APPENDIX I

Forest Spatial Patterns

LOOKING AT THE LANDSCAPE

Patch
Looking down from the air the landscape can be divided into relatively uniform *patches* that differ from their surroundings in nature or appearance. *Patch typ*e is a classification that distinguishes different types of vegetation, soil, or other variables. Each patch is classified as a different type than adjacent patches.

Grain and Resolution
Resolution is the degree of precision of a measurement. When looking at landscape maps the term *grain* is a synonym. Grain is the finest level of resolution possible within a given data set. Satellite imaging, for example, often divides the landscape into squares 30 m on a side. Any patch too small to show up in a square is ignored. Another common way to express resolution is minimum mapping unit, which is the smallest size a patch can be and still show up on a map. One map may include lakes larger than 50 acres, but no smaller, while another may include ponds as small as 1 acre. Figure 1 illustrates two different grain sizes. Some studies suggest that when analyzing habitat, grain size should be less than 1% of the home range size of the species in question (Schultz and Joyce 1992).

Mosaic
A group of patches forms a mosaic. When a single patch type dominates a landscape, it is called a *matrix*. Matrix types are expected in relatively uniform landscapes, such as agricultural regions, but more complex landscapes can also have a matrix if patch types are classified only into broad categories. If, for example, northeast Minnesota were classified into general categories such as forest, lake, urban, agriculture, etc., the matrix would be forest. But if the forest were divided into patches of finely-classified types, there may be no single dominant patch type (Figure 2).

Shifting Mosaic
Over time patch types change. Forests of shade-intolerant trees succeed to shade-tolerant species. Beaver meadows appear and then are abandoned. Forests are altered by logging, windstorm, or fire. Development replaces forest. As a result the mosaic of patch types shifts (Figure 2). The shifting mosaic may maintain the same proportion of patch types (one patch of old pine forest is cut down in one place, but it is replaced somewhere else by another that reaches maturity), or some patch types may increase or decrease over time. Other parts of the Forest Spatial Analysis and Modeling Project have investigated the changes in forest patterns in northeast Minnesota over the past decades (Host and White, 2003a; 2003b, White and Host 2003).

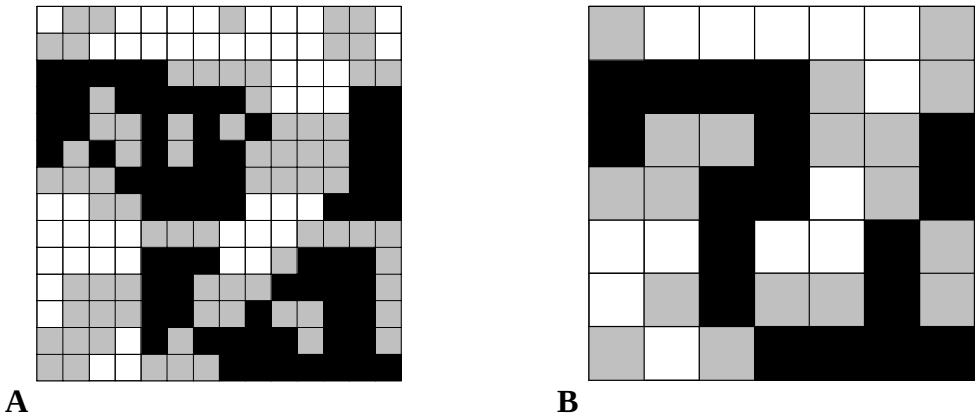


Figure 1. A landscape classified by 3 patch types with a small grain size (A) and a large grain size (B).

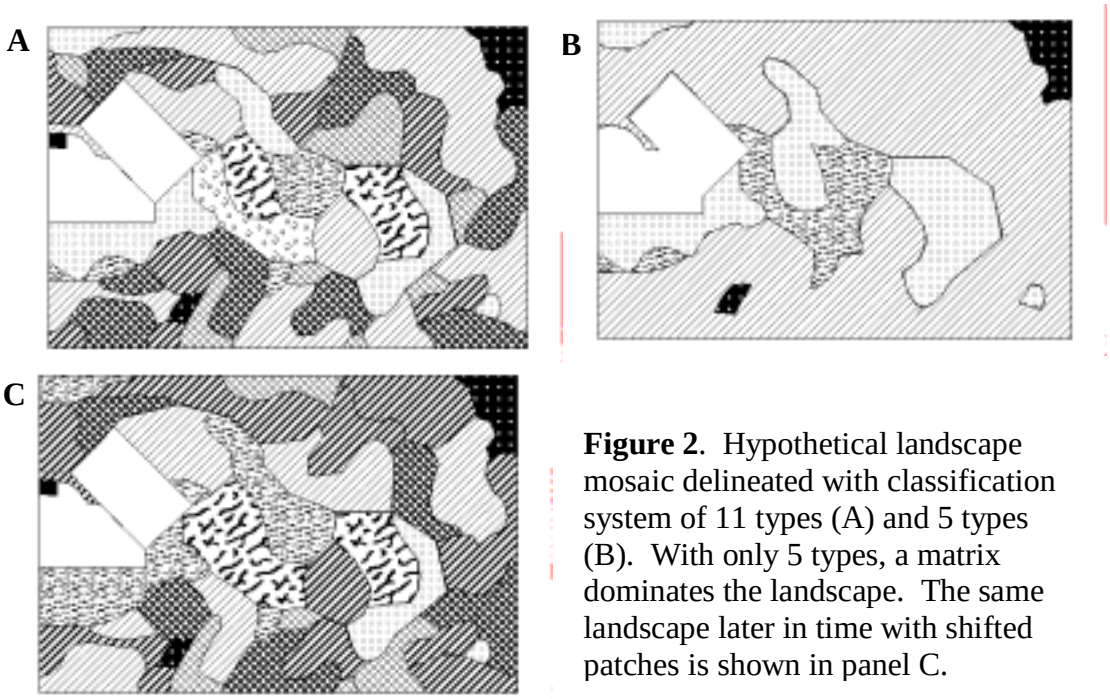


Figure 2. Hypothetical landscape mosaic delineated with classification system of 11 types (A) and 5 types (B). With only 5 types, a matrix dominates the landscape. The same landscape later in time with shifted patches is shown in panel C.

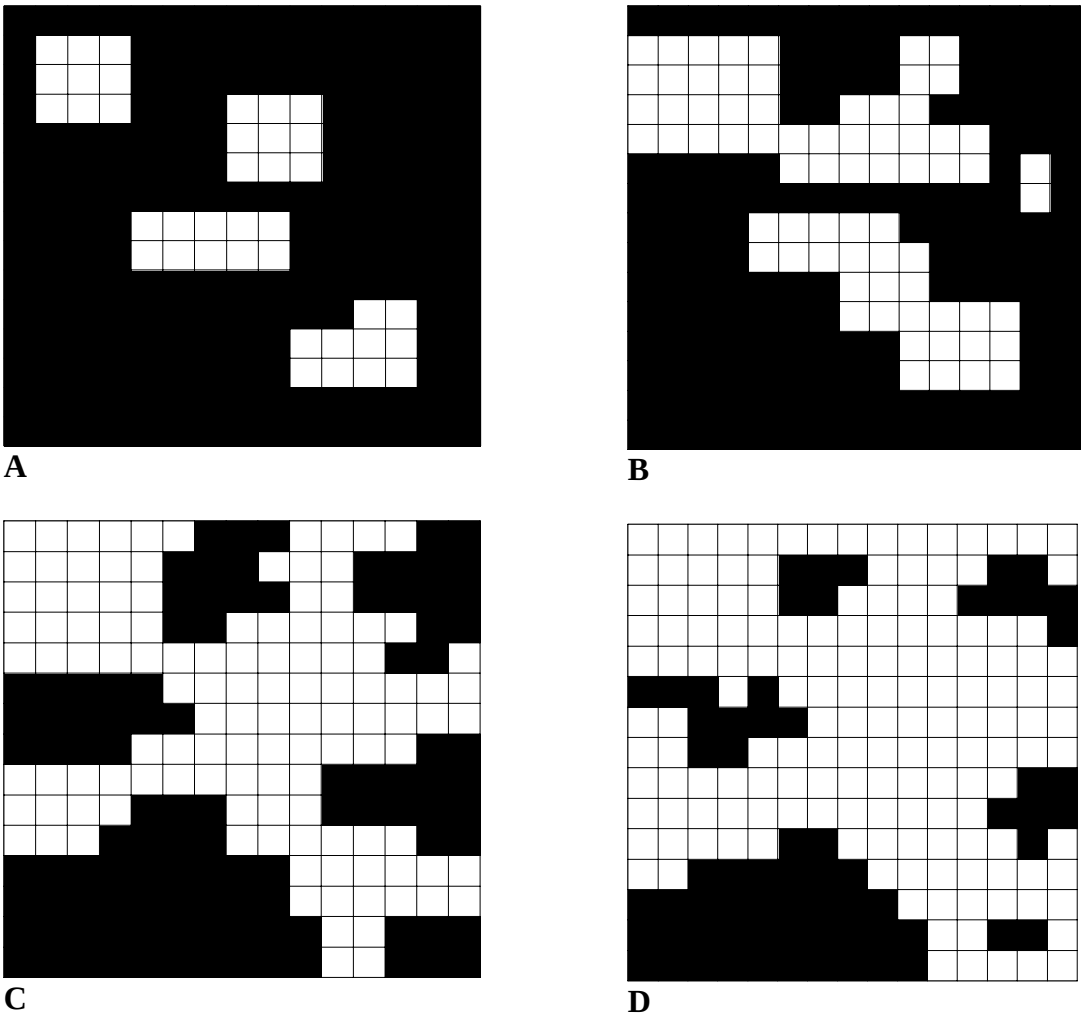
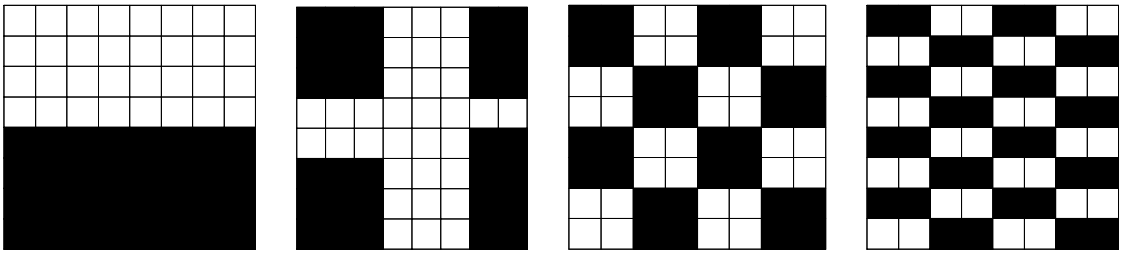


Figure 3. Habitat loss and fragmentation in a binary landscape (two patch types: habitat in black and non-habitat in white) on a scale from perforation (A) to remnant patches (D). As habitat availability declines, the components of fragmentation change: habitat patch size decreases, edge length increases (at first), and habitat patch isolation increases. As the proportion of habitat in the landscape falls from 83% to 68% to 47% to 30%, the total length of edge rises from 2.0 miles to 2.9 to 3.2, then falls back to 2.9 (assuming each square is 1 acre). In general, edge length reaches a maximum near 50% cover in binary landscapes.

Fragmentation
Fragmentation is the breaking up of a habitat (or patch type) into smaller, disconnected patches (Turner *et al*. 2001). The early stage of fragmentation, when holes are opened up within a large patch, is called *perforation*. As the holes expand, they connect with each other, and if they keep expanding, only fragments of the original large patch remain (Figure 3).

However, the term fragmentation has not been used consistently. Some studies include habitat loss as part of fragmentation, while others consider it a separate change. For the sake of clarity, whenever possible, we will not address the general concept of fragmentation, but instead its better-defined components (habitat loss, patch size, edge, and habitat isolation), along with other factors. Even if the amount of habitat stays the same, the other components of fragmentation can change (Figure 4). Many studies have investigated the effect of these distinct components on plant and animal species, but many others have investigated "forest fragmentation" more generally (i.e. on a scale of perforation to remnants).



A **B** **C** **D**

Figure 4. Four binary landscapes with the same amount of habitat (in black), but with varying levels of fragmentation, as measured by patch size and edge length. Average patch size declines from 32 acres in A (if each square is 1 acre) to 8 acres in B, 4 acres in C, and 2 acres in D. Edge length rises from 0.3 miles in A to 0.9 miles in B, 1.9 miles in C, and 3.2 miles in D.

SPATIAL PATTERNS

Six spatial patterns that affect plant and animal species will be emphasized here:

1. Patch size
2. Patch edges
3. Arrangement of patch types
4. Habitat availability
5. Habitat isolation and connectivity
6. Human presence and influence

Patch Size

Average patch size has decreased since the 1930s in the landscape of northern Minnesota (Host and White 2002; 2003). When patches are delineated to identify habitat for a particular species, the size of a habitat patch can determine whether the species can actually occupy it. A patch may provide habitat for a species, but if it is smaller than the area necessary to support a reproductive population, then the species cannot occupy it for long. For species with limited dispersal ability, a reproductive population may require a patch large enough for many individuals. A reproductive population of a bird, on the other hand, may require a patch just large enough for one pair's territory, or several territories if they have social requirements. A calculation of total available habitat will be an overestimate if it includes patches too small for the species in question.

Patch Edges

The amount of edge in the landscape of northern Minnesota has increased since the 1930s (Host and White 2002; 2003), and it tends to increase with decreasing patch size (Figure 3). Edges between patches provide a unique ecotone that is different from the patches on either side. Species that prefer these ecotones are called *edge species*. Other species avoid the edges of their habitat patches (or do less well there). These are called *interior species*. The influence of edges on both types of species is called the *edge effect*.

Measuring Edge

When all types of edges throughout a landscape are important, calculate:

- Ratio of total edge length to total landscape area

To take hard and soft edges into account, an alternative measure is:

- Contrast-weighted edge-to-area ratio

When the edges of just one patch type (Type A, for example) are important, there are two possible measurements:

- Ratio of Type A edge length to total landscape area (edge density)
- Average ratio of perimeter to area for all patches of Type A

This last metric reflects the shape of the patches. When the edge between two particular patch types (on a map of multiple patch types) is important, it can be measured by the:

- Length of adjacency between the types (divided by total area)

Roads and Trails
Roads, railroads, and trails can also form edges, even when the same patch type occupies both sides. They may be too narrow to show up on patch type maps (depending on the scale), but they can still influence plant and animal species. For one thing they can pose either a barrier or a conduit for the movement of various animals.

Arrangement of Patch Types

Species are affected not only by the amount of habitat, and the size of habitat patches, but also by how the patches are arranged on the landscape.

Landscape Diversity and Dominance
Landscape diversity refers to the diversity of patch types. The simplest measurement is:

- Richness, the number of patch types present

Richness can also be expressed as a percent of the total number of possible patch types (relative richness) or as the richness per unit area. Richness, however, does not indicate whether there are 50 patches of one patch type and 5 of each of the others, or 10 patches of each patch type. That is, richness does not indicate evenness. Taking evenness into account is the calculation of:

- Diversity, an index that increases with greater richness and evenness

The inverse of evenness is the index of:

- Dominance

Dominance increases as one, or a few, patch types occupy a greater proportion of the landscape.

Proximity of Two Patch Types
A species may require two or more patch types in close proximity (such as the boreal owl (Lane *et al.* 1997)), or a species in one patch type may be affected by the presence of adjacent or nearby patches of another type (such as forest songbirds that suffer nest parasitism from brown-headed cowbirds based in nearby agricultural or residential areas).

One metric is the:

- Probability of adjacency between two patch types

This metric could be adapted to measure the probability that the two patch types are within a certain distance of each other (rather than adjacent). Calculating available habitat for

species requiring two patch types necessitates excluding patches that are not within a certain distance of each other.

Habitat Availability

Calculating Habitat Availability

By Patch Type
In the simplest sense, quantifying the amount of habitat available for any species is a two-step process. First, the patch types that provide habitat for the species must be identified. Then the total area of these patch types in the landscape can be summed. This total area is often expressed as:

- Proportion of landscape providing habitat

The proportion of habitat can be compared to that from another point in time to measure habitat loss or gain. For species that are specialized for a certain patch type or types (such as the pitcher plant, which is restricted to peat bogs (Ellison and Parker 2002)), the process of calculating habitat availability could be as simple as this two-step process.

Variable Habitat Quality
For many species, however, identifying the patch types that provide suitable habitat is more difficult. When different patch types provide habitat at varying levels of quality, should low quality types be lumped with high quality types when calculating total available habitat? One way to address this issue is to quantify the proportion of habitat in different classes of quality, such as high, medium, and low. This quantification depends on expert knowledge or survey data.

Beyond Patch Type
For many species patch type is not the only factor to consider when quantifying available habitat. For example, pine warblers find their best habitat in pine-dominated forests, but other forest types provide suitable habitat if pines are mixed in. In this case pine density, rather than patch type, might be most relevant. In a wolf habitat study, patch type was only one significant factor. Other factors included deer density, land ownership, road density, and human population density (Mladenoff *et al*. 1995).

Multiple Factors
A variety of methods have been used to quantify available habitat when multiple factors are involved. These include habitat suitability indices (Burgman *et al*. 2001) and statistical models (e.g. Clarke *et al*. 1993, Mladenoff *et al*. 1995). A habitat suitability index uses expert knowledge to predict the amount and quality of habitat for a species in an area that has not been surveyed. They can be simple and powerful tools, but one of their weaknesses is that not all the habitat relationships are based on data. Statistical models use data collected in some places to predict habitat suitability across a wider area. A study of timber

wolves (Mladenoff *et al*. 1995), for example, calculated available habitat over three states on a scale of probability of occurrence (<10%, 10-25%, 25-50%, 50-75%, 75-95%, and >95%), based on data from one state. Models predicting abundance as a function of environmental variables do not have a great track record (Pearce and Ferrier 2001), but Mladenoff and colleagues (1999) were able to validate their 1995 model with new data. And building models is certainly cheaper than doing a field survey of all areas.

Habitat Isolation and Connectivity

Connectivity

Connectivity is sometimes considered the inverse of fragmentation (Turner *et al*. 2001), but a better definition of connectivity is the "degree to which a landscape facilitates or impedes movement of organisms among resource patches" (Taylor *et al*. 1993). Habitat isolation is an important factor affecting plant and animal species, but the real issue is how easily they (animals or plant seeds) can travel between patches of habitat. Thus, connectivity depends not only on the structure of the landscape, but also on the behavior of the organism in question. In the same landscape, connectivity will be greater for a species that travels easily than for one that does not.

Measuring Connectivity

Connectivity is more or less the inverse of habitat isolation, but measurement involves more than the distance between patches (Tischendorf and Fahrig 2000). There are indices of connectivity (Turner *et al*., 2001), but connectivity for a given species in a given landscape is more accurately determined by the rate of immigration into patches of appropriate habitat. According to Tischendorf and Fahrig (2000), comparing connectivity between landscapes or across time can be done by:

- Comparing immigration rates into small, equal-sized areas

When immigration data are unavailable, a related measure is:

- Functional distance

Functional distance (e.g. Bunn *et al*. 2000) is a measure of the distance between habitat patches, but it also takes into account the nature of the patch type(s) between patches and how easy or difficult it is for the species in question to move through it (them). Functional distance can involve estimates of the permeability of the intervening landscape and the rate of mortality during movement (Figure 5).

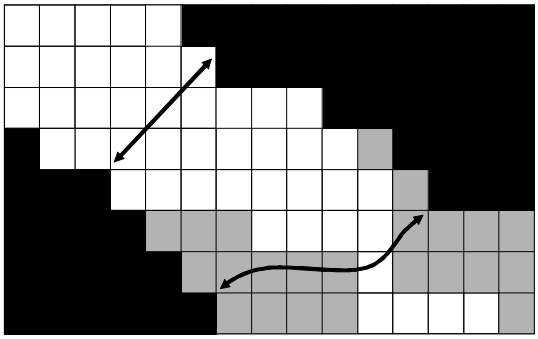


Figure 5. A simple schematic of functional distance between habitat patches (in black). The shortest distance between the patches is 3 squares (at diagonal). If one non-habitat patch type (gray) is 3 times more permeable for a species than another (white), the shortest functional distance for that species is 1 white square and 5 gray squares.

APPENDIX II

Conceptual Theories and Models

Several theories and models have been used to help explain the effects of habitat spatial pattern on species. Many of these form the basis for how spatial pattern is studied and interpreted. In the following section we provide a brief overview of some of the key theories and models including:

- Island biogeography
- Population structure and Metapopulation dynamics
- Source-sink dynamics

Island biogeography

The theory of island biogeography has influenced how land managers and ecologists consider the impact of spatial pattern and species presence/abundance. For many years it was the primary theory used to guide conservation reserve design (Shafer 1990). The theory was developed by MacArthur and Wilson (1963) in response to patterns of species diversity that had long been observed on oceanic islands. There were several general patterns that seemed to apply to islands, including relationships between:

1) the number of species and size of the island (larger islands often had more species than smaller islands)
2) the number of species and the degree of isolation of the island (islands farther from the mainland often had less species)
3) the rate of species "turnover" (rate at which species go extinct and then are replaced by other species) and the degree of island isolation (for example, less remote islands were thought to have lower species turnover rates in part because of lower immigration rates)

The theory of island biogeography was then applied to other isolated ecosystems and fragmented landscapes. It was suggested that there would be similar dynamics for species occurring in alpine communities on mountain tops and in caves (Turner *et al*. 2001) and species on oceanic islands, since the intervening habitat between these terrestrial types habitats was also inhospitable. The theory was then extended to the design of nature preserves in fragmented terrestrial landscapes (Soule and Simberloff 1986) and was one of the dominant theories of conservation biology in the 1970s and 1980s (Turner *et al*. 2001). The extension and use of the theory for nature preserves sparked much debate in the conservation community about reserve size and configuration. The primary focus of the debate was whether one large or several small reserves would protect the most species. The perceived tradeoffs were that one large

preserve might support more species, but also be more vulnerable to catastrophic events. Species occurring in several small reserves would be more likely to survive a catastrophic event but in general the smaller areas would not support as many species.

Many aspects of the theory have been questioned (Shafer 1990, Turner *et al*. 2001), including its applicability to species conservation in terrestrial systems. For example, unlike oceanic islands or caves, the matrix surrounding habitat fragments is not inhospitable to terrestrial species. For example, the matrix may support both invading species and/or provide marginal habitat for those species living in the fragment. In some cases small fragments may have higher species diversity because they contain both species associated with the fragments and invading species from the surrounding matrix, whereas larger fragments are less susceptible to invasion (see Webb and Vermaat 1990 in Turner *et al*. 2001).

Despite the criticisms, some predictions based on the theory of island biogeography tend to hold true and principles are still applied. For example, larger habitat patches will allow persistence of more species adapted to that habitat.

Population Structure and Metapopulation dynamics

Species tend to be distributed unevenly in space because of the patchy distribution of resources such as soil type, microclimate, host species, etc. Different species distributions, and hence population dynamics, can be thought of as different "population structures".

Several types of population structures are relevant to the subject of this background paper and the project area, including:

1) patchy population
2) classic metapopulation
3) source-sink and core-satellite.

In a patchy population, the population is divided into smaller subsets of individuals or "subpopulations" (or "local populations") (Figure 6). The subpopulations are functionally connected by dispersal. Individuals move between patches frequently enough that the patches do not support separate populations. The high degree of connectivity reduces the probability that any given subpopulation will go extinct as it is likely to be frequently colonized by new individuals.

As the number of individuals dispersing between patches decreases, at some point subpopulations begin to be more independent. That is, a subpopulation may go extinct (or be colonized) independently of the other subpopulations. Populations with these types of dynamics are referred to as "metapopulations" (Harrison 1991) (Figure 7). For the entire population to persist, colonization must be greater than extinction of subpopulations. Because of the extinction/colonization dynamics associated with

metapopulations, it is possible for a metapopulation to crash even if several occupied patches remain (Turner et al 2001). If, in addition, dispersal between subpopulations is reduced because of habitat fragmentation, the probability of extinction for the entire metapopulation is expected to increase.

In the “true” or “classic” metapopulation described above, all subpopulations are considered to have equal quantity and quality habitat, and equal probabilities of extinction (Levins 1970). However, habitat patch size and quality are typically variable and some patches are likely to provide better habitat than others. In fact, high quality patches may produce excess individuals that disperse to find additional habitat. In some cases these individuals may disperse to poor quality habitat, i.e. where there is little reproduction and/or high mortality rates. This type of population structure is called “source-sink” (Figure 8), (Pulliam and Dunning 1994). In cases where one large, high-quality habitat patch produces the majority of the individuals, and smaller or lower-quality patches primarily survive by receiving colonists from the large patch, the population structure is called “core-satellite” (or “mainland-island”) (Figure 9) (Harrison 1991).

Population structure will influence how a species responds to changes in habitat spatial pattern. For patchy populations, maintaining a high rate of connectivity between the patches is likely to be important. Persistence of a true metapopulation will require that colonization of patches exceeds extinction. Often species with a metapopulation structure are associated with temporary habitats created by disturbance. In this case, species are adapted to colonize new habitats as other habitat is degraded/destroyed, and persistence of these species is expected to be compatible with land uses that result in new habitat being created as other is lost. As a result of habitat fragmentation some species’ populations may resemble metapopulations, but may not be as well suited to persist as those adapted to this population structure. Metapopulation research has focused on animal species and less is known about plant metapopulation dynamics. Obviously, in a core-satellite (or source-sink) population, preserving the core is critical.

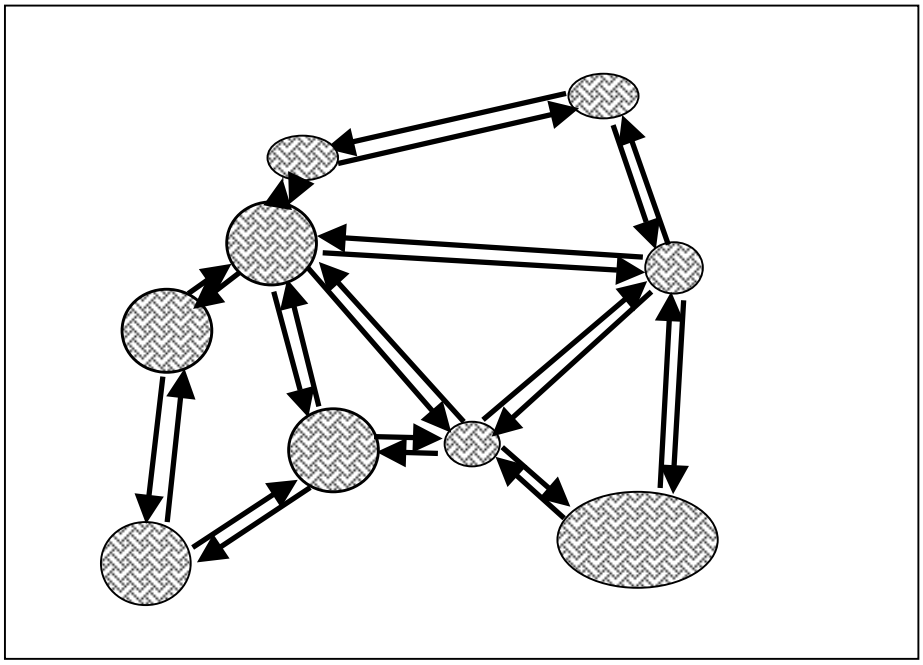


Figure 6. Patchy population structure. Dispersal between populations is high (indicated by heavy arrows) and habitat patches are usually occupied.

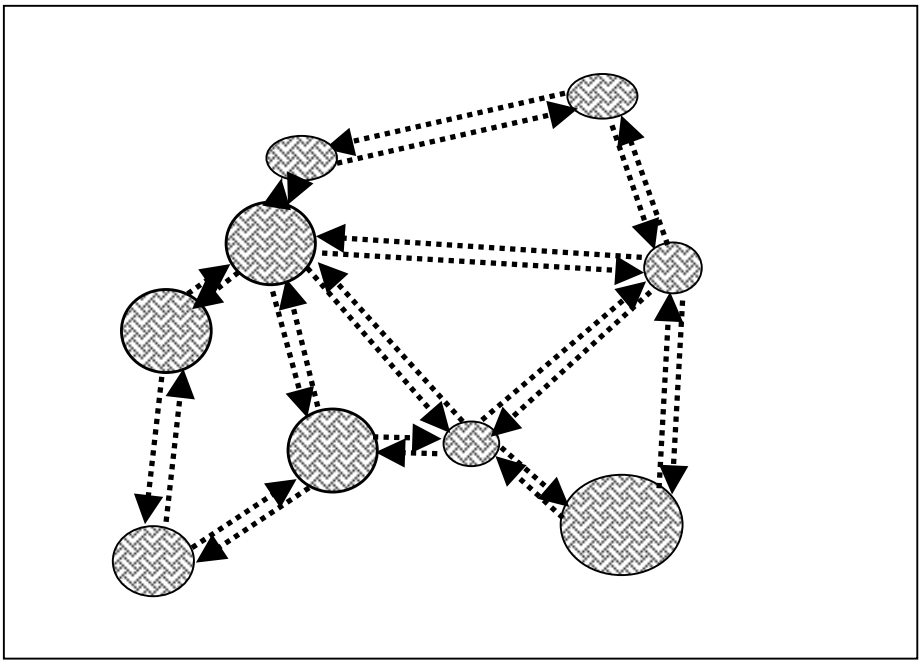


Figure 7. True metapopulation structure based on Levins (1970). Circles represent suitable habitat and arrows indicate dispersal (dotted to indicate limited dispersal between local populations).

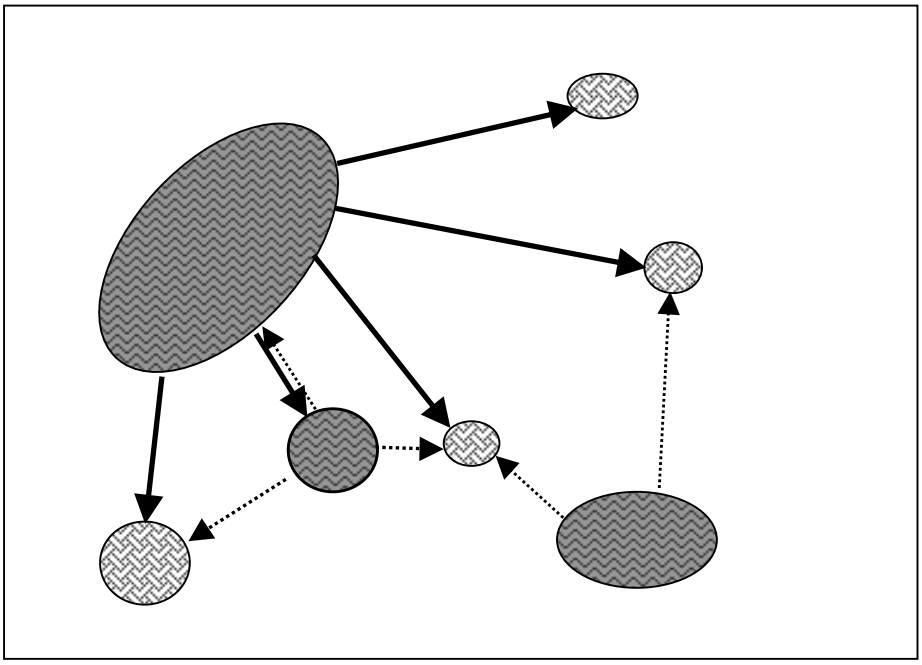


Figure 8. Source-sink population structure. Large and darker circles are sources, smaller circles are sink populations.

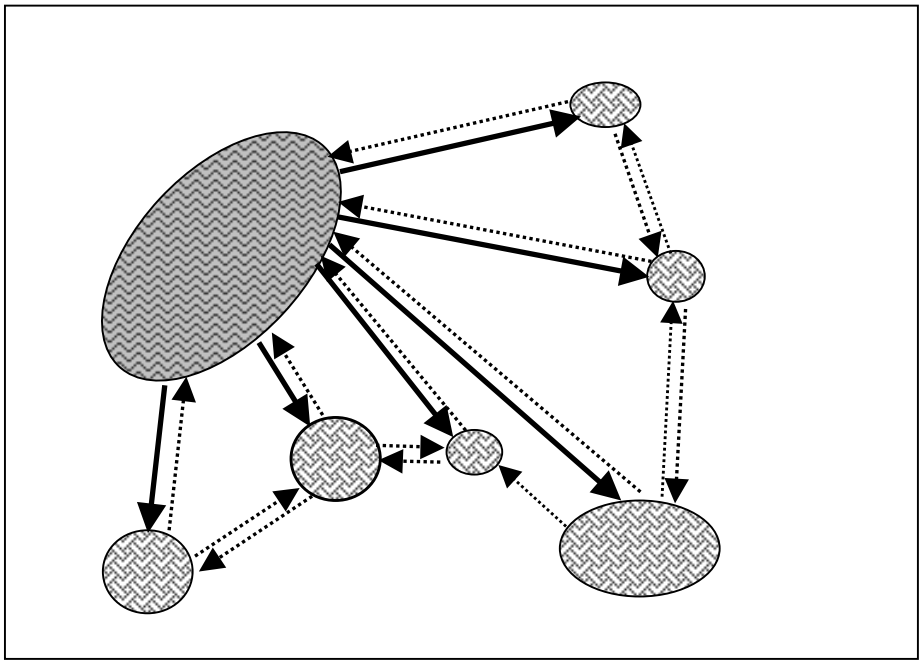


Figure 9. Core satellite population structure. Large, darker circle is core, smaller circles are satellite populations. Thicker arrows indicate greater numbers of individuals moving.

APPENDIX III

Species-Level Processes & Life History Characteristics

In this section we describe species-level processes known to be most susceptible to change in spatial pattern of habitat.

The effects of spatial pattern are known to vary between species, in particular between taxonomic groups. Where possible we use example species found in Minnesota or similar northern hardwood or boreal forest types. Our examples include a range of species (body size, trophic level, etc.) in each of the following five taxonomic groups:

- Birds
- Mammals
- Amphibians
- Insects
- Plants and Lichens

POPULATION DYNAMICS

One of the primary means by which spatial habitat pattern influences species persistence is by affecting population dynamics. Population dynamics is the change in the distribution and abundance of plant and animal populations through time and space. Understanding population fluctuations, including demographic processes such as birth, death, immigration and emigration and the interaction between these processes and the populations' environment, is critical to population conservation (Meffe and Carroll 1994).

There are four fundamental components influencing population dynamics which are often referred to as the "*BIDE* factors" (Figure 1):

- *B*irth rate
- *I*mmigration rate
- *D*eath rate
- *E*migration rate

Births and Deaths

Populations increase in size via reproduction (births) and dispersal into an area (immigration, and decrease via mortality (deaths) and dispersal out of an area (emigration). The iteration of these processes is also important; for example, if birth rates exceed death rates, the population will only be able to persist if there is immigration into

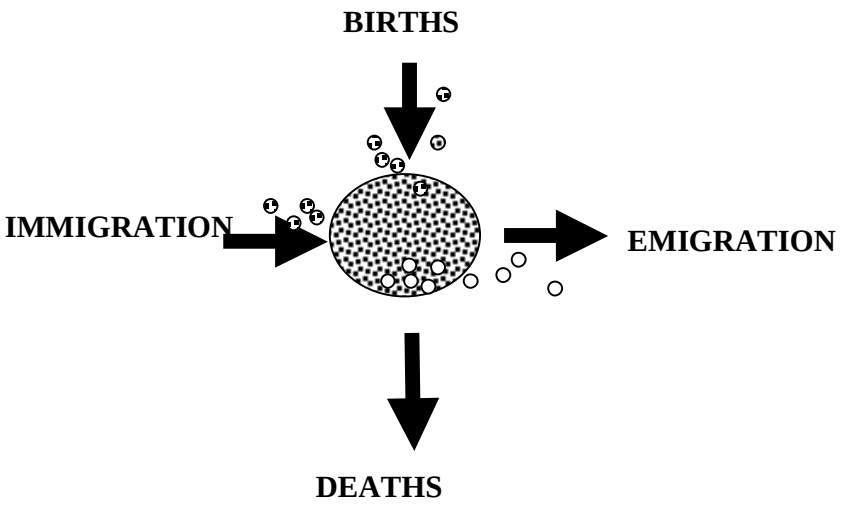


Figure 1. The four fundamental components influencing population dynamics.

the population area. In this section we will describe some of the key factors influencing birth and death rates.

Birth rate, or natality, is defined as the production of new individuals in a population per unit time. Births have a positive effect on population growth. A number of factors affect birth rates including the reproductive characteristics of the species, population size, and the influence of environmental conditions on reproduction.

Death rate, or mortality, is the number of individuals that die per unit population per unit time. Population growth is negatively affected by death rates. Death rates are determined by the physiological longevity associated with the species as well as the life expectancy of individuals in a population under a given set of environmental conditions. Species vary considerably in their longevity, from a few days in the case of some insects to thousands of years for some plants. Certain life stages are often more vulnerable to mortality, such as nesting stage in birds, the larval stage in insects and amphibians, and seed germination stage in plants. Insects and amphibians may experience greater than 90% mortality rates (Price 1984).

Factors influencing birth and death rates by taxa

The factors influencing birth and death rates vary between species and among taxonomic groups. In the following paragraphs, we provide a brief overview of some of the characteristics of natality and mortality for each taxonomic group.

Birds
Birds have low reproductive rates compared to most other taxa. Most species in the forested regions of northern Minnesota normally lay only one clutch per year. As a result, reproductive output does not vary between species as much as it does in other taxa. The size of the clutch is the major determinant. At the high end are species like the ruffed grouse with an average clutch size of 11 eggs. In the middle are species like the black-capped chickadee, which lays 6-8 eggs. And at the low end are species like the bald eagle, which usually lays 2 eggs, and a successful nest often fledges just one chick.

One of the most important factors causing mortality in birds is predation (on both nests and adults). For migratory birds there is significant additional mortality from windstorms and from collision with wires and buildings during migration. For resident birds there is significant mortality from cold/hunger in winter, and both residents and migrants can starve during cold spring weather. In forested regions parasites and diseases are not usually a major factor, except sometimes in colonial birds like swallows and herons, especially when they reuse their nests. Fish-eating birds like loons, ospreys and eagles are susceptible to mercury poisoning, and some waterfowl (particularly loons) die from ingesting lead sinkers. The full impact of West Nile virus is unknown at this time, but raptors appear to be heavily impacted in some places.

Mammals
Mammals have a greater variability in reproductive rate than birds. Many small mammals can have multiple litters each year. A female deer mouse, for example, can produce 4 litters averaging 5.3 offspring per litter. After taking into account the fact that female offspring from the first litter can produce their own litters before the end of the season, a single female can give rise to 35 young in a season (Millar *et al*. 1979). A pack of timber wolves usually has 5-10 pups per year, while each white-tailed doe usually has twins.

Predation and starvation are the major causes of mortality in mammals. Small mammals actually form the base of an elaborate vertebrate food web. When they are plentiful, they suffer tremendous mortality to both avian and mammalian carnivores. When they are scarce, many predators starve. White-tailed deer often starve during severe winters when snow buries browse and when extreme cold saps their energy faster than they can replenish it. Diseases and parasites, such as rabies, mange, chronic wasting disease (in deer), and brainworm (in moose) contribute additional mortality.

Amphibians
Amphibians have remarkably diverse reproductive strategies with varying reproductive rates. Frogs and toads use external fertilization and most species lay thousands of eggs, while salamanders rely on internal fertilization, often engage in a complex mating behavior, and have lower fecundity. For example, the American toad (*Bufo americanus*) lays 4,000 to 20,000 eggs, the blue-spotted salamander (*Ambystoma laterale*) lays 35-500 eggs, singly or in clusters of 6-10 eggs in water, while the wholly terrestrial redback salamander produces only 13-14 eggs (Oldfield and Moriarty, 1994; Harding, 1997).

Breeding populations can fluctuate by one to two orders of magnitude in a season due to a host of factors (Stebbins and Cohen, 1995; Harding, 1997). Amphibians are especially vulnerable to adverse weather (especially drought) and microclimate. In drought years, breeding ponds can disappear before larvae mature into adults, resulting in a total loss of young for that season. Species of frogs, toads and salamanders that overwinter in the soil suffer high mortality in cold winters when snow cover is insufficient to insulate the ground and frost penetration is deep. Amphibians are significant predators and sources of prey in their various life-stages. Predation by vertebrates and invertebrates of aquatic amphibian eggs or larvae are significant sources of amphibian mortality (Stebbins and Cohen, 1995). Amphibian population declines are occurring worldwide in a wide variety of habitats and have been attributed to several factors including habitat loss, chemical exposure, ultraviolet radiation exposure, and parasitism (Blaustein and Johnson, 2002). Collection for bait and biological supply houses are sources of mortality for some amphibian species (Oldfield and Moriarty, 1994).

Insects

Insects have a wide range of reproductive rates relative to birds and mammals. Characteristics contributing to high reproductive rates are: short generation times, the ability to lay many eggs or bear many live young, specializations associated with social insects, and asexual reproduction. For example, in the southern U.S. some aphid species have up to 15 generations per year. Egg laying in insects ranges from those insects that lay only one egg at a time (such as the tsetse fly), to insects that lay masses that contain hundreds of eggs, to social insects where one ant queen may lay thousands or up to a million eggs in her lifetime (Price 1984, Ricklefs 1990).

As a result, population sizes for insects can be quite large. Population numbers ranging from 50,000 to 100,000 were recorded for an alpine butterfly (*Euphydras anicia*, Ehrlich 1989). Lifetime in insects is also wide ranging, from a few hours to up to 17 years for the cicada in North America. For many moth or butterfly species, such as the forest tent caterpillar moth, adults live a few days to weeks and lay a few hundred eggs.

Insects typically experience high mortality rates, especially immature stages. Some common causes of mortality are: adverse weather, larval or pupal parasitism, adult predation by spiders and birds, starvation and indirect mortality as a result of habitat loss. Forest tent caterpillar larvae can experience high mortality rates in spring as a result of cold temperatures, rain, wind and snow, and/or the absence of leaves (food) due to frost damage (Coulson and Witter 1984). Parasitism rates can also be high. For example, over 75% of forest tent caterpillar larvae may be parasitized.

Plants and Lichens

Plants also have a wide range of reproductive abilities. A 45 year old aspen can produce an estimated 3,300,000 seeds (Scheiner 1975). Plants are able to reproduce sexually via seeds or spores, and asexually by vegetative means such as root sprouts (aspen) and runners (strawberries). Plant reproductive rates are influenced by whether mutualists, such as pollinators and dispersal agents are present.

Plants are often grouped based on their seasonal growth cycles as annuals, biennials, and perennials. Annuals complete their life cycle, from seed to flowering plant to seed in one growing season. Many wildflowers, weeds and vegetables are annuals. For biennials, two growing seasons are needed to complete their life cycle. A low-growing rosette of leaves is produced the first season of growth, followed by a flowering and fruiting stem the second season. Common mullein is a biennial. In perennials, vegetative parts of the plant live year after year. Examples include spring bulbs, and trees and shrubs.

Some of the causes of mortality in plants are seed predators, improper microsite for seedlings, adverse weather such as drought or flooding, herbivory, insects and diseases. Seeds and seedlings are especially sensitive to the effects of weather, microlimate, and topography, and at very small scales.

Lichens are a symbiotic relationship between a fungus (usually ascomycetes) and a green alga or cyanobacteria species. They may utilize three forms of reproduction including soredia, isidia and fragmentation. Soredia are very small, powdery propagules. Isidia are small outgrowths from the lichen and are typically larger than soredia. Lichens are also able to reproduce via fragments of the thallus (lichen "body"). In some species, the fungal component of the lichen is also able to produce spores, which, once dispersed from the parent, need to come in contact with the appropriate green algae of cyanobacteria to form a lichen.

As a group, lichens are sensitive to air pollution and as a result pollution is a primary mortality factor in large urban areas. Lichens are sensitive to microclimate and microclimate changes, and habitat alteration may eliminate populations (Essen and Renhorn 1998). Other causes of mortality for lichens are herbivory and wind damage – particularly for large, pendulous lichens (Essen and Renhorn 1998).

r and K selection

Some reproductive characteristics tend to be associated and facilitate different reproductive strategies. For example, some species have rapid development, early reproduction, small body size, are short-lived and produce numerous small, highly dispersible offspring. Many annual plants, insects and some amphibians are examples of a species with these characteristics. Individuals with these reproductive characteristics have been termed r-selected. In contrast, other species have individuals that are slow to develop and have delayed reproduction, large body size, are long-lived and reproduce repeatedly in their lifetime. Large mammals and many reptiles are examples of this strategy and species with these characteristics are called K-selected.

Density-independence and -dependence

Some influences on birth or death rates are independent of population size. For example, catastrophic weather conditions can result in high levels of mortality to insect or amphibian larvae or plant seedlings, regardless of the number of larvae or seedlings present. Another example of a density-independent mortality agent is insect mortality as a result of pesticide application.

Density-dependent effects on the birth or death rate per individual are a function of population size. Several factors that limit population size operate in a density-dependent manner include food quality, susceptibility to natural enemies, disease, and competition between members of different species (Coulson and Witter 1984).

Naturally rare/abundant populations

In any examination of population persistence, it is important to understand whether the species is characteristically abundant or rare. However, there are several forms of rarity (Rabinowitz *et al*. 1986) (Figure 2). Extreme forms of rarity include species that only occur in very specific habitats, at low population numbers and only in a small geographic area (Figure 2). Alternatively, species that occur over a large geographic range, are locally abundant, and have a large population in some area of their range may not be considered rare unless various factors, such as habitat destruction, have dramatically reduced population numbers (see, for example the federally endangered Karner blue butterfly, USFWS 2001).

	Geographic Range	**Large**		**Small**	
	Habitat specificity	**Broad**	**Restricted**	**Broad**	**Restricted**
Pop. Size	Somewhere large	Common	Locally abundant over a large range in specific habitat	Locally abundant in several habitats but restricted geographically	Locally abundant in a specific habitat but restricted geographically
	Everywhere small	Constantly sparse over a large range and in several habitats	Constantly sparse in a specific habitat but over a large range	Constantly sparse and geographically restricted in several habitats	Constantly sparse and geographically restricted in a specific habitat

Figure 2. Forms of Rarity. Modified from Meffe and Carroll (1994:127) (originally from Rabinowitz *et al*. 1986 and Holsinger 1993).

Immigration and Emigration

In addition to births and deaths, population dynamics are influenced by immigration (movement of new individuals into a population) and emigration (movement of individuals from the population).

Movement between populations, or areas of concentration, can enhance population persistence in a number of ways including:

1. Colonizing new habitat
2. Exploiting new food resources
3. Mate finding
4. Genetic invigoration

Because the quantity and location of habitat changes over time, even if at long time intervals, the colonization of new habitat is critical to species persistence. Similarly, as prey species populations increase in number or spatial extent, the movement of species feeding on that prey will facilitate the exploitation of those new resources. In some cases, moving to new habitat areas will increase the likelihood of finding a mate.

Movement in or out of a population can also have negative effects such as:

1. Deposition in unfavorable sites or on unfavorable hosts
2. Exposure to predators or other natural enemies
3. Exposure to unfavorable weather conditions
4. Difficulty in mate finding because of sparse population numbers

Populations may increase (immigration) or decrease (emigration) as a result of dispersal. Disrupting the process of dispersal is thought to be one of the primary effects of fragmentation. The following provides an overview of the dispersal process.

Definitions

Defining dispersal, migration and movement is a complex matter, and not entirely resolved. The definition and usage of these terms tends to vary between disciplines primarily because of fundamental differences in the life histories of different taxa and because of differences in how the disciplines developed (Macdonald and Smith 1991).

In this primer, we use the following definitions:

Dispersal:
Movement of organisms (usually juvenile animals or plant propagules) out of sites they or their parents previously occupied. (We are not including short-term excursions undertaken by some animals as dispersal).

Within-patch movement:
Movements, including short-term excursions, within habitat patches or sites occupied by their parents. Within-patch movement would include home range movements.

Migration:
"Mass directional movements of individuals of a species from one locality to another" (Macdonald and Smith 1991).

Several factors are known to influence dispersal rates including the size of the population, population growth rate and how rapidly the species moves in space. These characteristics typically vary between species and taxonomic group. One of the primary differences in dispersal between taxonomic groups is that for mobile animals, it is the individuals themselves that disperse to new habitats. Individuals can choose whether to stay or move out of the area where they were born and typically have some control over direction and distance. In contrast, dispersal by plants and immobile invertebrates occurs via offspring.

Birds

There are two types of dispersal in birds: natal dispersal (movement of an individual from its natal territory to the place where it settles to breed) and breeding dispersal (movement of a breeding adult to a new territory). Natal dispersal distance is generally greater than breeding dispersal, and many adults maintain the same territory throughout their lives. Birds have the ability to disperse great distances, and long distance dispersal occurs regularly, but at low frequency. Abundant species and species with broad geographic ranges have lower dispersal, while migratory species and species of wet habitats tend to disperse farther (Paradis *et al*. 1998). How far birds typically disperse to new territories is not well known. Numbers that are available are often based on very small samples. They range from a median of roughly 200 m in black-capped chickadees to a mean of 15-20 km in goshawks (Sutherland *et al*. 2000). Individuals that disperse farther are less likely to be recorded, making means and medians likely to be minimum estimates.

Mammals

Among mammals, large species and predators tend to disperse farther than small species and herbivores (Sutherland *et al*. 2000). As an example, timber wolves typically disperse 50-100 miles (Fritts and Mech 1981; Gese and Mech 1991), while in white-tailed deer, females often use the same summer range as their mother and males establish ranges up to 9.6 km away (Nelson and Mech 1984). Deer mice typically disperse 100 m or so, but they can travel up to 1 km (Sutherland *et al*. 2000). Dispersal distances in most species are not well-known.

Amphibians

Amphibians have relatively limited movement abilities compared with birds and mammals. Amphibians with larger hind limbs, such as bullfrogs (*Rana catesbiana*) are adapted for jumping and swimming, while species with shorter hind limbs walk, or hop (American toad, *Bufo americanus*). Salamander species walk or burrow, and are stout-bodied and short-limbed.

Although a few amphibians are strictly aquatic or terrestrial, many require both aquatic and terrestrial subhabitats to complete their life-cycles. Some amphibians breed in temporary pools (free from fish predators) while others breed in permanent or semi-permanent water bodies. Some species also rely on forests for one or more stages in their life-histories, such as breeding, juvenile dispersal, adult foraging, or overwintering. Some species overwinter in the duff on the forest floor (e.g., cold-resistant wood frog), while others overwinter underwater (Eastern newt may do this) or underground (e.g., Eastern tiger salamander). Amphibians using upland habitats for some part of their life

cycle typically move among distinct areas for breeding, summer, and winter, which together compose their home ranges. Some amphibians primarily use uplands during dispersal to other aquatic sites (e.g, Eastern newt) while others reside in uplands (e.g, blue-spotted salamander).

Amphibians exhibit strong site fidelity (Berven, 1990), with several field experiments demonstrating relatively long homing movements by displaced animals and little tendency to move away from activity areas when disturbed or handled (Stebbins and Cohen, 1995). Home range size is generally correlated with body size and movement abilities. Home ranges can shift in response to changes in factors such as competition, or unfavorable environmental conditions. Dispersal to new habitats usually occurs by young (newly metamorphosed) organisms, which typically travel greater distances than adults.

Home range sizes and dispersal distances of amphibians are relatively small compared with other vertebrates, and field measurements have been obtained for some species. Adult common toads (*Bufo bufo*) (not present in Minnesota) use a summer habitat of less than 100 sq. meters and an activity area for foraging of 1000 sq. meters, while the activity area of the young toads has a radius 6 times larger than that of the adults (Hofrichter, 2000). Adult leopard frogs (*Rana pipiens*) may travel up to 1.5 km (0.9 miles) from water if the cover has adequate moisture and humidity (Oldfield and Moriarty, 1994). Juveniles of the leopard frog (only 1-2" in length) can cover up to 800 m in a day, and can migration of 6-9 miles have been recorded (Hofrichter, 2000). In contrast, the terrestrial Northern red-backed salamander (*Plethodon cinereus*) has a very small home range of 3 to 5 sq. meters, with an activity radius of up to 25 sq. meters (Kleeberger and Werner, 1982).

Insects

Insects disperse by both active and passive means. Active dispersal in insects is accomplished by either flying or walking. Insects vary considerably in their flight ability, even within groups such as butterflies and moths. For example, the Monarch butterfly (*Danaus plexippu*s) has been shown to migrate up to 3000 km, whereas smaller, less mobile butterflies, such as the "blues" (Lycaenids), may move less than a km in their lifetime (New 1993). Dispersal distance is known to be influenced by the type of habitat and intervening areas. For example, Karner blue butterfly (*Lycaeides melissa samuelis*) females typically fly short distances (an average of 1.5 m/flight) within habitat patches (Lane 1999), and usually move less than 100 m between patches where habitat is a matrix of savanna and woodland, but may disperse 1-2 km to new habitat patches through open areas (King 1998).

The immature stages of many insects move by walking, for example the larval stage of butterflies. Many adult insects also move by walking, such as ground-foraging beetles. These movements are typically short distances. For example, some carabid beetles may only move a few hundred meters in a year (Baars 1979).

Passive dispersal is often associated with wind. For example, early stage gypsy moth larvae (*Lymantria dispar*) suspend themselves from trees on silk threads, and are then blown by wind. In open areas, the tiny larvae may be blown several miles (Johnson and Lyon 1988). Some insects, such as the spruce budworm, utilize both active (adult beetle flight) and passive dispersal (larvae and adults movement facilitated by wind).

Wind often plays a role in both passive and active insect dispersal and movement and often facilitates longer dispersal distances (Dingle 1972).

Plants and Lichens

Dispersal in plants and lichens occurs primarily via seed, spores, vegetative suckering or other forms of propagules. Plants have several adaptations for propagule dispersal such as winged (maple, *Acer* sp. or pine, *Pinus* sp.) or plumed seeds (dandelion, *Taraxacum officinale*) for wind transport, buoyant seeds for water transport (mangrove, *Rhizophora mangle* or coconut, *Cocos nucifera*), or structures to forcibly eject seeds such as dehiscent pods (wild lupine, *Lupinus* spp.).

For dispersal not involving animals, dispersal distance from the parent plant is influenced by 1) the height and distance of the propagule source, 2) the number of propagules produced and released, 3) propagule characteristics (type, weight, shape – wings, plumes, etc.), and 4) wind speed and direction (Harper 1977). Surrounding vegetation and topography can also influence dispersal distance and direction.

Seed dispersal often is facilitated by animals and many seed adaptations reflect this influence. Examples of seed adaptations to facilitate or attract dispersal by animals include: fleshy fruited seeds, seeds with barbs or sticky structures, acorns, and elaiosomes (or oil bodies) (Harper 1977). Where animals are involved in seed dispersal, the animal's feeding habits, territory and migratory behavior influence the distance and nature of the dispersal.

Seed bank

A unique phenomenon associated with plants is that the number of individuals present as dormant propagules greatly exceeds the numbers present as growing plants (Harper 1977). Some studies found 39,000 seeds/m^2 representing 47 species (Harper 1977). This store of seeds buried in the soil is known as the "seed bank". The seed bank is composed of dormant seeds distributed from plants in the area as well as those from elsewhere. Seeds from different species are often deposited at different soil depths. How long seeds persist in the soil depends on many factors including the species of plant. Many legumes (pea family plants) have water impermeable seed coats and in some cases may remain viable for hundreds of years.

Behavior

For animals, behavioral traits will also influence if and how far dispersing individuals might move. In the approach we take here, we have characterized species in terms of their dispersal-related behavior as either 1) resource-dependent or 2) resource-

independent. Species with resource-dependent dispersal typically will not cross areas of unsuitable habitat. Examples include some small mammal, insect and amphibian species (With 1999, Southwood 1962, deMaynadier and Hunter 2000). Species that disperse through areas that are not suitable habitat have resource-independent dispersal.

Dispersal behavior may vary within a species or with conditions. For example Western tent caterpillar populations have some individuals that are relatively inactive and lay eggs (oviposit) near their birth place, while other individuals tend to lay eggs further from their place of origin (Wellington in Price 1984). High population densities can increase dispersal rates, as has been shown for gypsy moth (Leonard in Price 1984).

INTERACTIONS WITH OTHER SPECIES

Predation, parasitism, herbivory, and mutualisms

Predation, parasitism and herbivory can have significant influences on population dynamics for prey species. It has been well documented for a wide variety of taxa that predator-prey relationships are influenced by the spatial structure of the habitat (Huffaker 1958, Roland 1993, Marzluff and Restani 1999, Kurki *et al*. 2000).

Here we describe the common types of predator-prey interactions, focusing on those most likely to be influenced by habitat loss or fragmentation.

Predation
Predators catch and kill their prey, typically eat more than one individual prey in their lifetime, and are free-living throughout their lifetime. Predators occur in many taxonomic groups including birds, mammals, amphibians and reptiles, insects and even plants. Predatory behavior can occur in all life stages or, as in the case of some insects, only certain life stages may be predaceous.

Predation occurs between many taxonomic groups including: ground nesting bird eggs by mammals (Robinson *et al*., 1995; Marzluff and Restani, 1999; Manolis *et al*., 2000), hares by lynx (Dunning *et al*., 1992), small invertebrates by forest amphibians (Stebbins and Cohen, 1995), and aphids by seven spotted lady beetle (*Coccinella septempunctata*) (Karieva, 1987). Some characteristics of predators are that they often defend their resources against competitors and occur in smaller numbers than prey (Rickleffs, 1990).

Parasitism
Parasites attack a range of animals, with various species infecting vertebrates or insects. In the case of vertebrate hosts, the parasite is usually in a different taxonomic class from its host, tends to be smaller than the host, and a single parasite rarely kills its host. In contrast, parasites of insects (often called parasitoids) are similar in size to the host, are often in the same taxonomic class, and require only one host to complete a life cycle.

Examples of parasitism include parasitism of ground-nesting birds by the brown-headed cowbird (Robinson 1992), which lays its egg(s) in another species' nest. The host species raises the cowbird, typically at some cost to its own reproduction. Many insects are parasitized by other insects (parasitoids). For example, forest tent caterpillar populations are affected by at least four parasitoid species (Roland and Taylor 1997).

Herbivory

Herbivory occurs when whole plants or plant parts are eaten by animals. Technically, all herbivory could be defined as either predation, entire plants eaten and killed, to parasitism, parts of plants eaten. However, the term "herbivory" is useful in identifying those forms of predation and parasitism that effect plants and we will use the term in this document.

Most plants experience some form of herbivory, and a wide range of animal species feed on plants. Examples include seed predation of *Trillium* by rodents (Jules and Rathcke 1999), seed predation and herbivory by deer on woody and understory vegetation (Alverson *et al*. 1988).

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