Ecological Strategies, LLC

Background paper:
Relationships between forest spatial patterns and plant and animal species in northern Minnesota

December 2003

***Submitted to*:**

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MNDNR Contract # A45867

Version 1.0

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INTRODUCTION

The Minnesota Forest Resources Council (MFRC), Minnesota Department of Natural Resources, Minnesota Forest Industries, The Nature Conservancy, Minnesota Audubon, and the US Forest Service are jointly sponsoring a project aimed at quantifying historical, current, and possible future spatial patterns of forests in north-central and northeastern Minnesota (Figure 1). The overall project focuses on spatial patterns (size, shape, and arrangement) of vegetation, land-use, and disturbance patches > 5 acres in size. The project aims to improve the scientific basis for sustainable forest management in Minnesota. This document is one component of the overall project, and is a synthesis of literature on the relationships between forest spatial patterns and plant and animal species.

Species vary widely in their responses to changes in forest spatial patterns, and relying on species-by-species analyses of responses can be complex and unwieldy. This document proposes a framework, called the Species Sensitivity Framework (Figure 2), to use as a tool for simplifying this problem. The purpose of the Framework is to categorize species, based on their characteristics, in terms of the response to spatial pattern changes. This way, the Framework can be used to anticipate how various spatial pattern changes will affect groups of species.

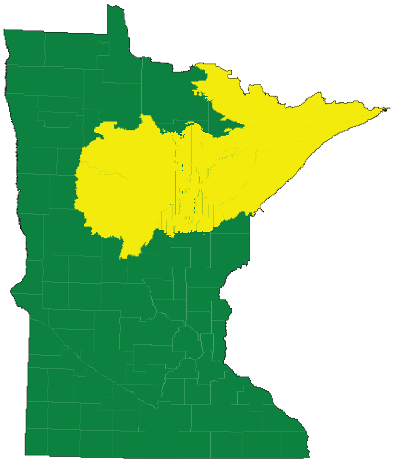


Figure 1. Project Area.

Figure 2. Species Sensitivity Framework.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low								
	Uncommon/ High								
	Uncommon/ Low								

In Section A, we identify the characteristics known to affect how species respond to changes in spatial patterns of their habitats. We use these characteristics as a tool for grouping species, and identify and categorize example species based on this system.

In Section B, we locate example species in the Species Sensitivity Framework, and we present known or hypothesized effects of several types of spatial pattern changes on these example species.

In Section C, we summarize how various types of spatial pattern changes likely affect the example species, attempting to generalize about how species within particular locations of the Species Sensitivity Framework respond to such changes. We then suggest how the Species Sensitivity Framework can be used a tool for informing the understanding of other species' responses to spatial pattern changes and we identify next steps in refining the Framework.

Background information on terms and definitions is provided in Appendix I. Some critical points need discussion here. Within the project area of north-central and northeastern Minnesota, many species use forested habitats of the landscape. Habitat is a physical space that provides essential resources for a species. Shifts in patterns of available habitat result from natural processes, such as succession, fire, and drought, as well as from human-induced changes in land-use. As people plant and harvest forested areas, construct or remove roads, and convert areas to or from agricultural or residential use, habitat patterns change. Depending on the scale of the changes in spatial pattern of habitat, there can be important consequences for a particular population of organisms, a species, or for several species.

Analyzing habitat for a certain species in a landscape requires using a patch type classification appropriate to that species. In some cases the appropriate classification might be traditional forestry cover types, which are usually defined by the dominant trees. In other cases, in order to fully define a habitat patch for a species, other information is needed, such as forest age as well as cover type, particular soil characteristics, or presence of suitable breeding pools. Appendix I describes terms and forms of measurement used to define spatial arrangements of habitat patches.

In Appendix II, we provide background information on theories and models used to explain the effects of habitat spatial pattern on populations of species, including island biogeography and metapopulation theory. These theories and models are the basis for how species' responses to spatial patterns are studied.

Several spatial pattern changes have occurred within the landscape of the project area. Since the late 1800s, Minnesota forests have experienced the following changes (Whitney, 1987; Host and White, 2002; Host and White, 2003):

- Smaller average patch size
- Increase in edge density
- Reduced core (interior forest) area
- Compositional changes

In recognition of these general trends within the project area, we specifically focus our discussion in Section B by addressing:

- patch size effects
- habitat patch quality effects
- patch edge effects
- effects of arrangement of patch types
- effects of habitat connectivity and isolation

This document is intended to provide planners, land managers, foresters and other decision-makers with a tools for understanding habitat spatial pattern changes, species-level processes, and the ways species are currently understood to respond to spatial change. We assume the audience for this document has a basic understanding of wildlife biology and ecology. Appendices provide detailed explanations of terms and usage.

This paper is intended to serve as a starting point, and will require refinement. This document is not intended to be a comprehensive literature review. The goal here is to develop a foundation and framework for further investigation, while illustrating important concepts with examples, and describing information gaps.

SECTION A

Example Species Selection and Categorization

As described in the introduction, we use example species to describe the general effects of forest spatial patterns and composition on plant and animal species. We use several criteria in selecting example species. Our goals are to:

1. represent a wide range of taxonomic groups
2. include species present in northern Minnesota
3. include a set of species that together represent a wide range of characteristics (see description of characteristics used below).

Selected species are also those for which:

4. information on biology and ecology is available
5. information on the effect of spatial pattern on the species biology or ecology is available.

CHARACTERISTICS

To facilitate comparing types of species-level characteristics to types of spatial patterns, we first chose to categorize the species based on the following species characteristics. These characteristics are the most important determinants of sensitivity to change in spatial patterns:

- Natural abundance type
- Dispersal type
- Interactions with other species
- Habitat specificity

This categorization scheme is then applied to example species (Table 1). In Section B, this categorization is used to locate species in the Species Sensitivity Framework (Table 2), in order to compare types of species trait combinations and effects of spatial patterns.

Current population size & Reproductive rate

- Current population size
- Reproductive rate

Dispersal (immigration and emigration processes)

- Dispersal distance

- Resource dependent and independent dispersal

Interactions with other species (predation, parasitism, herbivory), competitive ability, mutualists (pollinators and seed dispersers)

Habitat Specificity (influences many of the above processes)

Current population size & Reproductive rate

Abundance is an important determinant of of species sensitivity to changes in spatial patterns. In this paper we use current population size and reproductive rate as the main indicators of natural abundance (see Appendix II. for definitions of terms). Population size is based on the number of individuals that currently occur in a population, (versus historical population size), regardless of population structure (see Appendix III. for an overview of population structures). Where information is available, we provide estimates of current population size for that species. In many cases this number is not known, but general information is available on species abundance and these characteristics are used to help determine population size. We use this type of information to categorize population size as "common" or "uncommon" relative to other species in the taxonomic group.

We ranked reproductive rate based on several factors including; how quickly individuals typically mature to the reproductive stage, number of generations per year, and how many offspring are produced. We realize that a high reproductive rate does not necessarily mean large numbers of offspring will survive to maturity, however, the ability to produce large numbers of offspring in a short time frame is one indication of the potential for a species to build population size quickly. In addition, this type of information is available for many species. We used reproductive rate information to rank reproductive rates as "high" or "low".

Current population size and reproductive rate were used to categorize species as one of four types:

1. Common/High
2. Common/Low
3. Uncommon/High
4. Uncommon/Low

Dispersal

We use the following definition of dispersal in this paper: Movement of organisms (usually juvenile animals or plant propagules) out sites they or their parents previously occupied. This would not include short-term excursions undertaken by some animals.

The dispersal category is based on how far individuals, or in the case of plants and lichens, their offspring, disperse and how readily organisms can traverse non-habitat areas. We utilize quantitative information on a species' dispersal distance when available. When actual dispersal distances are not known, we rank dispersal distance based on available information about the species' dispersal characteristics, relative to other species in the taxonomic group.

We categorize dispersal behavior as "resource dependent" or "resource independent". For animals this is based on what is known about the species' behavior relative to dispersal (see discussion of dispersal behavior in Section A and Appendix III). For plants and lichens, we class dispersal based on what is known about their dispersal mechanism and how likely intervening areas influence dispersal distances. For example, for plants with ant-dispersed seeds, suitable ant habitat is needed for seeds to be dispersed. We classify these plants as resource dependent. In contrast, some plant propagules are less influenced by intervening habitat and are categorized as resource independent, for example wind-blown aspen seeds.

We combine the two dispersal characteristics to categorize two dispersal types. "Good dispersers" are those species that are known to disperse long distances relative to other species within that taxonomic group, that can and will disperse (or have their propagules dispersed) through non-habitat areas. "Poor dispersers" are those that disperse short distances and do not tend to traverse non-habitat areas (or have their propagules moved through non-habitat areas).

Interactions

Interactions with other species can often influence how spatial patterns affect species presence and abundance. For example, some bird species experience greater nest predation in edge areas. In plants, several factors are known to influence the effects of spatial pattern or composition such as whether the species is preferred as deer forage (Balgooyen & Waller, 1995; Rooney, 2001), its ability to compete with other plants (often correlated with whether it is native or non-native) (Hobbs and Mooney, 1998), and/or the type of pollination and/or dispersal mode (Rooney *et al*., in review).

Habitat Specificity and Type

Habitat specificity can play a primary factor in determining abundance and rarity and is also thought to influence sensitivity to habitat loss and/or change. Species with general habitat requirements are likely to be more resistant to alteration or changes to forest and pattern, as there is a higher probability that the new cover type will provide some measure of habitat. Species with very specific habitat requirements are more likely to experience habitat loss as a result of forest change, conversion to agriculture, or urbanization. Where known, we include notes about the species' local distribution, i.e., whether it is very narrowly or widely distributed.

Subhabitats

In some cases, a species may require recognizable components within its overall habitat. For example, some butterfly species utilize both open prairies and woodland areas, and the presence and close proximity of both of these habitat types (or "subhabitats") is important for population persistence (Lane, 1999; Lane and Andow, in press). We use the term subhabitat to describe these components of a species' habitat.

The type of habitat a species uses, such as whether it is a habitat generalist or specialist, can be a primary influence in how forest spatial pattern affects that species' persistence. For each species we describe the type of habitat used and assign one of the four types:

- Habitat generalist
- Interior forest
- Two or more subhabitats required
- Habitat specialist – specific successional stage, structure or other feature needed

For each taxonomic group we briefly provide the basis for example species selection and describe unique features for the group. It was challenging to assign species to categories for several reasons including lack of information and because there is often not a sharp delineation between the types of characteristics. However, categorization was a necessary step for moving beyond a species-by-species approach. *Please note* that the rankings for each characteristic in Table 1 are ranked relatively within taxonomic group. For example, the range from low to high reproductive rates for insects may be much greater than the range in birds, and a low reproductive rate for some insect species may still be greater than a high reproductive rate for most birds.

BIRDS

We chose 10 example bird species for this review (Table 1). Due to their ability to fly, most birds in northern Minnesota are good dispersers. In general, however, first-time breeders of migratory species settle farther away from their natal territory than those of resident species (Paradis *et al.*, 1998; Sutherland *et al.*, 2000). Therefore, when dispersal information was lacking or limited information suggested a moderate dispersal distance, we categorized migratory species as good dispersers and resident species as poor dispersers. This categorization is crude and based on little solid information. Only the black-capped chickadee, ruffed grouse, and spruce grouse were categorized as poor dispersers. These species are considered poor dispersers compared to other birds, not other kinds of animals. Poor-disperser birds may disperse farther than amphibians considered good dispersers.

Most birds in northern Minnesota forests are limited to one clutch per season, so most birds have low reproductive rates compared to other taxa. We considered species with clutch sizes over 10 to have high reproductive rates. Only the wood duck and the ruffed grouse fell into this category. We categorized species as common or uncommon in northeastern and north-central Minnesota based on Appendix A in Green (1995). All common species were either habitat generalists (red-eyed vireo, black-capped chickadee) or birds of the interior forest (ovenbird). ("Area-sensitive" may be a better term than "interior forest" to describe birds (Villard, 1998), but "interior forest" was better for all taxa combined.) Red-eyed vireos have been shown to be sensitive to forest cover in some studies (e.g. Dunford *et al*., 2002), but they use patches as small as 0.5 ha (Robbins & Dawson, 1989) and even some residential areas (Cimprich *et al*., 2000).

We chose the scarlet tanager as an example of uncommon interior forest species. The barred owl was another option, but there is less information on landscape effects for it. The three species that require multiple sub-habitats do so in very different ways. The good disperser wood duck requires both open water and mature trees. The poorly dispersing ruffed grouse strongly prefers aspen forests of different ages in close proximity. The boreal owl requires lowland conifer in proximity to mature upland mixed forest. The golden-winged warbler, which requires shrubby lowlands or other vegetation with similar structure, is an example of uncommon habitat specialists. Other options were the pine warbler, which requires mature pine forest, and the Connecticut warbler, which requires lowland conifers.

MAMMALS

We chose 11 example mammal species for this review (Table 1). Few, if any, mammals in northern Minnesota are specialists in particular vegetation types. Most are generalists and fall into just two categories: 1) common, poor dispersers with a high reproductive rate, and 2) uncommon, good dispersers with a low reproductive rate. The timber wolf represents the latter, though some information on red foxes is also presented because they respond differently to some landscapes than wolves do. Other species in this category include most weasels, all the bats, black bear, bobcat, and porcupine. We chose the deer mouse as an example of common, poor dispersers with high reproductive rates because lots of information on it has been published, but the snowshoe hare is also discussed because it is a major prey item for several large predators. Other species in this category include red squirrels, both chipmunk species, and most shrews and voles. The southern red-backed vole, however, is categorized as a forest interior species, based on studies showing an avoidance of edges and clearcuts (Halvorson, 1982; Martell, 1983; Mills, 1995). But other studies have found increases in clearcuts (reviewed in Kirkland, 1990); though they may be population sinks. In any case, red-backed voles have more specialized needs than deer mice (Gliwicz and Glowacka 2000). The American marten is the only other interior forest species.

In general large mammals disperse farther than small mammals, and predators disperse farther than herbivores (Sutherland *et al.*, 2000). Therefore, when dispersal information was lacking or limited information suggested a moderate dispersal distance, we categorized larger species and predators as good dispersers and smaller species and herbivores as poor dispersers. This categorization is crude and based on little solid information. The white-tailed deer is an example of uncommon species with low reproductive rates preferring multiple subhabitats (a mix of woodland and open areas), but some information for moose is also presented. Deer are much more common than moose, but the scale of mammal abundance includes some super-abundant small species. In comparison, deer and moose are both categorized as uncommon. Two other fairly common species in the same category as deer and moose are the mink and the beaver. For some of the mammal species in this table (such as pygmy shrew, water shrew, and star-nosed mole) little or nothing is known about landscape effects, but they are alone in their categories.

AMPHIBIANS

We chose 10 example amphibian species for this review (Table 1). Amphibians present in the project area of Minnesota have a wide variety of habitat requirements, and example species were selected to reflect this variety. Most amphibians require water and uplands for their life-cycle. Consequently, nearly all of these example species could be categorized here as requiring multiple habitats. However, some species, such as the American toad and Eastern tiger salamander, are able to use many types of breeding and upland habitats in comparison to other amphibians, and are therefore categorized as generalists. In contrast, the strictly terrestrial red-backed salamander relies on forested habitat for all of its life-stages, and is categorized as an interior forest species.

The other amphibians used as examples are all categorized as requiring multiple habitats. Within this categorization, they vary in terms of their habitat specificity as well as their other traits. The Northern leopard frog requires three subhabitats: shallow waters for breeding, open uplands for foraging and permanent waters for overwintering. As juveniles may cover distances as long as 800 m per day for many days at a time, this species is categorized as a good disperser. The Northern spring peeper has relatively broad habitat tolerances for breeding and foraging, and overwinters beneath logs, bark and fallen leaves. Gibbs (1998a) classifies this species as having intermediate dispersal tendencies, but also notes it has better dispersal than other amphibians categorized as intermediate. Based on this, the spring peeper is categorized here as a good disperser.

These remaining five example species are all considered forest-dependent. While they vary in degree in their other characteristics, they all rely on pools in forests for breeding. The blue-spotted salamander is perhaps the most common salamander in Minnesota forests. However, information about dispersal distances and behaviors was not obtained, so no final dispersal categorization was possible.

The spotted salamander is at the western edge of its range in Minnesota. The first records of occurrence in the state were in 2001, along the St. Croix river (Hall, http://www.dnr.state.mn.us/reptiles_amphibians/salamanders/spotted.html).

Although this species is extremely rare in the project area, it is included here because it is well-studied in other parts of its range. The wood frog breeds very early and rapidly in vernal pools, floodings, wooded swamps and quiet stream backwaters. It is a resident of moist deciduous, coniferous and mixed forests, overwintering on the forest floor. Based on Gibbs' (1998a) classification of both of these species as having low relative population density and intermediate dispersal tendencies, they are categorized here as uncommon and poor dispersers.

The Eastern newt has several subspecies, including the Central newt (*Notophthalmus viridescens louisianensis*) which is present in Minnesota, and the well-studied red-spotted newt (*N. v. viridescens*). This subspecies is at the edge of its range in the project area, and its distribution in patchy (Oldfield and Moriarty, 1994). The Eastern newt is unique among Minnesota salamanders in that it has a terrestrial eft stage dedicated to dispersal, with distances greater than 1 km recorded (Oldfield and Moriarty, 1994). The eft stage may only last 1-2 years in Minnesota, rather than 4-8 years elsewhere (Oldfield and Moriarty, 1994). This species is categorized as an uncommon good disperser.

The four-toed salamander is a special concern species in Minnesota. Its first occurrence in Minnesota was recorded in 1994, and it has since been found in several other counties in the project area. This small-bodied salamander relies on mature hardwood forest habitats, where it lays a relatively small number of eggs in moss near water. Based on these characteristics, it is categorized as an uncommon poor disperser.
(Hall, http://www.dnr.state.mn.us/reptiles_amphibians/salamanders/fourtoed.html).

INSECTS

We chose five example insect species for this review (Table 1). While insects represent the majority of species in the project area, insect biology and ecology are not well known. In fact, for many groups of insects species are still being named. Therefore for this group, information availability was a primary factor influencing species selection.

We selected two pest species, the forest tent caterpillar (*Malacomsoma disstria*) and spruce budworm (*Choristoneura fumiferana*), because their biology and ecology are relatively well known, they influence forest dynamics, they are important economic pests of forest trees, and because they are good examples of abundant, widely distributed, long distance, and resource-independent dispersers. Interactions between the forest tent caterpillar and its natural enemies have also been studied, providing a good example of interaction between an herbivore, its host plants and its natural enemies.

The northern blue butterfly is included because it is an example of a species that was historically locally abundant. It is now rare as a result of fire suppression and habitat change, but as a savanna/open woodland species, is likely to benefit from some types of forest management. Also, it is less mobile than the two pest species and its larval (immature stage) feeds only on one understory plant species.

Compared to many non-pest insects, the effects of spatial pattern on beetle species (Coleoptera) has been relatively well studied and three species are included as examples. Some ground beetles have very specific habitats and many are known to move very short distances. In addition, beetle species are numerically dominant and important to ecosystem processes. Hence they are useful for assessing the effect of habitat alteration on ground-dwelling insects (Golden & Crist, 2000).

PLANTS

We selected nine example plant species for this review (Table 1). Selected species represent a range of characteristics including those that have large population sizes and high reproductive rates, can grow competitively in a broad range of environments, and for which propagules are easily dispersed long distances, to those that have small population sizes, low reproductive rates, specific habitats and are dependent upon biotic pollinators and/or seed dispersers. We included the abundant native forest tree, quaking aspen (*Populus tremuloides*), the invasive native herbaceous plant, Canada goldenrod (*Solidago canadensis*) and the non-native grass, smooth brome (*Bromus inermis*). Aspen is included as an example of a common and economically important forest tree in northern Minnesota. Its biology and ecology are well-known and it is a good example of a plant species that does not depend on pollinators or seed dispersers and produces many wind-dispersed seeds. Coverage of aspen is increasing in several northern Minnesota forest types (Host and White, 2002). Also, interactions between aspen, its herbivores and their parasitoids have been studied.

We included another forest tree, white cedar (*Thuja occidentalis)*, because it is an example of a species that was once common in mesic hardwood forests but is now declining in abundance, in part because of poor regeneration. Cedar is able to function as an early successional species in some areas, seeding in after a ground disturbance. However, it is declining as a dominant species mesic hardwood forests (Meredith Cornett, pers. com.)

Understory and herbaceous plant species often respond differently to forest spatial pattern change than overstory species and therefore, several examples of understory species were included for which research had been conducted in northern forests (Table 1). Large flowered trillium (*Trillium grandiflorum)* and blue-bead lily (*Clintona borealis*) were included because pollination and/or seed dispersal are dependent upon biotic agents (animals) for dispersal. We also included wild leek

(*Allium tricoccum*) because it also has short seed dispersal distances, it is gravity-dispersed, has very specific habitat requirements and appears to be sensitive to habitat disturbance. In addition to the former, which have been shown to be preferred as deer browse, we added Michigan lily (*Lilium michiganense*) because it is both uncommon and preferred as deer browse (Fletcher *et al.*, 2001).

Plants were categorized as habitat specialist or generalist based partly on the number of habitat types that the species occurs in (Curtis, 1959; University of Wisconsin Herbarium web site - http://www.botany.wisc.edu/wisflora/search.asp). For plants, we also included the "Coefficient of Conservatism" ranks. These ranks were given to native species in Wisconsin based on the species' tolerance for disturbance and fidelity to a particular pre-settlement plant community type (Wisconsin State Herbarium, Wisconsin Floristic Quality Assessment, http://www.botany.wisc.edu/wisflora/WFQA.asp). The scores range from 1 to 10. A score of 10 applies to plants that are have restricted habitats and are intolerant of disturbance, such as calypso orchid (*Calypso bulbosa* var. *americanum*). A rank of 1 is applied to those plants that occur in many habitats, including disturbed areas, such as Canada goldenrod (*Solidago canadensis*).

LICHENS

We selected two lichen species that had different types of reproduction, soredia, spores, etc. (see Appendix I), different thallus types (foliose to fruiticose), and different habitat specificities.

SECTION B

Sensitivity Framework: Responses of Species to Spatial Pattern Changes

In this section, we present the effects of spatial pattern changes on example species. Based on the categorization system presented in Section A and Table 1, we are able to locate the example species within the Species Sensitivity Framework (Table 2). This Framework becomes a tool for comparing species' responses to spatial pattern changes based on species characteristics.

In presenting the spatial pattern effects on species, we focus on the following components of spatial composition and configuration (see Appendix I for detailed descriptions of the following spatial patterns):

- Patch size effects
- Habitat patch quality effects
- Edge effects
- Effects of arrangement of patch types
- Effects of habitat isolation and connectivity

In general patch size, habitat patch quality and edge effects influence species abundance and persistence at a within-patch scale. In contrast, arrangement of patch types, and habitat isolation and connectivity influence between-patch dynamics. Changes to spatial pattern often changes several metrics at once, and researchers attempt to analyze responses to these changes separately.

Under each category of spatial composition or configuration we provide a synthesis and summary of key species' information from the literature. We will include examples and research results from a wide range of species, habitat types, and locations, but wherever possible, we focus on those example species which occur in Minnesota and/or boreal/northern hardwood forest cover types.

Structure of following section:
For each of the five spatial pattern categories, we will present a summary of how the spatial pattern is known or likely to affect the example species. Based on the literature, we predict how the species likely respond to the types of spatial pattern changes documented in this project including: smaller average patch size, increased edge density, reduced core (interior forest) area, and a compositional change to younger forests and less conifers (Whitney, 1987; Host and White, 2002; Host and White, 2003). A simplified version of the species sensitivity table is associated with each summary section. Color-coding is as follows: light gray cells indicate a positive response, black cells indicate a negative response, and a cell with a double border indicates that either the response varies or is not known.

Patch Size Effects

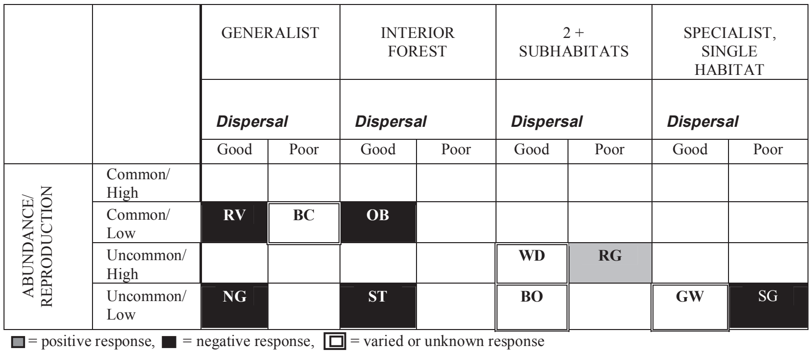
General

It is important to remember that patch size depends on the patch type classification system. For species like the ovenbird that use a wide variety of forest types, a patch of habitat more or less corresponds to the extent of forest cover, and a meaningful measure of patch size is the size of the forest. For specialists like the spruce grouse, however, the appropriate measure of patch size is the extent of black spruce and jack pine forest, even if it is embedded within a much wider forest.

Birds

Summary:

Species considered area-sensitive (categorized as “interior forest” species), such as ovenbirds (OB) and scarlet tanagers (ST), are most affected by forest patch size. In residential and agricultural portions of northern Minnesota, the abundance and reproductive success of these species depends on large patches. In the predominantly forested landscapes, larger patches probably continue to increase abundance. Resident species of mature forests, such as the spruce grouse (SG), barred owl, and northern goshawk (NG, migratory in some years), may also benefit from larger patches, as predicted by Bender *et al*. (1998). Non-forest species, including the golden-winged warbler (GW), also have minimum area requirements, but they tend to be lower than those for forest species. The ruffed grouse (RG), on the other hand, does best in landscape of small patches, as discussed in the Arrangement of Patch Types section.



		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low	■ RV	☐ BC	■ OB					
	Uncommon/ High					☐ WD	▨ RG		
	Uncommon/ Low	■ NG		■ ST		☐ BO		☐ GW	■ SG

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of responses:

Different bird species are affected by patch size in different ways. For example, a study in Spain showed that species with specialized foraging behavior occupied only the largest patches of forest, while generalists were found in all patches (Telleria & Santos, 1995). According to one prediction (Bender *et al.*, 1998), migratory species should be less affected by reductions in patch size than resident species, but Flather and Sauer (1996) found the opposite effect.

The northern goshawk, which migrates in some years but not others, was found to prefer larger patches of mature forest over smaller patches in Sweden (Wíden 1989), and they require stands of mature forest at least 40 ha for nesting in western Washington (Finn *et al.*, 2002). The non-migratory spruce grouse also tended to occupy larger patches of lowland conifers in Maine (Whitcomb *et al.*, 1996). However, most of the evidence for patch size effects in North America concerns migrants, either because those are the species most affected or because researchers have chosen to focus on them.

Abundance

Some species can use patches smaller than their territory size by using several separated patches, although this may impose a cost (Hinsley, 2000). Species that require large patches are called area-sensitive. Ovenbirds and scarlet tanagers are considered strongly area-sensitive forest-nesting birds, based on data from the Mid-Atlantic region (Robbins & Dawson, 1989) and other sources. The red-eyed vireo is also more abundant in large patches, but it does not require them to the extent that ovenbirds and tanagers do. Even in predominantly forested landscapes, larger patch sizes benefit ovenbirds, red-eyed vireos and other species (Van Horn *et al.*, 1995; Hawrot & Niemi, 1996; Burke & Nol, 2000; Manolis et al 2002).

In one study, scarlet tanagers were found to be completely absent from any patch of mature forest less than 10 ha in size, but density was similar in all larger patches (Roberts & Norment, 1999). Even more evidence is available for area-sensitivity in ovenbirds. In Missouri, for example, only patches of mature forest larger than 300 ha were assured of containing ovenbirds, but even those large patches were not optimal. Ovenbird density continued to increase as patch size grew past 800 ha (Wenny *et al.*, 1993). Male ovenbirds in continuous forest have larger body sizes than those in small patches, which are presumably unable to gain territories in the preferred larger patches (Mazerolle & Hobson, 2002).

Species of early successional forests generally demonstrate a lesser degree of area-sensitivity. Small groupcut harvesting in New Hampshire created forest canopy gaps large enough to attract early successional species in one study (King *et al.*, 2001), but not another (Costello *et al.*, 2000). These species generally benefit from open patches of at least 5 acres, preferably 10-40 acres (Thompson and Dessecker, 1997)

Some forest species may prefer large patches for behavioral reasons. For example, male hooded warblers (which do not occur in northern Minnesota) nesting in small patches spend more time outside their territories than those in continuous forest. They traveled up to 2.5 km to obtain extra-pair copulations, compared to a maximum distance of 250 m in continuous forest. The cost of this additional travel may explain why hooded warblers are found less frequently in small patches (Norris & Stutchbury, 2001). Extra-pair copulations are prevalent in many bird species, and some may avoid small patches altogether in order to have close neighbors for extra-pair copulations or other advantages.

Another possible mechanism explaining area-sensitivity is food supply. One study in an agricultural landscape that found increased ovenbird density in larger forest patches also found 10-36 times more prey biomass in larger patches. Territories in large patches also had deeper leaf litter, which is considered better habitat for ovenbirds (Burke and Nol, 1998a). However, in a forested landscape in New Brunswick, no difference was found in the amount of potential food in small patches of mature forest and a continuous forest (Sabine *et al.*, 1996).

Reproduction

Evidence is strong that reproductive success increases with patch size for some bird species, particularly mature forest species. For scarlet tanagers, fledging success increased with forest patch size, reaching a maximum of 64% in patches over 1000 ha (Roberts & Norment, 1999). The likelihood of territorial male ovenbirds attracting a mate increased with forest patch size (Van Horn *et al.*, 1995; Bayne & Hobson, 2001a), but according to one study the proportion of breeding males may not actually differ. Bayne and Hobson (2001a) found that the larger number of unpaired territorial males in small patches was balanced by the larger number of non-territorial males (floaters) in continuous forest. Once paired, however, forest patch size was the most important variable determining reproductive success in ovenbirds in a study comparing agricultural and forested landscapes in Ontario (Burke & Nol, 2000). The amount of forest in the landscape had no effect.

Increasing nest success with larger patch sizes may be a result of lower predation. In a study of artificial nests in northeast Alabama, predation by small mammals was not correlated with patch size, but predation by larger animals (blue jay, crow, gray fox, opossum, raccoon, and white-tailed deer) increased as patch size decreased (Keyser *et al.*, 1998). While evidence of increased reproductive success in larger patches is strong, it does not hold for all species in all areas. For example, in one study of early successional species, reproductive success was similar in small groupcuts and larger clearcuts (King *et al.*, 2001).

Winter Survival

One study in an agricultural landscape in Ohio found higher survival rates for Carolina chickadees, white-breasted nuthatches and downy woodpeckers in large woodland patches, compared to small patches (Doherty & Grubb, 2002). In forested landscapes, where forest patches are more likely to be perforated than isolated, this relationship between patch size and survival is unlikely.

Mammals

Summary:

In the residential and agricultural portions of northern Minnesota, patch size is likely important for the persistence of small forest mammals such as the red-backed vole (RV). In predominantly forested landscapes no mammal species are likely to depend on large patch sizes of particular forest types, but the habitat requirements of the marten (AM) is correlated with large patches of forest. Since patch size is usually correlated with diverse landscapes, white-tailed deer (WD), moose (M), and red fox (RF) probably respond positively to reduced patch size for the reasons discussed in the Arrangement of Patch Types section. Wolves (TW) benefit when deer increase.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High		▣ **DM** **SH** **SM**		■ **RV**		▣ **WS**		
	Common/ Low								
	Uncommon/ High								
	Uncommon/ Low	▨ **TW** **RF**	▣ **PS**	■ **AM**		▨ **WD** **M**			

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of responses:

Little research has been conducted on how mammals respond explicitly to patch size. More has been conducted on the related issue of edges. Many mammal species have larger home ranges than area-sensitive birds, and they may require extensive areas of habitat. However, their habitat does not need to consist of a single patch type, as it does for area-sensitive birds. An exception is the American marten. One study found that forest patches used by martens were larger than unused patches (Chapin *et al.*, 1998). Most of the research that has been conducted for mammals, however, concerns mammalian predation on bird nests.

One review (Chalfoun *et al.*, 2002) concluded that responses by nest predators to forest fragmentation is complex, species-specific, and depends on the landscape context. Increases in predators in smaller forest patches are more common in agricultural landscapes, but have also been found in forested landscapes. Contrary to this trend, the density of red squirrels in an agricultural landscape in Alberta actually increased with forest patch size (Bayne & Hobson, 2000a).

Amphibians

Summary:
Amphibians have relatively small home ranges and complex life-cycles involving movements by amphibian adults and juveniles between subhabitats. Consequently, changes in patch size per se (meaning the size of the breeding pool, or the size of an adjoining forest patch or open area) are often addressed in terms of studies of changes in patch habitat quality, patch edges, or in landscape-scale studies about relationships between species occurrences and forest patch sizes and forest and pond adjacency. These are discussed in subsequent sections of this document.

However, some conclusions can be made. Species that are uncommon, poor dispersers and dependent on particular forms of subhabitats such as the Four-Toed Salamander (FTS), are most sensitive to changes in the sizes of their subhabitats. Not only do decreased patch sizes mean less habitat is available for reproduction, foraging and overwintering, the decrease can also make the existing patches too far apart for dispersal. This effectively isolates the populations, making them more vulnerable to extirpation in the event of a drought or other catastrophic change to their habitat. In contrast, decreases in forest patch size, per se, may have relatively little effect or even be beneficial to the American toad (AT) a common species that disperses easily and uses a wide variety of upland and breeding habitats.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	**AT**							
	Common/ Low								
	Uncommon/ High								
	Uncommon/ Low						**FTS**		

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Insects

Little information was found on the effects of forest patch size on Minnesota insect species. Research on the Northern blue butterfly (NB) suggests that currently small habitat patches are a result of lack of disturbance and change in forest cover type and may limit the abundance of this species. Results from beetle studies are variable in regard to patch size, although small and larger patches supported a greater abundance and diversity of insects in some studies (Ground beetles: *Calosoma frigidum* [CF], *Platynus decentis* [CF]).

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low				CF				PD
	Uncommon/ High								
	Uncommon/ Low							NB	

▨= positive response, ■ = negative response, □ = varied or unknown response

Detailed overview of effects:

Patch size can affect insect species diversity, species presence and abundance, and predation rates (Bach, 1984; Kareiva, 1985; Shure and Phillips, 1991; Trumbo and Bloch, 2000; Mitchell *et al*., 2002; Ranius, 2002). Carabid beetle species richness was not different between habitat remnants and continuous forest in Australia (Davies & Margules, 1998). Studies in tropical openings and forested areas found beetle density to be greater in the large host patches located in forested areas than in open areas (Bach, 1984).

Ant species composition was shown to vary with patch size (research in conducted Appalachian Highlands, Mitchell *et al*., 2002). Contrary to what was predicted, ant abundance and species richness was greater in small patches and lower in large patches. In addition, the small patches had a history of more intense land use than larger patches. In the large patches, *Aphaenogaster fulva* dominated, possibly because of a greater tolerance to shade and preference for mesic conditions. *Camponotus* and *Formica* spp. tended to dominated smaller patches. The findings have implications for ant dispersed seeds as there seem to be advantages to dispersal by *A. fulva* (see Plants section below).

A study conducted in the Southern Appalachian Mountains found that arthropod abundance and composition varied with size of canopy opening (Shure and Phillips, 1991). Smaller canopy openings (0.016 ha) were found to have the highest herbivore biomass and species diversity, followed by large canopy openings (10 ha). The mid-sized patches (0.08, 0.4 ha) had the lowest herbivore abundance and diversity, possibly because the sparse vegetative cover and high sunlight and/or temperatures associated with this size opening may not have provided suitable habitat for many species. Which species were found in the openings and at what abundances was associated with how similar the environmental conditions in the openings were to the surrounding forest.

Insect abundance is often (but not always) associated with host plant abundance. For example, one factor correlated with Karner blue butterfly (*Lycaeides melissa samuelis*) abundance, a close relative of the northern blue butterfly, is host plant abundance (Lane, 1999). The northern blue butterfly is thought to be rare in Minnesota and Wisconsin because of the currently rare and patchy distribution of its host plant, dwarf bilberry (*Vaccinium caespitosum*) (Wolf, 1993). The small size of habitat patches is thought to be partly a result of lack of disturbance and change in forest cover type. Some beetle species associated with trunk hollows in Sweden and were not present (*Elater ferrugineus)* or rarely present (*Tenebrio opacus*) in stands with less than 10 hollow trees (Ranius, 2002).

Small patches, especially in developed areas, tend to have higher numbers of vertebrate scavengers (raccoons, skunks, etc.) which may compete with burying beetles for small mammal carrion, resulting in reduced abundance of woodland burying beetles (Trumbo and Bloch, 2000)

Plants and Lichens

Summary:

Plants such as large flowered trillium (LT) or yellow blue-bead lily (YL) are likely to be less abundant in small patches. This is in part because they require animals for pollination or seed dispersal and therefore reproduction rates may be reduced if these animals are not present or are less attracted to plants in small patches. Wind dispersed species, including aspen (A) and Canada goldenrod (CG), may be less sensitive to patch size as they are not dependent on pollinators and can disperse seeds longer distances. The incidence of dwarf mistletoe (DM) infection may increase with reduced patch size and smaller clear-cuts. In cases where reduced patch size is also associated with disturbance, greater edge and canopy opening, species with characteristics similar to aspen and Canada goldenrod are likely to increase in abundance. The negative effects of edge, such as adverse microclimate and competition with invasive species, will tend to be greater for small patches where the edge to area ratio is greater (see Edge Effects, Plants).

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	▨ **A** **CG** **DM**							
	Common/ Low			■ **LT**					
	Uncommon/ High								
	Uncommon/ Low							■ **YL**	

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of responses:

Patch size may influence plant species by affecting the abundance and/or behavior of pollination and dispersal agents, seed predators, microclimate and edge effects

(Cunningham, 2000; Jacquemyn *et al*., 2002; Pearson *et al*., 1998; Burke & Nol, 1998b). In general, small forest patches may tend to lack habitat specialists (Burke & Nol, 1998b). Large forest patches tend to have a greater presence and abundance of forest herbs than small patches (Pearson *et al.*, 1998; Jacquemyn *et al.*, 2002). Plants in the lily family were particularly likely to be more abundant in larger patches (Pearson *et al.*, 1998). Similarly, the herbaceous perennial *Primula elatior* was more likely to be present and support viable populations in larger forest patches (studies in Belgium, Jacquemyn *et al*., 2002).

Plants can also be affected if patch size influences their pollinators or seed dispersers. Lack of pollination was found to limit reproduction in small, isolated patches (Groom, 1998). Plants with ant dispersed seeds were found to be absent, or reduced in abundance, in smaller woodland patches (North Carolina study, Pearson *et al*., 1998). In the same study, ferns and composites, which have wind-dispersed seeds, were not affected by patch size and isolation. Dispersal of seeds by ants may be influenced by patch size as different species of ants were found to predominate in large patches (*Aphaenogaster fulva*), versus small patches, (*Camponotus* and *Formica* spp.) (Mitchell *et al*., 2002). *A. fulva* is very effective at rapidly collecting seeds and moving seeds, which may help reduce rodent predation on seeds. *Camponotus* sp. may not be as beneficial as seed dispersers because they may be less likely to move seeds to suitable germination sites and more likely to eat seeds. The behavior of dispersal agents can also be influenced by patch size. For example, birds may be more attracted to using large patches and deposit more seeds in those patches (Yao *et al.*, 1999).

Also, smaller forest patches may be less likely to receive seeds or types of propagules. Studies on lichens in Oregon (Sillett *et al.*, 2000) suggested that preserving remnant trees dispersed throughout forest openings could assist the inoculation of younger surrounding trees with lichen propagules.

Some of the observed effects in small patches were linked to the relatively greater proportion of edge in small patches and associated edge effects such as adverse microclimate (hot, dry, high light) and/or competition with invasive species (Burke and Nol, 1998b) (see discussion of edge effects below).

Forest patch and clearcut size can influence dwarf mistletoe infection rates (Anderson, 1949; Ostry, 1978). Anderson (1949) found that large, densely-stocked, even-aged black spruce stands with a small amount of edge are least likely to become infected. Black spruce trees in or adjacent to smaller forest openings, such as small clearcuts, may have a higher probability of becoming infected by dwarf mistletoe because birds and small mammals, vectors of dwarf mistletoe seeds, are attracted to small openings (Ostry 1978).

Habitat Patch Quality

Birds

Summary:
The types of changes in forest spatial pattern and composition documented in this project (White and Host 2003, Host and White 2003) have some general implications for habitat patch quality. A reduction in the proportion of mature forest since the late 1800s likely reduced the quality of a forest as habitat for species that prefer attributes of mature forest, including ovenbirds (OB), goshawks (NG), boreal owls (BO), and barred owls. Creating openings and younger age classes increases the quality of the forest for species associated with disturbance like chestnut-sided warblers and mourning warblers (1995) and also, to some degree, for golden-winged warblers (GW), a shrub specialist (Confer 1992). Increases in disturbance rates can improve habitat for ruffed grouse (RG), a species that requires both younger and older forests. These forest changes are neutral or slightly positive for generalists like the black-capped chickadee.

Decline in conifer cover (White and Host, Host and White 2003) has likely resulted in reductions in bird populations associated with conifers, including the Blackburnian warbler, northern parula, and pine warbler (Green, 1995), and presumably an increase in species associated with deciduous trees, such as red-eyed vireos (RV). For spruce grouse (SG) the overall decline in conifers could be offset if logging creates denser 4-6 m coniferous regrowth (1992).

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		*Dispersal*		*Dispersal*		*Dispersal*	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low	▨ **RV**	☐ **BC**	■ **OB**					
	Uncommon/ High					☐ **WD**	▨ **RG**		
	Uncommon/ Low	■ **NG**		☐ **ST**		■ **BO**		▨ **GW**	☐ **SG**

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

Ovenbird
Ovenbird abundance increased in a New Hampshire northern hardwood forest as it matured (Holmes & Sherry, 2001). They declined in a large forest patch (2000 ha) in

a fragmented Illinois landscape after the creation of small gaps by group and single-tree selection cutting (Robinson and Robinson, 1999). In New Brunswick selectively logged forest produced only 23% of ovenbird fledglings even though it was 50% of the sample. Nest success didn't differ, so the difference was due to the lower density (Bourque & Villard, 2001). The success in attracting a mate in one study was determined by local habitat quality, as measured by leaf litter depth (Rodewald & Yahner, 2000).

Northern Goshawk
In Minnesota goshawks prefer upland deciduous and coniferous forests at least 25 years old. Old (>50 years) aspen and birch was most preferred (Boal *et al*., in press).

Barred Owl
As an uncommon, forest area-sensitive species, barred owls are in the same sensitivity category as scarlet tanagers. In boreal forests they usually nest in natural cavities, but also in some hawk and corvid nests or other platforms. Old mixed forest was the only type that provided trees large enough for cavities, and they generally hunt in the same forest where they nest (Mazur *et al.*, 1997). Eighty percent of cavity nests were successful in a Michigan study, producing 1.97 young per nest, while only 31% of attempts in hawk nests or other open sites were successful, producing 1.0 young per nest. The difference was due primarily to owlets falling out prematurely. Nests in open sites are probably a result of a shortage of cavities (Postupalsky *et al.*, 1997). Therefore, older forests with abundant cavities are the highest quality habitat for this species.

Ruffed Grouse
Ruffed grouse are found at densities of 1-2 drumming males per 40 ha in northern hardwoods, and 4-8 drumming males per 40 ha in Great Lakes aspen forest (Dessecker & McAuley, 2001). Drumming and nesting sites require dense brushland (Stoll *et al.*, 1979); Thompson *et al.*, 1987). Chicks up to 10 days old eat only insects and they presumably choose habitat with more insects. After they start to eat plant material they used alder lowland 64% of time and upland 13% of time in a northern Minnesota study (Godfrey, 1975).

Golden-winged Warbler
The nesting success of birds that nest in dense shrublands is often higher than that of birds nesting in mature forest (Yahner & Cypher, 1987; Hanski *et al.*, 1996).

Mammals

Summary:
Changes in forest composition have likely had fewer impacts on mammal species than on birds. With a mature forest preference, martens are affected negatively by a younger forest with more openings. The effect on red-backed voles is less

predictable, but they also tend to prefer older, moister forests. Deer mice may have a neutral response to increases in younger forest, but snowshoe hares have likely benefited. White-tailed deer and moose, species that prefer a mix of forest and open areas, are strongly favored by the types of changes in forest composition seen over the last century, and wolves probably benefit as a result. Based on information discussed in the Arrangement of Patch Types section, red fox have also probably increased.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High		▨ **SH**		■ **RV**		▢ **WS**		
	Common/ Low		▢ **SM**						
	Uncommon/ High								
	Uncommon/ Low	▨ **TW** **RF**	▢ **PS**	■ **AM**		▨ **WD** **M**			

▨ = positive response, ■ = negative response, ▢ = varied or unknown response

Detailed overview of effects:

Unlike birds, there are few mammal species that require conifers. However, Martens and snowshoe hares prefer conifers for meeting some of their needs. Like birds, mammals can be affected by changes in the quality of forest types.

American Marten

Martens generally prefer dense, undisturbed old-growth conifers, but they also use mixed forests, clearcuts and shrublands, particularly when feeding on raspberries (primarily juveniles). The older forests provide better protection from predation, homeothermic management, and access to prey (Bissonette & Broekhvizen, 1995). In cold weather and deep snow martens used resting site under the snow formed by coarse woody debris. These sites tended to be in the oldest forest (Wilbert *et al.*, 2000). Resting sites in tree cavities and logs were in large-diameter trees with heartrot (Bull & Heater, 2000).

Small amounts of logging is not detrimental, but populations are much reduced in heavily logged forests (Bissonette and Broekhvizen, 1995). In an industrial forest in Maine, martens used home ranges with as little as 60% forest cover at least 6 m tall (Chapin *et al.*, 1998). In Ontario, however, indices of marten abundance were 90% greater in uncut forest than 3-40 year old logged forest, due to higher mortality and lower productivity in the young forest (Thompson, 2000). Martens use forests killed by spruce budworm to a greater degree than clearcuts because the budworm-killed forests had many more snags, logs, and root masses (Payer & Harrison, 2000).

Southern Red-backed Vole

According to a review by Kirkland (1990), southern red-backed voles generally increase after clearcutting, but in many studies they have been absent from clearcuts (Halvorson, 1982; Martell, 1983; Mills, 1995). In a study in Minnesota and Michigan, red-backed voles were most abundant in sapling stands (4-12 years), moderate in mature stands (45-75 years) and least numerous in recent clearcuts (Probst & Rakstad, 1987). In a jack pine forest in Minnesota they were most abundant on cut, unburned sites (slightly higher than in uncut forest), but least abundant on cut and burned sites (Ahlgren, 1966). The voles have more specialized dietary needs than deer mice (Martell, 1981; Gliwicz & Glowacka, 2000), which are apparently met in some clearcuts, but not others. They rely heavily on fungi and lichens even in clearcuts, where these foods are less available (Gliwicz and Glowacka, 2000). They are absent from beaver meadows in Minnesota, even when abundant in the adjacent forest (Terwilliger & Pastor, 1999).

Deer Mouse

Populations of deer mice generally increase after clearcutting conifers, but decrease after clearcutting deciduous forests (Kirkland, 1990). They have a generalist diet, which allows them to invade disturbed sites (Martell & Macauley, 1981). Even when the population increases after logging, however, clearcuts may be sink habitats (Sullivan, 1979; Martell, 1983), meaning that there are fewer births than deaths and the population is supported by immigration. In a study in Minnesota and Michigan deer mice were most abundant in mature stands (45-75 years old), but they had the greatest relative dominance over other small mammal species in recent clearcuts (Probst & Rakstad, 1987). Mature stands had the highest overall populations of small mammals. Clearcut spruce-fir in Maine had a low abundance, but moderate diversity of small mammals, while budworm-killed forest had a diverse and abundant small mammal community (Clough, 1987).

Snowshoe Hare

As common generalists, snowshoe hares are in the same sensitivity category as deer mice, and like mice and voles, hares are a primary food source for many predators. They use the densest cover available, whether hardwoods or conifers, but conifers support higher hare densities because they provide better cover from predators and climatic extremes. Following clearcutting hares decline, but they recolonize 6-7 years later, and increase to a peak at 20-25 years (Litvaitis *et al.*, 1985). As population increases, hares begin to use habitats of less vegetative density, but as predation increases and the population declines, the hares contract back into the densest habitat (Wolff, 1980).

White-tailed Deer and Moose

In summer the most important factor governing deer use of habitat types is the availability of preferred forage, including maple, aspen and *Diervilla* browse, as well as forbs like strawberry, purple pea, goldenrod, and aster. In northern Minnesota they use upland deciduous and mixed forest extensively, including edges and openings, and they generally avoid fields and lowlands (Kohn & Mooty, 1971). In early winter in northern Minnesota deer use open cut-over land and deciduous forest, where they browse maple and dogwood. Later in winter they use conifer stands, especially fir and cedar, for thermal cover, even though there may be less available browse (Wetzel *et al.*, 1975).

Like deer, the quality of moose habitat depends on the amount of available browse. In winter in the southern part of the moose's range, however, they prefer lowland conifer and pine-poplar mixed forest, over the more prevalent deciduous-dominated forest. Compared to the conifer-dominated boreal forests, where winter cover is abundant, in the south shelter is more important than food supply. At a larger scale, however, moose prefer areas at least one third logged, (Forbes & Theberge, 1993). As habitat quality improves for deer, however, moose usually decline, at least in places where snow is not deep enough to give them an advantage. The decline in moose, often attributed to a brainworm (*Parelaphostrongylus tenuis*) carried by deer, is probably due mostly to other factors such as competition (Whitlaw & Lankester, 1994).

Amphibians

Summary:

Many studies have been conducted concerning the responses of forest-dependent amphibians to changes in quality and type of upland and breeding habitats, particularly in order to understand the implications of forest management actions.

Overall, clearcuts are associated with lower amphibian abundances than interior forest areas, with salamanders showing a stronger negative response than frogs and toads. Strictly terrestrial salamander species (in the Plethodontid family, e.g. red-backed salamander (RBS)) show the strongest negative response. Microhabitat features associated with several amphibians have been described, including for the red-backed salamander, the Eastern newt and wood frog (EN and WF - both forest-dependent species requiring multiple subhabitats) as well as the generalist American toad (AT). Where forest management occurs, modifying forest management methods to increase appropriate microhabitat features will benefit these forest-dependent amphibians, as well as generalist amphibians.

Breeding pool quality can affect amphibian species by affecting reproductive success and mortality from predators. Temporary pools created from forest management practices may lack adequate hydroperiods to serve as suitable breeding habitat for pond-breeding amphibians, and have been found to have negative effects on reproduction of early-breeding wood frogs (WF), specifically (DiMauro and Hunter, 2002). Permanent man-made ponds stocked with fish are common in extensively modified landscapes, and are inadequate breeding pools for some amphibian species. In a study of such a landscape, American toads are not affected by the presence of fish predators, while *Ambystomatid* species were never found in ponds with predatory fish. Leopard frogs (NLF), wood frogs (WF) and spring peeper (NSP) (which all have palatable larvae) were negatively affected by the presence of predatory fish.

Highlighted boxes refer to the responses of these species to clearcutting and changes in pond quality described above.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	▣ **AT**				▣ **NLF** **NSP**	■ **BSS?**		
	Common/ Low				■ **RBS**				
	Uncommon/ High					■ **EN**	■ **SS** **WF**		
	Uncommon/ Low								

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of effects:

Clearcuts vs. forested control sites

Clearcutting has at least a short-term negative impact on amphibian abundance (deMaynadier & Hunter, 1995; Dupuis *et al*, 1995; deMaynadier & Hunter, 1998). A review of 18 studies of effects of clearcutting on amphibians shows a 3.5-fold difference in median capture between control stands vs. clearcut stands (deMaynadier & Hunter, 1995). None of the reviewed studies were from Minnesota and few were from the midwest. Salamanders were found to be more sensitive to clearcutting than frogs and toads, as demonstrated by the differences in their respective median ratios of abundance on control vs. clear-cut stands. Salamanders had a median ratio of 4.3 (and Plethodontids, the strictly terrestrial salamanders, had a ratio of 5.0), compared with 1.7 for frogs and toads. This difference may be explained by the tolerance of frogs and toads to higher temperatures, and their ability to store and absorb large quantities of water, compared with salamanders. Similarly, in studies in North Carolina (Petranka *et al*, 1993; Ash, 1997) Missouri (Herbeck and Larsen, 1999) and west-coast Canada (Dupuis *et al*, 1995), salamander densities in mature forest stands were much higher than in recent clearcuts. While it is clear that salamander populations will not persist long-term without forested habitats, patterns of lowered abundance of amphibians in recent clearcuts are not fully understood, and may be explained several ways: the animals die, they disperse off-site, or they persist on-site, underground, in a reduced state of activity (deMaynadier and Hunter, 1995; Ash and Bruce, 1994; Petranka, 1994).

Importance of microhabitat features

Studies have attempted to identify the preferred microhabitat features of forest amphibians so that forest management can be conducted while maintaining these features. In their review of 18 studies (again, none from Minnesota, few from

Midwest), deMaynadier and Hunter (1995) found several microhabitat features of documented importance to many forest amphibians, including the presence of large, moderately to well-decayed hardwood and conifer logs, coarse woody debris, and forest litter. These features are understood to provide protection from mortality due to desiccation.

Various microhabitat features are associated with the Minnesota amphibian species: red-backed salamanders are associated with litter depth, understory vegetation and canopy closure; Eastern newts with understory vegetation, canopy closure and moisture; wood frogs with canopy closure and moisture; and American toads with understory vegetation (deMaynadier and Hunter, 1995). Changes in microhabitat features resulting from clearcutting are expected to affect physical characteristics of individual salamanders, although this was not found in an experimental study comparing several physical features of individual *Ambystoma talpoideum* salamanders placed in recent clearcut areas and 40-year-old pine forest lots (Chazal and Niewarowski, 1998). The authors note that there are limits to the interpretation of these results because the individual salamanders were not exposed to the mechanical disturbances of clearcutting and site preparation. These studies suggest that identifying and then implementing potential modifications to forest management practices that allow for persistence of microhabitat features required by forest amphibians has the potential to help improve habitat quality for amphibians in managed forests.

An understanding of the microhabitat requirements of forest amphibians, combined with a better understanding of their responses to the regenerating clearcuts or other forms of managed forests, will be valuable in determining at what point regeneration provides adequate forest habitat. While in general microhabitat variables often increase with stand age, there is considerable stand-specific variability due to several factors, including natural and silvicultural disturbance history, regional climate and soil differences, elevation, proximity to streams and seepages, and other environmental variables (deMaynadier & Hunter, 1995). This variability illustrates that stand age alone is not necessarily adequate for predicting responses of amphibians to managed forests.

For example, several terrestrial salamander species were found to return to recent North Carolina clearcuts in 4-6 years, and the timing of this return appears to be closely correlated with timing of litter layer reformation (Ash, 1997). In contrast, terrestrial salamander populations in southern Appalachian hardwood forests significantly declined within 3 years after partial removal of the forest canopy on low-elevation south-facing slopes (Harpole & Haas, 1999). In a review of the effects of clearcuts in floodplains of the southeast U.S., Lockaby et. al., (1997) report that amphibian diversity recovered within 6 months of harvests, but that the time required for re-establishment of pre-harvest amphibian populations (if this is possible) is unknown.

Breeding habitats
Decreases in the quality of breeding pools can negatively affect population if reproductive success falls. Temporary pools that dry out too easily, or pools that are stocked with predators are two examples. Pools are created during forest-management activities, and have the potential to be breeding sites for some amphibian species relying on temporary pools. These species include wood frogs, spotted salamanders and blue-spotted salamanders. DiMauro and Hunter (2002) found that anthropogenic pools may function as ecological traps for breeding wood frogs in most years, and they should be avoided or designed with adequate size, depth, and shading to maintain adequate hydroperiod. In this study, anthropogenic pools were more common than natural pools in the landscape, both types of pools typically had the same numbers of wood frog eggs, and only 56% of the natural pools dried before wood frogs could emerge, as compared with 75% of anthropogenic pools. This resulted in a potential anthropogenic pool “trap effect” of 19% for wood frogs.

In extensively transformed landscapes with many permanent ponds stocked with fish, the presence of predatory fish has a negative effect on amphibians (Hecnar and M’Closkey, 1996). In a landscape-scale study in southwest Ontario, amphibian species richness was lower in ponds with predatory fish, compared to ponds with non-predatory fish, and fish-free ponds, although not all amphibians were negatively affected (Hecnar and M’Closkey, 1996). Species with large bodies and large clutch sizes co-occurred with predatory fish more often than small-bodied species. The American toad (AT) with toxic eggs, larvae and adults, was not affected by the presence of predatory fish, while *Ambystoma spp.* (BSS and SS) never occurred with predatory fish. Leopard frogs (NLF) wood frogs (WF) and spring peepers (NSP) all with palatable larvae were negatively affected by the presence of predatory fish.

Insects

Summary:

The impacts of forest spatial pattern to insects will often be related to effects on host plant presence and abundance, plant structure and factors such as woody debris. Some disturbances associated with forest management practices, such as the creation of openings associated with roads and landing areas, are likely to increase host plant abundance and improve habitat patch quality for the Northern blue butterfly (NB) (USDA FS, 2002b). Both the northern blue and forest beetle, *Platynus decentis* (PD), may be negatively impacted by conversion from mixed deciduous-coniferous forest to conifers (where this occurs) because of negative effects on host plants and/or the lack of deciduous leaf litter. It is unknown how changes to habitat quality occurring in Minnesota forest might influence habitat quality for the ground beetle *Calosoma frigidum* (CF).

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low				**CF**				**PD**
	Uncommon/ High								
	Uncommon/ Low							**NB**	

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of effects:

Several factors influence patch quality for insects including host plant presence and abundance and forest structure. Host plants for immature stages are required, and in some cases a particular species of plant is needed, particularly for immature stage feeding. For example, Northern blue butterfly (NB) larvae feed solely on dwarf bilberry (*Vaccinium caespitosum*)(Wolf, 1993). Habitat quality for Northern blue butterflies may be reduced by conversion to red pine forest because larval host plant and adult nectar plant populations may be reduced or eliminated (USDA FS, 2002b). For many insects, such as butterflies and moths, adults typically have different food requirements than immature stages and may need flowers for nectaring or dung for nutrition. In the case of the forest tent caterpillar, the increase in larval food abundance is one factor contributing to large populations (see edge effects below). A diversity of host plants is important for many butterfly species as a diversity of hosts helps buffer against starvation as a result of year to year variation in plant abundance and phenology (Carey, 1994). Therefore, spatial pattern effects that influence the presence or abundance of plant resources for an insect species will often impact the presence and abundance of the associated insect herbivores (see sections on “Plants”).

Some insect species show preferences for certain site characteristics including stand age, areas with Sphagnum moss, or deciduous leaf litter (Coulson and Witter, 1984; Koivula, 2003). Similarly, particular habitat attributes contribute to outbreaks of the spruce budworm (*Choristoneura fumiferana*), including: a high proportion of preferred host species in the stand, the age of the trees is greater than 50 years old with overmature host trees that are producing flowers, the tops of the host trees protrude through the canopy and are in direct sunlight, and the stand is under water stress (Coulson and Witter, 1984). Studies conducted in northern Wisconsin and Michigan found that species tended to be associated with one of the following forest types: managed sites, old growth forest, northern hardwood forests, eastern hemlock dominated forests; or forest structures: even-aged or uneven-aged canopy structure

(Werner & Raffa, 2000). The authors concluded that a range of forest types was needed to maintain beetle biodiversity. For example:

- *Platynus decentis* (PD)– habitat specialist in mature/old growth forests, high abundance in eastern hemlock-hardwood forest types
- *Calosoma frigidum* (CF)– associated with northern hardwood species, feeds on butterfly larvae and may be important predator of butterfly or moth (Lepidopteran) pests.
- Some species were more commonly observed in managed forests, including *Nicrophorus orbicollis* and *N. sa*yi
- Habitat generalists – presence/abundance for some species was not related to forest management or type, for example *Calathus ingratus* and *Pterostichus melanarius*

Insects also often have particular requirements for egglaying and/or overwintering sites (Lane, 1999; Bernays and Chapman, 1994). Some beetle species were consistently associated with forests and a closed canopy (Koivula, 2003).

Insects are not able to internally regulate their body temperature and often require specific microclimates in order to conduct various activities, including flight, mating and egg-laying (Clench, 1967; Jones, 1977). Because of this trait, and the low mobility of some stages, high temperatures can be detrimental to insects (Lane, 1999). Both forest patch size and openings in the canopy will influence temperature conditions (Geiger, 1965).

Habitat quality for many invertebrates is also linked to that of their mutualists and/or natural enemies (Price *et al*., 1980; Cottrell, 1984). For example, habitat quality for large blue butterfly (*Maculinea rebeli*) operates at the smaller scale habitat of the ant (*Myrmica schencki*) that tends the butterfly's larval stages (Clarke *et al.*, 1997). Birds are one of many predators on the spruce budworm. In a low budworm population, birds consumed 84% of the larvae and pupae. During the transition into an epidemic, all birds shifted their diet more heavily onto budworms and some species increased numerically, but they consumed only 22% of the larvae and pupae. During the epidemic, bird predation was ineffectual (Crawford & Jennings, 1989). The authors concluded that birds were capable of "dampening the seriousness of spruce budworm infestations." In a review of similar dynamics, Holmes (1990) concluded that birds help maintain low abundances of insect populations at endemic levels, but once an outbreak gets started, bird predation has little impact.

Plants & Lichens

Summary:

Changes to plant habitat quality associated with large canopy openings (immediately following clearcutting or conversion to agriculture), or subsequent canopy closure of clearcuts, are likely to have the most impact on species intolerant of high heat and/or light conditions in openings and/or dense canopy cover. In addition, any negative effects on pollinator or dispersal agent habitat, is likely to reduce plant reproduction. Many understory forest herbs would fall in one of these categories including wild leek (WL) and large flowered trillium (LT).

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low			■ LT					■ WL
	Uncommon/ High								
	Uncommon/ Low								

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

The environmental conditions associated with clearcuts can be detrimental to forest insect species (Meier *et al.*, 1995). As compared with forest interiors, clearcuts can have higher solar radiation, higher daytime and lower nighttime temperatures, drier soil conditions and a higher proportion of bare soil, a decrease in litter, and stronger winds (Chen *et al.*, 1992; Meier *et al.*, 1995; Jules *et al.*, 1999). Shallow rooted herbaceous species are likely to be most susceptible to these changes (Meier *et al.*; 1995). Other environmental characteristics such as pits and mounds and rotting logs provide important habitat for some plant species (Cornett *et al.*, 1998; Cornett *et al.*, 2000). In comparison to forest canopy gaps, clearcuts also have less environmental spatial and temporal heterogeneity (Bormann and Likens, 1979).

As clearcuts regenerate, the dense canopy of young successional forests may create environments where light levels are too low to allow many understory herbaceous species that typically depend upon forest canopy gaps or the environments associated with these partially shaded conditions to grow (Bormann and Likens, 1979). In addition, plants occurring in early successional stage forests in Michigan, including *Lilium* sp. have been shown to experiences higher herbivory rates by chipmunks (Fletcher *et al.*, 2001).

Edge Effects

Birds

Summary:

In residential and agricultural portions of northern Minnesota, forest edges are detrimental to many forest songbirds such as the ovenbird (OB), scarlet tanager (ST), and perhaps even the red-eyed vireo (RV), due to increased nest predation and brood parasitism by brown-headed cowbirds. In predominantly forested landscapes the cowbird is rare or absent, but in some places at least, clearcut edges increase nest predation enough to cause a local population sink for ovenbirds. If edges become more prevalent in the forested landscape, and sink habitats expand, the populations of some of these area-sensitive species could decline. In fact, the ovenbird has experienced a substantial population decline in recent years in parts of the study area (Lind et. al 2000). In general, more edges probably indicate better conditions for ruffed grouse (RG) because they prefer several age classes of aspen in close proximity.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low	**RV**	**BC**	**OB**					
	Uncommon/ High					**WD**	**RG**		
	Uncommon/ Low	**NG**		**ST**		**BO**		**GW**	SG

▨ = positive response, ■ = negative response, ▢ = varied or unknown response

Detailed overview of effects:

Forest edges have traditionally been known as places of high diversity, primarily because species of both forests and open areas are found there (see the Arrangement of Patch Types section). Some species, such as the black-capped chickadee, are often more abundant at forest edges than in the interior (Smith 1993). Edges are not uniformly beneficial to all species, however. Flather and Sauer (1996) found that in general Neotropical migrants were less abundant in landscapes with more edges, while short-distance migrants were associated with edges. Neotropical migrants are more sensitive to competition from generalists and increased predation near edges because they have a shorter breeding season, small clutch size, and a life span of only 1-2 years on average (Green, 1995).

Reproduction

Some studies have shown a lower abundance of species like ovenbirds and scarlet tanagers near edges (Ortega & Capen, 1999; Rosenberg *et al.*, 1999; Lee *et al.*, 2002), but overall there is little evidence that edge-sensitive species actually avoid edges during the breeding season (Villard, 1998). Instead most evidence of edge effects concern reproduction. For example, the likelihood of attracting a mate for male ovenbirds in Missouri was significantly lower within 300 m of forest edges (Van Horn *et al.*, 1995). On the other hand, pairing success in red-eyed vireos was not related to distance to edge (Dunford *et al.*, 2002).

Many studies have investigated the effect of forest edges on nesting success. Nests near edges are often less successful than interior nests due to an abundance of nest predators and brown-headed cowbirds, which lay their eggs in other birds' nests (Chalfoun *et al.*, 2002). However, a major study found higher nest predation near edges only in a highly fragmented landscape, and not in a predominantly forested landscape (Donovan *et al.*, 1997). This study also showed lower cowbird abundance in forested landscapes. Two reviews reinforced these results (Andrén, 1995; Marzluff and Restani, 1999), making the case that a diversity of nest predators in forested landscapes assures an even distribution of nest predation regardless of edge. Another review, however, demonstrated that many of the studies that did not find an edge effect had such low statistical power that they could not have detected even large declines in nesting success (Manolis *et al.*, 2000). A majority of studies with sufficient power in predominantly forested landscapes of the northern hardwood-conifer region did detect lower success near forest edges.

In the region of northern Minnesota and Wisconsin several studies have investigated this edge effect. The results vary. In a study in the southern Chippewa National Forest the predation rate on natural bird nests was not related to distance to edge (Hanski *et al.*, 1996), but in the same study area artificial nests near edges suffered higher predation than interior nests (Fenske-Crawford & Niemi, 1997). In this case a high diversity of mammalian predators (fisher, eastern chipmunk, red-backed vole, red squirrel, deer mouse, black bear, gray squirrel and skunk) did not even out the distribution of nest predation.

In a Wisconsin study ovenbird nest success was lower within 300m of clearcut edges, but clutch size was larger, which balanced out their productivity (Flaspohler *et al.*, 2001). Both edge areas and interior areas appeared to be population sources, meaning that births outnumbered deaths. In the northern Chippewa National Forest distance from clearcut edge was the strongest predictor of nest predation for ovenbirds and hermit thrushes (Manolis *et al.*, 2002). Areas within 100 m of clearcuts were sinks for ovenbirds, where reproduction was lower than mortality. A study in New Hampshire found that the edges of small groupcuts increased predation on artificial nests as much as clearcut edges did (King, DeGraaf and Griffin, 1998).

Narrow roads through forests create less dramatic edges than clearcutting, and there is less evidence of an effect on reproduction. Near unpaved roads in Vermont ovenbird density was lower, they had larger territories, and pairing success was lower, but not significantly so (Ortega & Capen, 1999). In New Hampshire fledging success was not related to the distance to unsurfaced roads (King & DeGraaf, 2002). And in Pennsylvania a comparison of predation at different edge types found the strongest effect at clearcut edges and no effect near logging roads (Yahner & Mahan, 1997).

Compared to all the research into edge effect penetrating into forest, very few studies have investigated the effect of forest edges on birds nesting in early successional patches. No edge effect was found for early successional songbirds nesting in clearcuts and smaller groupcuts in New Hampshire (King *et al.*, 2001). One study did find higher predation on indigo bunting nests near hard edges than soft edges (Suarez *et al.*, 1997). Confer (1992) reported that golden-winged warblers prefer their shrubland habitat to be at the edge of a forest.

Migration

Even for forest birds with increased predation at the edges of forests, edges can provide some benefits. During fall migration 9 species were more abundant along forest edge than the interior, and they moved more slowly there, perhaps because of greater food availability (Rodewald & Brittingham, 2002). Edges also provide habitat for individuals that will enter the breeding population later (Howe *et al.*, 1991).

Winter Edge Avoidance

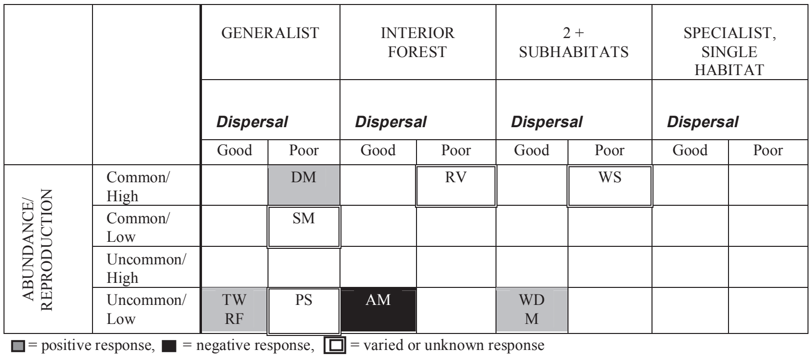
In a Canadian agricultural landscape black-capped chickadees foraging near forest edges went toward the interior to cache food, especially near the edges of wide unforested areas (Brotons *et al.*, 2001). The energetic cost of retrieving the food in winter is lower in the interior, compared to the edges exposed to wind. Another study showed that in fragmented landscapes chickadees are willing to go farther into the open (risking predation) to reach food trays, compared to less-fragmented landscapes (Turcotte & Desrochers, 2003). This willingness stems from increased energy stress in winter in highly fragmented landscapes. Where chickadees had been well fed, they showed no willingness to venture into open areas. Whether edges in predominantly forested landscapes also lead to energy stress is unknown.

In a fragmented Scandinavian landscape forests provided protection from predators for several small woodland bird species. They used the exposed side of forest edges mainly when predation pressure was low, and large flocks were more likely to cross over the edge (Rodriguez *et al.*, 2001).

Mammals

Summary:

Other than the American marten (AM), most mammals show either positive or neutral relationships to edges. Red-backed voles (RV) sometimes avoid edges, but this has not been reported universally. Red fox (RF) and deer mice (DM) do show preferences for edge. Species like the white-tailed deer (WD), which prefer multiple subhabitats in proximity to each other, also tend to prefer edges, and wolves (TW) may benefit as a result.



		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High		DM		RV		WS		
	Common/ Low		SM						
	Uncommon/ High								
	Uncommon/ Low	TW RF	PS	AM		WD M			

▨ = positive response, ■ = negative response, ▢ = varied or unknown response

Detailed overview of effects:

Mammals respond to edges in different ways, depending on the species and the landscape. Increases in small and medium sized mammals at edges are more likely in agricultural areas, but have also been found in forested landscapes (Chalfoun *et al.*, 2002) Like chickadees, martens do not like to stray too far from trees, where they can escape from predators (Bissonette & Broekhvizen, 1995), though one study did not find an avoidance of forest edges (Chapin *et al.*, 1998). White-tailed deer, on the other hand, benefit from an increase in edges (Clark and Gilbert, 1982; Alverson *et al.*, 1988).

Deer mice showed a positive edge effect in one study in Alberta (Bayne and Hobson, 1998). White-footed mice, which are closely related to deer mice, were found to be less abundant near edges in one study, even though several studies have reported higher densities in small forest fragments (Wolf & Batzli, 2002).

One study of red-backed voles in Oregon found six times more voles in the interior, compared to the edge, corresponding to the distribution of their primary food source, mycorrhizal fungi (Mills, 1995). On the other hand, chipmunks and red squirrels, which are forest species like red-backed voles, were shown to be most abundant along clearcut edges, compared to the interior forest and the interior clearcut, where they were least abundant (King, Griffin and DeGraaf, 1998).

Foxes and coyotes, but not raccoons, demonstrated an affinity for edges in winter in New Hampshire (Oehler & Litvaitis, 1996).

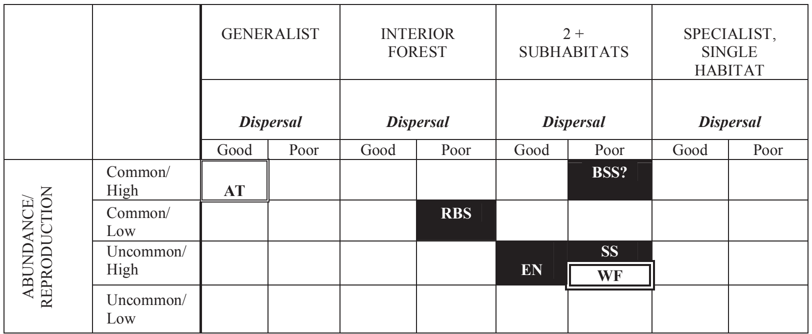
Amphibians

Summary:
Various types of edges along amphibian subhabitats can affect species by decreasing habitat quality, or by interfering with adult movements or juvenile dispersal.

Along high-contrast edges (clearcut vs. forest interior and plantation vs. forest interior), forest-dependent amphibians show reduced density and abundance. Strongest negative responses are shown by red-backed salamander (RBS), blue-spotted salamander (BSS), spotted salamander (SS), and wood frog (WF) with a weaker negative response from the Eastern newt (EN). Negative effects along an edge gradient to a depth of 25-35 m have been found for these four species, although another study found that the edge effect for RBS to be more shallow.

Responses to edges formed by roads (roadside abundance and road-crossing rate) vary widely among amphibian species, and among life-stages of amphibians as a group. One study found that roads presented no barrier effects for four frog species, and may even be a preferred habitat for American toads (AT) and juvenile wood frogs (WF), though they were less suitable for four salamander species. For amphibians as a group, dispersing juveniles showed the highest rates of road-crossing, followed by adults migrating in fall, and adults moving within home ranges. Decreased juvenile dispersal rates in old field habitats compared with forests were found not only for known a forest-associated species (wood frog, WF), but also for the generalist American toad (AT). These findings suggest that in fragmented landscapes, decreased dispersal will have potentially negative consequences for those populations. A more full understanding of juvenile dispersal behavior across edges of various kinds is important in order to evaluate the effects of spatial pattern change on amphibian populations.

The figure below shows the responses of amphibian species to forest-road edges, based on the information above.



		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		*Dispersal*		*Dispersal*		*Dispersal*	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	□ AT					■ BSS?		
	Common/ Low				■ RBS				
	Uncommon/ High					■ EN	■ SS □ WF		
	Uncommon/ Low								

▨ = positive response, ■ = negative response, □ = varied or unknown response

Detailed overview of effects:

Edges created through forest management practices

Forest management practices can create high-contrast edges such as clearcut vs. forest interior and plantation vs. forest interior. Higher ambient light and wind along these high-contrast edges are likely to result in lower moisture, as compared with the forest interior. Amphibian responses to high-contrast edges include reduced density and abundance (deMaynadier & Hunter, 1998; DeGraaf & Yamasaki, 2002).

In a study conducted in Maine (deMaynadier and Hunter, 1998) red-backed salamanders and mole salamanders (*Ambystoma spp.*) were most abundant along forest interior portions of the edge gradient, while the terrestrial form of the Eastern newt, the red eft, was less closely associated with forest interior habitats. Territoriality of red-backed salamanders is suggested as a contributor to their sensitivity to forest changes, as open areas create "sink" habitat for non-breeding individuals that are excluded from mature forest territories (deMaynadier & Hunter, 1998). Wood frogs were more abundant in mature, closed-canopy locations than were American toads (a generalist) or any ranid species.

Edge gradients of varying distances (or depths) can have effects on species as well. Four species termed "management-sensitive" (redback salamanders, spotted salamanders, blue-spotted salamanders and wood frogs) were negatively effected to a distance of 25-35 m along silvicultural edges as old as 11 years (deMaynadier and Hunter, 1998). The role of edge contrast was examined as well, using ambient light as a measure, and results for capture rates of these "management-sensitive" species were consistent with the hypothesis that edge effects are strongest along high-contrast stand boundaries. In another study in New Hampshire, red-backed salamanders also showed negative effects along silvicultural edges, but for shorter distances (DeGraaf & Yamasaki, 2002). Across an edge gradient running from relatively mature forest-interior habitat (70-90 yr old) to recently clearcut habitat (2-11 yr old), abundance of both juveniles and adults of wood frogs and spotted salamanders declined sharply (deMaynadier & Hunter, 1999).

Roads

When roads or open areas adjoin forest areas, these edges may affect amphibian movements, including adult movements to or from breeding ponds, or dispersal of juveniles (deMaynadier and Hunter, 2000; Gibbs, 1998b). Clear differences exist among species in terms of forest road crossing rates, in a study conducted in Maine of a heavily trafficked logging road (deMaynadier & Hunter, 2000). No barrier effects of roads were found for four frog species, and roadside habitat may even be selected by some species and life stages (such as American toads and juvenile wood frogs). In contrast, forest road habitats appeared less suitable for four salamander species, in terms of both abundance alongside roads and road crossing rates. For the amphibians as a group, road crossing rates varied by life-stage, with highest rates of crossing by young-of-the-year (22.1%), followed by adults in fall migration (17.0%) and adults moving within their home ranges (9.2%) (deMaynadier and Hunter, 2000).

In a study of the movements of 6 amphibian species in Connecticut, roads hindered the movements of all species, and forest edges associated with open lands (residential areas) were much more permeable to amphibian movements than were road edges (Gibbs, 1998b). Species included were forest-dependent spotted salamander, red-spotted newt, red-backed salamander, and wood frog, as well as the pickerel frog and marbled salamander (not a Minnesota spp.). Somewhat surprisingly, in this study spotted salamanders and marbled salamanders (forest-dependent species) were found to cross forest edges to access breeding pools in open habitat. And in contrast to deMaynadier and Hunter's (1998) findings, red-spotted newts (a subspp. of Eastern newts) were the species most strongly negatively affected by forest edges; they were among the two most commonly captured species, but at edges their capture rates were lowest (Gibbs 1998b).

Juvenile response to edges

Juveniles are the major lifestage in amphibians for dispersal to new habitats, and factors affecting their movements can affect populations. In an experimental study of response to silvicultural edges, juvenile wood frogs were found to prefer closed-canopy habitat for emigration immediately upon metamorphosis, and their highest capture rates occurred in microhabitats characterized by dense foliage in understory and canopy layers (deMaynadier & Hunter, 1999). In a natural population of wood frogs and spotted salamanders, juveniles of both species appeared to be even more discriminating than adults in their choice of closed overstory canopy forested habitat for upland movements (deMaynadier & Hunter, 1999).

An experimental study in Missouri of larval amphibians of the spotted salamander, small-mouthed salamander and American toad, comparisons were made of the initial orientation, distance and rates of movement of juveniles dispersing from artificial pools into old fields or forest (Rothermel & Semlitsch, 2002). Spotted salamanders and American toads were significantly biased toward forest in their initial orientation. Importantly, juvenile American toads avoided open-canopy habitat, an indication that predictions of juvenile dispersal behavior based on adult habitat use may be misleading. Movement behavior and dehydration rates suggest that old field habitats offer greater resistance to dispersing juveniles of these species than do forests. Based on these findings, the authors suggest that with increases in old field habitats, decreased dispersal rates are likely to occur between populations of these species, with potentially negative consequences for population persistence in altered landscapes (Rothermel and Semlitsch, 2002).

Insects

Summary:

Patch edge has been shown to influence insect species by altering microhabitat, affecting the behavior or effectiveness of natural enemies, or by influencing movement patterns. Adverse microhabitat, and possibly competition with open habitat species, is likely to reduce habitat quality for forest interior species such as *Platynus decentis* (PD). The forest tent caterpillar (FT) is known to experience lower parasitism rates in forests with a greater proportion of edge – such as some northern Minnesota forests.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	**FT**							
	Common/ Low								**PD**
	Uncommon/ High								
	Uncommon/ Low								

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

Patch edge has been shown to influence insect species by altering microhabitat, affecting the behavior or effectiveness of natural enemies, or by influencing movement patterns. Habitat edge was found to affect ground-dwelling insects more than habitat area (Golden & Crist, 2000). Beetle community structure (species occurrence and abundance) was also significantly affected by edge effects (Davies *et al.*, 2001). Edge areas typically contain mixtures of species found in forest and open habitats, and therefore, edges of forests may be subject to invasion by insects from the surrounding matrix (Koivula, 2003).

Survival of the larval stage of the forest tent caterpillar was found to be associated with an increase in edge area (Rothman & Roland, 1998). While the smallest parasitoid species attacking forest tent caterpillar caused higher rates of parasitism at forest edges, the other three, larger parasitoids examined were more effective at parasitizing caterpillars in contiguous forests (Roland & Taylor, 1997).

Patch edge can influence insect behavior also. Designed experiments on beetle behavior found that beetles were less likely to move into patches that had less edge and/or high contrast boundaries (Collinge & Palmer, 2002).

Plants and lichens

Summary:

Plant and lichen species that are intolerant of the high light, heat and/or wind conditions associated with edge may be negatively affected by the increase in forest edge in Minnesota, such as the pendulous lichen (PL), *Usnea longissima* and wild leek (WL). Negative effects of competition with invasive species associated with edges are most likely to inhibit low stature, slow growing understory herbaceous species such as yellow blue-bead lily (YL). The types of plants most sensitive to deer browse will typically be those with low reproductive rates, low propagule dispersal abilities, and that are preferred deer food, such as yellow blue-bead lily and large flowered trillium (LT). However, woody species like white cedar (WC) can also be significantly impacted by deer browse if browse rates and conditions are high enough to reduce or prevent seedling growth or survival.

Plant species that are tolerant of edge microhabitats, such as smooth brome (SB) and beaked hazelnut (BH) are likely to benefit from an increase in edge habitat (depending on the type of edge). Understory species with high reproductive rates that are good competitors with other plant species, and are not preferred deer food, i.e. most grasses, sedges and ferns, are also likely to increase in abundance with increased edge. Species similar to Canada goldenrod, which in addition to the above characteristics, have seeds capable of moving long distances, will have an additional means of reaching and utilizing suitable edge habitats.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	**CG**	**SB**		**PL**				
	Common/ Low			**LT**					**WL**
	Uncommon/ High							**WC**	
	Uncommon/ Low							**YL**	

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

Plant or lichen growth in edge areas can either be positively or negatively influenced by edge conditions. Several responses to edges have been documented for woody species including higher numbers of small trees (Ranney *et al*., 1981; Chen *et al*., 1992), increased tree mortality (Chen *et al*., 1992) and higher plant species richness (Ranney *et al*., 1981). Canopy density has been observed to increase or decrease in edge areas depending upon plant species and conditions (Palik and Murphy, 1990; Laurance, 1991; Chen *et al*., 1992). Understory species response to edge also varies. Studies in northern Wisconsin found that some species, such as Pennsylvania sedge

(*Carex pensylvanica*) and harebell (*Campanula rotundifolia*) had higher abundance in edge adjacent to clear-cut areas (Euskirchen *et al.*, 2001). Alternatively, yellow blue-bead lily was most abundant in interior forest (jack pine forest) or edge-interior areas (red pine forest).

Edge can influence plant or lichen presence and abundance by effecting environmental conditions such as microclimate, or by influencing competing plant species and herbivorous animals. Some lichen species have been shown to have a higher growth rate in edge areas between old growth forest and young regenerating forests than in interior forest areas because of increased light levels. Other lichen species, such as *Alectoria sarmentosa*, were negatively influenced by edge up to 20-50 m into the forest (Sillett *et al.*, 2000). Studies on pendulous lichens in the boreal forests of Sweden found lower growth and survival rates in edge areas where higher winds broke off large pieces of the lichen thallus (Esseen and Ericson, 1982). Studies conducted in Douglas Fir forests in Oregan found that some lichen species grew as rapidly in young forests as old growth (*Lobaria pulmonaria*), but transplants of another species (*Lobaria oregano*) had decreased biomass and more injuries in clearcuts than forested areas (Sillet *et al.*, 2000).

Edge can also affect forest plant species by influencing pollinators, herbivores and/or competing plants. Studies in Oregon found lower pollination rates for *Trillium ovatum* flowers and reduced seed production in edge areas (Jules & Rathcke, 1999).

Increased white-tail deer abundance and associated browse in fragmented forests (see mammal section above) has had direct and indirect effects on many plant species (Alverson *et al.*, 1988; Waller and Alverson, 1997). Reduced recruitment of several woody species, such as white cedar (*Thuja occidentalis*) and hemlock (*Tsuga canadensis*), has been linked to excessive deer browse (Alverson *et al.*, 1988; Cornett *et al.*, 2000; Rooney, 2001). Understory species are also impacted by deer browse (Balgooyen and Waller, 1995; Fletcher *et al.*, 2001; Rooney, 2001; Weigmann *et al.*, in prep.). Dicots, lilies and orchids tend to be preferred, over grasses, sedges and ferns (Augustine, 1997; Fletcher *et al.*, 2001). Many of these preferred species are especially vulnerable to herbivory because they are bulbous species, long-lived, reproduce sexually, and/or are non-clonal. Deer not only remove flowers and foliage from understory plants, but can impact future generations by reducing reproductive success. In addition, understory species are never able to escape the reach of browsing deer - an option that is available for woody species if browse pressure is alleviated for a number of years. In addition to deer browse, increased seed predation by rodents (*Trillium ovatum*, Oregon study) has been documented for edge areas (Jules & Rathcke, 1999).

Some woody and understory species are known to increase in abundance with high rates of fragmentation and deer browse. Studies in northern Wisconsin found that species thriving in heavily browsed habitats are those that are unpalatable or resistant to browse, and as a result they are able to reproduce in heavily browsed habitats

(Weigmann *et al*. in prep.). These species tend to be grasses, sedges, and ferns, and are often non-native species (Weigmann *et al*. in prep).

Invasive species abundance is often higher in edge areas (Burke and Nol 1998b). Invasive species tend to be good competitors and hence may out-compete other desirable species in edge areas, and/or edge areas may serve as a point of invasion for more interior forest areas (Ranney *et al*., 1981, Burke and Nol, 1998b). In Minnesota, wild roses, blackberries, and grapevines are associated with edges (Jaakko Poyry Consulting, Inc., 1992).

Edge can also affect plant species composition (Ranney *et al.*, 1981), and effects can vary with aspect of clearcut (Euskirchen *et al.*, 2001).

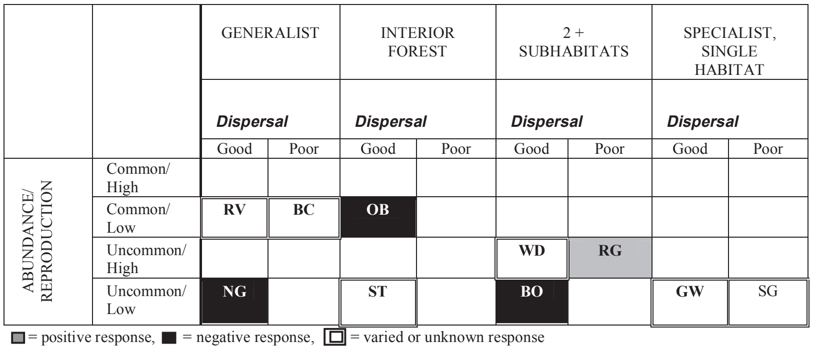
BETWEEN PATCH SCALE

Effects of Arrangement of Patch Types

(Includes Landscape Diversity and Human Influence)

Birds

Summary:
In general, a higher diversity of patch types, such as forest of different ages, increases the diversity of bird species, because more species are able to find habitat within the landscape. However, individual species can have positive or negative responses to this increased diversity, and the edges between older forest and very young forest (i.e. clearcuts) can have negative effects. Ruffed grouse (RG) and boreal owls (BO) are two species that prefer specific arrangements of different forest patches.



		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		*Dispersal*		*Dispersal*		*Dispersal*	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low	**RV**	**BC**	**OB**					
	Uncommon/ High					**WD**	**RG**		
	Uncommon/ Low	**NG**		**ST**		**BO**		**GW**	SG

▨ = positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

Birds in northern Minnesota are adapted to dynamic forest landscapes, where natural disturbances create shifting mosaics of patch types (Green 1995). As landscape diversity is increased even further, through such actions as logging and settlement, short-distance migrant species benefit (Flather and Sauer, 1996). The northern goshawk, on the other hand, was associated with lower landscape diversity in western Washington, and it preferred areas with a high proportion of older forest and less than 20% cover of regenerating forest (Finn *et al.*, 2002).

Forest Perforation
One way that landscape diversity can be increased is by perforating a continuous forest with openings. Forests containing a mix of patches of different ages support

more bird species than forests left uncut or selectively logged. In northern hardwoods of New Hampshire (similar to Minnesota) a forest managed with clearcuts up to 15 ha on an 80-120 year rotation had a higher diversity of species than uncut forest because the inclusions of young forest brought in new species. All species in uncut areas were also found in managed areas. Only the ovenbird was less abundant in the managed areas, but it was still the third most abundant species there (Welsh & Healy, 1993). Openings in the forest increases edge length, however, which can have negative effects on reproduction (see Edge Effects sections).

In Missouri a managed hardwood forest (75% pole/sawtimber, 12% regeneration, 13% sapling) had lower density of scarlet tanagers, red-eyed vireos, and pine warblers than unmanaged forest (100% pole/sawtimber). The ovenbird showed no difference in density. Other forest bird species were more abundant in the managed forest, plus there were additional species not found in the unmanaged forest (Thompson *et al.*, 1992). A study of bird species of concern (uncommon or potentially threatened species) in Missouri found that some species were found only in clearcuts and shelterwood cuts, while other species were found only in mature uncut or selectively cut forest (Annand & Thompson, 1997). The authors suggest that to maintain all bird species of concern the forest should contain a combination of even-aged and uneven-aged patches.

Ruffed Grouse

Quaking aspen trees provide the best habitat for ruffed grouse, and the dense cover of 6-15 year old aspen forest is especially important for drumming males and rearing broods. Patches of mature aspen forest is also important because the dormant flower buds of mature male aspens provide an excellent food source in winter and early spring (Dessecker & McAuley, 2001). In a Habitat Suitability Index model for grouse, the optimal habitat within a 10 ha territory is an even distribution of 4 aspen age classes: 0-12 years old for brood cover, 13-25 years old for spring and fall cover, 26-38 years old for nesting cover and food, and 38+ years old for winter food (Rickers *et al.*, 1995). Aspen managed on a 40-year rotation with 1-2 ha clearcuts maximizes the interspersion of protective cover and winter food (Dessecker and McAuley, 2001). Clearcuts of 10-20 acres also produces healthy populations, though not maximum (1996).

Although grouse prefer dense young aspen on recent clearcuts for its protective cover when rearing broods, one study found that the abundance of arthropods preferred by grouse was greatest in mature forest and on logging roads planted with herbaceous vegetation after use. When planted logging roads traverse dense young aspen stands, grouse are provided with both good cover and a good food source (Hollifield & Dimmick, 1995).

Boreal Owl

Male boreal owls use lowland conifers for roosting and mature upland mixed forests for nesting (Lane *et al.*, 1997). Their average home range is 1202 ha, but they concentrate activity within smaller areas. These smaller areas must contain both patch types to support a pair of the owls, which may become more difficult if mature mixed forests are replaced by younger forests.

Mammals

Summary:

Higher landscape diversity tends to benefit habitat generalists, and since most mammals in Minnesota are generalists, most probably respond positively to increased diversity. This has not been studied for most small mammals, however. White-tailed deer (WD) and moose (M) benefit from a diversity of forest ages. Their major predator, the wolf (TW), likely responds to increases in deer and moose, but not when the increases occur in areas of high road density. American martens (AM) decline when increased diversity means more clearcuts. Red foxes (RF) increase with limited amounts of development.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High		DM SH SM		RV		WS		
	Common/ Low								
	Uncommon/ High								
	Uncommon/ Low	TW RF	PS	AM		WD M			

▨ = positive response, ■ = negative response, ▢ = varied or unknown response

Detailed overview of effects:

Landscape Diversity

The more heterogeneous the landscape, the higher the expected proportion of generalist small mammals that can take advantage of all the patch types. Habitat for specialists may be too scattered for them to utilize (Kozakiewicz & Szacki, 1995). With greater heterogeneity there is a greater diversity of prey species, so generalist predators gain an advantage over specialists. When this occurs, population cycles driven by specialist predators tend to level out (Oksanen & Schneider, 1995).

When the landscape is more diverse, the mobility of small mammals increases because there is a greater chance that a patch will not contain all the necessary resources. In addition, they can take advantage of additional resources in nearby patches (Kozakiewicz & Szacki, 1995).

Logging is beneficial to moose when it leaves a mosaic of age classes, especially when no roads provide hunter access (Rempel *et al.*, 1997). White-tailed deer likely respond the same way to landscape diversity, due to their preference for a mix of forest and open areas. In the eastern part of the upper Michigan, which is less diversified than the western part, deer traveled an average of 1.8 miles further between summer and winter ranges (Verme, 1973).

In New Hampshire, raccoons, foxes, and coyotes were more abundant in more diverse landscapes. Landscape diversity is increased by fragmentation, which is correlated with human-dominated patches. These generalist predators increased when 7-27% of the landscape was human-domintated (Oehler & Litvaitis, 1996). In a boreal forest landscape in Sweden red fox abundance increase with the amount of young forest and agriculture, but peaked when agriculture covered 20-30% of the landscape (Kurki *et al.*, 1998).

Developed areas have the opposite effect on timber wolves. Many studies have shown that they avoid roads in particular (Thiel, 1985; Jensen *et al.*, 1986; Mech, 1989). Road density and fractal dimension were the most important predictors of wolf presence in a model for Wisconsin, but fractal dimension didn't add much predictive power (Mladenoff *et al.*, 1995). High road density and high wolf density at Camp Ripley Military Reservation is an exception to this rule (Merrill, 2000).) In the Kenai National Wildlife Refuge wolves avoided roads with public access, but were attracted to gated roads. They also avoided settled areas. Their absence was due to behavioral avoidance, not mortality (Thurber *et al.*, 1994). Away from developed areas, however, wolves would likely respond positively to increased deer in diverse landscapes.

Perforation

For martens in Utah, if open patches in the forest become so prevalent that the width of the forest between openings averages less than 100 m, the forest becomes unsuitable. They are absent from landscapes with over 25% non-forest cover. Even when small mammal populations are higher in clearcuts, marten abundance is correlated with forest cover, not the abundance of prey (Hargis *et al.*, 1999). In an industrial forest in Maine they preferred forest patches close to a forest preserve (Chapin *et al.*, 1998), and another study demonstrated a partial avoidance of roads (Robitaille & Aubry, 2000).

Neighborhood Effect

The abundance of some species in a patch of forest can be influenced by the patch type(s) surrounding it. In one study in Alberta the abundance of small mammals was lower in forest patches surrounded by clearcuts than in contiguous forest or patches surrounded by farmland. This pattern was due partly to an abundance of red squirrels and flying squirrels in farm woodlots (Bayne & Hobson, 1998).

Amphibians

Summary:

Clearcutting may be less damaging to terrestrial salamander populations than alternative timber-harvest methods if clearcutting is concentrated in small areas (a few hectares in size), rather than having low-intensity harvests spread over a larger portion of the landscape. In a study of abundance and species richness, spatial pattern changes that increase conversion of natural, mixed-species into conifer plantations may be detrimental to spotted salamander (SS), red-backed salamander (RBS), spring peeper (NSP) and wood frog (WF), though less so for American toads (AT).

When a forested landscape is increasingly converted to agriculture, forest habitat loss is the most obvious consequence. In addition, however, is the risk of decreasing the adjacency of ponds and forest, posing particular threats to amphibian populations that have small home ranges and relatively short dispersal distances and relatively poor abilities to cross inhospitable habitats. Studies of species occurrences in agriculturally fragmented landscapes suggest that decreases in pond-forest adjacency will result in a decreases in the presence on the landscape of wood frogs (WF), Eastern newts (EN), spotted salamanders (SS), and salamanders of the blue-spotted/Jefferson complex (similar to the blue-spotted salamander - BSS). However, such a pattern may potentially benefit generalist amphibian species including American toad (AT) and the Northern leopard frog (NLF), while the response of the Northern spring peeper (NSP) is unclear.

At a landscape-scale, more amphibian species are present on landscapes with a greater diversity of types of breeding sites. As spatial pattern change takes place, maintaining a diversity of breeding sites will benefit amphibian species as a whole.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	▨ AT				▨ NLF ▣ NSP	■ BSS?		
	Common/ Low					■ EN			
	Uncommon/ High						■ SS WF		
	Uncommon/ Low								

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of effects:

Comparison of clearcuts and alternative timber-harvest methods

No difference in the decline in terrestrial salamander abundance was found in an experimental study in Virginia comparing clearcutting with alternatives involving canopy removal on a 2-ha scale (Knapp *et al*, 2003). Alternative methods like groupcuts and shelterwood cuts require re-entry into the site after a period of years, exposing salamanders again to drier environments and soil compaction. If populations are not recovered from the previous cutting, these repeated disturbances may result in a long-term decline of the populations. The authors conclude that because larger areas must be disturbed more frequently in order to get the same amount of timber, alternative methods may be more detrimental to salamander populations than clearcutting. However, clearcutting larger patches will create areas with higher edge-to-area ratio, likely lowering rates of recolonization. The authors suggest that the next important step in understanding the landscape-level effects of clearcutting on salamander populations is to study how clearcut size affects the decline and recovery of salamander species.

Conversion from natural forest to plantation

In a study conducted in New Brunswick, Canada, conversion of natural, mixed-species forest into black spruce (*Picea mariana*) conifer plantations was found to be most detrimental to spotted salamander, redback salamander, spring peeper and wood frog, and less so for American toads, based on abundance and species richness (Waldick *et al.*, 1999). In addition, densities of spotted salamanders and wood frogs breeding in ponds in plantations were most strongly related to distance to nearest natural forest.

Ponds and agricultural land vs. ponds and forests

In a study of the effect of composition and spatial arrangement of patches in a forest and agricultural landscape on 9 amphibians in northeastern Maine, overall results suggest that the composition of the landscape surrounding breeding ponds is associated with occurrence of all 9 species studied, and that landscape configuration is also important for a small subset of species (Guerry & Hunter, 2002). In this study, 7 of 9 amphibian species were associated with forest area. Wood frogs, green frogs, Eastern newts, spotted salamanders and salamanders of the blue-spotted/Jefferson's complex were more likely to occupy ponds in areas with more forest, consistent with what is known of their ecology as forest-dependent species. Leopard frogs and American toads were negatively associated with forest area, consistent with their affinity for open areas. This study showed little evidence of thresholds of forest area affecting occupancy for these 9 species, but weak evidence for a forest area threshold for Eastern newts. Three species were associated with pond-forest adjacency. Spotted salamanders and salamanders of the blue-spotted/Jefferson's complex were more likely to occupy ponds adjacent to forest. Of these species in this study, these are the least vagile (able to move) and even small distances between upland and wetland habitats may serve as a barrier to their movement across the landscape. In areas with little forest, leopard frogs were more likely to occupy adjacent ponds, but in areas with extensive forests, they were less likely to occupy adjacent ponds. Mink frogs (*Rana septentrionalis*) were nearly ubiquitous and not associated with forest area. The spring peeper, which was expected to be associated to forest area, was distributed independently of forest area and pond-forest adjacency (Guerry and Hunter, 2002).

Landscape diversity

At a landscape-scale, the presence of a diversity of types of breeding sites is an important characteristic associated with amphibian species richness. In an agriculturally-fragmented landscape, sites dominated by seasonal or semi-permanent wetlands or sites containing a mixture of wetlands with various water regimes had highest amphibian species richness (Kolozsvary and Swihart, 1999). This finding provides an example of a factor which is separate from a spatial effect (area or proximity), which is capable of altering the distribution of amphibians.

In a study of 14 species of frogs and toads in Iowa and Wisconsin, species abundance and richness were highest where habitat patch diversity was high or where there were forested wetland edges. Forest variables had positive associations for many frog and toad guilds, not just those that require forest in some part of their life-cycle (Knutson *et al.*, 1999).

Plants

The arrangement of cover types can influence plants species diversity and composition (Hersperger and Forman, 2002). Studies in forests in Canada (Hersperger and Forman, 2002) found that plant species' presence in woodland patches was influenced by the type of cover adjacent to the woodland. In particular, where woodland was adjacent to shrubland, the woodlands contained a higher proportion of native species. Adjacent to grassland, the woodlands had a higher proportion of weedy and introduced plants.

Effects of Habitat Isolation and Connectivity

Birds

Summary:

The proportion of forest in the landscape is a major factor influencing forest bird abundance and reproduction, particularly for ovenbirds (OB), even at the local level. The predominantly forested nature of northern Minnesota ensures habitat connectivity for many species and provides at least a partial buffer against the negative influences of edges and small patch sizes. It probably provides a better landscape even for species like the golden-winged warbler that do not nest in mature forest.

Although crossing open spaces places small species at greater risk of predation or winter energy stress, they do make the crossings when necessary, and most species are widely distributed over the appropriate habitat. With the current level of forest cover, the landscape cannot be considered at risk of becoming disconnected for most birds in northern Minnesota, but increasing forest gaps and patch isolation would make dispersal increasingly risky for them.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High								
	Common/ Low	**RV**	**BC**	**OB**					
	Uncommon/ High					**WD**	**RG**		
	Uncommon/ Low	**NG**		**ST**		**BO**		**GW**	SG

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of effects:

Although birds are extremely mobile animals, habitat isolation can still have an effect on many species. In one study in a relatively fragmented landscape in Ontario (up to 67% forested) that investigated the separate effects of habitat loss and isolation, scarlet tanagers and several other species were less likely to be present as the mean nearest-neighbor distance between forest patches increased. Some species were influenced by habitat loss, some by isolation or other configuration patterns, and some by both loss and configuration (Villard *et al.*, 1999). In another similar study, however, many species were affected by habitat loss, but only two by measures of fragmentation, one positively and one negatively (Trzcinski *et al.*, 1999). A review of field studies demonstrated that, in general, the amount of habitat in a landscape has a much larger effect on bird abundance than the degree of fragmentation of the remaining habitat, as predicted by computer models (Fahrig, 2002). In most studies, however, the isolation of habitat is not investigated separately from the amount of habitat in the surrounding landscape (i.e. habitat availability).

Habitat Availability

Many studies have investigated the influence of the amount of forest in the landscape on forest bird abundance and reproduction. In the short term, the removal of forest can result in temporary increases in density as the "homeless" birds pack into the remaining forest (Hagan *et al*., 1996; Schmiegelow *et al*., 1997). In the long term, less habitat supports fewer individuals. However, the relationship between habitat availability and abundance is not necessarily linear. Reductions in forest cover may result not only in lower overall abundance, but also in lower density in the remaining habitat, and reproduction may be reduced as well.

A continental analysis of Breeding Bird Survey results showed that, in general, Neotropical migrants had denser populations in landscapes with more forest and wetland (Flather and Sauer, 1996). In boreal forests, Schmiegelow and Mönkkönen (2002) predicted that resident species, such as boreal owls and black-backed woodpeckers, would be more sensitive to habitat loss because of their lower abundance and large home ranges.

A study comparing 3 landscapes in southern boreal Quebec found that even in the same forest types there were more generalist and early successional species in an industrial forest and an agricultural landscape than in a natural disturbance forest (Drapeau *et al*., 2000). Ovenbirds were more likely to be present in Ontario landscapes (up to 67% forested) with more forest cover (Villard *et al*., 1999), and had denser populations in continuous forest in Missouri, compared to fragmented forest (Porneluzi and Faaborg, 1999). In one study the density of male red-eyed vireos increased with the percent of forest within 2 km, but there was no relationship to the amount of forest within 10 km (Dunford *et al*., 2002). In another study, red-eyed vireos were not sensitive to the amount of forest in an agricultural landscape (Lee *et al*. 2002). Scarlet tanagers are significantly affected by forest fragmentation in the Northeast, Midwest, and Atlantic Coast, but not in the Northern Forest (including Minnesota), where abundance is low (Rosenberg *et al*., 1999).

The ability of male ovenbirds to attract mates was correlated with the amount of forest in the landscape in some studies (Gibbs and Faaborg, 1990; Hagan *et al*., 1996; Lee *et al*., 2002), but not others (Porneluzi and Faaborg, 1999; Rodewald and Yahner, 2000).

A major study across the Midwest demonstrated that nesting success for forest songbirds (including ovenbirds) is greater when forest cover is greater (Robinson *et al*., 1995) and populations in fragmented landscapes may be sustained by immigration from continuous forests (Donovan *et al*., 1995). Lower nesting success in fragmented landscapes is due to higher nest predation by mammalian and avian predators and a higher abundance of brown-headed cowbirds, which lay their eggs in other birds' nests (Donovan *et al*., 1997). This pattern of greater reproductive success in predominantly forested landscapes held up for artificial nests in Saskatchewan (Bayne and Hobson, 1997), but not for ovenbird nests in Ontario (Burke and Nol, 2000).

Another impact of reducing the amount of forest in the landscape is an increase in winter energy stress in black-capped chickadees due to greater exposure to wind (Turcotte and Desrochers, 2003).

Landscape Permeability

Landscapes with different amounts of forest provide different levels of permeability to birds traveling across them. For example, when ovenbirds and white-throated sparrows were moved 2 km away from their territories, only the intervening landscape type was a significant predictor of the probability of return and the time of return. For ovenbirds, permeability increased with the proportion of forest in the landscape. An agricultural landscape was least permeable to them, followed by a harvested forest landscape and naturally patchy landscapes. For white-throated sparrows naturally patchy landscapes were the least permeable (Gobeil and Villard, 2002).

In another study in an agricultural landscape in Quebec, the time for both ovenbirds and black-capped chickadees to return to their territories decreased and the probability of successful return increased as forest cover increased. The configuration of the forest, such as mean nearest-neighbor distance between forest patches, had no effect (Bélisle *et al*., 2001).

Gap-crossing

Large bird species cross gaps more readily than small species. In an agricultural landscape in Ohio the proportion of species willing to cross a particular gap between two forest patches depended on the amount of woodland in the surrounding landscape (Grubb and Doherty, 1999).

In an agricultural landscape in Saskatchewan open farmland was not a barrier to male ovenbirds without young, but males with young rarely left their fragment of forest. With young they were willing to cross roads and power line corridors (Bayne and Hobson, 2001b).

Three studies have investigated the willingness of forest birds to cross clearcuts and other forest openings, using recordings of chickadee mobbing calls as an attractant. Several species, including black-capped chickadee and red-eyed vireo, were twice as likely to cross 50 m of forest as 50 m of either clearcut (without residual trees) or pasture. A majority of chickadees and yellow-rumped warblers preferred traveling through woodland even if it meant doubling or tripling (respectively) the route length (Desrochers and Hannon, 1997). Chickadees were unwilling to cross gaps over 50 m across when there was a forest alternative, but they sometimes crossed over 200 m gaps when there was no alternative (St. Clair *et al*., 1998). Several bird species took short cuts across gaps when they could do so without venturing farther than 25 m from the forest edge (Bélisle and Desrochers, 2002).

The reluctance to cross small gaps is surprising, especially for species that migrate thousands of miles. However, migration takes place at night, but gap crossing takes place during the day when predation risk from raptors is greater. The preference for many species to travel through forest, as opposed to gaps, increases the functional distance between habitat patches, even for generalist species and in forested landscapes.

Corridors

A subject related to the willingness to cross gaps is the question of whether forest corridors ease the movement of birds and maintain the connectivity between forest fragments. In an agricultural landscape in North Dakota, robins moved more readily between woodland patches when connected by a woodland corridor (Haas, 1995). In a forested landscape in Alberta, forest fragments connected by a riparian corridor had the same number of birds as unconnected fragments, but resident species, particularly black-capped chickadees, were more abundant. Also, western tanagers and black-throated green warblers, the only two old forest specialists, were more abundant in the connected fragments in some years (Hannon and Schmiegelow, 2002).

The same riparian corridors were used by dispersing juvenile birds unwilling to cross recent clearcuts. Four years later most juveniles had begun to move through the regenerating forest, but ovenbirds, red-eyed vireos and red-breasted nuthatches continued to avoid the regenerating forest and traveled along the corridor (Robichaud *et al*., 2002).

Isolation within Natural Patch Types

Most studies of habitat isolation and connectivity investigate the relationship between natural patches, such as forest, and human-created patches, such as clearcuts or agriculture. Very few have investigated the isolation of one natural patch type within a continuous landscape of other natural patch types. In Rocky Mountain National Park, patches of aspen are separated by other natural vegetation types. No matter how far apart the aspen patches were, bird species richness was the same (Turchi *et al*., 1995), suggesting that the birds that use aspen forest have no trouble finding it in the landscape.

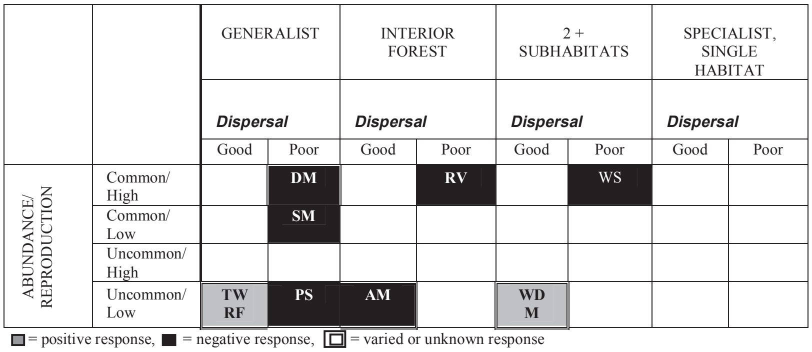
In an Alberta study, on the other hand, even when patches of one forest type were isolated by another forest type, there were fewer species and lower numbers of Neotropical migrants and residents, compared to control sites in continuous forest of the same patch type (Schmiegelow and Hannon, 1999).

These studies may be applicable to species like the golden-winged warbler, pine warbler, or spruce grouse with specific habitat requirements that may in some cases be met only by widely separated patches. Spruce grouse in isolated habitat patches, for example, had to disperse farther than those in continuous habitat, and occupied patches were closer together than unoccupied patches (Whitcomb *et al*., 1996).

Mammals

Summary:

Roads and wide-open spaces tend to reduce the dispersal ability of many small mammals and probably some larger mammals like martens. As a result, some species may be absent from isolated patches of appropriate habitat in residential or agricultural portions of northern Minnesota. It is also possible that populations of small mammals like deer mice or red-backed voles may be effectively isolated from each other by major highways like Route 53. The landscape as a whole contains enough natural vegetation to remain connected for most or all mammal species at this time, but increasing patch isolation would eventually have negative consequences for poor-disperser species.



		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High		■ **DM**		■ **RV**		■ WS		
	Common/ Low		■ **SM**						
	Uncommon/ High								
	Uncommon/ Low	▨ **TW** **RF**	■ **PS**	■ **AM**		▨ **WD** **M**			

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Less information is available on barriers to the movement of mammals across the landscape. Due to body size, small mammals are confronted with more barriers than large species. In general, when the habitat for a small mammal is fragmented, it means a longer transit time during dispersal and decreased survival (Gaines and McClenaghan, 1980; Diffendorfer *et al*., 1995).

In one study some small mammals such as deer mice, chipmunks, and gray squirrels were reluctant to cross roads when the distance between forest edges was greater than 20 m. Open country species, on the other hand, such as the meadow vole, were more willing to cross roads (Oxley *et al*., 1974). In another study, the movement of white-footed mice (closely related to deer mice) across a narrow gravel road was very infrequent, but they did cross occasionally, including lactating (possibly pregnant) females (Merriam *et al*., 1989).

In another study, white-footed mice placed in an open agricultural field were unable to orient toward forest (suitable habitat) as close as 30 m away (Zollner and Lima, 1997). This casts doubt on their ability to cross inhospitable habitat. However, another study found that they swam up to 765 ft between islands and the mainland by orienting toward trees. Only when released more than 1000 ft offshore were they unable to orient toward land (Sheppe, 1965).

Amphibians

Summary:

Landscape-scale studies of amphibian responses to spatial pattern change are often focused on agricultural and urbanizing landscapes. Amphibians were found to respond differently to forest area and proximity, wetland area and proximity, and wetland permanence depending on their life-history attributes (Kolozsvary and Swihart, 1999). The American toad (AT) and the gray tree frog (*Hyla versicolor*) were found to thrive in an agriculturally fragmented landscape. Other species occurred primarily near suitable breeding habitats, including tiger salamander (ETS), smallmouth salamander (*Ambystoma texanum)* and green frog (*Rana clamitans*). Forest-dependent species either were absent or showed the greatest sensitivity to reductions in forest area – these include spotted salamander (SS), wood frog (WF) and redback salamander (RBS). The Northern leopard frog (NLF) and two other species of ranids (green frog and pickerel frog, (*Rana palustris*)) were positively related to proximity to wetlands and sensitive to isolation from wetlands. Red-backed salamander (RBS) was most sensitive to forest patch area.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	▨ **AT**				■ **NLF**			
	Common/ Low	**ETS**			■ **RBS**				
	Uncommon/ High						■ **SS** **WF**		
	Uncommon/ Low								

▨= positive response, ■ = negative response, ▢ = varied or unknown response

Response to agriculturally fragmented landscape

In one study, amphibian species richness decreased as the density of roads increased and wetland isolation increased (the distance to nearest neighbor wetland) (Lehtinen *et al*., 1999). In urbanizing and rural landscapes, threshold effects of forest cover have been found for some species. Wood frogs (WF) and spotted salamanders (SS), were absent where forest cover was reduced below 30%, and red-spotted newts (a subspecies of Eastern newt - EN) which were absent where forest cover was reduced to about 50%. No threshold was found for red-backed salamander (RSP) or spring peeper (NSP) (Gibbs, 1998a). These finding suggest that among forest-dependent and interior forest amphibians, those with low population densities (WF, SS and EN) are at greater risk from loss of forest area.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High					**NSP**			
	Common/ Low				**RBS**				
	Uncommon/ High					**EN**	**SS** **WF**		
	Uncommon/ Low								

▨= positive response, ■ = negative response, ☐ = varied or unknown response

Response to forest area thresholds
(negative response = shows evidence of thresholds)

Detailed overview of responses:

Area and proximity

In a study of species occurrence, forest area and proximity, wetland area and proximity, and wetland permanence in the agriculturally-fragmented landscape of west-central Indiana, Kolozsvary and Swihart (1999) found that amphibian species responded differently to fragmented landscapes, depending on their life-history attributes. Species with high vagility, broad environmental tolerances, desiccation resistance or general seasonal requirements for breeding (they breed in a wide variety of wetland types) were less severely affected and may actually benefit from fragmentation of wetland landscapes by agriculture. In contrast, species with limited mobility, that require large forest tracts, or have specific seasonal requirements for breeding (breed only in ephemeral wetlands, for example) were more severely affected by fragmentation, as characterized by decreased wetlands and forest and increased cropland.

Some species, including American toad and the gray tree frog, were found to thrive in an agriculturally fragmented landscape. Other species occurred primarily near suitable breeding habitats, including tiger salamander, smallmouth salamander, and green frog. Forest-dependent species either were absent or showed the greatest sensitivity to reductions in forest area – these include spotted salamander, wood frog, and redback salamander. In particular, three species of ranids (green frog, Northern leopard frog and pickerel frog) were positively related to proximity to wetlands (and sensitive to isolation from wetlands). Red-backed salamanders were most sensitive to forest patch area. This species was found in the largest contiguous forest and in small or moderately sized woodlots in close proximity to the large forest tract. This distribution suggests that immigration of salamanders from the large tract may rescue those in the smaller sites, preventing extinction or increasing chances of recolonization (Kolozsvary and Swihart, 1999).

Connectivity

In a study of amphibians in fragmented agricultural and urban landscapes, wetland species richness decreased with decreased landscape connectivity (e.g. site isolation, road density and land use) (Lehtinen *et al*., 1999). The most important predictors of species richness were the density of roads and wetland isolation (distance to nearest neighbor wetland).

Thresholds

Thresholds may occur, in which forest patch size or forest cover drops too low for a species to remain present. Guerry and Hunter (2002) had weak evidence for a threshold effect in Eastern newts; this species was not present in any pond with less than 144 hectares of adjacent forest. Thresholds for forest cover were found in a study in an urbanizing and rural landscape in Connecticut (Gibbs, 1998a). Distribution of five forest amphibian species with different life history characteristics was studied in a 10 km-long site along a continuous forest fragmentation gradient in deciduous forest. Wood frogs and spotted salamanders were absent from portions of a forest fragmentation gradient where forest cover was reduced below 30%, and red-spotted newts (a subspecies of Eastern newt) were not present below a forest cover threshold of about 50%. No threshold was found for red-backed salamander (RSP) or spring peeper (Gibbs, 1998a).

The resulting patterns contrast with a common notion that populations of the best dispersers are those most tolerant of habitat fragmentation. Instead, correlations between species' biological traits and their fragmentation tolerances imply that low density, population variability and high mobility coupled with restricted habitat needs predispose woodland amphibians to local extinction caused by habitat fragmentation (Gibbs, 1998a). This study analyzed correlations in species abundance and indices of fragmentation across the landscape. Two quite contrasting life cycles are suggested to confer relative resistance to habitat fragmentation on forest amphibians. A species with restricted dispersal ability and restricted habitat use was relatively resistant (e.g. red-backed salamander), as was a species with extensive dispersal ability and habitat flexibility (e.g. spring peeper). Low population density apparently predisposes populations to susceptibility to fragmentation (e.g. the wood frog, spotted salamander and red-spotted newt). Susceptibility to fragmentation was highest for the red-spotted newt, which not only has low population density but high habitat specificity and high dispersal tendency, as well (Gibbs, 1998a).

Insects

Summary:

Insects that can fly (such as the spruce budworm SB moth), and that are strong fliers, can generally disperse greater distances than walking insects (such as the ground beetles, PB, CF). The ability and willingness of an insect to cross areas of unsuitable habitat will also influence dispersal distance and success. Barriers to dispersal are highly variable between species and even within closely related groups such as butterflies. Dispersal between habitats for species such as the northern blue butterfly (NB), which utilizes open structured forests, can be facilitated by corridors that have partially to open canopy, and contain host plants.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	**SB**							
	Common/ Low				**CF**				**PD**
	Uncommon/ High								
	Uncommon/ Low							**NB**	

▨ = positive response, ■ = negative response, ▣ = varied or unknown response

Detailed overview of effects:

Isolation and connectivity have a number of influences on insect species depending in large part on the dispersal abilities/preferences of the insect when moving within and among habitat patches (Wiens *et al*., 1997). For example, dispersal rates are very low between trees for beetle species associated with trunk hollows (*Elater ferrugineus* and *Tenebrio opacus*); therefore populations are easily isolated (Ranius, 2002). The northern blue butterfly is able to disperse farther than walking insects (although among butterflies is a relatively weak flier) and dispersal can be facilitated if there are open canopied patches or roadsides are located between habitat patches.

The higher rate of parasitism observed for the forest tent caterpillar (*Malacosoma disstria)* in contiguous forests is thought to be a result of the effect of habitat structure on parasitoid movement (Roland and Taylor, 1997).

The matrix between habitat patches has a large effect on isolation for butterflies. For example, studies on six butterfly taxa in Colorado found that conifer cover was more of a movement barrier than willow for four of the six taxa (Ricketts, 2001). Some of the species that frequented meadows were less likely to leave meadow patches regardless of the type of intervening habitat. The group of butterflies with the largest mean wing length was the most mobile and few barriers to movement were observed.

Dispersal can also be influenced by paved and gravel roads (and railroads) which can stimulate longitudinal movements and reduce the rate of immigration into isolated habitat patches (Mader *et al*., 1990).

Plants and lichens

Summary:

Aspen (A) and Canada goldenrod (CG) are likely to be less sensitive to loss of reduced forest connectivity because they produce large amounts of wind-blown seed that is able to establish in many microhabitats. Also, once established, both species are often able to out-compete other plant species. Species that have low reproductive rates and are poor dispersers, such as wild leek (WL), are expected to be more sensitive to reduced habitat connectivity. For species that are dispersed by animals, such as large flowered trillium (LT), how far seeds move will depend on whether ants or deer are moving the seeds and how the intervening matrix influences their behavior.

		GENERALIST		INTERIOR FOREST		2 + SUBHABITATS		SPECIALIST, SINGLE HABITAT	
		Dispersal		***Dispersal***		***Dispersal***		***Dispersal***	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
ABUNDANCE/ REPRODUCTION	Common/ High	**A** **CG**							
	Common/ Low				**LT**				**WL**
	Uncommon/ High								
	Uncommon/ Low								

▨= positive response, ■ = negative response, ☐ = varied or unknown response

Detailed overview of effects:

Whether habitat is functionally connected for any given plant species will depend upon whether its propagules (seeds or vegetative structures) are able to successfully disperse between suitable habitat areas and/or establish in the intervening matrix. Plant species that produce many seeds at a young age and have seeds that are wind or bird dispersed, tend to be the most successful at dispersing between suitable habitat patches (Higgens *et al*., 2003). For wind-dispersed propagules, the morphology, prevailing winds, and structure of vegetation will influence how far propagules disperse and in what directions (Harper, 1977; Sillett *et al*., 2000; Higgins & Revilla, 2003). For animal-dispersed seeds, how the intervening matrix between habitat patches affects the dispersal agent is the main factor (Higgins & Revilla, 2003, see discussion of animal dispersal above).

The conditions required for seed germination and seed or propagule survival will determine whether a plant species can establish and grow in matrix areas. For example, aspen is able to tolerate a wide range of soil types and conditions, can spread by vegetative means and is able to compete with other species because it is fast growing. Studies on lichen species in Oregon (Sillett *et al*.; 2000) found that lichen species differed in their ability to survive and grow in clearcut areas.

Habitat Loss Thresholds

As habitat is fragmented (broken into smaller, disconnected patches), several landscape patterns change at once: the amount of habitat decreases, patch size decreases, patch isolation increases, and edge length increases. Many field studies have shown that, in general, the amount of habitat in a landscape has a much larger effect on bird abundance than arrangement of habitat, as predicted by computer models (Fahrig, 2002). Another review of studies revealed that the relationship between habitat availability and species abundance is not linear. As habitat cover declines below 30% of the landscape, declines in species population or species richness become greater than expected from habitat loss alone. Below the threshold of 30%, the effects of fragmentation (i.e. patch size, edge, and isolation) magnify the effects of habitat loss (Andrén, 1994).

Results of computer modeling predict habitat loss thresholds at which a landscape can no longer support the species. One model predicted a 20% threshold, with some minor variation due to the demographics of the species in question (Fahrig, 1997). Three other models predict thresholds at varying levels of habitat loss, depending on various factors: habitat quality (With *et al*., 1997), species edge sensitivity and the particular landscape pattern (With and King, 2001), and reproductive rate and emigration rate (Fahrig, 2001).

Although these models differ in the effect of the components of fragmentation on population persistence at the habitat loss threshold, the same effect occurs at the threshold: the species suddenly becomes unable to disperse between the remaining patches, and extinction becomes probable. The quality of the matrix between patches has a moderate effect on the level of the threshold. Maintaining a diverse landscape for improved connectivity can prolong population persistence with lower amounts of habitat (Fahrig, 2001). Reducing fragmentation can also lower the threshold to some extent (Fahrig, 2002).

The major lesson is that the amount of habitat in the landscape is the most important factor determining the survival of a species, and conservation efforts should focus primarily on maintaining high quality habitat wherever it is. Only when habitat loss reaches a threshold do patch size, edge length, and isolation become as important as habitat availability. The same landscape may be at a threshold for some species, but not others, depending on how much habitat there is for each and the species characteristics. Given the choice, habitat protection and restoration is more beneficial in places with a higher proportion of habitat nearby (e.g. Austen *et al*., 2001).

INFORMATION GAPS

During the collection of information for the project, we have encountered several types of information gaps. The gaps in information identified here may need to be filled either with a more in-depth review of the scientific literature, the results of research currently underway, or new scientific research. Gaps in the following types of information are identified for each taxonomic group: measurements of population sizes, reproductive rates, distribution; dispersal distances and other dispersal-related characteristics, and effects of spatial pattern changes.

Population sizes, reproductive rates, distribution

Mammals

Population sizes for most species, especially small mammals, are just educated guesses. They have been estimated for small areas, but not for the region as a whole.

Amphibians

Within the project area, status of amphibian species is not well-known, because of lack of quantitative data on population sizes, distribution and abundance (Casper, 2002). The Terrestrial Wildlife Committee for the Lake Superior Management Plan is proposing that a set of baseline data collection sites be established for monitoring amphibians of the Lake Superior Watershed, which can serve as control sites for comparative studies, in order to identify population trends, causal factors, and contribute to conservation management (Casper, 2003).

Insects

Insects represent the largest number of species in the project area, but most insect groups are not well surveyed or studied. Basic information on the presence, abundance and distribution of the majority of the insect species Minnesota is not known.

Dispersal

Dispersal distances are difficult to measure. Most estimates tend to underestimate dispersal distances because the low probability of detecting the longest dispersal distances for most organisms.

Birds

Except for the ruffed grouse, we lack basic information on how far young birds settle from their natal site. It is also poorly known how they choose the site and their behaviour during movement. Do they prefer to travel within forest? Do they require any particular resources during dispersal? Do migratory species choose a spot before their first fall migration or when they return the following spring?

Mammals

Dispersal distances are not known for snowshoe hare, moles, shrews, or voles. Nor is it known what types of landscapes they are willing and unwilling to cross.

Amphibians

More information is needed from the literature about dispersal distances and behaviors of amphibian species. Understanding juvenile dispersal behaviors is an important research focus.

Insects

Dispersal distances can be especially difficult and labor intensive to quantify for insects, in part because of their small size. A common method for estimating dispersal distances for butterflies or moths is mark-release-recapture methods where large numbers (hundreds to thousands) of individuals are marked and then recaptured. Dispersal distances are then estimated using various types of calculations. As described above, one of the difficulties with this and similar methods is capturing the long distance dispersers.

Plants and Lichens

More information is needed on animal dispersal in general and how spatial pattern influences to animals in turn affects plant dispersal.

Habitat requirements

Mammals

Habitat requirements are more or less understood for many mammals, but more could be learned about what makes some clearcuts suitable for red-backed voles and others not. Also, habitat for pygmy shrews is not well understood.

Amphibians

Determining microhabitat associations of amphibians within the project landscape would be useful for helping determine how forest management might improve protection of these features.

Insects

Habitat requirements for some of the common and pest species are relatively well known, but much more information is needed about the basic ecology and habitat requirements of most insects.

Effects of spatial pattern changes

Studies often do not distinguish between effects of different variables that may be correlated and confounded. For example, as mentioned previously, the effects of forest loss and forest fragmentation are often not distinguished. Future studies should be careful to tease apart such correlated effects when possible, and offer caveats in conclusions if such effects cannot be distinguished.

Birds

Several studies have separated habitat availability, isolation, edge length, and patch size effects, but there is still much to learn. In particular more can be done to study the effects of these patterns within predominantly forested landscapes, rather than only comparing forested landscapes to fragmented (or only within fragmented landscapes).

Many studies have investigated the effects of edges and the amount of habitat in the landscape, but only for a few forest songbirds, particularly the ovenbird. Less is known even about scarlet tanagers and red-eyed vireos. Are they area-sensitive in northern Minnesota? Do birds other than ovenbirds experience negative edge effects? Little is known about patch size and connectivity issues for many species. Arrangement of patch types has been studied for ruffed grouse, but for few other species.

Mammals

Studies of road crossing by small mammals have begun to describe that dispersal barrier, but the degree of connectivity across forested landscapes is unknown. There has been little study of patch size for any species, and this is one of the major changes in the landscape of northern Minnesota. Very little is known about shrews and moles.

Many questions remain. How much forest cover would need to be lost before the landscape is disconnected for good dispersers (mostly large species) and for poor dispersers (mostly small)? How well do mammal species persist in the developed parts of the region? If they are rare or absent from some areas, which patterns cause it?

Amphibians

More information is needed to understand at what point amphibian habitat becomes disconnected in forested landscapes. Studies of clearcut size and impacts on amphibian populations will be useful.

Insects

The majority of the studies on insects and spatial pattern were conducted in other parts of the country or world, with only a few examining insect species and forest spatial pattern in the great lakes and/or boreal forest region.

Plants

The preferences and effects of deer browse on plants (which tend to increase with the types of forest spatial pattern and composition changes that have occurred) are relatively well understood. More information is needed on how to aid the recovery of plant populations that have been reduced from deer browse or other land-use impacts, and how spatial pattern may alleviate or exacerbate these impacts.

SECTION C

Conclusions and Next Steps

CONCLUSIONS

Our evaluation of the effects of forest spatial pattern and composition on example plant and animal species (Section B) identified some general patterns and tendencies. Based on these patterns and tendencies we suggest that species with similar characteristics (and grouped together in the same cells or sections in Table 1) tend to have similar responses to change in forest spatial pattern and/or composition. In Section B, we also described some of the known exceptions to these patterns. In this section we provide an overview of the general tendencies and exceptions, with the underlying knowledge that Minnesota forests have experienced the following changes since the late 1800's (Whitney, 1987, Host and White, 2003a, 2003b; White and Host 2003):

1. Smaller average patch size
2. Increase in edge density
3. Reduced core (interior forest) area
4. Compositional changes – younger forests, fewer conifers

Please note that species in the same cell of the Sensitivity Framework are grouped together based on similar characteristics - but that the categorization of traits was relative within each taxonomic group. Therefore, values such as dispersal distance can range widely between species in the same cell for different taxonomic groups. For example, the American toad, moving up to 1000 m, is categorized as a good disperser and is located in the same cell as the spruce budworm which can move up to 250 km.

The information reviewed in Section B suggests that species will have positive, neutral, or negative responses to the types of spatial pattern changes detected in northern Minnesota (Whitney, 1987, Host and White, 2003a, 2003b; White and Host 2003), depending on several key species characteristics. These are summarized in Fig. 3.

Figure 3. General characteristics of species likely to have positive, neutral, or negative responses to the types of changes in spatial patterns seen in the last century in Minnesota.

Positive or neutral response	***Negative response***
♦ Common, large population size ♦ High Reproductive rate ♦ Good Disperser ♦ Habitat generalist ♦ Good competitor	♦ Uncommon, small population size ♦ Low reproductive rate ♦ Poor disperser, resource dependent ♦ Habitat specialist – interior forest/area-sensitive, single habitat ♦ Poor competitor

Positive or Neutral Response

In general, species that have large populations are more resilient to perturbations. Species with high reproductive rates are often able to respond or rebound quickly to the creation of new habitat. Species with the ability to disperse easily and/or long distances to new locations, and can survive in a broad array of habitats, will be most likely to utilize new habitat patches as they are created. Several factors accentuate these tendencies, such as the competitive ability of the species.

Example species with these traits include the American toad, forest tent caterpillar, spruce budworm, aspen and Canada goldenrod. The American toad is currently very abundant, has a high reproductive rate, and is able to disperse relatively long distances (as compared with other amphibians). Also, even though the toad requires two subhabitats to complete reproduction, it can utilize a wide range of upland and wetland habitat types. The spruce budworm is an example of an insect pest that occurs in high numbers, has the ability to increase rapidly in numbers, can readily disperse to new host plants and feeds on a wide range of deciduous tree species. Aspen tends to respond positively to the types of forest changes that have occurred in Minnesota. Aspen produces large numbers of seeds that are both wind-pollinated and dispersed, and it tolerates a wide range of environmental conditions.

Other species share some of these traits, but not others, and predicting response to landscape changes is more difficult. The pygmy shrew, for example, is uncommon and a poor disperser, characteristics typical of a negative response. But it is also a habitat generalist. Not enough is known about the species to say which characteristic has the greater effect on response.

Some species with more available information have likely displayed neutral or positive responses to changes in landscape pattern. Deer mice, for example, are abundant habitat generalists with a high reproductive rate, but are poor dispersers. Black-capped chickadees are also common habitat generalists, but with relatively low reproductive rates and dispersal distance. With an ability to use a variety of forest types of different ages, neither of these species has probably changed dramatically in abundance as a result of spatial patterns, although chickadees have possibly increased with more edges. Only if total forest cover of all ages decreases significantly would these species be expected to decline.

Timber wolves and red foxes are in the same category, but do not necessarily respond the same way to landscape changes. Increases in forest openings, including agriculture, have likely benefited red fox. The wolf generally avoids agricultural and other developed areas, but like the fox, it probably benefits from forest openings because its main prey, the white-tailed deer, favors a mix of forest and openings.

Species that require two subhabitats may be more sensitive to landscape change, but the changes in northern Minnesota have helped several species in this category. The decline in patch size and increase in edges has increased available habitat for white-tailed deer, which use both forest and openings. The decline in patch size, coupled with an increase in young aspen has also benefited the ruffed grouse, which prefers aspen in different age classes in close proximity. The beaver has also likely benefited from increased aspen when it grows near aquatic subhabitat. The water shrew requires forest habitat alongside water (preferably running), but the forest type is not important, so it is not likely impacted by landscape changes, unless total forest cover declines significantly.

Changes in the composition of the landscape have also affected many species. American toads have an affinity for open areas and may even benefit from forest change that increases the amount of open habitat, such as agriculture, although juvenile toads appear to prefer to disperse in forests, rather than old fields. More deciduous forest has likely led to an increase in the red-eyed vireo. Snowshoe hares may have benefited from more young, dense regrowth that protects them from predators. According to habitat modeling done at the Natural Resources Research Institute, an increase in short-statured, deciduous habitat in Minnesota has probably led to an increase in golden-winged warblers. An increase is counter-intuitive for a habitat specialist, but when the specialized habitat increases, the specialist will benefit. Other species in the same category that specialize in declining habitats have had the opposite response.

Connectivity between habitat patches can be influenced by roads and other openings. Some juvenile amphibians, such as American toads and wood frogs, have been found to be unaffected by forest roads, and may even select roadside habitat for dispersal. Insects that utilize open habitats, such as the northern blue butterfly, may use roadsides as corridors if needed plant resources are present near roads.

Competitive ability can either accentuate a positive response, or shift the response more toward a positive response, of a species to forest change. In the case of Canada goldenrod, which has all the traits of a positive response species, its strong competitive ability amplifies the tendency for this plant species to proliferate. In the case of smooth brome, which has many characteristics of a species with a positive response, but is a poor disperser, its strong competitive ability gives it an advantage over less competitive species.

If a species' natural enemy is negatively influenced by a change in spatial pattern, this can accentuate a positive response. For example, the majority of parasitoid species attacking the forest tent caterpillar parasitize fewer larvae as forest edge increases, resulting in higher survival rates for the caterpillar.

Negative response

Species with small population sizes and/or low reproductive rates may be negatively affected if forest changes eliminate or reduce habitat further. Many issues with small population size come into play in this scenario, such as difficulty finding mates or genetic issues, as does the ability for the species to rebound if new habitat is created. A species is also likely to be sensitive to spatial pattern and/or composition change if it has specific habitat needs and is a poor disperser. Examples of species with small population sizes, low reproductive rates, and specific habitat needs include spruce grouse, American marten, four-toed salamander, and calypso orchid.

A reduction in average patch size is often associated with greater distances between patches and reduced habitat connectivity. This is particularly relevant for those forest species that have poor dispersal abilities, and especially for those species unwilling or able to cross edges, open areas, or other intervening types of matrix. For example, the four-toed salamander and calypso orchid have low, resource-dependent dispersal characteristics that result in short dispersal distances. The four-toed salamander is small-bodied and requires mature hardwood forests and wetlands as habitat. It is unlikely to disperse far or be able to cross non-habitat areas. For some species, such as the red-spotted newt (a subspecies of this project area's Eastern newt), a behavioral tendency to disperse can contribute to high mortality rates if dispersing individuals are not able to reach suitable habitat.

Many forest bird species, including the black-capped chickadee, are reluctant to cross forest gaps, and roads can present barriers to dispersal for some species of small mammals, amphibians and insects. The current configuration of roads and forest gaps has apparently not disconnected the landscape for birds or small mammals, although additional movement barriers could eventually do so. Forest road habitats tended to be less suitable for four salamander species, in terms of both abundance along roads and road-crossing rates. Roads can stimulate longitudinal movements or reduce the rate of crossing for ground-dwelling, flightless, beetle species.

Significant amounts or types of habitat loss for these sensitive species are expected to result in population reductions or extirpations. Particularly sensitive are those species that have specific habitat requirements such as ovenbird, scarlet tanager, American marten, northern blue butterfly, ground beetles, and calypso orchid. For some species an important component of habitat is patch size. Forest interior birds like ovenbirds tend to have greater reproductive success in larger patches, even in predominantly forested landscapes. Insects, specifically burying beetles, may experience less competition from vertebrate predators for food. Plants may have higher pollination and/or plant propagule dispersal rates in areas with great resources for these animals, and also experience less competition with invasive plant species or unsuitable microhabitats in edge areas.

Also sensitive to habitat loss are some species that require two subhabitats or that have very specific habitat requirements. For example, many of the amphibians and some bird species require two or more separate subhabitats (recognizable subsets of the species' habitat that may also be spatially distinct) and are expected to decline if one of the two of the key subhabitat types is missing. In general, amphibians are especially prone to local extinction and recolonization processes, and may represent organisms with the greatest dependence on maintenance of dispersal connections. Boreal owls require mature mixed forest and lowland conifers within each territory. Reductions in the amount of mature mixed forest near lowland conifers will reduce habitat availability for them.

Habitat quality for many species is linked to the composition and structure of the vegetation. A general trend in Minnesota has been from older coniferous forest cover and to younger forests. Conversion of mixed-species forest into conifer plantations has been shown to be detrimental to spotted salamander, redback salamander, spring peeper and wood frog. The trend toward younger forests may be detrimental to species that prefer older upland deciduous or coniferous forests such as northern goshawk. Red-backed voles are absent from some clearcuts, so logging may have reduced their population, although they are still one of the most abundant mammals in northern Minnesota. The loss of conifers has likely resulted in lower populations of bird species that prefer conifers, including the pine warbler, Blackburnian warbler, and northern parula (Green, 1995). The spruce grouse could also be affected, but the overall loss of conifers may be offset by denser 4-6 m coniferous regrowth after logging. Several amphibian species depend upon other attributes of the forest such as litter depth, understory vegetation, canopy closure and moisture, and consequently have lower abundance in clearcut areas. Species linked to one specific community type also tend to be vulnerable. Lowland hardwood forest is the only habitat where the calypso orchid is found, and this, combined with the plant's low tolerance to disturbance, make it vulnerable to the loss or degradation of this forest type.

Any negative effects can be exacerbated by several factors. For example, predation of ovenbird nests tends to increase as patch size decreases and with proximity to forest edge. Any negative effects on associated pollinators and/or dispersal agents are likely to reduce reproductive and dispersal rates for plants like large flowered trillium or yellow blue-bead lily.

USE OF INFORMATION AND NEXT STEPS

We developed the species categorization and sensitivity framework to help evaluate the influence of spatial pattern on animal and plant species. In general, we found that species in the same sensitivity category (see Table 2), with similar reproductive rate, dispersal ability and habitat specificity characteristics, tend to respond to spatial pattern in similar ways. However, there are also many exceptions that are important to consider.

The framework could be strengthened by adding more species and by refining the framework structure. Information about additional species and their interactions with spatial pattern could be added to the framework to reinforce observed patterns or elucidate exceptions to the patterns. As more information is added, it may become clear that changes to the structure of the framework itself would be advantageous.

The existing information and framework can be applied in various ways. In particular, if the management goal is to move away from a species-by-species approach, the framework can serve as a means for evaluating the effects of known forest spatial patterns on groups of species with similar characteristics. In doing so, however, it will be important to consider the different scales at which these interactions occur, for example the different dispersal distances and habitat sizes between species. In addition, managing for multiple species poses many problems. Not the least of these problems is the fact that different species respond in dramatically different ways to the same landscape patterns. It would be impossible, for example, to maximize populations of both ruffed grouse and ovenbirds. One solution might be to manage different areas for different spatial patterns, each of which would be best for a different suite of species. These management areas could be matched with regions that have natural disturbance regimes tending to produce the desired spatial patterns.

In some cases species-level management is still needed, such as when managing for game species or federally listed species. In these cases, and when information on these species is lacking, the framework and accompanying materials can be used as an initial guide for management planning. To use the framework in this way, the types of information we used in this paper should be compiled (where available) for the target species and then categorized using the same methods as Section B. Based on the categorization of these characteristics, determine where the species fits on the species' sensitivity framework. Note how interactions with other species might shift the magnitude of the effect. Also note known exceptions to the patterns that might apply to the target species. If used in this way, the framework and associated materials should help formulate possible species responses to management actions, which could be tested using simulation models and adaptive management and monitoring methods.

This report is a first step in evaluating the effects of forest spatial pattern and composition on plant and animals species in Minnesota. It is qualitative in nature, and is meant to provide general guidance and the basic background information to aid in developing more quantitative models. The next logical and necessary step in determining the effects of forest spatial pattern and composition on these species will be to relate actual values of the characteristics included to the spatial metrics and compositional makeup of this landscape (see Host and White 2002, 2003).

ACKNOWLEDGEMENTS

This project was funded by the Minnesota Forest Resources Council, through the Minnesota Department of Natural Resources. Jim Manolis and members of the Strategy and Technical teams provided invaluable comments throughout the process of developing this document. Lawson Gerdes, and two anonymous reviewers provided useful comments on early drafts. Tom Rooney, Meredith Cornett, and Welby Smith contributed their expertise on various plant related topics. Editorial assistance was provided by Joanna Kadi.

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Table 1. Species characteristics and categorization for example species. See Section A text for explanation of column categories.
(Multiple subhabitats = 2 or more subhabitats)

	Population size/ Reproductive rate		**Inter-actions**	**Dispersal**			**Habitat**	**References**
TAXONOMIC GROUP	**Current population size**	**Reproductive rate**		**Distance**	**Resource dependent, independent**	*Type*		
BIRDS								
Red-eyed vireo *Vireo olivaceus*	**Common**	**Low** Average of 3 eggs/year		**Long** No specific information	**Resource Independent**	**Good disperser**	**Generalist** Deciduous and mixed forests as young as 8 years old, some residential areas with sufficient shrub and tree cover	Green 1995 Cimprich et al. 2000
Black-capped chickadee *Poecile atricapilla*	**Common**	**Low** 6-8 eggs/year		**Short** Median of 200 m, recorded up to 20 km	**Resource Independent** Reluctant to cross open areas	**Poor disperser**	**Generalist** Deciduous and mixed forest, parks, thickets, suburbs	Smith 1993 Green 1995
Northern goshawk *Accipiter gentiles*	**Uncommon**	**Low** 2-4 eggs/year, 2-3 fledge per successf. nest	Predator of various bird and small mammals species	**Long** Mean of 15-20 km with limited data, known ex. of 100 km	**Resource Independent**	**Good disperser**	**Generalist** Upland coniferous and deciduous forest >25 years old	Green 1995 Squires and Reynolds 1997 Boal et al. in press
Ovenbird *Seiurus aurocapillus*	**Common**	**Low** Average of 4 eggs/year	Increased mammalian nest predation along forest edges	**Long** No specific information	**Resource Independent**	**Good disperser**	**Interior forest** Upland coniferous and deciduous forest	Van Horn and Donovan 1994 Green 1995 Manolis et al. 2002
Scarlet tanager *Piranga olivacea*	**Uncommon**	**Low** Average of 4 eggs/year		**Long** No specific information	**Resource Independent**	**Good disperser**	**Interior forest** Mature deciduous and mixed forest	Green 1995 Mowbray 1999 Roberts and Norment 1999
Wood duck *Aix sponsa*	**Uncommon**	**High** Average of 11 eggs/year		**Long** After fledging, juveniles move up to 11 km before migration	**Resource Independent**	**Good disperser**	**Multiple subhabitats** Swamps, marshes, ponds, creeks, and rivers with mature trees nearby for nesting	Green 1995 Hepp and Bellrose 1995
Boreal owl *Aegolius funereus*	**Uncommon**	**Low** 3-4 eggs/year	Population fluctuates with small mammal populations	**Long** Frequently disperses long distances	**Resource Independent**	**Good disperser**	**Multiple subhabitats** Requires mature mixed upland forest for nesting and lowland conifer for foraging	Hayward and Hayward 1993 Green 1995 Lane et al. 1997

	Population size/ Reproductive rate		Inter- actions	Dispersal			Habitat	References
Ruffed grouse *Bonasa umbellus*	**Uncommon**	**High** Average of 11 eggs/year	Population cycles, maybe in response to cycles of snowshoe hare predators	**Short?** Mean of 6.4 km for males, 9.6 km for females	**Resource Independent**	**Poor disperser**	**Multiple subhabitats** Strongly prefers aspen forest of varying ages in close proximity	Green 1995 Rusch et al. 2000.
Golden-winged warbler *Vermivora chrysoptera*	**Uncommon**	**Low** Average of 5 eggs/year		**Long** None of 88 banded nestlings returned to natal area	**Resource Independent**	**Good disperser**	**Specialist** Most often in shrubby lowlands, sometimes in upland deciduous regeneration if not too dense	Confer 1992 Green 1995
Spruce grouse *Falcipennis canadensis*	**Uncommon**	**Low** 5-6 eggs/year		**Short?** Mean 2.3 km	**Resource Independent**	**Poor disperser**	**Specialist** Forests of jack pine and black spruce, usually young and dense	Boag and Schroeder 1992 Green 1995 Whitcomb et al. 1996
MAMMALS								
Deer mouse *Peromyscus maniculatus*	**Common**	**High** Several litters of 4-5.5 per year		**Short** Median 50 m for males, 150 m for females, rec. up to 1 km	**Resource dependent**	**Poor disperser**	**Generalist** Woodlands and clearcuts	Timm 1974 Hazard 1982 Sutherland et al. 2000
Snowshoe hare *Lepus americanus*	**Common**	**High** 3-4 litters of 3-4 per year	Population crashes cyclically, depending on browse avail. and predation	**Short?** Up to 20 km has been recorded	**Resource dependent**	**Poor disperser**	**Generalist** Dense coniferous or deciduous cover	Hazard 1982 Sutherland et al. 2000
Timber wolf *Canis lupus*	**Uncommon**	**Low** 4-7 young per pack per year	Heavily dependent on deer population	**Long** Typically 50-100 miles; recorded up to 550 miles	**Resource independent**	**Good disperser**	**Generalist** Wherever prey is	Hazard 1982 Fritts and Mech 1981 Fritts 1983 Gese and Mech 1991
Red fox *Vulpes vulpes*	**Uncommon**	**Low** 4-6 young/year		**Long** Median 22 km for males, 3 km for females, up to 300 km for either	**Resource independent**	**Good disperser**	**Generalist** Variety of habitats, preferring semi-open areas over continuous forest	Storm et al. 1976 Hazard 1982
Star-nosed mole *Condylura cristata*	**Common**	**Low** Average of 5 young/year		**Short** A different mole species has dispersed up to 800 m	**Resource dependent**	**Poor disperser**	**Generalist** Moist deciduous or cedar forests near water	Timm 1974 Hazard 1982 Sutherland et al. 2000

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
Pygmy shrew *Microsorex hoyi*	**Uncommon**	**Low** 5-6 young/year		**Short** A European shrew has dispersed up to 870 m	**Resource dependent**	**Poor disperser**	**Generalist** Wide habitat tolerance, but may be most Common in mixed moist and dry veg.	Long 1974 Hazard 1982 Baumgardner et al. 1999
American marten *Martes americana*	**Uncommon**	**Low** 3-4 young/year	Generalist predator	**Long** Up to 61 km has been recorded	**Resource independent**	**Good disperser**	**Interior forest** Conifer and mixed forest, preferably, but not exclusively, old-growth	Hazard 1982 Chapin et al. 1997 Chapin et al. 1998 Sutherland et al. 2000 Wilbert et al. 2000
Southern red-backed vole *Clethrinomys gapperi*	**Common**	**High** Several litters of 4-5 per year		**Short** A European cogenitor has dispersed up to 400 m	**Resource dependent**	**Poor disperser**	**Interior forest** Moist conifer and mixed forest. Avoids some edges and clearcuts, but not others.	Timm 1974 Hazard 1982 Martell 1983 Kirkland 1990 Mills 1995 Sutherland et al. 2000
White-tailed deer *Odocoileus virginianus*	**Uncommon**	**Low** 2 young/year	Population depends primarily on winter severity	**Long** Up to 9.6 km (sometimes 40 km between summer and winter range)	**Resource independent**	**Good disperser**	**Multiple subhabitats** Prefers a mix of deciduous forest and open areas, and conifer stands in winter	Wetzel et al. 1975 Seal et al. 1978 Hazard 1982 Nelson and Mech 1984
Moose *Alces alces*	**Uncommon**	**Low** 1-2 young/year	Susceptible to brainworm carried by deer.	**Long** Up to 118 km has been recorded	**Resource independent**	**Good disperser**	**Multiple subhabitats** Prefers a mix of forest and open areas	Hazard 1982 Sutherland et al. 2000
Water shrew *Sorex palustris*	**Common**	**High** 2-3 litters of 5-8 per year		**Short** A European shrew has dispersed up to 870 m	**Resource dependent**	**Poor disperser**	**Multiple subhabitats** Boreal and mixed forests, usually near water, especially running water	Timm 1974 Hazard 1982 Sutherland et al. 2000

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
AMPHIBIANS								
Frogs and toads								
American toad *Bufo americanus*	**Common**	**High** 2,000 – 20,000 eggs	Co-occurs with fish predators.	**Long** Moves up to 1000 m after breeding.	**Resource-independent**	**Good disperser**	**Generalist** Breeds in variety of water types, and uses many types of uplands. Overwinters in sandy soils.	Casper 2002. deMaynadier and Hunter 2000 Gerry and Hunter 2002 Harding 1997 Hecnar and M'Closkey 1996 Kolozsvary and Swihart 1999 Oldfield and Moriarty 1994
Northern leopard frog *Rana pipiens*	**Common?** Formerly common, now only locally abundant in favorable conditions.	**High** 300 –6,000 eggs, laid in communal sites.	More common in pools without fish predators. Collected for biological supply houses and fish bait trade.	**Long** Juveniles may cover up to 800 m/day. May travel up to 1.5 km to over-wintering sites, and > 1km from these sites.	**Resource-dependent** Requires adequate cover for movement.	**Good disperser**	**Multiple subhabitats** Breeds in shallow wetlands. Disperses and forages in open uplands. Overwinters in permanent waters. Requires 3 sub habitats; none are forests.	Casper 2002 Gerry and Hunter 2002 Hecnar and M'Closkey 1996 Oldfield and Moriarty 1994
Northern spring peeper *Pseudacris crucifer crucifer*	**Common** Intermediate relative population density	**High** 750-1,300 eggs, laid singly or in small clusters	More common in ponds with non-predatory fish vs. ones with predatory fish.	**?**	**Resource-dependent**	**Good disperser**	**Multiple subhabitats** Broad habitat tolerances. Breeds in temporary or permanent waters surrounded by uplands. Disperses into mixed habitat Overwinters beneath logs, bark and fallen leaves.	Casper 2002 Gibbs 1998b Harding 1997 Hecnar and M'Closkey 1996 Kolozsvary and Swihart 1999 Oldfield and Moriarty 1994
Wood frog *Rana sylvatica*	**Uncommon** Low relative population density. Few data on pop. trends in N. MN.	**High** 500 to 3,000 eggs in masses in communal nesting sites.	Susceptible to fish predation and drought.	**Long** Dispersal distances as great as 2.5 km	**Resource-dependent**	**Poor disperser**	**Multiple subhabitats** **Forest-dependent** Breeds in vernal pools, Resident in moist deciduous, coniferous and mixed forests. Overwinters on forest floor.	Berven and Grudzien, 1990 Casper 2002 deMaynadier and Hunter 1999; 2000. DiMauro and Hunter 2002 Gibbs 1998a; 1998b Hecnar and M'Closkey 1996 Oldfield and Moriarty 1994

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
Salamanders								
Eastern tiger salamander *Ambystoma tigrinum tigrinum*	**Common** Abundant in MN, but at limit of range in N. MN.	**Low** 18 – 100 eggs. Long-lived – captives have survived 20+ years.	Suspectible to fish predation, with high mortality in egg to metamorph stages.	**?**	**Resource-independent**	**Good disperser**	**Generalist** Breeds in permanent to semi-permanent, preferably fishless, water bodies. Lives underground in various types of uplands. Less forest-dependent than other *Ambystoma* spp.	Casper 2002 Harding 1997 Oldfield and Moriarty 1994
Red-backed salamander *Plethodon cinereus*	**Common**	**Low** 3-14 eggs laid on land. Has stable populations, takes 3-6 years to sexual maturity.	Interspecific competition for home ranges.	**Short.** Activity range of males and young is 13 m^2; of females, 25 m^2.	**Resource-dependent** Low dispersal tendency	**Poor disperser**	**Interior forest** Completely terrestrial. Uses deciduous, coniferous and mixed forests.	Casper 2002 deMaynadier and Hunter, 2000 Gibbs 1998b Harding 1997 Heatwole,1962 Harpole and Haas 1999 Oldfield and Moriarty 1994
Blue-spotted salamander *Ambystoma laterale*	**Common**	**High** Lays a total of 35-500 eggs (avg of 225), singly or in clusters of 6-10.	Suspectible to fish predation.	**?**	**?**	**?**	**Multiple subhabitats** **Forest-dependent** Breeds in small ponds and woodland potholes. Resident in variety of forests, on forest floor. Overwinters at pond edges.	Casper 2002 deMaynadier and Hunter, 2000. Hecnar and M'Closkey 1996 Oldfield and Moriarty 1994
Eastern newt *Notophthalmus viridescens*	**Uncommon** Low relative density	**High** 6-10 eggs laid as often as 30 times a season.	All life stages have toxic skin secretions for protection against predators.	**Long** Dispersal distances >=1 km, from natal to breeding areas. Has eft stage dedicated to dispersal	**Resource-dependent**	**Good disperser**	**Multiple subhabitats** **Forest-dependent** Breeds in water, and may reside and/or overwinter in either water or forested uplands. Disperses in coniferous and deciduous forests.	Casper 2002 Oldfield and Moriarty 1994 Hecnar and M'Closkey 1996 *On subspp. - red-spotted newt -* deMaynadier and Hunter, 2000. Gibbs 1998a
Spotted salamander *Ambystoma maculatum*	**Uncommon** Low relative density.	**High** 50-250 eggs, laid in masses.	Suspectible to fish predation – prefer temporary pools	**?**	**Resource-dependent**	**Poor disperser**	**Multiple subhabitats** **Forest-dependent** Breeds in water. Resident in uplands.	Casper 2002 deMaynadier and Hunter 1999; 2000. DiMauro and Hunter 2002 Gibbs 1998a Hall, MN DNR website Harding 1997 Hecnar and M'Closkey 1996 Oldfield and Moriarty 1994

	Population size/ Reproductive rate		Inter- actions	Dispersal			Habitat	References
Four-toed salamander *Hemidactylum scutatum*	**Uncommon** Special concern species in MN.	**Low** Lays 15-64 eggs in moss by water.		**Short**	**Resource-dependent**	**Poor Disperser**	**Multliple subhabitats.** **Forest-dependent** Must have moss for nesting. Breeds in spring-fed creeks, sphagnum seepages, bogs. Resident in mature hardwood forests. Overwinters on forest floor or underground.	Casper 2002 Hall, MN DNR website Harding 1997
INSECTS								
Butterflies & moths								
Forest tent caterpillar *Malacosoma disstria*	**Common** Pest of aspen and other deciduous trees 10^8 larvae/ha	**High** Average of 200 eggs, 1 egg mass	Parasitism rates affected by spatial pattern of aspen. High potential larval mortality from parasitism and/or adverse weather	**Long**	**Resource independent?**	**Good disperser**	**Generalist** Aspen-birch forest Mixed deciduous forest	Coulson and Witter 1984 Roland and Taylor 1997
Spruce bud worm *Choristoneura fumiferana*	**Common**	**High** Average of 170 eggs, 5-10 clusters	Preyed upon by birds and many other predators	**Long** Adults - 80 km, up to 250 km (50 mi.)	**Resource independent?**	**Good disperser**	**Generalist** Coniferous forests Continuous, even-aged forests, balsam fir and spruce	Coulson and Witter 1984 Jennings and Crawford 1985

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
Northern blue butterfly *Lycaeides idas nabokovi*	**Uncommon** Less than 10 sites documented. Population estimates ranged from 4,000-5,000 and approx. 1000 at 2 sites, plus several smaller sites in WI and MN. Historic distribution and population size much larger	**Low** 30 eggs, may be low estimate One life cycle per year	Mutualistc ant (*Formica* sp.), tends larvae, 62% mortality rate from egg parasitoids	**Long** < 100 m common, 1-5 km – rare to occasional 1km in fragmented landscape and with currently low pop. numbers	**Resource dependent** Open vegetation with abundant nectar sources	**Good disperser** But short distances of current dispersal distances may be related to closed forest structure	**Specialist** Openings in mixed evergreen forest, White, red or jack pine savannas, one host plant = *Vaccinium caespitosum*, will nectar on non-native sp., habitat = disturbance dependent	Wolf 1993
Beetles								
Ground beetle *Calosoma frigidum*	**Common** 40 beetles/ spruce tree, associated with spruce budworm	**Low**	Preys on spruce budworm and forest tent caterpillar larvae	**Short** may be less than 10 m in months	**Resource dependent**	**Poor disperser**	**Interior forest?** Northern hardwoods/ Coniferous forests	Jennings and Crawford 1985 Werner and Raffa 2000
Ground beetle *Platynus decentis*	**Common?**	**Low**		**Short** may be less than 10 m in months	**Resource dependent**	**Poor disperser**	**Interior forest** Old growth forests, Eastern Hemlock	Werner and Raffa 2000

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
PLANTS & LICHENS								
Trees								
Aspen *Populus tremuloides*	**Common**	**High** Sexual & asexual reproduction, mature tree may produce over 1 million seeds, clonal	Herbivory by Forest tent caterpillar	**Long** Several to many kilometers, wind dispersed finely plumed seed, vegetative shoots	**Resource independent** Wind dispersed Seed dispersal is affected by pattern/matrix – affect of existing trees on wind patterns, etc. –	**Good disperser** Relative to other trees	**Generalist** Wide range of soil types and conditions COC = 2	Perala 1983 Harper 1977 http://www.botany.wisc.edu/wisflora/search.asp
White cedar *Thuja occidentalis*	**Uncommon** & declining	**High** 60,000 to 260,000 seeds per tree, vegetative reproduction	Deer browse reduces/ eliminates recruitment	**Long?** 45-60 m (150-200 ft.) Winged seed	**Resource independent**	**Good disperser**	**Specialist** Cool, moist, nutrient rich sites, organic soils near water, or calcareous mineral soils; shade tolerant COC = 9 Seed bed conditions = constant moisture and warm temperatures, decaying logs and stumps, Sensitive to changes in hydrology	Johnson and Booker 1983 Cornett et al. 2000 Tom Rooney pers. com. http://www.botany.wisc.edu/wisflora/search.asp
Understory herbs								
Canada goldenrod *Solidago canadensis*	**Common**	**High**	Strong competitor	**Long** Wind dispersed seeds, plumed seed	**Resource independent** Seeds can be blown over unsuitable habitat	**Good disperser**	**Generalist** Disturbed areas and openings COC = 1	McLachlan & Bazely 2000 http://www.botany.wisc.edu/wisflora/search.asp
Smooth brome *Bromus inermis* [NON-NATIVE]	**Common**	**High**	Strong competitor Pollination = wind	**Short?** Gravity dispersed	**Resource independent**	**Poor disperser**	**Generalist** COC = not ranked	Welby Smith pers. com. 2003 http://www.botany.wisc.edu/wisflora/search.asp

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
Wild Lily-of-the-Valley or Canada mayflower *Maianthemum canadense*	**Common** Can be the dominant understory herb	**Low** Ussually small number of seeds, Clonal growth helps persistence & expansion	Preferred deer food	**Long** Bird dispersed fruits, fleshy fruit	**Resource independ**ent Many birds will fly over unsuitable habitat	**Good disperser**	**Generalist** Northern hardwood forests, often associated with aspen , interior forest and edge species. Tolerant of disturbance. COC = 5	McLachlan & Bazely 2000 Euskirchen et al. 2001 Rooney 2001 Balgooyen and Waller 1995 Tom Rooney pers. com. 2003 Welby Smith pers. com. 2003 http://www.botany.wisc.edu/wisflora/search.asp
Large flowered trillium *Trillium grandiflorum*	**Common**	**Low** 20 seeds/year, >15 years to reproduce, few seeds germinate and establish, < 10% survive	Preferred deer food Pollination = insects	**Long** Ants <60cm, bees up to 900m, may also be dispersed by deer (dispersal distances for *T. ovatum*)	**Resource dependent** Habitat for ants needed	**Good disperser**	**Interior forest** Mixed deciduous forests Tolerant of edge in some cases. Large colonies or scattered individuals COC = 6	Rooney 2001 Alverson et al. 1988 Jules and Rathcke 1998 Jules 1998 Tom Rooney pers. com. Meier et al. 1995 http://www.botany.wisc.edu/wisflora/search.asp
Wild leek *Allium tricoccum*	**Common?**	**Low** Few seeds produced, spread vegetatively		**Short** Gravity dispersed	**Resource independent**	**Poor disperser**	**Specialist** Wet areas, undisturbed forest habitat, sensitive to hydrologic changes COC = 6	USFS FS 2002b Gehlhausen et al. 2000 Welby Smith pers. com. 2003 http://www.botany.wisc.edu/wisflora/search.asp
Michigan lily *Lilium michiganense*	**Uncommon**	**Low** Small number of seeds	Preferred deer and small mammal food	**Short** Gravity dispersed?		**Poor disperser**	**Generalist** Bogs, meadows, low woods and wet prairies COC = 6	Fletcher et al. 2001 Welby Smith pers. com. 2003 http://www.botany.wisc.edu/wisflora/search.asp
Yellow blue-bead lily *Clintonia borealis*	**Uncommon**	**Low**	Pollinated by insects	**Long** Bird dispersed	**Resource independent**	**Good disperser**	**Generalist** Boreal forest, northern forest, pine barrens, bog Sensitive to disturbance COC = 7	Balgooyen and Waller 1995 Meier et al 1995 http://www.botany.wisc.edu/wisflora/search.asp
Calypso orchid *Calypso bulbosa* var. *americanum*	**Uncommon**	**Low** Long time to reproduction	May be preferred deer food Pollination = bumblebees	**Short** Gravity	**Resource independent**	**Poor disperser**	**Specialist** Lowland coniferous Forests, under cedar, spruce and fir COC = 10	Smith 1993 http://www.botany.wisc.edu/wisflora/search.asp

	Population size/ Reproductive rate		Inter-actions	Dispersal			Habitat	References
Lichens								
Pendulous lichen species *Usnea longissima*	**Common**	**High?**	Damaged by high winds	**Short?** Primarily by thallus fragments blown by wind, 200 m?	**Resource independent**	**Poor disperser?**	**Interior forest** Northern mixed and southern hardwood forests Old growth forests	USFS FS 2002b Clifford Wetmore pers. com. 2003
Foliose lichen species *Lobaria pulmonaria*	**Common**	**High?**		**Long** Small soredia or isidia	**Resource independent**	**Good disperser**	**Interior forest** More common on old growth sites	USFS FS 2002b Clifford Wetmore pers. com. 2003
Parasite on trees								
Dwarf mistletoe *Arceuthobium pusillum*	**Common**	**High?**		15 m, seeds ejected by hydrostatic pressure, also by birds and small mammals	**Resource independent**	**Good disperser**	**Generalist?** Parasite on black spruce, also on while spruce, red pine, white pine and jack pine	Ostry and Nicholls 1979

Table 2. Species sensitivity framework for example species.
(Multiple subhabitats = 2 or more subhabitats)

		HABITAT GENERALIST		INTERIOR FOREST		TWO OR MORE SUBHABITATS[1] REQUIRED		HABITAT SPECIALIST, SINGLE HABITAT	
		Dispersal		**Dispersal**		**Dispersal**		**Dispersal**	
		Good	Poor	Good	Poor	Good	Poor	Good	Poor
POPULATION SIZE/REPRODUCTIVE RATE	Common/ High	American toad Forest tent caterpillar Spruce bud-worm Aspen Canada goldenrod Dwarf mistletoe?	Deer mouse Snowshoe hare Smooth brome	Foliose lichen – *L. pulmonaria*	Red-backed vole? Pendulous lichen – *U. longissima*	Northern leopard frog Northern spring peeper	Water shrew? Blue-spotted salamander?		
	Common/ Low	Red-eyed vireo Eastern tiger salamander Wild lily-of-the-valley	Black-capped chickadee Star-nosed mole?	Ovenbird Large flowered trillium	Red–backed salamander Ground beetle – *C. frigidum?*				Wild leek Ground beetle – *P. decentis*
	Uncommon/ High					Wood duck Eastern newt	Ruffed grouse Spotted salamander? Wood frog	White cedar	
	Uncommon/ Low	Northern goshawk Timber wolf Red fox	Pygmy shrew Michigan lily	Scarlet tanager American marten		Boreal owl White-tailed deer Moose	Four-toed salamander	Golden-winged warbler Yellow blue-bead lily Northern blue butterfly	Spruce grouse Calypso orchid

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[1] Subhabitat – recognizable compositional or structural subset of a species' habitat that is required to complete life cycle (Lane 1999).