is divided into 5 or 6 kingdoms comprising some 5 to 30 million species worldwide, approximately 1.4 million of which have been named and many fewer studied (Wilson 1988a). For the species studied, we still have difficulty predicting their distribution over large areas (Van Horne and Wiens 1991). The cost of collecting better information has been high (e.g., spotted owl, Thomas et al. 1990). Furthermore, the limited information base is biased towards useful (to humans), cuddly, annoying and, more generally, visible species. Fungi and insects have been neglected, as have Monerans (Archaebacteria and Eubacteria) and Protistans. The problem increases if

genetic diversity is considered: a single insect may contain from 1 billion to 10 billion bits of information (Davis 1993). The vast scope of biodiversity generates enormous uncertainty in conservation efforts. How is the success of conservation of biodiversity to be judged when there are too many species to monitor? Measurements of biodiversity should ideally consider all species, even those which have not been identified.

Given the requirements of a measurement of biodiversity in the context of conservation in managed forests, I re-examine measurements at gene, species and ecosystem levels. Genes are inappropriate measurements of biodiversity because genes generate too much information to be used over large areas and genetic variation is not readily predictable. Species approaches which attempt to be comprehensive suffer from similar problems as gene approaches. Focusing on a specific species or on a few species allows large areas to be considered and impacts to be predicted, but sacrifices comprehensiveness. Focusing on a specific species may be appropriate where the species is threatened or endangered.

"Species diversity" (Whitaker, 1972) is a common measurement of biodiversity, used in scientific studies (but see criticisms in Hurlbert 1971). Measurements of species diversity consider richness (number of species) and evenness (degree of equality in abundance of each species). In terms of conservation, species diversity is an inadequate representation of biodiversity. At a global scale, species diversity (i.e., all species) would represent biodiversity adequately. However, species diversity cannot be measured comprehensively at large scales. Assuming that any measurement of biodiversity must be a sample of limited area and scope, it follows that a measurement should be sensitive to local factors which influence global biodiversity. Changes in biodiversity at the global scale result from the extirpation of populations (loss of genetic diversity) and extinction of species at smaller scales. Species diversity measured at smaller scales is insensitive to extirpation and extinction.

The lack of sensitivity of species diversity to impacts on biodiversity results from two factors acting together. First, species diversity is a sample of a limited area including limited taxa.

Second, species diversity treats all species as equal; it does not track species composition. Because species are counted but not identified, a species may be extirpated and replaced by another without influencing measurements of species diversity. Furthermore, local measurements cannot be aggregated to provide a broader picture because species composition is not tracked. Measurements of biodiversity should retain information about composition of the sample so that samples can be combined to provide information about larger areas.

Diversity indices are used in misleading ways in conservation planning (Noss and Harris, 1986). For example, Terbough and Winter (1983) suggest the richest sites (of endemic birds) in Ecuador and Columbia be given priority for reservation without considering the unique species contributed by each site. They explicitly assume that centres of richness of other taxa coincide. Problematically, conservation action taken for one group of species may not serve other groups particularly well (Scudder 1994). Samson and Knopf (1982) point out that maintenance of species diversity over a large area cannot be achieved by maximizing diversity at several smaller sites because high diversity sites may contain less regionally unique species than low diversity sites. It is not surprising that representing ecological complexity with one or two numeric measurements is inadequate.

Ecosystems provide the best measurement of biodiversity for conservation purposes. Because of their relatively large size and small number, ecosystems can be used to assess large spatial scales. Major changes in ecosystem distributions over time can be predicted. Ecosystem-based measurements can retain information describing the composition of ecosystem types because of the small number of ecosystems (relative to species). Thus, ecosystem-based measurements will be sensitive to loss of ecosystem types and samples can be aggregated to examine larger areas. To the extent that ecosystems are correlated with species, preventing loss of ecosystem types will minimize extinction. Some factors, (e.g., hunting) capable of causing extinction, will not be detected by ecosystem-based measurements, however, habitat loss is the major cause of current extinctions (Ehrlich 1988). Ecosystem-based approaches to conserving biodiversity have been recommended because ecosystems may better protect habitat (Orians

1993), and because there are simply too many species to use species-based approaches (Franklin 1993). Conversely, ecosystem-based approaches have been criticized because ecosystems lack definite boundaries and can exist in different stable states (Merriam 1988).

There is an additional and compelling reason to use ecosystems to represent biodiversity in managed forests: feasibility for management. Land links all forest values. Forest managers may focus on timber, recreation, wildlife or other resources, but viewed broadly, forest managers do not manage resources—they manage land. In particular, (in the case of tree farming), they manage the rate, timing, intensity and spatial pattern of disturbances impacting the land, which in turn influences the patterns of flora and fauna on the landscape. Management involves weighing costs and benefits of alternative actions (e.g., multi-criteria decision techniques; Kangas and Kuusipalo 1993). Biodiversity must be linked with the condition of the landscape so that it may be easily evaluated and assessed in conjunction with other values. Ecosystems link flora and fauna with the landscape.

## Incorporating "biodiversity" into forest management

While there are many good general recommendations and approaches for predicting impacts of land management on species, there are no approaches which provide a general, comprehensive picture of biodiversity that is simple enough to apply to land management. I propose a simple operational representation of biodiversity for land managers based on ecosystems. Then I propose a framework for assessing impacts of management on biodiversity. Finally, I propose that research is required to support management for biodiversity.

Assessing biodiversity in land use planning requires four steps: (1) representing biodiversity; (2) predicting changes in biodiversity; and (3) assessing biodiversity in relation to (4) targets for biodiversity.

**Representing biodiversity**

For the purpose of land use planning, I propose that biodiversity is represented sufficiently by ecosystems and that ecosystems are defined adequately by three components: an abiotic component, a succession component and a remnant-structure component. I assume the following:

1. plant species depend on the abiotic environment and on seral stage (which depends on the timing and intensity of the last disturbance);
2. vegetation structure (i.e., spatial arrangement of shrubs, trees, snags, etc.) reflects seral stage and remnant-structure (vegetation structure remaining after major disturbance);
3. insect species are correlated with plant species; and
4. vertebrate species are correlated with vegetation structure.

Each ecosystem component varies across a landscape, reflecting relatively continuous climatic and geological gradients and relatively discrete disturbance events. To allow for management planning, each component can be divided into categories or classes with distinct boundaries on the landscape. The detail represented in each land class depends on several factors, including whether the focus is on plants or animals and whether information is available to map biophysical variation or to predict plant succession. For example, in areas of approximately 5,000 to 50,000 ha, abiotic classes may be defined as combinations of Biogeoclimatic zone and site productivity; seral stages may include grass/forb/shrub, deciduous tree, young conifer, mature conifer and old conifer; remnant-structure classes may be dichotomous—with remnant structure and without.

**Predicting changes in biodiversity**

At a landscape scale, disturbance events such as fire and insect damage greatly influence vegetation patterns. I suggest that abiotic conditions and disturbance (including active forest management) timing and intensity provide a sufficient basis to predict seral stage development and

remnant structure. For simplicity, I assume that abiotic conditions will not change greatly over time or because of disturbance (this may not be true; loss of soil or climate change may greatly affect the abiotic environment). Disturbance, including forestry, removes portions of the biota from a site. Following disturbance, vegetation and animals recolonize the area, following broadly predictable patterns of secondary succession which depend in part on the abiotic site conditions and the intensity of disturbance (Bunnell and Eastman 1976, Schoonmaker and McKee 1988, Bunnell and Kremsater 1990). Forest structure depends on both the remnant structure surviving the last disturbance and the development of new structure with succession and stand development (seral stage). Thus, given information describing the landscape (abiotic, remnant structure, and seral stage variation) and describing proposed disturbance events (which may include predicted natural disturbances), future ecological patterns can be predicted.

**Assessing biodiversity**

Two broad measurements are needed to assess biodiversity on the landscape: (1) composition (relative abundance of ecosystems) and (2) pattern (spatial arrangement of ecosystems). Landscape composition is more important than landscape pattern because each ecosystem represents a unique aspect of biodiversity; pattern only influences the value of each ecosystem. I suggest that composition is best assessed by focusing on seral stage distributions and then by considering the distribution of each abiotic class and of each remnant-structure class within each seral stage. I assume that, within forests, seral stage is the most important factor because of its major influence on both plant species and animal species. Also, the relative importance of remnant-structure likely depends on seral stage and predictions of seral stage development already account for some abiotic variation.

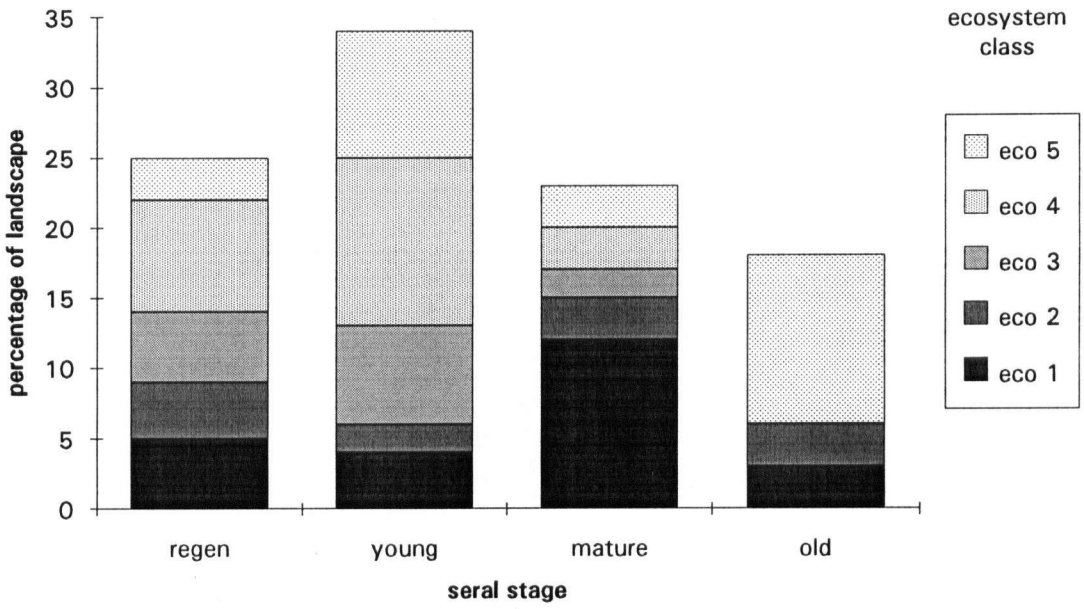
Measurements of the spatial arrangement of land classes are also important. The majority of work describing the biological consequences of landscape pattern focuses on vertebrates. Although examples of the importance of pattern to plants exist, I base my discussion of landscape pattern on vertebrates. I suggest that both patch size and edge effects should be considered.

The distribution of patch sizes in each seral stage provides a simple measurement of pattern. For example, the proportion of the landscape in each seral stage could be divided into five patch size classes: 0-10 ha, 10-100 ha, 100-1,000 ha, 1,000-10,000 and 10,000+ ha. Patch size is important because it relates to the number of species found in a patch (Chapter 3, MacArthur and Wilson 1967).

The relative proportions of core and edge habitat of seral stages should be measured. The positive and negative effects of edge habitat (or ecotones) have been well documented for a number of species (Angelstam 1992). Effects include microclimatic changes, juxtaposition of cover with food, and increased competition and predation. I assume that the most important edge effects to consider are those occurring in the older seral stages and that these areas are only influenced by very structurally-different habitats (i.e., younger seral stages). This assumption reduces the number of landscape classes considered and simplifies comparison of landscape patterns. The depth of the edge influence determines the proportion of area in edge habitat. While the influence of edge is usually species specific, a depth of one or two tree heights seems a reasonable starting point because climatic effects of adjacent openings tend to penetrate this distance (Harris 1984, Chen et al. 1992). Unfortunately, at present, there are no generalizations describing desirable ratios of edge habitat on a landscape.

The main benefit of using ecosystems to represent biodiversity is that landscape composition and pattern may be considered comprehensively and explicitly in land management decisions. For example, Figure 2.1 illustrates how a landscape may be described by the composition and pattern of its ecosystems. Such descriptions are sensitive to loss or fragmentation of ecosystem types and may be used to monitor changes in landscape conditions over time. The ecosystem components that I have described above are probably appropriate for planning in areas of 5,000 to 50,000 ha. Other more appropriate components may be defined at other scales.

a)




b)

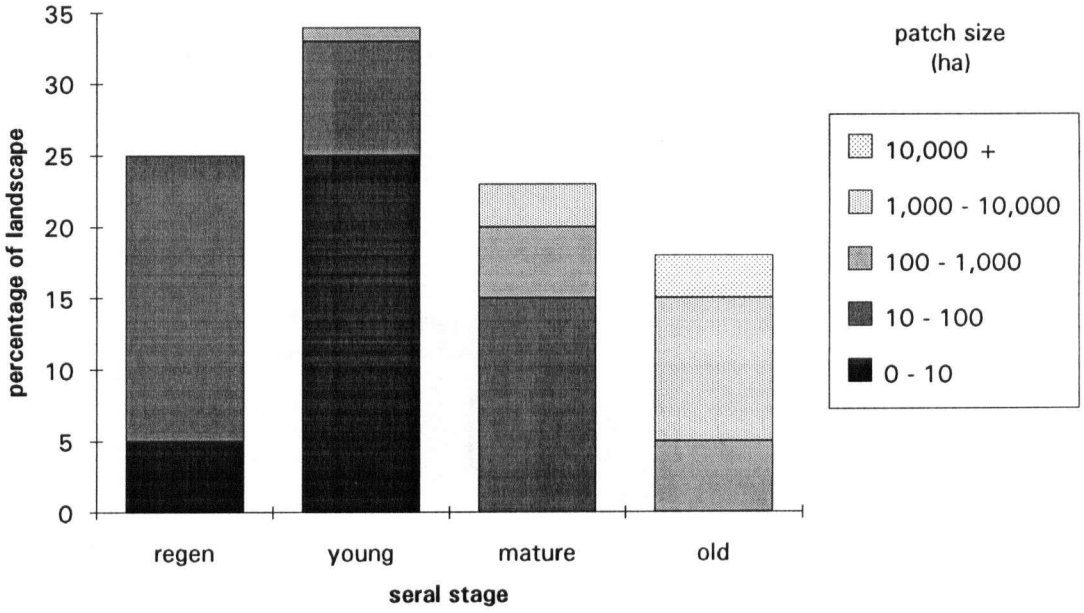



Figure 2.1 Proportion of hypothetical landscape occupied by (a) different ecosystem classes in different seral stages and (b) different patch sizes in different seral stages.

## Targets for biodiversity

I have described an approach to measurement which uses ecosystems to represent biodiversity, but I have not described the target landscape composition and pattern to maintain biodiversity. While the range of landscape conditions which will maintain biodiversity is largely unknown, one line of reasoning provides some guidance. If species are adapted to regional natural disturbance patterns (Bunnell 1994), landscape compositions and patterns similar to those created by natural disturbances may conserve biodiversity.

## Research and adaptive management

Management for biodiversity requires the support of research. Sufficient information exists to propose an operational representation of biodiversity, but the strength of this representation is unclear. Research is required to challenge basic premises and to refine the representation. The range of landscape conditions which conserve the species of a region is also unclear. Research is required to assess the influence of different landscape compositions and patterns on selected species. Biodiversity research need not focus on ecosystems to support ecosystem-based management. A focus on the mechanisms that determine the distribution of individuals and populations may provide more rigorously testable hypothesis and hence a relatively solid base of information. However, effort must be directed to translating this information into a form useful for management.

Two research approaches can be applied to resource management issues. Traditional research tries to define mechanisms leading to observed patterns and in doing so is often limited to examining small components of a problem. Adaptive management is a less reductionist approach which can examine the larger context of a management problem. Adaptive management designs resource use policies which probe for better understanding (Walters 1986). Adaptive management tests or challenges existing research findings and theories; done well it includes all

aspects of research design including replication and tests of alternative hypothesis; it compliments traditional research.

I have suggested that the complexity of biodiversity should be represented by ecosystems for land management purposes and in doing so have made several assumptions which should be tested by research:

1. plant species distributions depend on the abiotic environment and on the timing and intensity of disturbance;
2. vegetation structure, including newly generated structure and remnant structure, can be predicted from the abiotic environment and from the timing and intensity of disturbance;
3. insect species distributions depend on plant species distributions;
4. vertebrate species distributions depend on vegetation structure;
5. patch size and arrangement influences species distributions; and
6. edge habitat influences species distributions

In addition to testing specific assumptions, broad questions regarding the relationship of landscapes with species should be examined. Which land classes are correlated with different species and what are appropriate class boundaries? What factors other than seral stage, disturbance class and stand age are broadly correlated with species distributions? What range of landscape composition and pattern maintains a population? What is the importance of landscape composition relative to landscape pattern? Answering such questions will require study of large areas and many taxa, partly because correlations of species with landscape variables are often scale specific. Mechanisms responsible for such correlations will be more difficult to determine. Mechanisms are essential to know because changes in habitat may not generate immediate, obvious changes in species abundance but may cause changes in population dynamics leading to

population declines. Four types of species may provide more generally applicable feedback in research studies (Noss 1990):

1. ecological indicators: species whose response to change is characteristic of several others;
2. keystones: species on which a large part of the community depend;
3. umbrellas: species with large area requirements which, if present, indicate protection of sufficient area for many other species; and
4. vulnerables: species that, for some reason, are prone to extinction in human dominated landscapes.

## Discussion

This chapter has discussed biodiversity as the variety of life and its linking processes, symbolizing potential resources, our life support system and the intrinsic rights of other creatures. At a fundamental level, biodiversity is concerned with genes, but it may be considered from the levels of species and ecosystems. Humans can readily observe some variety between individuals and more variety between species. Intuitively, the species level seems an obvious choice as a practical measurement of biodiversity. However, formal definitions of biodiversity extend this intuition in two important ways, setting a global scale for biodiversity ("all life") and including less-visible variation (e.g., genes, processes, unobserved species). Measurements of biodiversity should hence be relevant to the global scale and should capture less-readily-observable variation: they should be comprehensive.

Because measurements of biodiversity (at any level) usually consider areas substantially smaller than the globe, they should be sensitive to events at small scales that might affect global biodiversity. Extirpation of populations influences global biodiversity; hence any measurement of biodiversity should be sensitive to the loss of populations. Species-level as well as ecosystem-level measurements must track components of the sample to identify decreasing abundance of a

species or ecosystem. Diversity indices which do not retain constituent identities do not address biodiversity because they cannot identify extirpations. The commonly used indices of species diversity do not represent biodiversity.

To be useful in the context of forest management, measurements of biodiversity must apply over large spatial and temporal scales and must recognize the uncertainty associated with prediction. As an additional constraint, land managers have limited resources to apply to the task of conservation, and cannot use complex measurements of genes and species. Thus biodiversity must be represented simply. Any practical measurements of biodiversity will compromise scope in one of two ways, lacking either precision (small scale variety) or breadth (variety in different regions).

I suggest that ecosystem-level measurements of biodiversity are appropriate for forest management. Because resource management is concerned fundamentally with the allocation of land to different uses, biodiversity must be linked with land. I propose that biodiversity should be represented by ecosystems described by abiotic variation, seral stage variation and remnant-structure variation. Ecosystem measurements are comprehensive and cover relatively large areas. They identify constituent pieces, and are hence sensitive to extirpations (within the limits of accuracy). Broad changes in the distribution of ecosystems on a landscape can be predicted with better certainty than can the distribution of species or genes. Impacts can be assessed by predicting landscapes (collections of ecosystems) resulting from proposed developments, and examining their composition and pattern.

Ecosystem-level measurements are limited in both precision and accuracy. Because ecosystems belonging to the same class will have different constituent species, populations may be extinguished even when all classes of ecosystem exist. Many constituent species, however, will be adequately represented. Also, a comprehensive ecosystem approach ensures that conservation efforts do not jump from issue to issue or from species to species depending on local bias.

The simplicity of an ecosystem approach facilitates management but may link weakly with real biodiversity. This link should be a research priority. Research and adaptive management can

aid management by clarifying relationships between the landscape and selected species and by improving predictions of landscape response to management. Land managers and researchers must collaborate to conserve biodiversity. Scientists, however, have different objectives than resource managers (Bunnell 1989). With regard to biodiversity, the roles and approaches of scientists should be clearly distinguished from those of land managers. Land managers make decisions based on several criteria and a few broad, but crude relationships, whereas scientists describe relationships with precision but often without breadth. A single interpretation or measurement of biodiversity is unlikely to meet the needs of both land managers and researchers.

A general strategy for measuring biodiversity should focus on several levels. Many approaches to conservation of biodiversity feature species or their habitat. I do not suggest an end to traditional species-based approaches but instead suggest that ecosystem-based approaches be combined with species-based approaches to provide a coarse and fine filter combination similar to that used by the Nature Conservancy (Noss 1987).

# Chapter 3.

# The Influence of Home Range and Dispersal on Species Distributions in Fragmented Landscapes: a Model.

"Big fleas have little fleas

Upon their backs to bite 'em;

The little ones have lesser ones,

And so *ad infinitum*."

Haldane 1985 pp. 103

adapted from Jonathan Swift 1733, "On Poetry"

## Introduction

Forest fragmentation occurs when urbanization and agricultural development create a patchwork from contiguous forest (Burgess and Sharpe 1981). Contiguous areas of old forest habitat are also fragmented when natural disturbance events (e.g., fire, windthrow) and forestry practices convert portions of an area to younger forest. Physical consequences of forest fragmentation include increased edge, increased isolation of old forest patches, reduced patch sizes and, more obviously, reduced total area of old forest habitat (Harris 1984). Biological consequences vary by species. Increased edge habitat is beneficial to some species and detrimental to others (Angelstam 1992). Increased isolation of habitat patches negatively affects species with low dispersal capability (Diamond 1975). Reduced patch size negatively affects species with large home ranges or territories (Diamond 1975). Generally, population size declines as habitat abundance declines. Some species, however, prefer the modified landscape over the original forest (Rudnicky and Hunter 1993). Benefits for some species can have costs for other species through increased levels of competition and predation (Whitcomb et al. 1981).

Forest managers charged with conservation face two critical questions: (1) how much old forest should be preserved and (2) how should the forested patches be arranged? No general theory describes the effects of forest fragmentation sufficiently well to address these questions. Island biogeography (MacArthur and Wilson 1967) provides some background, describing the effects of isolation and size in island systems, but its relevance to forested ecosystems, where "islands" of suitable habitat are quite similar to the "sea" of unsuitable habitat, is questionable (Margules et al. 1982). Growing understanding of edge effects in fragmented forests also provides useful guidance.

The relationship between landscape pattern and species distributions is being addressed by studies using two broad approaches. The first approach focuses on general descriptions of pattern; the second focuses on population dynamics in fragmented habitats. Many indices describe landscape pattern. Rogers (1993) reviews 70 indices and identifies several which best

distinguish test patterns. She notes redundancy in many of the indices and the inability of any index to characterize landscape structure adequately. In addition, the biological significance of many of these indices is not obvious. Percolation theory (Stauffer 1985) describes the connectivity of habitat in relation to the total amount of habitat. As the percentage of randomly located habitat on a map approaches 60%, the map becomes connected from boundary to boundary. The point of connectivity is an abrupt threshold. The pattern of habitat determines the habitat percentage at which the threshold occurs. For 27 real landscapes, the threshold varied from 42% to 70% before the landscape was connected (Gardner et al. 1991).

The influence of animal mobility on population dynamics was recognized by Levins (1970) who proposed that dispersal of individuals between sub-populations counteracted local extinction. Studies of patchy populations support this theory (e.g., Fahrig and Merriam 1985). Recently, Wiens et al. (1993) described a comprehensive framework for modelling population dynamics on fragmented landscapes. Models of population dynamics on fragmented landscapes are still relatively uncommon (but see Thomas et al. 1990) because insufficient data exist to develop such models for many species.

Neither description of physical patterns nor understanding the population dynamics of a single species (alone or in combination) sufficiently addresses the biological consequences of forest fragmentation. Ideally, the impacts of fragmentation on a wide range of species should be considered. Some modelling studies have included life history traits of a variety of species to provide more broadly applicable results. Toth et al. (1986) predict species richness in different patches using home range size and habitat requirements. They also consider juxtaposition of patches for species requiring different habitats for breeding and foraging. Gardner et al. (1991) model different dispersal strategies on real and simulated landscapes. Wilcove et al. (1986) present an interesting model examining the influence of fragmentation on two groups of species, the first with large area requirements and limited dispersal and the second with less stringent area requirements and larger dispersal. They use data from real landscapes, describing patch size and inter-patch distance, and model colonization and extinction processes based on island

biogeography theory. They do not specifically address the influence of each factor (area required, dispersal, patch size and habitat abundance).

This chapter presents a simple model which explores in detail the relationship between animal spatial requirements (home range, dispersal range, and viable population size) and landscape pattern (patch size and habitat abundance) over a range of spatial scales. I systematically vary home range, dispersal range, patch size and habitat abundance to determine the influence of each.

## Methods

### Approach

My model examines the general relationship between animal mobility and landscape pattern. I assume that four factors determine the distribution of species on a landscape. First, species have diverse habitat requirements; some species prefer old forest patches (Bunnell and Kremsater 1990). Second, the habitat value of patch edges may differ from interiors (Temple 1986). Third, each species has a characteristic home range and dispersal range which reflects its mobility (Wiens 1989, Holling 1992) . Fourth, barriers to movement influence survival of the individual and the population (Wiens et al. 1993). I use spatially-explicit simulation to model the relationship between mobility and landscape pattern.

In the simulation, I create habitat patches within the background mosaic of a raster map (large two-dimensional matrix) and then determine the suitability of the raster landscape for simulated animals, with assigned mobility. To survive, simulated animals require both contiguous habitat in excess of their assigned home range size and other home ranges within their dispersal range. Rather than modelling real species and landscapes, I explore the relationship between movement ability (home range, dispersal range) and landscape pattern systematically.

The model is scale-independent; i.e., the relative magnitude (ratios) of the variables, and hence the behaviour of the model, does not change with scale. Changing the size of the landscape is similar to photo-reducing or photo-enlarging a paper map: the size of patches and distance between patches will be reduced, but the relative geometry will be unchanged. Animals also show scale-independent traits: over a range of body sizes, the ratio of dispersal distance to home range radius does not differ greatly (approximately 15x to 27x for omnivores; Figure 3.1). Other factors (e.g., terrain traversed during dispersal) add to variation in this ratio and thus reduce the importance of body size. The model uses constant ratios of dispersal range to home range radius to remain scale-independent.

I examine edge effects on a subset of the landscapes. I assume that edge depth does not vary with patch size, thus edge effects depend on scale. To study edge, I use the same simulation approach described above, but assign absolute values to patch size and edge depth. The purpose of this portion of the study is to demonstrate how edge influences the general model, not to explore the influence of edge effects in detail.

The model has several assumptions and limitations:

- it assumes habitat is either usable or not usable with no gradation;
- it ignores animals which depend on more than one habitat type;
- it assumes that contiguous habitat is required for a home range and that home range size is fixed;
- it ignores the influence of population dynamics on emigration rates and colonization success;
- it ignores the influence of competition and predation on dispersal and colonization success; in reality, different patch sizes may have different suites of competitors and predators;
- it ignores the influence of ground cover on dispersal; and
- it does not include a temporal dimension and thus cannot assess the importance of habitat dynamics in relation to chance events such as dispersal.

**Model parameters**

In the model, landscapes are square (500 x 500 raster cells), consist of two land classes (habitat and a non-habitat background mosaic) and are defined by habitat abundance and patch size (Table 3.1). The proportion of habitat varies from 5%- 40% and the remainder of the landscape is defined as unusable. Forty percent is a reasonable upper limit because landscapes with 60% habitat and randomly located patches are connected from boundary to boundary (Stauffer 1985) and hence are not greatly fragmented.

Landscapes contain either patches of equal size or patches of mixed size. Equal patch sizes are expressed as a ratio of home range size and vary from 1/10x to 10,000x. On landscapes with mixed patch sizes, patch sizes range over four orders of magnitude and habitat is divided equally between patch-size classes. On these latter landscapes, I express patch sizes as a ratio of the largest patch size to home range size (arbitrarily). Patch locations are assigned randomly. I assume landscapes are sufficiently large that landscape boundaries do not influence results.

Home range and dispersal range describe the mobility of different species (Table 3.1). Variation in home range size covers at least four orders of magnitude (Figure 17 in Holling 1992). For example, omnivores ranging in size from 31 grams to 343 kg have home ranges which vary from 1 ha to 10,000 ha ($10^0$-$10^4$ ha; ). My model expresses home range in a ratio with patch size (PS/HR; Table 3.1). This ratio also expresses the number of home ranges in a patch. My model expresses dispersal distance as a ratio of home range radius (DD/HRR) and uses three DD/HRR ratios which encompass the range of maximum dispersal (5x, 20x, 50x) and one that assumes a complete barrier to dispersal (0x; Figure 3.1).

Simulated animals all use the same habitat, but habitat value may be modified by the proximity of patch boundaries (Table 3.1). I define three classes of animals: "Neutral" animals are not influenced by patch boundaries; "Edge" animals only use habitat within 100 m of a patch boundary; "Core" animals only use habitat greater than 100 m from a patch boundary (Harris

Table 3.1. Parameters used to define model landscapes and animal mobility.

| Parameter | Range of input values |
|---|---|
| habitat abundance | 5%, 10%, 20%, 40% |
| patch size / home range | 1/10, 1, 10, 100, 1,000, 10,000 (equal patch size) |
| maximum patch size[1] / home range | 1/10, 1, 10, 100, 1,000 (mixed patch size)<br>includes patches of 1, 10, 100, 1,000 cells; probability of occurrence = 1 / number of cells per patch |
| Dispersal / Home Range Radius | 0x, 5x, 20x, 50x |
| Edge Preference | Neutral: not influenced by patch boundary<br>Edge: use habitat ≤ 100 m from boundary<br>Core: use habitat ≥ 100 m from boundary |
| Minimum Viable Area | 500, 5,000 home ranges |

1. i.e., pactches with 1000 cells are the largest.

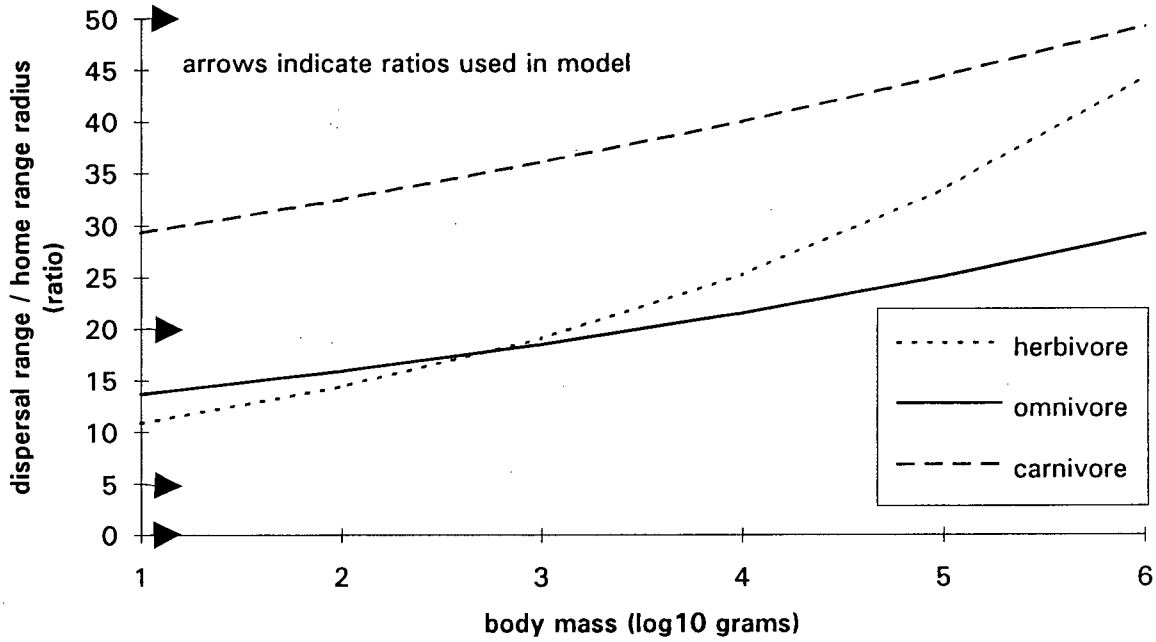



Figure 3.1. Ratio of dispersal range to home range radius versus body size for herbivores, omnivores and carnivores. Based on data from Holling (1992) and Sutherland (unpublished, University of British Columbia).

1984). In simulations examining edge effect, I fix the scale of the model and set home range size at either one hectare or ten hectares; I calculate other parameter values using ratios in Table 3.1.

I assume that, to be viable, populations of animals require an area of usable habitat which exceeds 500x home range size (see Shaffer 1981). I also examine the possibility that an area greater than 5000x home range size is required.

**Spatial simulation algorithms**

The simulation proceeds in four stages:

1) Creating the landscape: The model creates a 500 cell by 500 cell raster grid. Patches of suitable habitat of either a single size or a mix of sizes are generated by placing concentric squares around a randomly located center cell until the desired patch size is reached. Patch shape may not be completely square because formation of the last concentric square is terminated when the desired patch size is reached. As patches are generated, they may touch or overlap. Patch generation is ended when the specified amount (5%, 10%, 20% or 40%) of the landscape is covered in habitat. In simulations considering edge or core animals, habitat cells which are within 100 m of adjacent mosaic cells are flagged as edge cells. Edge cells are the only usable cells for edge animals and are unusable for core animals.
2) Identifying home ranges: Candidate home ranges are formed from contiguous patches of habitat. The size of each candidate home range is then calculated and those larger than the home range parameter are flagged as usable home range (or simply home range). Although the patch size specified in step one may be smaller than a home range, adjacent patches may merge to form a candidate home range. Raster cells touching at the sides or the corners are considered adjacent. Subsequently, patch size refers to the patch size originally

generated in step 1 (1, 10, 100, 1000, 10000 cells), not to the size that is created by merging overlapping or touching patches.

3) Identifying dispersal ranges: The model calculates the minimum distance from each landscape cell to the nearest home range cell using dynamic programming. Minimum distances are compared to the dispersal distance parameter to identify portions of the landscape that are accessible. Portions of the landscape connected by dispersal are flagged and contiguous portions are aggregated into dispersal regions.

4) Determining landscape suitability: *Landscape suitability* is defined as the area of home range within regions connected by dispersal, where home range area within the region exceeds the specified minimum area for a viable population. If the area of connected home ranges is less than the area required for a viable population, landscape suitability is zero.

The number of patches and number of home ranges created in a simulation limits the range of PS/HR parameters which can be examined (Table 3.2). In a particular simulation, raster cell size is either set equal to home range size or to patch size. These cell sizes provide the necessary precision to model home range, dispersal and patch location, but they limit the range of PS/HR which can be modelled. Reducing the precision of the home range and dispersal simulation is feasible but reducing the precision of patch placement is not: patch locations cannot be modelled when cell size exceeds patch size. Simulating PS/HR ratios smaller than 1/10 is not possible without reducing total landscape area to less than the area of a viable population.

I performed three replicates of each of one hundred and seventy-six scale-independent simulations (11 PS/HR x 4 DD/HRR x 4 habitat abundance). Additional simulations examined edge effects and viable area requirements equal to 5000 home ranges. On landscapes with mixed patches, I used several grain sizes and combined the results. In some of the simulations with large patches, I increased cell size by one or two orders of magnitude to determine if the small number of patches influenced the results. To explore an observed threshold effect, I

calculated largest connected area (i.e., maximum home range size) for habitat abundances ranging from 35% to 45% (1% increments) on landscapes where PS/HR equaled one.

Table 3.2. Number of patches, potential number of home ranges and cell size used in simulations with different ratios of patch size to home range size on landscapes with 250,000 raster cells, equal patch size and 5% habitat abundance (12,500 raster cells of habitat).

| | patch size / home range size | | | | | |
|---|---|---|---|---|---|---|
| | **1/10** | **1** | **10** | **100** | **1000** | **10000** |
| **n patches**[1] | 12500 | 12500 | 1250 | 125 | 12.5 | 1.25 |
| **n HRs**[2] | 1250 | 12500 | 12500 | 12500 | 12500 | 12500 |
| **cells / patch** | 1 | 1 | 10 | 100 | 1000 | 10000 |
| **cells / HR** | 10 | 1 | 1 | 1 | 1 | 1 |

1. Number of suitable patches
2. Maximum possible number of home ranges

## Results

### General model behaviour

On most landscapes, suitability was either high or zero; few landscapes were partially suitable (Table 3.3). When suitability was high or low each replicate produced near identical scores. When a landscape was partially suitable, the variation in scores between replicates increased. Cell size did not greatly influence results. All figures and tables are based on mean suitability scores derived from the three replicates with the same cell size.

### Effects of home range and dispersal

Home range and dispersal range limited landscape suitability. When patch size was smaller than home range size, home ranges usually could not be created. However, on landscapes with 40% habitat abundance, many patches partially overlapped or were adjacent;

Table 3.3. Landscape suitability for neutral animals grouped by the ratio of patch size to home range size, dispersal range and habitat abundance. Suitability is expressed in quartiles: "x" = 1%-25%; "xx" = 26%-50%; "xxx" = 51%-75%; "xxxx" = 76%-100%; and blank cells < 1%.

| Habitat Abundance | DR[3] | single patch size: patch size / home range[1] -1 | 0 | 1 | 2 | 3 | mixed patch sizes: max patch size / home range[2] -1 | 0 | 1 | 2 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 5% | 0x | | | | | xxxx | | | | | xx |
| | 5x | | | | | xxxx | | | | | xx |
| | 20x | | xxxx | xx | x | xxxx | | | xxx | xxxx | xxxx |
| | 50x | | xxxx | xxxx | xxx | xxxx | | xx | xxx | xxxx | xxxx |
| 10% | 0x | | | | | xxxx | | | | | x |
| | 5x | | x | | x | xxxx | | | | | xx |
| | 20x | | xxxx | xxxx | xx | xxxx | | xx | xxx | xxxx | xxxx |
| | 50x | | xxxx | xxxx | xxxx | xxxx | | xx | xxx | xxxx | xxxx |
| 20% | 0x | | | | x | xxxx | | | | xx | xx |
| | 5x | | xxxx | x | x | xxxx | | | x | xx | xx |
| | 20x | x | xxxx | xxxx | xxxx | xxxx | x | xx | xxx | xxxx | xxxx |
| | 50x | x | xxxx | xxxx | xxxx | xxxx | x | xx | xxx | xxxx | xxxx |
| 40% | 0x | xx | xxx | xx | xxx | xxxx | | | | x | xx |
| | 5x | xxxx | xxxx | xxxx | xxxx | xxxx | x | xx | xxx | xxxx | xxxx |
| | 20x | xxxx | xxxx | xxxx | xxxx | xxxx | x | xx | xxx | xxxx | xxxx |
| | 50x | xxxx | xxxx | xxxx | xxxx | xxxx | x | xx | xxx | xxxx | xxxx |

1. Ratio of patch size to home range size ($\log_{10}$ ); ratios of 4 produced the same results as 3.
2. Ratio of maximum patch size in mixed patch size landscape to home range size ($\log_{10}$ ).
3. Dispersal ratio (dispersal range / home range radius).

thus, large home ranges could be created from many small touching patches (Figure 3.2). Further exploration revealed that a connectivity threshold occurs near 40% habitat abundance (PS/HR = 1; largest connected area is about 2,500 cells at 38% and about 84,000 cells at 42%). At 40% habitat abundance, the largest connected area is about 24,000 cells (PS/HR = 1). The connection of home ranges into larger regions by dispersal showed a similar threshold response. As dispersal distance increased, landscapes moved from mostly unconnected to mostly connected at a threshold distance equal to the mean inter-patch distance. For example, landscapes which were largely unconnected for an animal with 5x dispersal became mostly connected when dispersal was increased to 20x (Figure 3.3).

Landscape suitability depends on habitat abundance, relative patch size (PS/HR) and relative dispersal range (DD/HRR; Figure 3.4, 3.5). Suitability increases as habitat abundance increases, but, relative patch size interacts with habitat abundance to complicate this relationship. For example, when patch size is less than home range size, variation in habitat abundance from 5%-10% does not affect suitability. The relationship between suitability and relative patch size tends to follow two general patterns: first, when relative dispersal is small (0x, 5x) and the distance between patches is high (5% or 10% habitat abundance), suitability tends to be low until patch size exceeds 1000x home range size (each patch able to support a viable population); second, where relative dispersal or habitat abundance is higher, suitability tends to be low until patch size equals or exceeds home range size (each patch able to support an individual). Note however that suitability may drop when patch sizes are 10x to 100x larger than the home range because inter-patch distance increases as patch size increases (see Appendix 1). Effects of patch size are less pronounced on landscapes with greater habitat abundance. On these landscapes, larger home ranges can be created because patches touch or overlap. When dispersal is sufficiently high (50x) patch sizes larger than the home range have little influence on suitability.

On landscapes with mixed patch sizes, suitability is highest when home ranges are relatively small and dispersal is relatively high (Figure 3.6). As home range increases and dispersal range decreases, suitability decreases. Suitability is higher on landscapes with higher

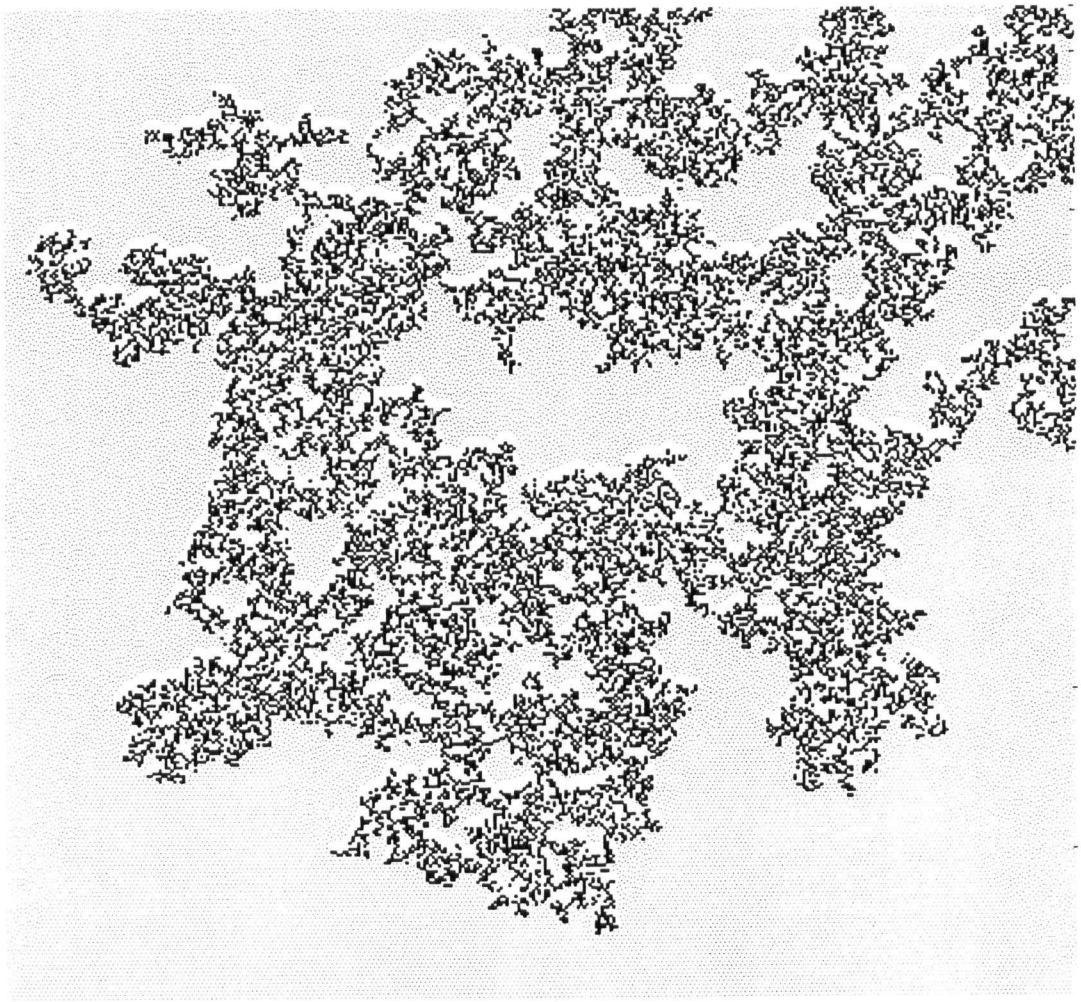



Figure 3.2. Map of home range area for simulated animals requiring 1000 ha home ranges on a landscape with one ha patches and 40% habitat abundance.

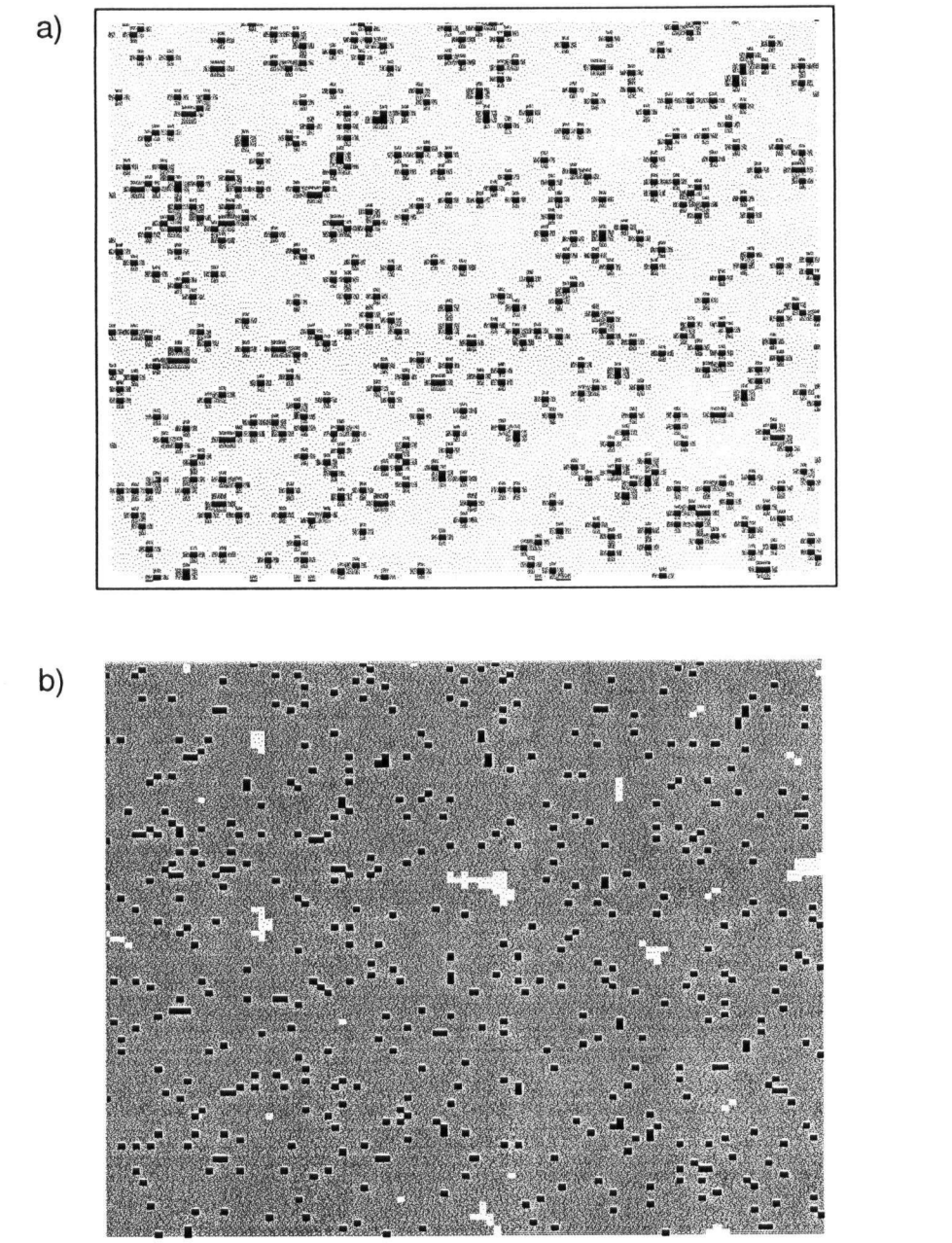



Figure 3.3. Map of landscapes with one ha patches and 5% habitat abundance for simulated animals with one hectare home ranges and (a) 5x dispersal and (b) 20x dispersal.

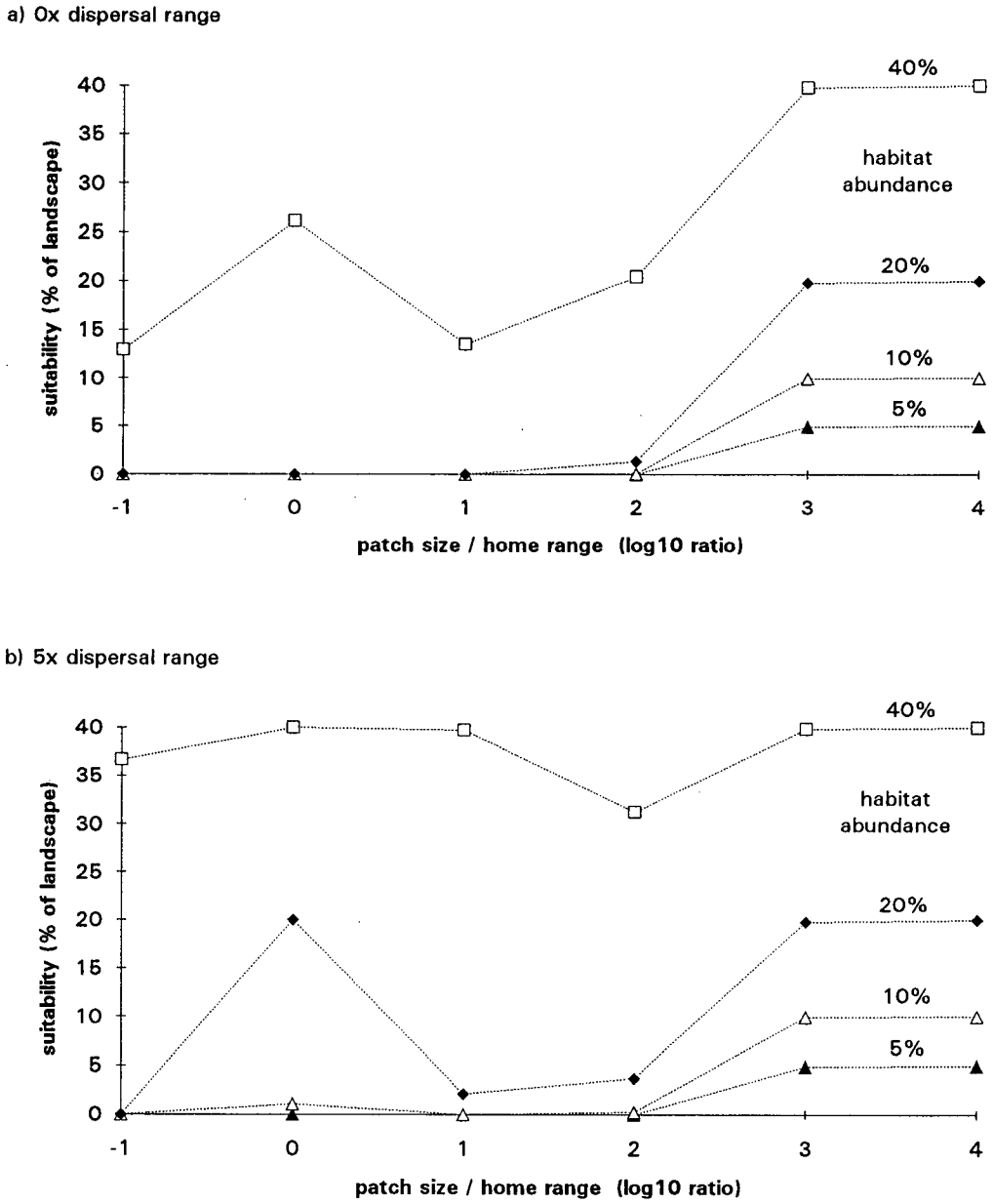
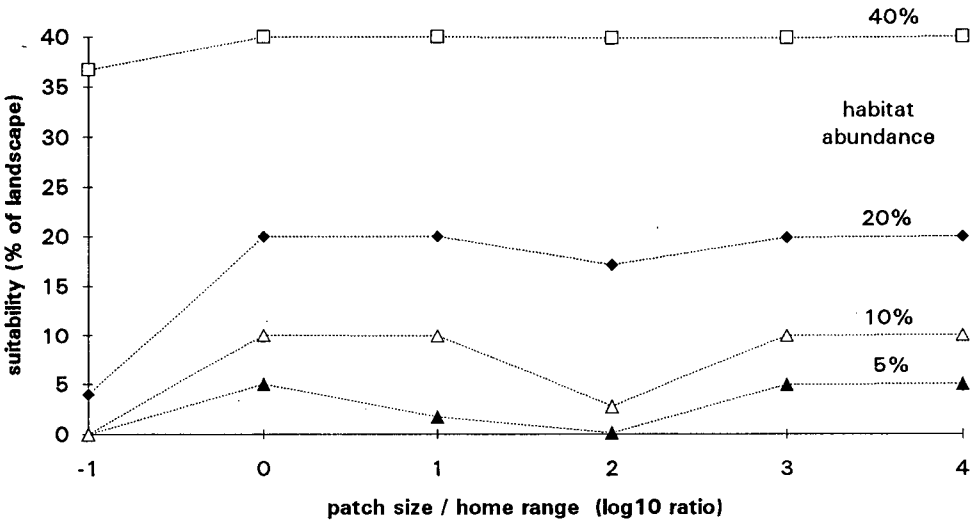



Figure 3.4. Landscape suitability versus the ratio of patch size to home range size for different habitat abundances and for dispersal ranges of (a) 0x and (b) 5x.

a) 20x dispersal range




b) 50x dispersal range

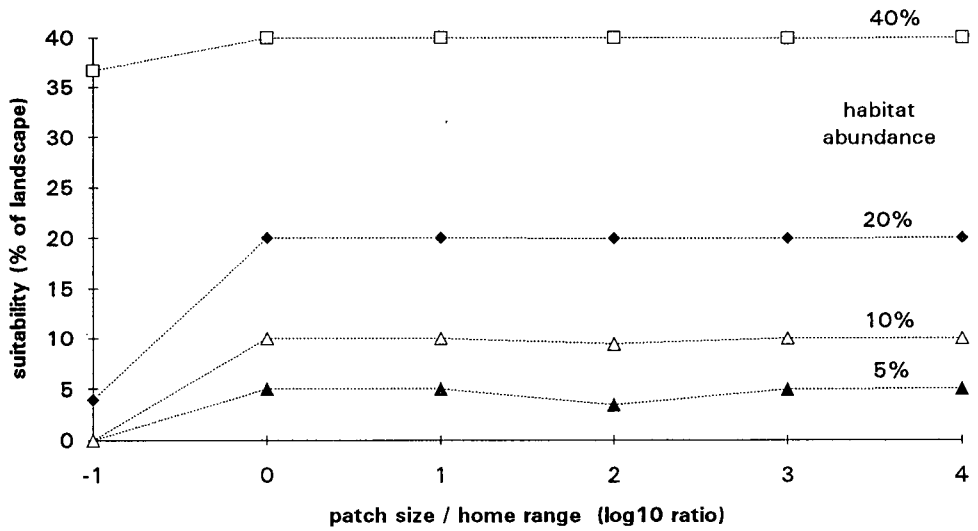



Figure 3.5. Landscape suitability versus the ratio of patch size to home range size for different habitat abundances and for dispersal ranges of (a) 20x and (b) 50x.

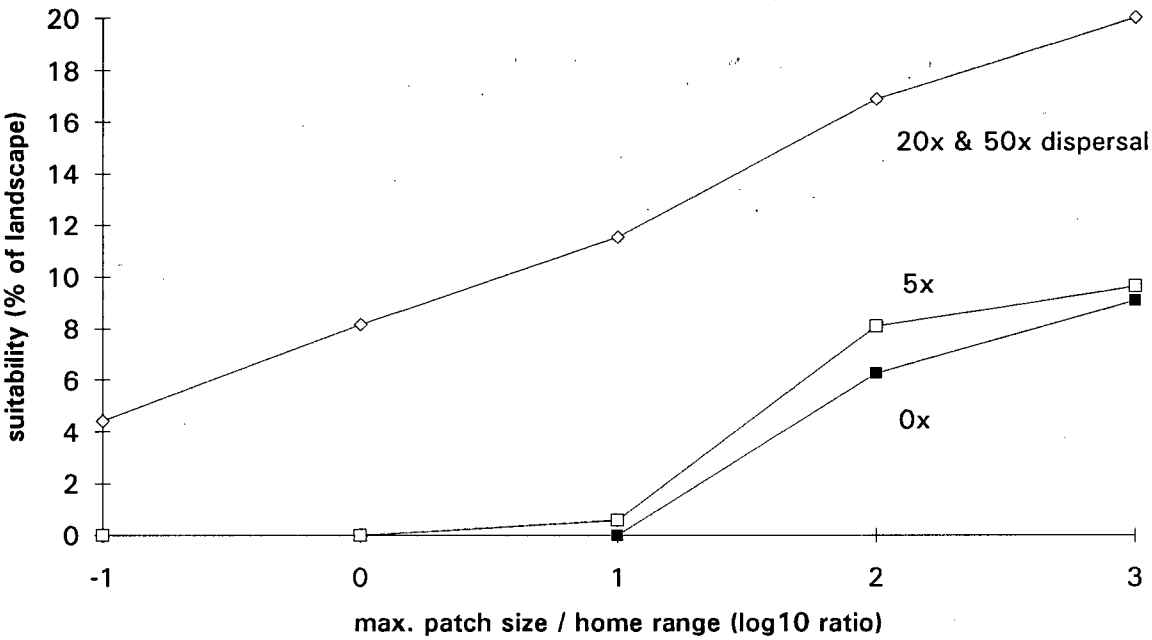



Figure 3.6. Landscape suitability versus the ratio of patch size to home range size for different dispersal ranges on landscapes with mixed patch sizes and 20% habitat abundance.

habitat abundance (Table 3.3). Overall, landscape suitability is higher for animals with relatively small home ranges and relatively large dispersal ranges (Table 3.3).

**Effects of edge**

Landscape suitability was calculated for core and edge animals with 1 and 10 ha home ranges and various dispersal ranges on landscapes with 20% habitat abundance and patch sizes ranging from 1 to 10,000 ha. Results for this section cannot be scaled because of the assumption that edge depth is a constant 100 m. Edge habitat dominates small patches and core habitat dominates large patches (Figure 3.7). Suitability for edge animals with one ha home ranges is highest on landscapes with 1 ha patches and declines as patch size increases (Table 3.4). Suitability for edge animals with 10 ha home ranges is highest on landscapes with 10 ha patches and declines as patch size increases or decreases. Suitability increases with increasing dispersal range. With a complete dispersal barrier (0x), suitability for edge animals is zero on all landscapes. Landscape suitability for core animals (Table 3.4) is similar to that for neutral animals, being high on landscapes with patches of 1000x home range size. Unlike neutral animals, however, suitability is not high when patch size equals home range size, because most of the patch is edge habitat.

**Effects of viable population size**

When viable area requirements increase from 500 to 5000 home ranges, patches of 100x to 1000x home range size have lower suitability (Figure 3.8). The two measures of suitability are equal at smaller and larger patch sizes.

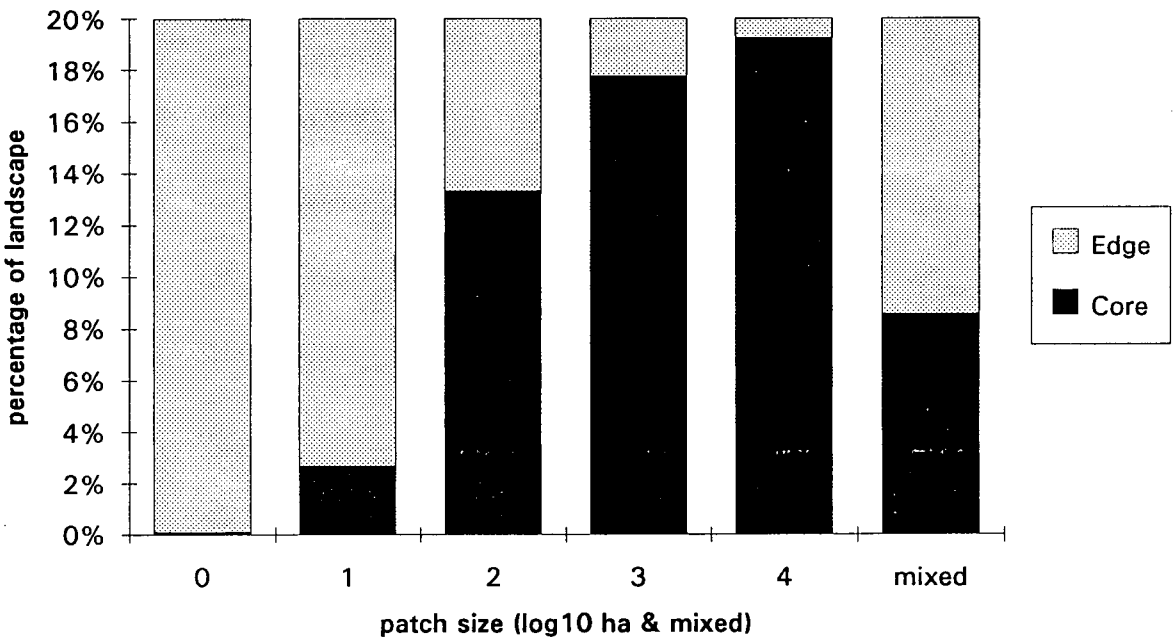



Figure 3.7. Percentage of core and edge habitat versus patch size on landscapes with 20% habitat abundance.

Table 3.4 Landscape suitability for neutral, core and edge animals grouped by patch size, home range size, and dispersal range for landscapes with 20% habitat abundance. Suitability is expressed in quartiles: "x" = 1%-25%; "xx" = 26%-50%; "xxx" = 51%-75%; "xxxx" = 76%-100%; and blank cells < 1%.

| | | neutral animals | | | | | | core animals | | | | | | edge animals | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | patch size ($log_{10}$ ha & mixed) | | | | | | patch size ($log_{10}$ ha & mixed) | | | | | | patch size ($log_{10}$ ha & mixed) | | | | | |
| hr[1] | dr[2] | 0 | 1 | 2 | 3 | 4 | m | 0 | 1 | 2 | 3 | 4 | m | 0 | 1 | 2 | 3 | 4 | m |
| | 0x | | | x | xxxx | xxxx | xx | | | x | xxxx | xxxx | xx | | | | | | |
| 0 | 5x | xxxx | x | x | xxxx | xxxx | xx | | | x | xxxx | xxxx | xx | xxxx | x | | | | x |
| | 20x | xxxx | xxxx | xxxx | xxxx | xxxx | xxxx | | xxx | xxxx | xxxx | xxxx | xxx | xxxx | xxxx | x | x | | xxx |
| | 50x | xxxx | xxxx | xxxx | xxxx | xxxx | xxxx | | xxx | xxxx | xxxx | xxxx | xxxx | xxxx | xxxx | xx | x | | xxx |
| | 0x | | | | x | xxxx | xx | | | | | xxxx | | | | | | | |
| 1 | 5x | | xxxx | x | x | xxxx | xx | | | | xx | xxxx | | | xxx | | | | |
| | 20x | x | xxxx | xxxx | xxxx | xxxx | xxxx | | | xxxx | xxxx | xxxx | xxx | x | xxx | xx | | | xx |
| | 50x | x | xxxx | xxxx | xxxx | xxxx | xxxx | | | xxxx | xxxx | xxxx | xxxx | x | xxx | xx | x | | xx |

1. Home range area ($log_{10}$ ha)
2. Dispersal ratio (dispersal range / home range radius).

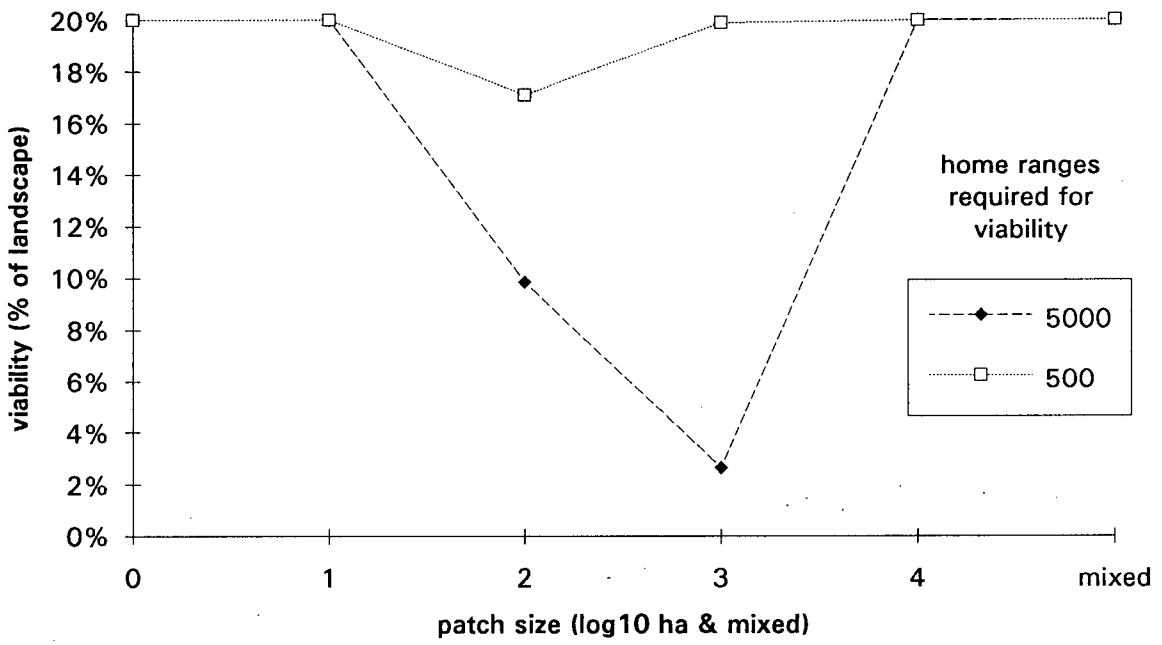



Figure 3.8. Landscape suitability versus the ratio of patch size to home range size for different viable area requirements. Dispersal is 20x and habitat abundance is 20%.

## Discussion

My results suggest some interesting geometric relationships and identify key parameters and assumptions worthy of further research. They can be extrapolated to provide general guidance for land managers.

### Geometry

Habitat abundance and patch size interact with home range, dispersal range and area required for a viable population to determine landscape suitability in the model. Edge habitat also influences suitability.

The relationship between the mobility of animals and landscape pattern showed three major trends. First and somewhat surprisingly, suitability decreased as patch size increased beyond home range size (until patches supported a viable population). Second, suitability increased as habitat abundance increased. Third, once large patches supported viable populations, other parameters ceased to be important. Two key interactions determined the suitability of the landscape when single patches did not support viable populations. First the ratio of patch size to home range size determined if home ranges could be created on landscapes where habitat abundance was less than 40%. Second, the ratio of dispersal distance to inter-patch distance determined if dispersal between home ranges was possible.

Appendix 1 describes a graphical model relating landscape pattern to animal mobility. The graphical model illustrates the interaction of patch size, inter-patch distance and habitat abundance and then relates these landscape variables to animal mobility. It generates the same pattern of results as the simulation: landscapes with large patches (relative to home range size) and low habitat abundance have inter-patch distances which exceed the maximum dispersal distance of an animal (Figure 3.9). The simulations presented above and the graphical model predict reduced dispersal success on landscapes (5-10% habitat abundance) with habitat patches

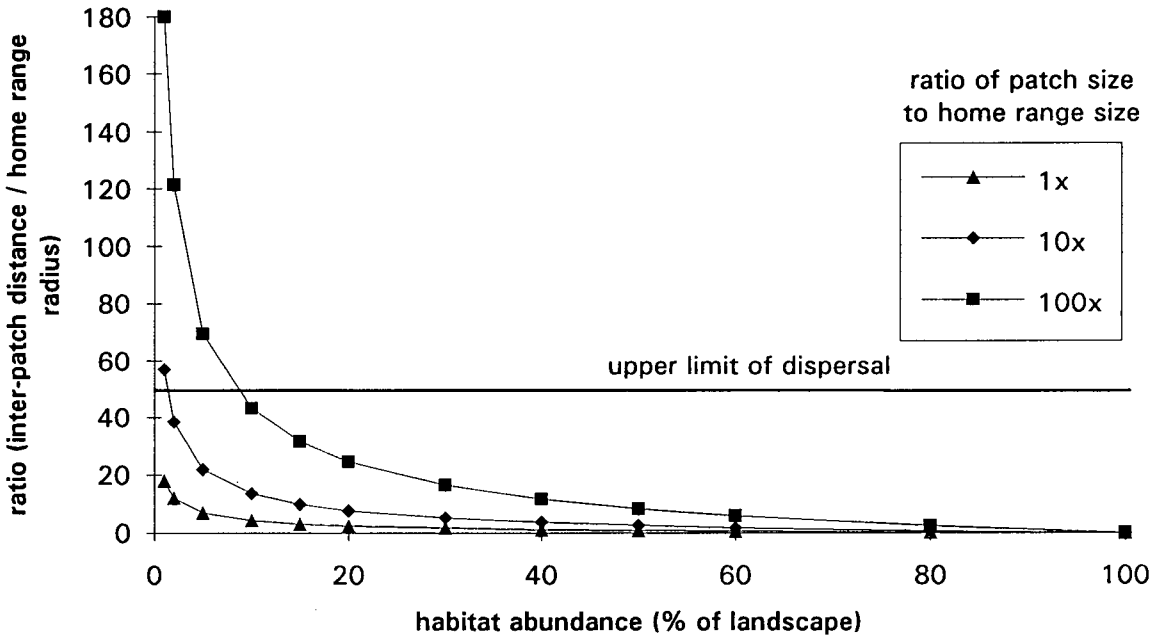



Figure 3.9. Ratio of inter-patch distance to home range radius versus habitat abundance for different ratios of patch size to home range size on a simple model landscape (square patches of equal size, evenly distributed in a regular grid).

of 10x-100x home range size relative to landscapes with smaller and larger patches. I also predict decreased long-term presence and abundance of species for the same situation.

On landscapes with mixed patch sizes, habitat abundance is divided equally between four different patch sizes. The abundance of usable patches for animals with the large home ranges is one quarter of the total habitat abundance. For animals with small home ranges, the mean inter-patch distance is higher on landscapes with mixed patch sizes than on landscapes with small patch sizes. Attempting to meet the requirements of diverse groups of species means that less resources are available for any one group.

With a fixed edge depth of 100 meters, edge accounts for the majority of habitat in 1 ha and 10 ha patches. Core animals with small home ranges cannot use landscapes where the patch size equals the home range size because little or no core habitat exists in these patches. When patches reach sufficient size to contain core habitat, the larger inter-patch distance associated with larger patches, further increased by the need to cross edge habitat, reduces connectivity for core animals. Core animals require either (1) patches large enough to support viable populations or (2) higher habitat abundance than animals which are unaffected by edge habitat.

The model shows two thresholds of connectivity, one with home range and one with dispersal. As habitat abundance increases, the increasing probability of randomly-located patches touching allows large home ranges to be created. This phenomena occurs near 40% habitat abundance in this model. A similar threshold effect occurs with dispersal. For a given dispersal range, landscapes move from mostly unconnected to mostly connected as habitat abundance increases. This threshold effect is described by percolation theory (Stauffer 1985). Because of these threshold effects, there may be little warning before a population collapses.

My model differs from the standard percolation model by connecting cell corners as well as cell edges and by having patches that are larger than the cell size (i.e., increased resolution). Percolation models do not strictly apply when patch sizes are larger than cell size. Essentially, finer cell sizes allow better distinction of gaps between patches.

**Key parameters and assumptions**

This model assumes contiguous habitat is necessary for a home range and that home range size is fixed. However, home range size may vary with resource density (Thomas et al. 1990). The relationship between resource density and habitat value must be better understood because forestry modifies resource densities.

Data describing maximum dispersal distance were useful for determining the range of parameters to model. However, in a real population, home ranges would have to be much closer than the maximum dispersal distance to maintain the population. The actual distance required will vary with rates of immigration (a function of population size and growth rate) and mortality. Vegetation cover may also affect maximum dispersal distance. The influence of vegetation cover on dispersal is important to know because of the significant influence of forestry on vegetation cover.

Minimum viable population size is an important factor under specific conditions in the model. When patch size is large relative to home range size, the connectivity of home ranges is relatively low. Whether or not such large patches support a viable population is a critical factor. When patch size is closer to home range size, patches tend to be mostly connected or mostly unconnected depending on habitat abundance; hence, on a large landscape, minimum viable population size is not an important factor when patch size is similar to home range size.

**Management implications**

Heated debate over what constitutes a "good" landscape pattern has at times dominated the conservation literature. The argument was captured with the acronym SLOSS referring to the options of Single Large Or Several Small reserves. Different assumptions suggest different patterns. My model illustrates the relationship between animal mobility and landscape pattern, and provides one perspective on what constitutes a good landscape. Conservation of biodiversity requires consideration of a wide range of species. This section combines selected results from

my model and applies them to a particular scale to increase their relevance to conservation issues.

I measure overall conservation value of a landscape pattern as the number of mobility strategies (i.e., home range and dispersal range) which have non-zero landscape suitability. I assume that increased landscape suitability is of little benefit once the threshold for viability is achieved. I consider animal home ranges from 1 ha to 10,000 ha and patch sizes from 1 ha to 10,000 ha. I assume that variation in home range size from 1 ha to 10,000 ha sufficiently represents natural variation.

Results of the scale-independent model do not consider situations where home range size exceeds patch size by more than 10x. When home range size exceeds patch size by more than 10x, I assume that landscape suitability is zero at habitat abundances of 5%, 10% and 20% and that landscape suitability is non-zero at 40% habitat abundance. Data from 1/10x PS/HR and maps from 1/100x and 1/1000x PS/HR support these assumptions.

The number of mobility strategies with non-zero landscape suitability increases with habitat abundance and in most cases increases with patch size (Figure 3.10). Patch size and habitat abundance interact. Patch size has less influence when habitat abundance is high (40%), because home ranges can be created from patches of less than home range size and because patches are relatively close. Mixed patches, from 1 ha to 1,000 ha, have lower landscape suitability than equal patches of 1,000 ha, but higher suitability than equal patches of smaller size. The decision to ignore landscape suitability beyond the viability threshold favours mixed patches because only a portion of these landscapes are suitable in many cases.

The model suggests that large or mixed patches are better than small patches. More importantly, it suggests that habitat abundance is the key factor influencing the biological consequences of patch size. Large patches are of greatest benefit where habitat abundance is low or where dispersal barriers exist. Wilcove et al. (1986), using a model with a different formulation, arrived at some similar conclusions. They found that extirpations began when

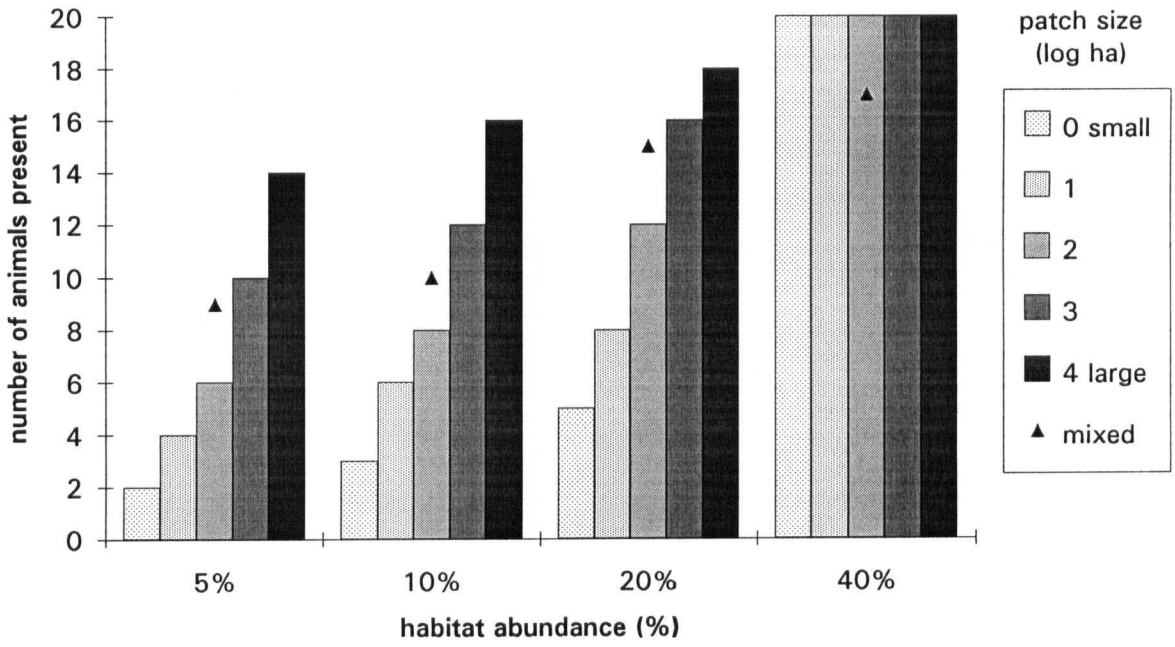



Figure 3.10. Number of mobility strategies with non-zero landscape suitability versus habitat abundance and patch size.

habitat abundance was reduced below approximately 40% and that one large patch maintained more species than a fragmented landscape. From these general patterns, I suggest courses of action for managers of forest land in relation to habitat abundance and patch size.

Reducing habitat abundance causes two types of negative impacts on species: first, it reduces the total number of sites available for home ranges; and second, it reduces the connectivity of available home ranges. The model shows a qualitative shift in behaviour when habitat abundance is 40%: landscape suitability at this abundance is much less sensitive to assumptions about home range, dispersal range and patch size. This shift in behaviour reflects a connectivity threshold. However, the 40% threshold point depends on the assumptions used in this model. In a study of 27 mapped landscapes in Georgia, threshold habitat abundance ranged from 42% to 70% (Gardner et al. 1991). Remembering the limitations of the 40% figure, two options for land management are proposed:

1. Play it safe: keep approximately 40% (well distributed) of the landscape in natural conditions and support limited biological research.
2. Push the limit: keep < 40% of the landscape in natural conditions, worry about the size and arrangement of patches, and invest heavily in research to better understand factors influencing dispersal success. Even with large investments in research and management, the risk of unforeseen events reduces the desirability of this option.

Patch size had a large influence on suitability, particularly on landscapes with lower habitat abundance. The model suggests two options for patch size:

1. Large patch size: Large patches maintained the highest range of mobility strategies. Large patches are large enough for viable populations of smaller animals. Large animals can disperse between patches. However, animals of intermediate size may find large patches

too small for a viable population and too far apart for dispersal. Where dispersal barriers exist, large patches are beneficial simply because they support viable populations.

2. Mixed patch size: Landscapes with mixed patch sizes maintained a moderate range of mobility strategies. Landscapes with large patches scored better, but may fare worse if species interactions are modelled. If competition and predation influence survival and if patches of different size contain different combinations of species, then suitability for some species is increased by the absence of others in some patches.

Forest fragmentation occurs at scales and patterns reflecting current technology and government regulations. We know the benefits of resource use but we have poor understanding of the costs to us and to other species. Our understanding of ecosystems is not yet sufficient to describe appropriate management strategies in detail, however as this model suggests, the more extensively we modify a system, the more likely we will be to negatively impact other species. What level of management we finally choose depends on how we weigh the costs and benefits and how much risk we wish to take. Paradoxically, those charged with land management seem better versed with the direct benefits than the direct and indirect costs.

# Chapter 4.

## SIMFOR: Software for Simulating Forest Management and Assessing Biodiversity

"Every program has at least one bug and can be shortened by at least one instruction—from which, by induction, one can deduce that every program can be reduced to one instruction which doesn't work."

from /usr/games/fortune, UNIX Fortune Cookie, unixg.ubc.ca

## Introduction

Chapter 2 developed an approach for measuring biodiveristy in managed forests. This chapter describes a model which employs that approach, illustrating its application with an example. Explicit modelling is an essential component of forest management for at least two reasons. First, management acts on complex and inter-connected ecosystems where impacts extend beyond the target resource. Second, the impacts of forestry accumulate over time and over large areas. Models can track and graphically display interactions, multiple consequences and cumulative effects. Models are quickly and easily manipulated relative to real systems, and, if they adequately characterize the real system, they can indicate its response to manipulation.

Models, ranging from simple equations to linear programs and simulations, have been used to aid forest management decisions at stand and landscape scales. With computer-based approaches, more aspects of real systems, including biological and economic processes, may be simulated but this added complexity can also obscure key assumptions and limitations of the model. Many of the newer models are better at graphically depicting key processes. They can be used to gain understanding of forest ecosystems rather than to simply generate solutions. Recently, geographic information systems (GIS), have been applied in forest management for cartography and resource analysis (Jordan 1992). The use of GIS has highlighted the importance of spatial relationships in forest management: resources are linked with the landscape, and extracting one resource from a specific location impacts others in that area and in surrounding areas. Several recent forest planning models combine spatial simulation with temporal simulation in an attempt to link clearly some of the important interactions in managed forests, at the stand level (e.g., Alvarez-Buylla and Garcia-Barrios 1993) and the landscape level (e.g., Baskent and Jordan 1991, Nelson and Finn 1991, Sessions and Sessions 1991). Ignoring spatial information may significantly influence predicted levels of sustainable resource use (Daust and Nelson 1993).

Wildlife modelling has followed similar trends to forest modelling, moving from non-spatial models of populations and habitat to models which include the spatial pattern of habitat

resources (Daust and Bunnell 1994). With recent concern for biodiversity and recognition of the importance of patterns of forest fragmentation (Harris 1984), spatial modelling of the impacts of forest management on wildlife has become more common (e.g., Thomas et al. 1990).

Conservation efforts in managed forests are complicated by the broad scope of biodiversity. Rules or guidelines, developed by "experts", are used to help managers develop plans to conserve biodiversity. Several models are capable of simulating forest dynamics and of predicting the consequences of such rules and guidelines on timber supply and economic indicators (e.g., Nelson and Finn 1991). Several models predict the habitat value of different forested stands (e.g., Van Horne and Wiens 1991). Software is available to measure landscape patterns (Fragstats; McGarigal and Marks in prep.) which may indicate broad impacts on biodiversity. General modelling approaches for assessing vertebrate diversity in forests have also been described (Daust and Bunnell 1992, Davis and Barrett 1992, Hansen et al. 1993). Integrated software specifically designed to assess impacts of forest management on biodiversity by analyzing landscape pattern, forest structure and vertebrate habitat has not been described. In this chapter, I describe such software. I demonstrate the application of this software with a case study.

## Description of SIMFOR

### Overview

SIMFOR simulates changes due to growth, succession and planned forest operations in a 5,000 to 50,000 ha forested area over an approximate 300 year period; it calculates landscape statistics, tracks forest structure and determines habitat distributions of selected species at specified sampling intervals. SIMFOR is a gaming tool: it simulates alternative management plans and generates descriptive information. SIMFOR provides insight not answers: it does not identify the best management option, rather where possible, it provides information describing why a condition (e.g., poor habitat for a species) is predicted.

In SIMFOR, the condition of the forest landscape in any location at any time is described by ecosystem class, disturbance class and stand age (time since disturbance). Ecosystem class reflects abiotic variation and site productivity. Disturbance class refers to characteristic forest structures that remain after site disturbance (e.g., from fire, insect damage or selection cutting). Note that disturbance class includes both natural disturbance and forest management treatments. Stand age is measured in years. Ecosystem class, disturbance class and stand age are used to predict vegetation structure at the stand scale. Stand structure is described by a suite of forest attributes. For each ecosystem class and disturbance class, a set of curves defines the abundance of selected forest attributes at different stand ages so that at any location and any point in time in the simulation, the amount of each forest attribute may be quantified. Landscape statistics are derived from the composition and pattern of ecosystem classes and seral stages. Seral stages are different stages in the succession and development of forest stands and the rate of seral stage development depends on ecosystem class and disturbance class. Structural attributes of stands play important roles in the ecology of forests and, in SIMFOR, vertebrate habitat depends on the distribution of forest attributes on the landscape.

Before use, SIMFOR requires information describing the current forest landscape, the rates of succession and growth of selected forest attributes and the locations of proposed harvest units. Current forest conditions are often described by existing forest inventories. Harvest plans must be developed externally (manually or using other models). The rates of development and decline of forest attributes (e.g., snags) may not be readily available and will have to be developed from existing inventory data or new research. The following steps are required to set up SIMFOR for a new area:

1. using forest inventory data, create maps of stand age, ecosystem class (usually a combination of Biogeoclimatic subzone [Pojar et al. 1987] and site index) and disturbance class (describing the degree to which the last natural disturbance or management treatment maintained forest structure) and translate these maps to SIMFOR format;

2. for each combination of disturbance class and ecosystem class, create curves describing the development and decline of forest attributes over time (see below for further detail);
3. translate harvest unit maps to SIMFOR format;
4. specify the timing and new disturbance class (describing the type of harvesting) applied to each harvest unit;
5. define parameters used to calculate landscape statistics, including age limits of different seral stages, depth of edge effect and neighbouring seral classes which cause edge effect; and
6. define species groups to be used in the habitat calculations.

For habitat calculations, SIMFOR uses a database listing the requirements of different species (Daust et al.1993). This database requires minor modifications for different regions of British Columbia. Simulations without habitat calculations may take a few minutes to run while those which include several species and use spatial information in habitat calculations may take hours on a 33 MHZ Intel 80486 computer. The results of a particular simulation are examined in the viewing module of SIMFOR. Results include plots describing change over time and maps showing spatial patterns at selected sampling intervals (Table 4.1).

Desirable management options are selected using a gaming approach. Gaming consists of selecting landscape indices and species that are most relevant for the region and then simulating alternative management strategies. Several management plans may be developed beforehand or new strategies may be developed considering the results of the first simulation. If the timing or type of harvest is altered, then only the harvest schedule file needs to be changed to begin a new simulation. If harvest unit boundaries change, a new map must be imported. Text files store results used in plots (Table 4.1) and these files may be used to document the most favorable options.

Table 4.1. Output generated by SIMFOR.

| Type | Description |
|---|---|
| **Forest Cover** | |
| map | ecosystem class |
| map | stand age |
| map | disturbance class |
| map | harvest units |
| plot, map | any forest attribute |
| **Landscape Statistics** | |
| plot, map | seral stage distribution in each ecosystem class and for the entire landscape |
| plot, map | seral stage distribution in each patch size class |
| plot, map | proportion of edge habitat in each seral stage |
| **Habitat (for a selected species)** | |
| plot, map | areas with required forest attributes |
| plot, map | areas with required attributes which are large enough for home ranges |
| plot, map | areas with home ranges which are connected by dispersal |

In addition to its interface, SIMFOR consists of three modules which perform calculations. The first simulates disturbance and consequent changes in forest structure; the second calculates indices of landscape pattern; and the third calculates habitat distributions. I describe the major steps used in each module below.

**Simulating landscape composition and stand structure**

In SIMFOR, forest management is viewed to have impacts at two scales: the landscape scale and the stand scale. At the landscape scale, forest management alters the distribution of disturbance classes and stand ages. At the stand scale, changes to disturbance class and stand age are translated to changes in stand structure. Stand structure is represented in the model by a suite

of 10 forest attributes (Table 4.2). The abundance of each attribute is a function of ecosystem class, disturbance class and stand age. A database of forest attribute curves describes the change in abundance (per ha) of each forest attribute with stand age for each combination of disturbance class and ecosystem class.

Table 4.2. Forest attributes used to represent stand structure in SIMFOR.

| Attribute Name[1] | Description |
|---|---|
| large conifers | number of live stems / ha exceeding 30 cm diameter at breast height (DBH) |
| small conifers | number of live stems / ha of 10 to 30 cm DBH |
| large snags | number of dead stems / ha exceeding 30 cm DBH |
| small snags | number of dead stems / ha of 10 to 30 cm DBH |
| down-wood | total number of dead and down stems / ha exceeding 30 cm DBH |
| shrubs | percentage ground cover of shrubs |
| grasses and forbs | percentage ground cover of grasses and forbs |
| canopy | percentage ground cover of tree canopies |
| lichen | percentage of trees with obvious lichen cover |
| litter | depth in centimeters |

1 Attributes are easily changed to reflect local conditions.

When simulations begin, the state of the forest is described by maps of ecosystem class, disturbance class and stand age derived from the forest inventory. Ecosystem class varies with location but is constant over time. As time progresses in the simulation, the harvest schedule is checked to determine which areas are to be harvested. The harvest schedule file lists the year of logging and the new disturbance class to be assigned to each harvest unit. Harvesting is simulated by updating disturbance class and by resetting stand age to zero at the location specified by the harvest unit. Age is incremented in areas which are not logged. Forest attribute abundance is not updated until forest attribute information is used in a calculation. The simulation continues until the end of the specified planning horizon.

**Assessing landscape pattern**

Numerous indices are available to describe landscape pattern, however, the biological relevance of many of these is questionable. Patch type, patch size and patch boundaries are used to describe landscape pattern in the model because they have biological relevance, are easily interpreted and efficiently calculated. Theoretical evidence suggests that patch abundance and patch size are important factors influencing habitat value (MacArthur and Wilson 1967) and that patch boundaries also influence habitat value (Angelstam 1992). In Chapter 2, I described possible links between landscape classes (e.g., seral stage, ecosystem type) and biodiversity.

In SIMFOR, landscape statistics are calculated, each sampling period, in three steps. First, the proportion of each seral stage in each ecosystem class and in the entire landscape is calculated. Each seral stage is defined by a lower and upper stand age boundary which may vary between ecosystem classes. In this way, the structural character of fast and slow growing stands may be represented with the same seral stage classification. Second, the distribution of patch sizes in each seral stage is calculated. Contiguous raster cells (including those touching at their corners) of the same seral stage are joined into patches. Sizes are calculated and patches are divided into size categories defined by the analyst. Third, the proportion of each "primary" seral stage within the specified edge depth of a "contrast" seral stage is calculated. Primary and contrast seral stages and the depth of edge effect are defined by the analyst. Edge calculations are performed at a higher resolution (16 x as many cells) than the raster grid to increase precision. Patch size and edge effect are both calculated because patches of complex shape may be large but still greatly influenced by edge.

**Predicting distributions of forest-dwelling vertebrates**

Many habitat suitability calculations employ complex equations without clear rationale and without considering the spatial pattern of resources (Van Horne and Wiens 1991). Habitat suitability calculations in SIMFOR are based on a simple supply (of attributes generated by the forest) and demand (for attributes by selected species) approach and may include spatial information if desired.

At any point in time, the distribution of forest attributes on the landscape is determined using the forest attribute database and a state description of the forest landscape. The requirements of species (forest-dwelling vertebrates of British Columbia) for these attributes, along with their home ranges and dispersal ranges are stored in another database used by SIMFOR. The species database describes the degree of use of each forest attribute with one of three terms: not used, used or required. Given the qualitative nature of this data, I translate these terms into abundance categories (nil, low and high) for use in the model. The validity of assuming that a strong requirement means that a high abundance is required is debatable. Better data, describing the density of resources required by species, are not available.

Three different habitat suitability calculations are performed. The first ignores spatial information and compares the supply of forest attributes in each raster cell with the attribute abundance demanded by a selected species. If the abundance of each required attribute is met or exceeded, the raster cell is deemed suitable, otherwise it is deemed unsuitable. Areas where at least half the requirements are met are also identified. This approach may be criticized because attribute requirements may not be additive. Conversely, the approach is simple and general and allows various combinations of resource requirements to be tested.

The second habitat calculation uses the home range of each species, in addition to the attribute requirements. An approximately square area (squareness limited by resolution of raster grid) equal to the size of the home range is overlaid on the map and the mean abundance of each required forest attribute is calculated for the area. This mean supply of attributes is compared to the abundance required by the species. If the abundance of attributes supplied meets or exceeds

the requirements, the center 10% (approximately square) of the home range is flagged as suitable, otherwise it is flagged as unsuitable. The home range calculation moves systematically along the map until all cells are flagged. I assume that an animal whose home range is centered on the edge of the area rather than the center will experience greater movement costs to access this habitat and thus the calculated habitat suitability applies only to the center of the area, not the whole area. This assumption also eliminates bias associated with the starting location for the home range calculation. The home range calculation is more rigorous than the non-spatial calculation because a few cells with low attribute supply can change the habitat designation from suitable to unsuitable for animals with high resource requirements. This home range caluclation implicitly assumes that species requiring high abundances of several forest attributes over large areas are rare.

The third calculation determines if the identified home ranges are connected by dispersal. I calculate the distance from each cell to the nearest home range and flag regions as being accessible or inaccessible to dispersal. I then determine which accessible region has the most home ranges and identify this as the largest connected area. The area of home range within the largest accessible region (expressed as a percentage of the land base area) is the final and most conservative measure of habitat value. I do not consider the influence of habitat type crossed on dispersal distance since I did not find sufficient data relating dispersal distance to habitat type. However, variation in dispersal with habitat type is likely an important process to model.

In summary, the demand for attributes by selected species is compared to the attributes supplied by the forest in the habitat calculations. In the non-spatial habitat assessment, supply is compared to demand in each raster cell. When spatial information is included, mean supply is calculated for the home range area and dispersal is modelled between home ranges. The dispersal calculation identifies regions that may be difficult to cross.

## Demonstration of SIMFOR: Nehalliston Case Study

### Description of Study Area

The Nehalliston Creek drainage (approximately 8000 ha) is located near Kamloops in south, central British Columbia. The area encompasses four Biogeoclimatic zones and includes several lakes and one large river. Resource use in the area includes timber extraction, recreation and watershed protection. Don Thibodeau of the Forest Engineering Research Institute of Canada (FERIC) investigated the economic impacts of three alternative forest management plans for the Nehalliston Creek drainage (Thibodeau 1994). The plans represent past, present and possible future generations of Integrated Resource Management guidelines and will be referred to as follows:

- FOLIO: Nehalliston Resource Folio, past development plan in effect from 1982 to 1992;
- LRUP: Nehalliston Local Resource Use Plan, currently in effect;
- BIOD: Local Resource Use Plan with proposed biodiversity guidelines added.

I evaluate the impacts of these alternative plans on indicators of biodiversity using SIMFOR.

### Methods

Digital maps and forest inventory data for the Nehalliston Creek drainage were provided by Walt Klenner, Kamloops Forest Region and by Don Thibodeau, FERIC. Ecosystem class, stand age and disturbance class were derived from these maps. Biogeoclimatic subzones were used to represent ecosystem class. Information describing historical disturbance events for the area was sparse so past disturbance was classified as natural or clearcut.

Maps of proposed harvest units, developed by FERIC, were translated to SIMFOR. The three forest management plans, developed by FERIC, specify the location, the timing and the type of harvest treatment for each harvest unit. Harvest treatments, including clearcutting, selection

cutting, clearcutting with retention and selection cutting with retention, were translated directly to disturbance classes in SIMFOR. Two intensities of selection cutting (25% or 33% per entry) were used by FERIC but were not differentiated in SIMFOR because resulting stand structures are likely to be similar. Where retention is indicated, 15% of the gross stand volume (mainly snags and unmerchantable stems) is retained on the site. Retention is necessary in selection cutting systems to maintain old trees and snags.

In SIMFOR, forest attribute curves are required for each combination of ecosystem class and disturbance class. Information describing the response of forest attributes to various disturbances is largely unavailable in British Columbia. Research and silviculture staff from the Kamloops Forest Region provided local knowledge in the form of hand drawn curves of selected forest attributes for various combinations of harvesting and silviculture treatments. I adapted these curves to the specific treatments used by FERIC and divided the attribute abundance into categories of nil, low, medium and high for use in SIMFOR.

SIMFOR was used to examine changes in landscape pattern and in habitat distributions in the Nehalliston Creek drainage over a 120 year planning horizon (the duration of the management plans developed by FERIC) for each management plan. In the FOLIO, clearcutting is the only harvest treatment and regulations limiting the area harvested are the least restrictive. In the LRUP, clearcutting and selection cutting are proposed. In the BIOD, clearcutting with retention and selection cutting with retention are used and regulations limiting the area harvested are the most restrictive. For more details, see the FERIC report (Thibodeau 1994).

For landscape statistics calculations, seral stage classes are defined as follows:

- **Regeneration**: stand age of 0 to 20 years for all ecosystem types;
- **Pole**: stand age of 21 to 60 years for all ecosystem types;
- **Mature**: stand age of 61 to 120 years for all ecosystem types;
- **Old**: stand age greater than 121 years for all ecosystem types;
- **Mixed**: all aged stand resulting from selection cutting.

Patch size classes were defined in orders of magnitude: 1 to 10 ha; 10 to 100 ha; 100 to 1,000 ha; 1000 to 10,000 ha. Edge depth was set at 100 m and adjacent patches causing edge effects were:

- Old next to Regeneration or Pole;
- Mature next to Regeneration; and
- Mixed next to Regeneration.

For habitat calculations, three groups of species with different attribute requirements and different home ranges and dispersal ranges were chosen (Daust et al. 1993):

- "Shrew group": requires at least low abundance of down-wood and litter; home range = 0.02 ha and dispersal range = 100 m.
- "Vole group": requires at least low abundance of down-wood, brush and grass; home range = 0.5 ha and dispersal range = 1000 m.
- (Pileated) "Woodpecker group": requires at least low abundance of large conifers, large snags, and down wood; home range = 300 ha and dispersal range = 10000 m.

**Results**

SIMFOR was used to summarize the land classes presently found in the Nehalliston Creek drainage. The land base consists of 91% forest, 5% lakes and 4% non-forest or non-productive forest types. Eighty-two percent of the area has not been harvested and 9% has been clearcut. The majority of the land base (73%) is covered with Mature forest . Results are divided into landscape statistics and habitat distributions.

**Landscape statistics**

Landscape statistics are used to describe changes in disturbance classes, seral stage classes, patch sizes and edge habitat over the 120 year simulation. In all three scenarios, the proportion of the land base in the natural disturbance class decreased and areas disturbed by various types of forest management increased (Table 4.3). At year 120, the area managed by clearcut harvesting is largest in the FOLIO; the natural (unharvested) area is highest in BIOD but does not differ greatly between scenarios.

Table 4.3. Percentage of forested area in each disturbance class for different scenarios at year 0 and year 120.

| Disturbance Class[1] | Year 0 ALL | Year 120 FOLIO | Year 120 LRUP | Year 120 BIOD |
|---|---|---|---|---|
| • Natural | 82 | 31 | 32 | 36 |
| • Clearcut | 9 | 60 | 31 | 4 |
| • Selection cut | | | 28 | |
| • Clearcut with retention | | | | 26 |
| • Selection cut with retention | | | | 25 |
| • Non-forest | 9 | 9 | 9 | 9 |

1. disturbance class indicates the last treatment applied to a site and is not influenced by stand age.

In all scenarios, the area of forest in the Old seral stage increases until approximately year 60 when it begins to decline (Figure 4.1). The area of mature forest greatly decreases over the first 20 years as a large tract of mature forest moves to the Old age class. Over time, harvesting practices increase the area of Pole and maintain the area of Regeneration seral stages. The seral stage distribution stabilizes near the end of the planning horizon. At this point, the area

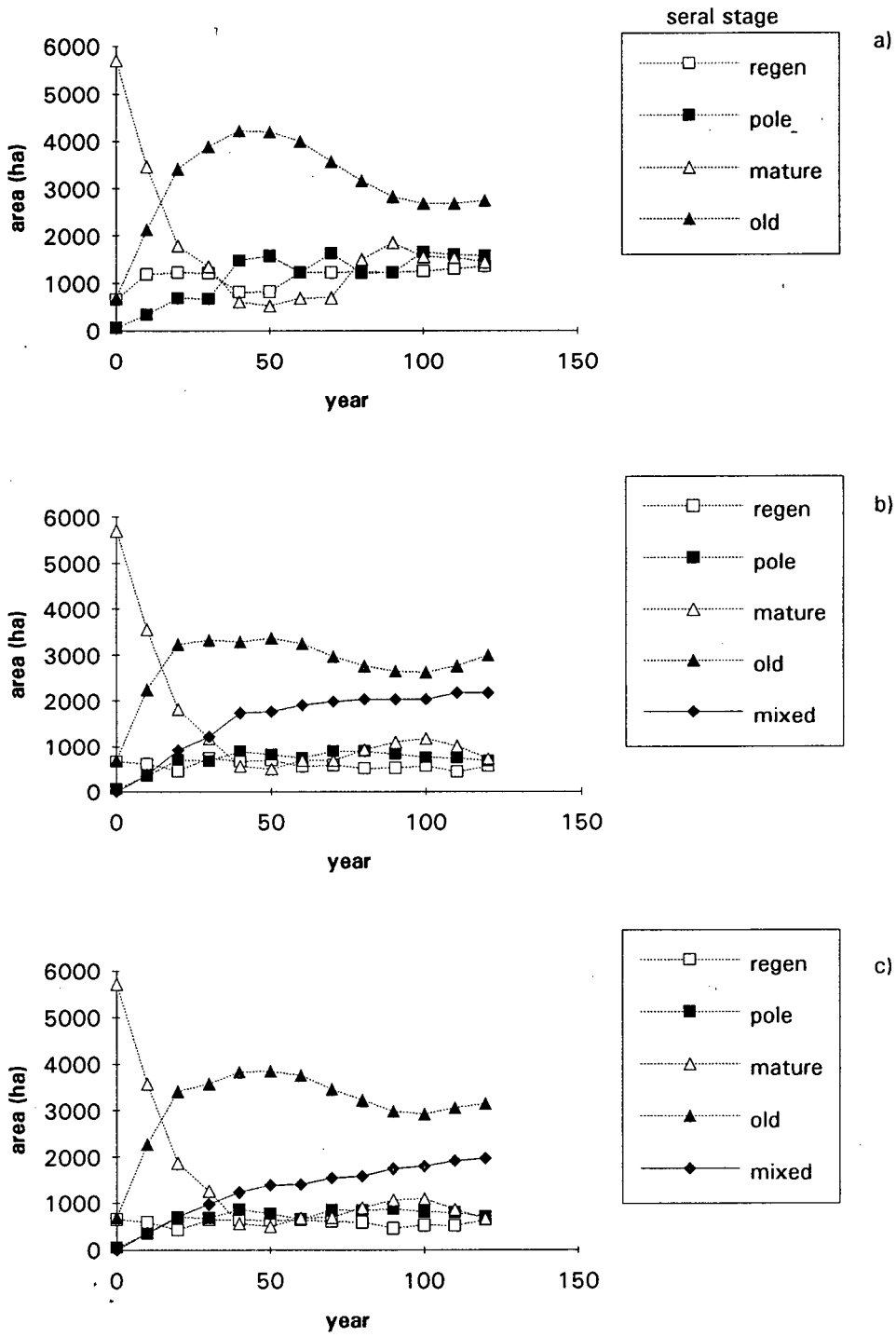



Figure 4.1. Seral stage area versus time for a) FOLIO, b) LRUP and c) BIOD.

of Old seral stage is highest in BIOD, however, the area of Mature and Old seral stages is highest in the FOLIO because Mature seral stages are not generated by selection cuts used in the LRUP and BIOD (Table 4.4). Regeneration and Pole seral stages account for more than twice as much area (18% and 23% respectively) in the FOLIO scenario than they do in the other scenarios. In most scenarios, seral stage distributions are only slightly biased by ecosystem type and tend to be biased in the same direction (Table 4.5). However, ICH has a high abundance of Old seral area in the LRUP and BIOD, but has low abundance in the FOLIO. In the last three decades of the simulation, ESSF has the least amount of the Old seral stage in all three scenarios.

Table 4.4. Mean percentage of forest area (averaged from sample years 100, 110 and 120) in each seral stage (all ecosystems) for each simulation.

| | Regeneration | Pole | Mature | Old | Mixed |
|---|---|---|---|---|---|
| **FOLIO** | 18% | 23% | 21% | 38% | 0% |
| **LRUP** | 7% | 10% | 14% | 39% | 30% |
| **BIOD** | 8% | 11% | 12% | 43% | 26% |

Table 4.5 Mean percentage of forest area (averaged from sample years 100, 110 and 120) in the Old seral stage by ecosystem class for each simulation.

| | ALL | ESSF[1] | SBS[2] | IDF[3] | ICH[4] |
|---|---|---|---|---|---|
| **FOLIO** | 38% | 27% | 40% | 45% | 27% |
| **LRUP** | 39% | 25% | 41% | 46% | 74% |
| **BIOD** | 43% | 31% | 43% | 53% | 77% |

1. Engelmann Spruce - Subalpine Fir
2. Sub-Boreal Spruce
3. Interior Douglas-Fir
4. Interior Cedar-Hemlock

At the beginning of the simulation, patches of Mature seral stage exceeding 1000 ha dominate the landscape (Figure 4.2). As the forest ages, this large contiguous area becomes Old seral stage; patches of Mature never again exceed 1000 ha in the simulation. In LRUP and BIOD, the majority of the Old seral stage remains in patches of greater than 1000 ha for the entire simulation (Figure 4.3). At approximately year 100 of the FOLIO, patches of Old seral of greater than 1000 ha disappear as harvesting severs linkages connecting patches. The implied higher fragmentation in the FOLIO is corroborated by the higher percentage of edge habitat in the Old seral stage seen in the FOLIO towards the end of the planning horizon (Figure 4.4).

**Habitat distributions**

Habitat was evaluated for the shrew, vole and woodpecker attribute dependency groups. Habitat abundance, calculated using spatial information, was highest in BIOD and lowest in FOLIO for all three species groups examined (Figure 4.5). Habitat abundance was intermediate in the LRUP scenario. The vole group was least affected by differences in the scenarios. By year 120, the percentage of the land base flagged as suitable habitat in BIOD exceeds that flagged in FOLIO by 16% for the shrew group, 3% for the vole group, and 61% for the woodpecker group. In the FOLIO scenario, habitat is generally abundant for the shrew and vole group (exceeding 75% of the land base at year 120), however, habitat for the woodpecker group is limited (30%). The spatial habitat calculation is the most conservative of the habitat calculations, including requirements for attributes, home range and dispersal. Examining the different calculations provides some explanation for decreasing habitat abundance. For example, for the woodpecker group in the FOLIO scenario, habitat abundance calculated using spatial information declines to 30%, whereas habitat abundance calculated without spatial information declines to only 49% over the planning horizon (Figure 4.6). This suggests that part of the decline in habitat abundance was due to insufficient forest attributes and that part of the decline was due to the spatial arrangement of the attributes.

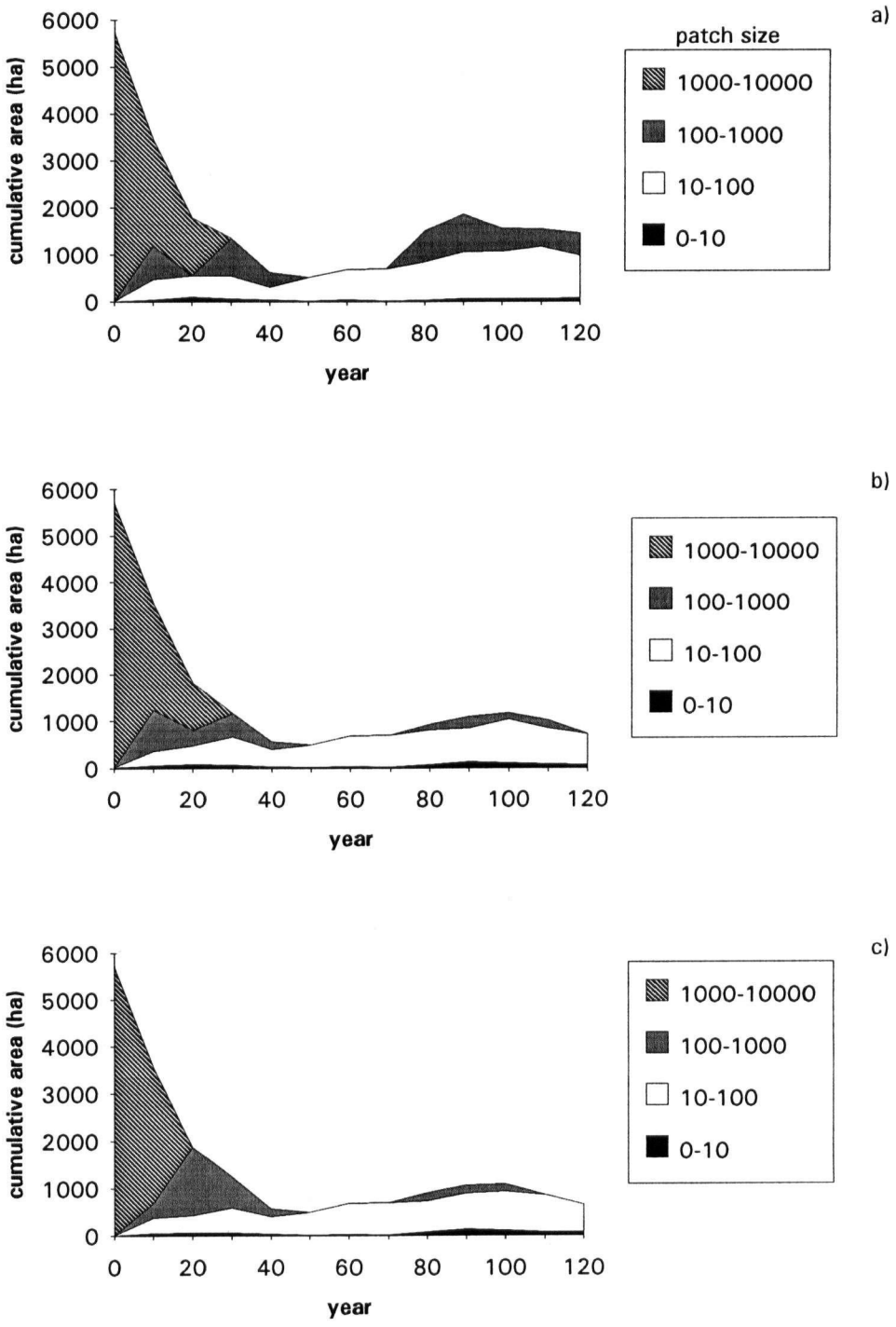



Figure 4.2. Mature seral stage area, grouped by patch size class, versus time for a) FOLIO, b) LRUP and c) BIOD.

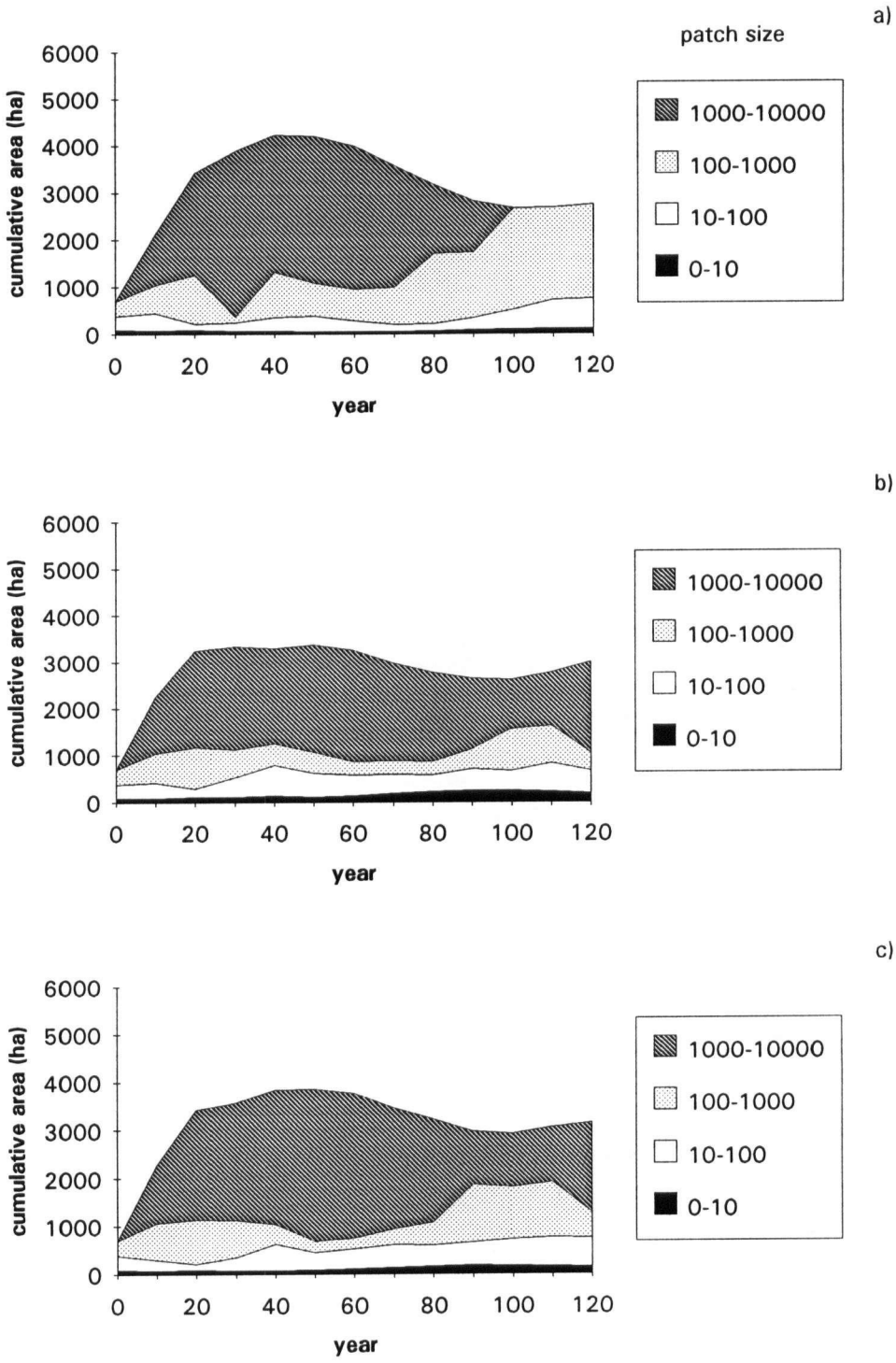



Figure 4.3. Old seral stage area, grouped by patch size class, versus time for a) FOLIO, b) LRUP and c) BIOD.

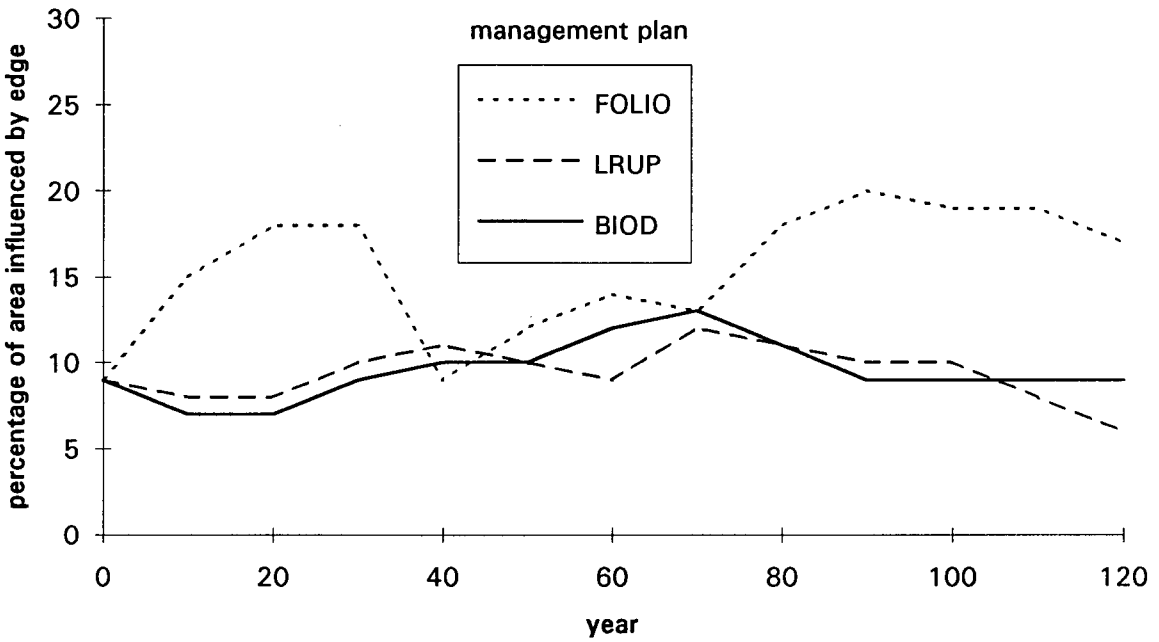



Figure 4.4. Percentage of Old seral stage, within 100 m of a Regeneration or Pole seral stage, versus time for each management scenario.

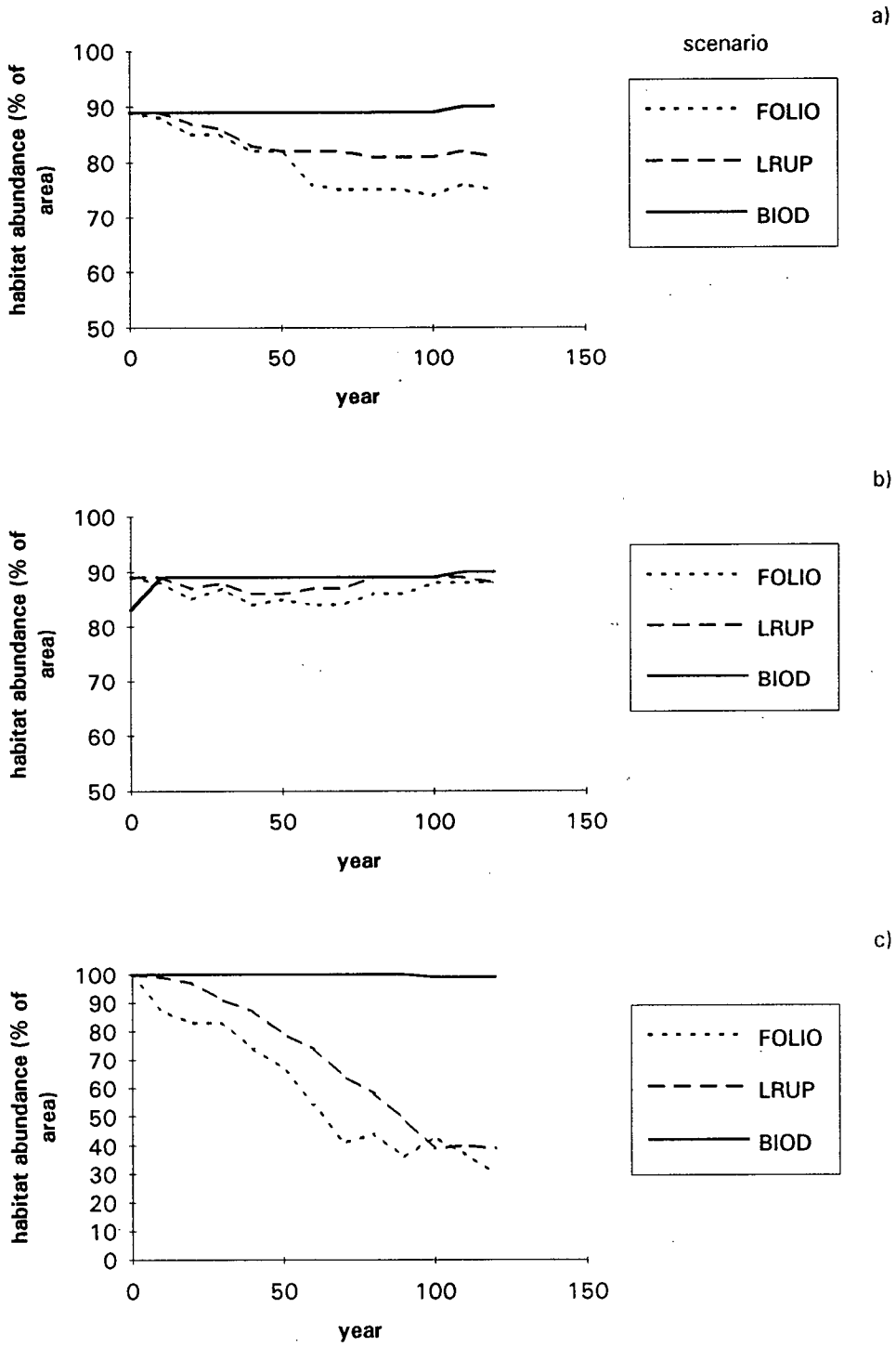



Figure 4.5. Habitat abundance (calculated with spatial information) versus time for each management scenario for a) the shrew group, b) the vole group and c) the woodpecker group.

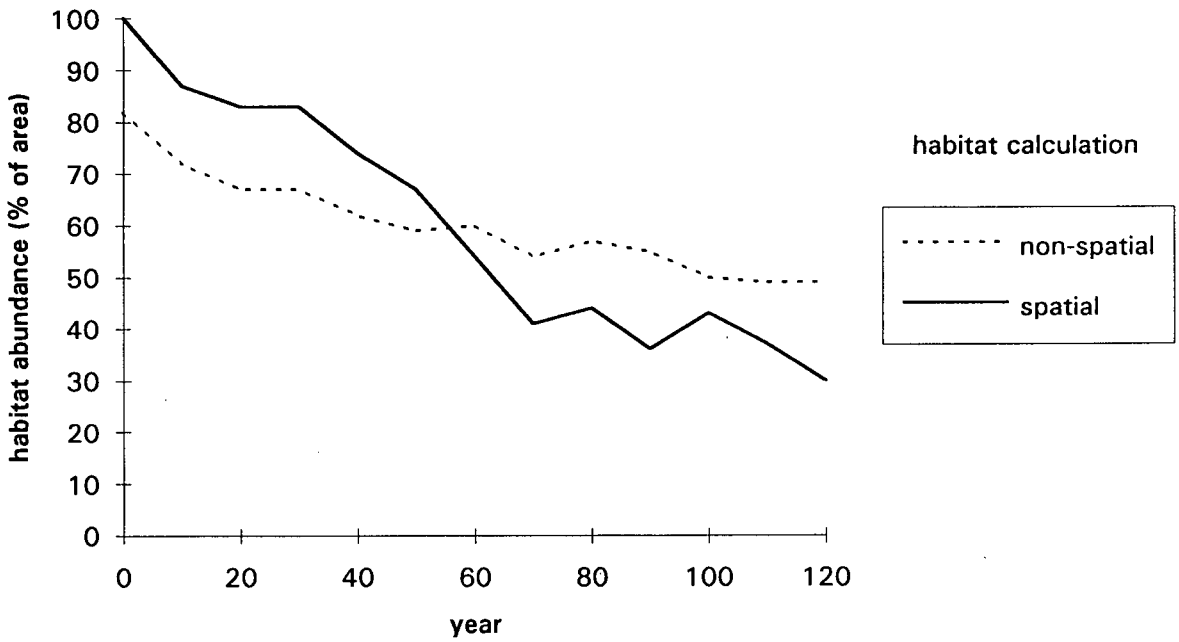



Figure 4.6. Habitat abundance versus time for different types of habitat calculations for the woodpecker group in FOLIO.

The woodpecker group requires large snags, large conifers and downed wood. In FOLIO, the mean abundance (over the entire landscape) of large conifers and downed wood declined over the planning horizon and the mean abundance of large snags remained fairly constant (Figure 4.7a). In BIOD, the mean abundance of large conifers declined but the mean abundance of down-wood and large snags increased (Figure 4.7b). Results for the LRUP were intermediate between those of the FOLIO and the BIOD. Mean attribute abundance does not account for spatial variation in attribute distributions but it no doubt relates to habitat requirements of animals with large home ranges.

**Discussion of Nehalliston Case Study**

Guidelines enacted to protect non-timber values significantly influence expected timber yields and harvesting costs in the Nehalliston creek drainage (Thibodeau, 1994). The mean annual volume harvested in the BIOD scenario (10,520 $m^3$) is 81% of that harvested in the LRUP scenario and 69% of that harvested in the FOLIO scenario. Total harvesting and management costs, estimated for the first two decades, are \$19.11 per $m^3$ for the FOLIO scenario, \$24.48 per m3 in the LRUP scenario and \$24.90 per $m^3$ in the BIOD.

Assessing impacts of these scenarios on biodiversity requires a more subjective evaluation. Rather than discussing the vast literature on habitat use and forest fragmentation here, I assume the following criteria are important:

- Old and Regeneration seral stages provide critical habitat;
- large patches conserve biodiversity better than smaller patches;
- excessive edge habitat negatively influences Old forest habitat; and
- habitat abundance for species with large home ranges, requiring large conifers, large snags and down-wood will be a good indicator of biodiversity.

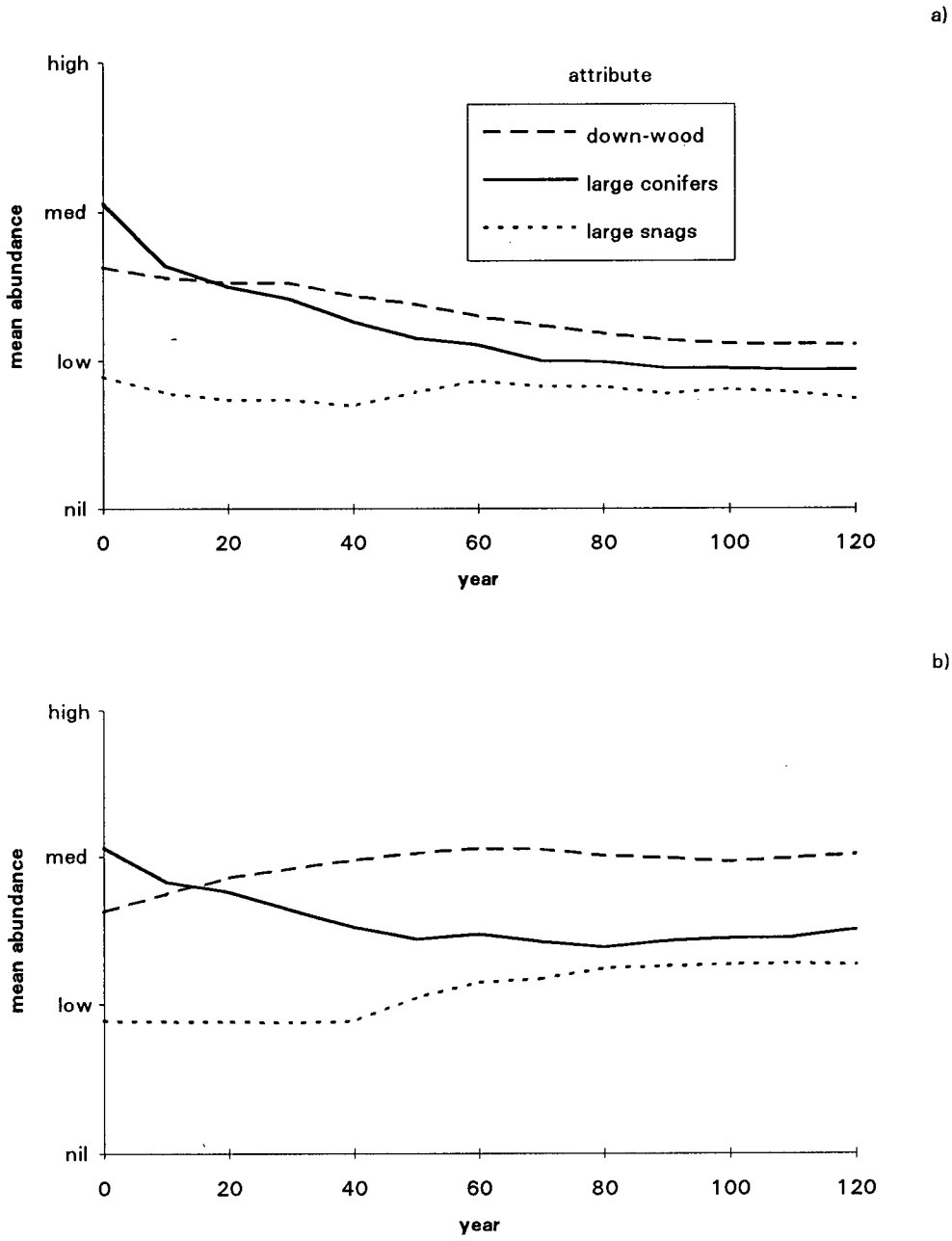



Figure 4.7. Mean abundance, across the landscape, of selected forest attributes versus time for a) FOLIO and b) BIOD.

In part these criteria are based on the assumption that because of logging and other human activities, large tracts of old forest are becoming a scarce and hence relatively valuable habitat type. This further implies that the requirements of species using regeneration seral stages and edge habitat are being met and that these types of species need not be considered. For this reason, I mainly discuss impacts on Old seral stages and on species requiring old forest attributes. I also focus on the end of the planning horizon, because it is at this point (and beyond) where the full effects of planned management are best displayed.

Based on these assumptions, the results of this study suggest that biodiversity will be best conserved under the BIOD scenario, then under the LRUP scenario and finally under the FOLIO scenario. At the end of the planning horizon, the BIOD scenario has more area of the old seral stage than the other scenarios. The BIOD scenario has more area in patches exceeding 1000 ha than the FOLIO scenario and less edge habitat than the FOLIO scenario. None of the scenarios showed seral stage distributions that were greatly biased by ecosystem type. Seral stage measurements do not reflect stand-level management, impacting forest structure, but habitat measurements do. Habitat abundance for each of the three species groups examined was highest in the BIOD scenario. Most noticeably, woodpecker habitat declined to very low levels in the FOLIO scenario. The LRUP scenario showed intermediate habitat abundances.

Trends in habitat abundance may to some extent be explained by examining the non-spatial habitat calculations and the trends in attribute abundance. For the woodpecker group in the FOLIO scenario, declining abundance of down-wood and of large conifers led to reductions of the habitat value of individual raster cells as shown by the non-spatial habitat calculation. These factors only accounted for part of the decline in habitat. Further habitat decline resulted largely because of reduced density of attributes over the home range. Increased forest fragmentation in the FOLIO scenario likely contributed to reduced attribute density.

This study highlighted several limitations in applying SIMFOR and presented some interesting research questions:

Nehalliston case study limitations:

- data describing the response of forest attributes to various forestry treatments were not available so expert opinion was used;
- the case study area was too small to properly assess landscape patterns;
- ecosystem classes should have included some measure of site productivity as well as broad Biogeoclimatic variation; and
- natural disturbance processes are not modelled but may greatly influence results.

SIMFOR limitations:

- habitat requirements of different species are a first approximation and are based on a broad survey of the literature; data describing home range and dispersal range are particularly weak;
- habitat calculations do not include the influence of edge habitat, water courses, roads or non-forest habitat;
- home ranges are modelled as fixed size when likely they vary with resource density; and
- the dispersal model is simplistic and does not include the influence of different habitat types.

Future Research Questions:

- how do old forest, mature forest, and selectively harvested forest differ in species composition and in ecological processes;
- what range of seral stage distributions will conserve biodiversity; and
- at what spatial scale should landscape and habitat analysis be performed?

Deciding which scenario to adopt depends largely on the weights assigned to the various economic and environmental costs and benefits. SIMFOR does not provide the answer, but it does provide some guidance.

## General Discussion

A plethora of rules and regulations guide forest management in British Columbia today. With recent advances in spatial simulation, the impacts of these regulations on timber supply and economic costs can be reasonably well predicted. The question of whether the guidelines achieve their stated objectives often remains unanswered. Guidelines enacted to conserve biodiversity are particularly difficult to evaluate because of the broad scope of biodiversity. SIMFOR models forest management and provides indicators of landscape pattern and wildlife habitat which can be used to assess impacts on biodiversity. SIMFOR may be characterized as a spatial forest dynamics model, which not only tracks changing forest structure over time but also over space. SIMFOR focuses on forests as ecosystems, rather than forests as trees and uses ecologically based land classes rather than classes based on tree growth. Landscape statistics generated by SIMFOR attempt to provide an ecological view of the forest rather than a "timber-centric" view. The advantage of using such an approach is that the ecological state of the forest can be used to predict the potential output of a wide variety of forest resources (e.g., wildlife habitat, recreation, timber volume).

Many rules applied to forest land are designed to protect a single value. In areas with multiple resource values, such rules and regulations can become redundant; each additional rule increases the complexity of management but has little effect on the landscape. Many rules specify the timing and type of harvesting and silvicultural treatments that may be performed but do not consider the current state of the forest. This regulatory approach leaps directly from desired resource outputs to rules guiding practice. As an alternative approach, one could focus on forest ecosystems and specify a range of desirable landscape states described by selected landscape

statistics. With such an approach, outputs are calculated based on the state of the forest and management must aim to keep the forest within the range of desired states. For example, rather than enforcing retention in clearcuts, mean minimum densities of forest attributes over some area could be specified; rather than specifying clearcut sizes, the patch size distributions of various seral stages could be specified. Timber, recreation and wildlife are outputs of the landscape and would need to be calculated given the range of desired landscape states. This approach has several problems. Questions of scale of management and appropriate statistics to describe the system have yet to be resolved. Few strong generalizations have emerged from studies of plants and animals to help us define appropriate statistics for conserving biodiversity. I suggest ecosystem class, disturbance class, seral stage, patch size and edge habitat are important factors to consider. An ecosystem focused approach has benefits. It allows natural disturbance events which alter the state of the system to be considered explicitly in management. It consolidates a variety of different rules and guidelines into one system and increases the flexibility of management treatments. Most importantly, it shifts the focus from resource outputs to the forest ecosystem which is what forestry actually manipulates.

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# Appendix 1

## The relationship between habitat abundance, patch size and inter-patch distance on a simple, regular landscape.

The survival of populations depends upon the size and isolation of habitat patches in a fragmented landscape (Whitcomb et al. 1981). While many studies have examined the influence of habitat abundance, patch size and patch isolation on species survival, none have described the geometric relationship between these factors. This appendix describes an algebraic model relating (1) patch size, (2) inter-patch distance and (3) habitat abundance (total area) on a simple landscape. The model is extended to express inter-patch distance as a ratio of home range radius, to allow determination of landscape connectivity.

**A model relating patch size, inter-patch distance and habitat abundance**

Consider an infinite landscape with square patches of equal size, distributed in a regular grid (Figure A1.1).

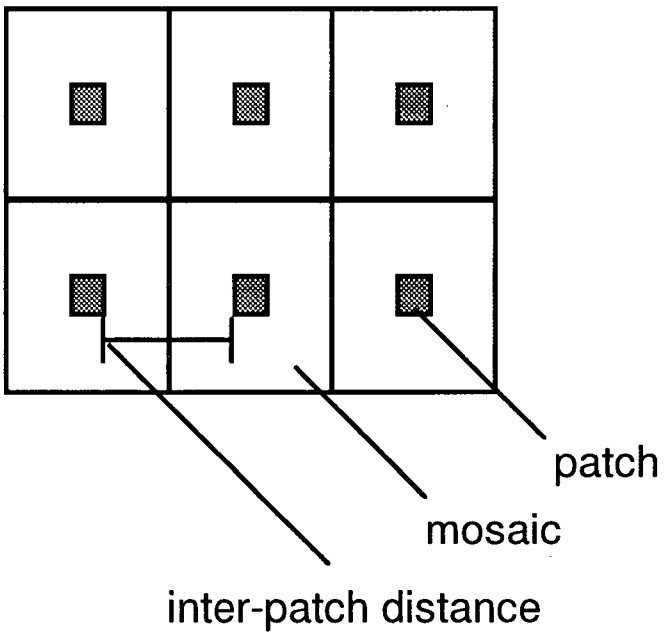


Figure A1.1. Hypothetical landscape consisting of square patches of equal size arranged in a regular grid on a background mosaic.

Three parameters describe the pattern on this landscape: habitat abundance (i.e., total area of patches), patch size and inter-patch distance. The landscape area which is not part of a patch makes up the background mosaic. For patches to be distributed evenly, each patch center must be surrounded by an equal area (patch plus mosaic). Defining any two of the parameters determines the third and completely describes the landscape. Simple equations relate the parameters:

Let

*Pp* = percent of landscape defined as patch habitat
*Pm* = percent of landscape defined as mosaic
*Ap* = area of a single patch
*Am* = area of mosaic apportioned to each patch center to ensure even distribution
*Dc* = distance between patch centers
*Dp* = minimum inter-patch distance

Then

$Pm = 100 - Pp$
$Am = Pm / Pp \times Ap$
$Dc = \sqrt{(Am + Ap)}$
$Dp = Dc - \sqrt{Ap}$

For example

Given: $Pp = 6.25\%$ and $Ap = 1$ unit$^2$

Find *Dp*:

$Pm = 100 - 6.25 = 93.75\%$
$Am = 93.75/6.25 \times 1 = 15$ units$^2$
$Dc = \sqrt{(15 + 1)} = 4$ units
$Dp = 4 - \sqrt{1} = 3$ units

Over a range of parameters, these equations show how habitat abundance influences the relationship between patch size and inter-patch distance (Figure A1.2). Inter-patch distance increases as habitat abundance decreases and as patch size increases. Note that while inter-patch distance changes with patch size, the relationship between these variables is constant across

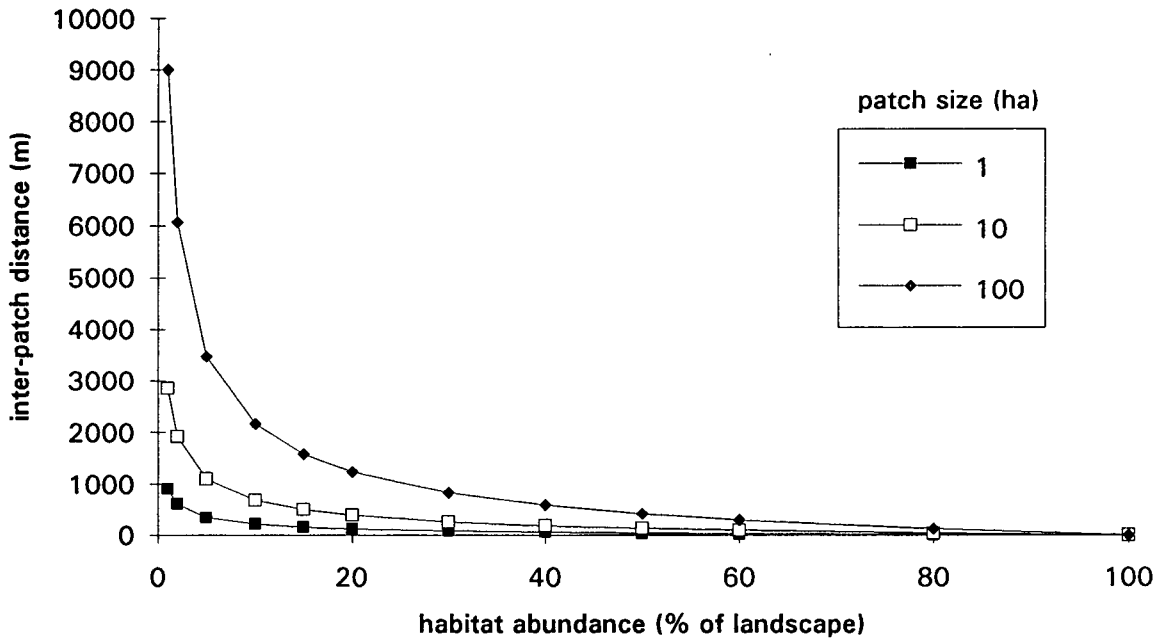


Figure A1.2. Inter-patch distance versus habitat abundance for different patch sizes on the model landscape.

different scales; that is, the ratio of inter-patch distance to patch width is fixed for a given habitat abundance (Figure A1.3). For example, if patch width is doubled, the distance between patches is doubled.

## A model relating dispersal to inter-patch distance

The ratio of dispersal distance to home range radius is approximately constant for species of different body sizes (Figure 3.1 in Chapter 3). For a given habitat abundance, inter-patch distance is a constant ratio of patch size on the simple landscape described above. Thus, the relationship between home range size and patch size (assuming patches are suitable and the mosaic is not) determines the relationship between dispersal distance and inter-patch distance. Inter-patch distance can be expressed as a ratio of home range radius and compared to the ratio of dispersal distance over home range radius to faciltate assessment of landscape connectivity for different species (Figure A1.4).

## Discussion

Much of the conservation literature focusses on the size and arrangement of habitat patches (Murphy 1989). Habitat abundance (total area of patches) has been received less attention, yet it is a critical factor determining the range of possible landscape patterns. On a hypothetical landscape, habitat abundance in combination with patch size determines inter-patch distance; in combination with inter-patch distance, it determines patch size. The landscape model shows the exponential increase in patch isolation as habitat abundance decreases. Real landscapes on which forestry or agricultural policies create a regular patchwork will show properties similar to those described in the model.

The general, scale-independant relationship between animal mobility and landscape pattern is shown by the extended landscape model, which expresses patch size as a ratio of home range

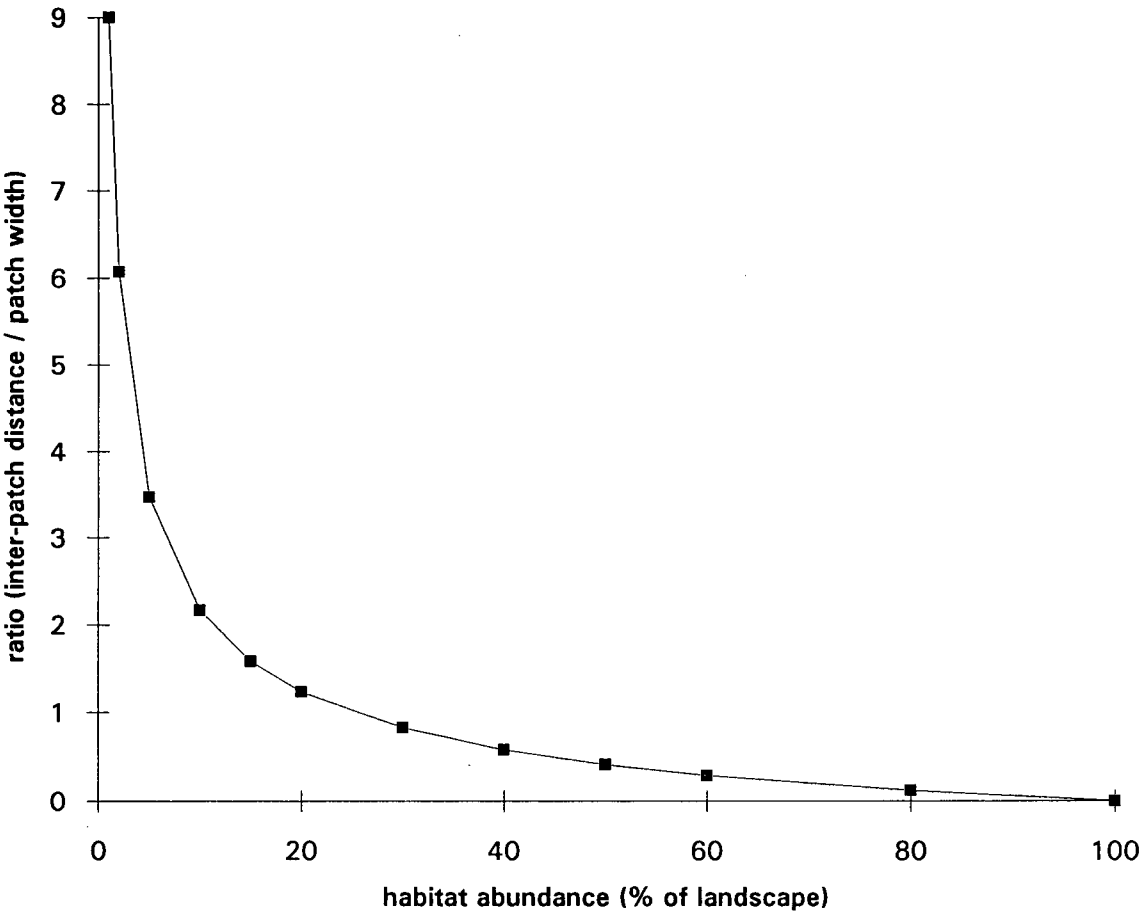


Figure A1.3. Ratio of inter-patch distance to patch width versus habitat abundance on the model landscape.

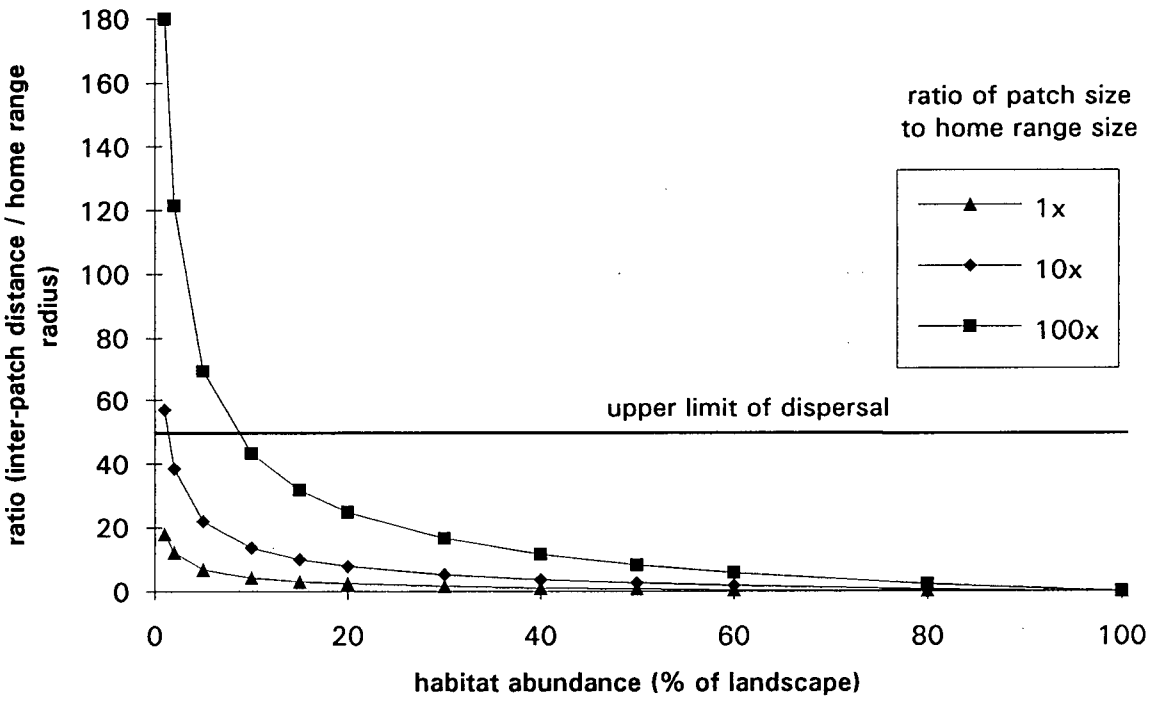


Figure A1.4. Ratio of inter-patch distance to home range radius versus habitat abundance for different ratios of patch size to home range size on the model landscape.

size and inter-patch distance as a ratio of home range radius. The ratio of inter-patch distance to home range radius increases as patch size increases relative to home range size and as habitat abundance decreases. It can be compared to the relative dispersal ability of groups of species (e.g., omnivores) to determine if the landscape is connected. Two apsects of landscape pattern can reduce the connectivity of a landscape for a species. When habitat abundance is too low, dispersal between patches will not be possible. When patch size is too large, dispersal between patches will not be possible even with fairly high habitat abundance. Each species moves at a particular spatial scale (Holling 1992). As relative patch size increases, the scale of the landscape pattern is increased beyond the scale of the animal mobility.

The extended model provides insight into a key conservation question: how much land should be preserved? This question is complicated because different species, which use different habitats at different spatial scales, will find the same landscape to be of different value. I ignore variation in habitat requirements and ask how much land is required to conserve species with different mobilities. If a species is to survive on a landscape, patches of habitat must either support a viable population or support some individuals and be connected by dispersal. Because inter-patch distance increases with patch size, the point where a patch almost supports a viable population will be the point where connectivity is lowest for a species. When a variety of species with different mobilities are considered, one or more species will encounter patches which are not quite large enough to support a viable population. Thus, dispersal must be possible between patches which almost support a viable population to maintain a variety of species on the landscape. For example, assume

- an area equivalent to 101 home ranges supports a viable population of any species; smaller areas must be connected to other areas by dispersal;

- an inter-patch distance equivalent to 25x home range radius will allow dispersal between patches by any species.

Note that in the extended model, habitat abundance does not depend on absolute patch size, however, patches must be sufficently large to support animals with the largest home ranges.

Based on the extended model, a habitat abundance of 20% allows patch sizes of 100x home range size to be connected (inter-patch distance of 25x). If patch size needs to be 501x home range size to support a viable population, approximately 40% habitat abundance is required. These habitat abundances are much larger than those required to maintain a single species. For one species, patch size may be set equal to home range size; habitat abundance of 1% provides an inter-patch distance of less than 25x. This comparison illustrates that more habitat is required to maintain a diversity of species than to maintain a single species because the scale of the landscape pattern does not match the scale of mobility of all species.

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