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Quantifying Terrestrial Habitat Loss and Fragmentation: A Protocol

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Abstract

Anthropogenic habitat loss and fragmentation have been implicated as among the key drivers of the burgeoning global biodiversity crisis. In response, there is a growing mandate among natural resource managers to evaluate the impacts of proposed management actions on the extent and fragmentation of habitats. Unfortunately, few guidelines exist to help managers understand the many complex issues involved in the quantitative assessment of habitat loss and fragmentation. In our Primer, we explore habitat fragmentation as a landscape-level process in which a specific habitat is progressively sub-divided into smaller, geometrically altered, and more isolated fragments as a result of both natural and human activities. We describe alternative perspectives on fragmentation in which habitat patches are viewed either as analogs of oceanic islands embedded in an ecologically neutral sea or as patches of variable quality embedded within a complex and heterogeneous mosaic of patches of varying suitability and affects on habitat connectivity. In the conventional island biogeographic perspective, habitat loss and fragmentation is described as a landscape transformation process involving several recognizable phases that are demarcated by significant changes in the pattern or function of the landscape. We describe the key spatial components of habitat loss and fragmentation: habitat extent, subdivision, geometry, isolation, and connectivity, and their affects on individual behavior and habitat use, population structure and viability, and interspecific interactions. Finally, we view the evidence, both theoretical and empirical, regarding the issue of when is habitat fragmentation important, and conclude that it depends not only on the pattern of habitat distribution but on the life history characteristics (e.g., dispersal capabilities) of the target organism(s).

The Primer on habitat fragmentation provides the foundation for examining several key issues in the analysis of habitat loss and fragmentation. First, what constitutes habitat. Second, how do we represent landscape structure in a digital data model. Third, what are the components of habitat loss and fragmentation. Fourth, what is the appropriate scale of analysis, Fifth, what is the relevant spatiotemporal context for assessing habitat loss and fragmentation. Finally, how are habitat loss and fragmentation measured.

The conceptual overview (i.e., Primer) on habitat fragmentation and discussion of important analytical issues provides the foundation for a step-by-step protocol for quantitatively assessing habitat loss and fragmentation. This protocol consists of five steps and is intended to serve as a general guideline for the quantitative assessment process, but one that must be tailored to meet the specific conditions of any particular application.

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PURPOSE AND ORGANIZATION

Many scientists believe that the earth is facing a mass extinction (Lawton and May 1995, Vitousek et al. 1997, Wilson 1999, Myers and Knoll 2001, Balmford et al. 2003). Current global extinction rates for animals and plants are as much as 1,000 times higher than the background rate in the fossil record (Wilson 1999) and vertebrate animal taxa are disappearing at disproportionately high rates (Baillie et al. 2004). Anthropogenic habitat loss and fragmentation have been implicated as among the key drivers of this global biodiversity crisis (Wilcox and Murphy 1985, Saunders et al. 1991, Andren 1994, Myers and Knoll 2001, Balmford et al. 2003). In response, there is a growing mandate for natural resource managers to evaluate the impacts of proposed management actions on the extent and fragmentation of habitats (Fahrig and Merriam 1985, Lubchenco et al. 1991, Hobbs 1993). For example, habitat fragmentation is currently listed by the Chief of the Forest Service as one of the "four threats" of greatest concern in management of National Forest Lands. Unfortunately, few guidelines exist to help managers understand the many complex issues involved in the quantitative assessment of habitat loss and fragmentation.

The main purpose of this document is to describe a protocol for quantitatively assessing terrestrial habitat loss and fragmentation. While the theoretical framework and concepts presented here are broadly applicable to any ecological system, the focus here is on terrestrial habitats in forested landscapes of North America. The motivation for this document, in part, stemmed from two regional conferences on forest fragmentation. The first conference entitled "Forest Fragmentation: Wildlife and Management Implications" was held in Portland, Oregon on 18-19 November, 1998. The conference was convened to provide a synthesis of the current state of knowledge related to fragmentation in managed forests of the Pacific Northwest and resulted in an edited book (Rochelle et al. 1999). The second conference entitled "Forest Fragmentation in the Southern Rocky Mountains" was held in Fort Collins, Colorado on ??-?? ??, 1999. The conference was similarly convened to provide a synthesis of the current state of knowledge related to fragmentation in forests of the southern Rocky Mountains and also resulted in an edited book (Knight et al. 2000). While the material presented at these conferences and in the subsequent books clearly demonstrated the rapid growth in our scientific understanding of fragmentation, it was clear that managers lack clear guidelines for implementing these scientific principles. The purpose of this document is to help bridge that gap between science and management in regard to habitat loss and fragmentation.

This document is organized into three major sections. The first section provides a primer on habitat fragmentation. Specifically, what is habitat fragmentation, what causes it, why it is important, and when does it matter? An understanding of the concepts presented in this section is prerequisite to full comprehension and appreciation of the material presented in the subsequent sections. The second section discusses several key issues in the analysis of habitat loss and fragmentation. Specifically, what constitutes habitat; how do we represent landscape structure in a digital data model; what are the components of habitat loss and fragmentation; what is the appropriate scale of analysis; what is the relevant spatiotemporal context for assessing habitat loss and fragmentation; and how are habitat loss and fragmentation measured? These two sections are designed to provide the conceptual framework needed to undertake a quantitative

assessment of habitat loss and fragmentation. The third and final section presents a step-by-step protocol for quantitatively assessing habitat loss and fragmentation, and is illustrated with an example from southwest Colorado.

A PRIMER ON HABITAT FRAGMENTATION

"Habitat fragmentation" has become a standard label used by conservation biologists in characterizing human-induced ecological degradation of the environment, despite that fact that the notion of "habitat fragmentation" is conceptually ambiguous (Haila 1999, Fahrig 2003). It mixes together several different but often confounded ecological processes, chief among them reduction in habitat area and change in habitat configuration (Fahrig 2003). Furthermore, as all natural environments are "fragmented" to a variable degree, both spatially and temporally, the assessment of human-caused fragmentation is much less straightforward than it is usually assumed. And to further complicate matters, despite the burgeoning literature on fragmentation, adequate empirical data on the actual effects of habitat fragmentation are amazingly scarce.

What is Habitat Fragmentation?

Despite decades of attention in the scientific literature and widespread application in conservation and management, there still is no consensus on the definition of "habitat fragmentation." In part, complacency on the part of the scientific community has impeded the development of a clear and precise definition. On the other hand, the lack of consensus also reflects genuine disagreement among scientists and conservationists on the proper definition. Perhaps most of all, however, it reflects the natural evolution of an ecological concept.

According to the dictionary, "fragmentation" means "the breaking apart or up into pieces" (Merriam-Webster Inc. 1987). It follows, then, that "habitat fragmentation" means the breaking apart of habitat into pieces. Unfortunately, this definition doesn't apply perfectly to habitat fragmentation in the real world. Using the analogy given by Fahrig (2000), when a porcelain vase is "fragmented", the amount of porcelain remains constant. Yet, habitat fragmentation generally occurs through a process of habitat removal, because the total area under consideration remains constant while the total area of habitat is reduced. Therefore, habitat loss and fragmentation per se (i.e., the subdivision of habitat into isolated fragments) are inextricably linked in real-world landscapes. It is worth noting, however, that it is possible to have habitat fragmentation without net loss of habitat under special conditions; specifically, when habitat loss is perfectly balanced against the creation of habitat through successional processes or restoration efforts. However, the more typical scenario is one of habitat fragmentation accompanied by simultaneous habitat loss, and for this reason, some authors have chosen to consider both components under the auspices of the term "fragmentation."

Distinguishing effects of habitat fragmentation from those due to habitat loss has important implications for conservation biology. As Fahrig (1997) notes, "if habitat (fragmentation) is important, then within some limits it should be possible to mitigate effects of habitat loss by

ensuring that remaining habitat is not fragmented. On the other hand, if the effects of fragmentation are trivial in comparison to effects of habitat loss, then the assumption that loss can be mitigated by reduced fragmentation has potentially dangerous consequences for conservation. If, for example, species go extinct mainly because of habitat loss, the solution is straightforward: habitat conservation and restoration. On the other hand, if species go extinct mainly because of the fragmentation or 'breaking apart' of habitat, the problem may appear less severe and at the same time more complex, and the solution seems less obvious. One might even conclude that: (1) loss of habitat is not a serious threat to species survival, as long as the remaining habitat is not broken apart; and (2) to restore endangered populations we need not restore large tracts of habitat, but just enough to connect up the 'broken apart' pieces of remaining habitat." Clearly, in light of these potentially erroneous conclusions, the precise definition of "habitat fragmentation" is not simply an issue of semantics.

For these and other reasons, the simple dictionary definition of "fragmentation" given above is simply inadequate to describe the complex, real-world changes that landscapes undergo during the fragmentation process. In particular, this definition fails to explicitly identify the scale and components of the fragmentation process, as well as the causes and consequences of this process. These additional shortcomings have fostered a great deal of confusion over what is meant exactly by the term "fragmentation." For our purposes, we will define habitat fragmentation as follows:

"Habitat fragmentation is a landscape-level process in which a specific habitat is progressively sub-divided into smaller, geometrically altered, and more isolated fragments as a result of both natural and human activities, and this process involves changes in landscape composition, structure, and function at many scales and occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances (McGarigal and McComb 1999)."

The above definition highlights the complexity of the fragmentation concept and makes explicit the following important considerations:

First, habitat fragmentation is a 'process' of landscape change. It is not a state or condition of the landscape at any snapshot in time, even though it is often meaningful to substitute space for time and compare the relative fragmentation of habitats among landscapes. Strictly speaking, however, habitat loss and fragmentation involve the progressive reduction and subdivision of habitat over time, which results in the alteration of landscape structure and function. This transformation process can be complex; it involves a number of physical changes in landscape structure and can proceed in different patterns and at different rates depending on the causal agent (e.g., natural disturbances, agricultural clearing, timber harvesting) and the ecological characteristics of the landscape. In other words, there are multiple possible scenarios of landscape transformation associated with fragmentation processes.

Second, habitat fragmentation is a landscape-level process, not a patch-level process. That is, fragmentation alters the spatial configuration of habitat patches within a broader habitat mosaic

or landscape, not merely the characteristics of a single patch (Fig. 1). Thus, although individual patches are affected by fragmentation (mainly through isolation from other patches), it is the entire landscape mosaic that is transformed by the fragmentation process. Unfortunately, failure to recognize this distinction has pervaded the "fragmentation" literature for decades (McGarigal and Cushman 2002). This failure is largely due to the fact that the fragmentation concept arose out of island biographic theory, which predicted that species number was a function of island (or patch) size and isolation (MacArthur and Wilson 1967). Quite simply, the theory predicts that smaller and more isolated islands will contain fewer species due to a tradeoff between colonization and extinction processes. Despite the many identified shortcomings of the theory, early empirical data lent support to its simple predictions. Thus, although the original theory was applied to true oceanic islands, the theory was quickly extrapolated to patches in a land mosaic, and it was theorized that the reduction in patch size and increased isolation associated with habitat loss and subdivision in landscapes undergoing agricultural and urban development would lead to a steady loss of species.

Failure to distinguish between island biogeography and fragmentation has led to serious confusion over the definition of habitat fragmentation and, perhaps more than any other issue, has clouded the conservation debate over the relative importance of habitat loss and fragmentation. Island biogeography, as applied to habitat patches in a land mosaic, involves the relationship between species richness or abundance and a variety of 'patch' characteristics, such as patch size and isolation. Specifically, the theory predicts that small and isolated habitat patches (i.e., area and isolation effects, respectively) will contain fewer species than large and less isolated habitat patches, and the empirical evidence for these effects is widespread (e.g., Dodd 1990, Robinson 1992, van Apeldoorn et al. 1992, Andren 1994, Celada et al. 1994, Hunter et al. 1995, Hinsley et al. 1996, Schmiegelow et al. 1997, Vos and Chardon 1998, Fahrig 2003). The predictions of island biogeographic theory have obvious conservation implications: large and "connected" habitat patches are likely to support viable populations of more species than small and isolated patches. Thus, island biogeography deals exclusively with processes operating at the patch level: An individual patch can be progressively reduced in size and, as a consequence, become more isolated over time, and the biological consequences of these changes are the subject of island biogeography (Fig. 1).

Habitat fragmentation, on the other hand, involves the subdivision of contiguous habitat into several pieces (Fig. 1). The biological consequences of the fragmented (subdivided) distribution of habitat patches across the landscape is the subject of fragmentation research. Thus, in contrast to island biogeography, fragmentation explicitly deals with processes operating at the landscape level. This does not imply that studying patch-level processes, such as island biogeography, is not relevant to the study of fragmentation. Quite the contrary. Understanding these patch-level processes allows us to understand some of the mechanisms contributing to fragmentation effects at the landscape level. However, relationships derived at the patch level can not be extrapolated to infer effects of habitat fragmentation (McGarigal and Cushman 2002). It is analogous to trying to understand metapopulation dynamics (a landscape-level process) by studying only one of the subpopulations (patch-level). Indeed, it is widely recognized that extrapolating findings across spatial scales, especially patch-level to landscape-level scales, can lead to erroneous conclusions

(Wiens et al. 1987 and 1993; Wiens 1989a,b; McGarigal and McComb 1995, 1999; Villard et al. 1999, Cushman and McGarigal 2004).

Third, habitat fragmentation is a habitat-specific process. That is, fragmentation occurs only in reference to a specific habitat. Landscapes don't undergo fragmentation, habitats within landscapes do. Since habitat is an organism-specific concept, the target habitats must be characterized in ways relevant to the organism(s) under consideration. For example, the target habitat might be forest, spruce-fir (*Picea-Abies*) forest, or 'old growth' spruce-fir forest. The choice of classification resolution should be driven by habitat specificity of the organism(s) under consideration. Attention to the resolution at which community types are distinguished is crucial because the fragmentation trajectory within the same landscape can differ markedly among habitats in relation to habitat specificity. For example, in some Pacific Northwest (PNW) landscapes, old-growth Douglas-fir (*Pseudotsuga menziesii*) forest has been highly fragmented by logging, yet late-seral forest (a broader, more inclusive classification) remains abundant and highly connected (McGarigal and McComb 1995). In addition, it is important to recognize that since organisms perceive and respond to habitats differently, not all organisms will be affected in similar ways by the same landscape changes. As one focal habitat undergoes fragmentation, some organisms will be adversely affected, some may actually benefit, whereas others will be unaffected.

Fourth, habitat fragmentation is a scale-dependent process, both in terms of how we (humans) perceive and measure fragmentation and in how organisms perceive and respond to fragmentation. The extent of the landscape considered, in particular, can have an important influence on the measured fragmentation level; a highly fragmented habitat at one scale may be comparatively unfragmented at a much coarser (or finer) scale (e.g., when fragmented woodlots occur within a forested region)(e.g., McGarigal and McComb 1995). In addition, for habitat fragmentation to be consequential, it must occur at a scale (both extent and grain) that is functionally relevant to the organism(s) under consideration. Yet more often than not, we do not know how organisms scale the environment (Wiens 1989, With 1994). The lack of correspondence between the scale at which we measure fragmentation and the scale at which organisms perceive and respond to fragmentation is a great challenge to our understanding.

Fifth, habitat fragmentation results from both natural and anthropogenic causes. Here, we explicitly recognize that habitats can be fragmented by natural causes as well as by a variety of human activities. From a conservation perspective, we are primarily interested in anthropogenic changes that cause the landscape to reside outside its expected range of natural variability, and the adverse impacts that this may have on organisms. Accordingly, most studies have focused on anthropogenic causes and ignored the backdrop of the natural patch mosaic created by changing landforms and natural disturbances.

The cause of fragmentation can dramatically influence the fragmentation process itself. Fragmentation caused by development, for example, usually results in a progressive and permanent loss and fragmentation of habitat; that is, habitat is permanently lost to development and remnant habitat patches effectively become isolated from each other as they are embedded in

an inhospitable matrix of nonhabitat. Much of the fragmentation dogma, for example, stems from field studies conducted in the eastern deciduous forest of North America on forest fragmentation caused by agricultural development and urbanization (i.e., land type conversions; e.g., Whitcomb et al. 1981, Robbins et al. 1989, Terborgh 1989). Commercial timber management, on the other hand, alters landscape structure by changing the areal extent and configuration of plant communities and seral stages across the landscape, and this usually occurs on a backdrop of a natural patch mosaic created by changing landforms and natural disturbances (Swanson et al. 1988). Commercial timber management is considered the major cause of late-seral forest loss and fragmentation in many forested landscapes (Lehmkuhl and Ruggiero 1991, Hunter et al. 1995, McGarigal and McComb 1995, Schmiegelow et al. 1997, Shinneman and Baker 2000). A natural forest landscape is a spatially and temporally dynamic mosaic of forest patches (i.e., shifting mosaic) driven by natural disturbances (e.g., fire and windthrow) and forest regrowth. It is the scale and structure of this mosaic that is dramatically altered by timber management activities (Swanson et al. 1990). Vertebrate population responses in forested landscapes altered by timber management activities are likely to differ from those in landscapes experiencing urbanization and agricultural development. Sharp forest/nonforest edges are transient in managed forest landscapes because of forest regrowth, and regenerating forest does not function as nonhabitat for many species, but rather as habitat of variable quality and permeability to animal movements. Late-seral forest patches may never be truly isolated or may be isolated for only a brief period of years. Moreover, vertebrate populations in dynamic forest landscapes have evolved in naturally heterogeneous environments and may have adaptations for coping with some of the ecological changes associated with habitat fragmentation. For these reasons, it is questionable whether all of the empirical findings on forest fragmentation from urban or agricultural landscapes extend to dynamic forest landscapes undergoing fragmentation by timber management (Hejl 1992).

Unfortunately, similar attention has not been given to forest fragmentation caused by natural disturbances. Yet, it is increasingly clear that coniferous forest landscapes in western North America are naturally highly dynamic, and that many forested habitats periodically experience rapid fragmentation and recovery following large fires (Romme and Despain 1989, Wallin et al. 1996, Knight and Reiners 2000, Veblen 2000). Anthropogenic disturbances, such as logging, primarily affect the scale, rate, and pattern of fragmentation in such landscapes. It is still unclear how native fauna in such landscapes are affected by additional anthropogenic fragmentation caused by timber harvesting.

Habitat Fragmentation Paradigms

To appreciate the range of current scientific thinking about habitat fragmentation one must recognize that there are several distinct perspectives representing different conceptualizations of landscape structure and change (Wiens 1994, With 1999). These perspectives largely differ in how the focal habitat is perceived and represented relative to other landscape elements, and whether the landscape structure is viewed as relatively static (i.e., unchanging) or dynamic (i.e., constantly changing). Although there exist many variations, two paradigms have emerged that provide alternative frameworks for conceptualizing the habitat loss and fragmentation process.

Static Island Biogeographic Model

The first paradigm we call the "static island biogeographic model." In this model, habitat fragments are viewed as analogues of oceanic islands in an inhospitable sea or ecologically neutral matrix (Fig. 2a). Under this perspective, discrete habitat patches (fragments) are seen as embedded in a uniform matrix of non-habitat. Connectivity is assessed by the size and proximity of habitat patches and whether they are physically connected via habitat corridors. The key attributes of the model are its representation of the landscape as a binary system of habitat and inhospitable matrix, and that, once lost, habitat remains matrix in perpetuity. In extreme cases, the process of habitat loss and fragmentation continues until the target habitat is eliminated entirely from the landscape. This scenario is perhaps best exemplified by urban sprawl and agricultural development, where remnant habitat fragments are maintained in an otherwise relatively static matrix or are eventually eliminated entirely from the landscape.

The static island biogeography paradigm has been the dominant perspective since the inception of the fragmentation concept. The major advantage of the island model is its simplicity. Given a focal habitat, it is quite simple to represent the structure of the landscape in terms of habitat patches contrasted sharply against a uniform matrix. Moreover, by considering the matrix as ecologically neutral, it invites ecologists to focus on those habitat patch attributes, such as size and isolation, that have the strongest effect on species persistence at the patch level. The major disadvantage of the strict island model is that it assumes a uniform and neutral matrix, which in most real-world cases is a drastic over-simplification of how organisms interact with landscape patterns. Not all matrix is created equal. Moreover, the strict island model usually assumes a static landscape structure, at least with respect to the matrix. Once habitat is lost, it remains matrix. This, too, is not realistic in many landscapes, especially those driven by natural disturbances and/or forest management activities.

The landscape transformation process as conceptualized under the idealized static island biogeographic model can be divided into several broad stages or phases that are demarcated by significant changes in the pattern or function of the landscape (Forman 1995; Fig. 3). In reality, these phases are not strictly separate from each other since they may take place simultaneously; however, a dominant phase can often be identified.

1. Perforation.—Often, the first stage of habitat loss and fragmentation involves the perforation of natural habitat through direct loss, usually resulting from conversion to other land uses (e.g., agricultural clearing, housing development, timber harvesting). Perforation creates holes in otherwise contiguous habitat. Here, there is both a direct loss of habitat and a change in the spatial distribution of remaining habitat. The degree of impact on habitat configuration will depend on the pattern of perforation (see below). However, at this stage, the habitat is still physically well connected.
2. Dissection.—The second stage of habitat loss and fragmentation involves the dissection of natural habitat. In most cases, a perforated pattern will become a dissected pattern at certain threshold levels of habitat loss. Dissection may precede or occur in conjunction

with perforation. A common route to habitat dissection is through the construction of roads or other transportation corridors that span the landscape. In most cases, there is relatively little reduction in habitat area caused by dissection. However, the resulting linear landscape elements can be a significant source of disruption to the natural community because they can provide avenues for the intrusion of edge predators, invasive species, exotics, diseases and pathogens that adversely affect the organisms of interest. In addition, these linear elements can affect landscape connectivity by altering movement patterns of organisms. Perhaps most importantly, some dissecting agents such as roads provide human access to the natural habitats and establish a network by which future habitat loss and alteration will occur. Of course, as in all cases, the effects of dissection will depend on the habitat and the organism(s) of interest.

3. Subdivision.—The third stage of habitat loss and fragmentation involves the subdivision of habitat into disjunct patches. Forman (1995) referred to this phase as “fragmentation”, but like Jaeger (2000), who referred to this phase as “dissipation”, we prefer to use the term fragmentation to refer to the entire sequence rather than a single phase. During this phase, the landscape undergoes an important phase transition from a landscape characterized by physically connected habitat to a landscape in which the habitat is broken up into disjunct fragments. At this point, the areal extent of habitat may still be quite large and may not yet be significantly limiting landscape function for the organism(s) of interest. However, at this point, the habitat is physically disconnected and may disrupt movement patterns of the target organism(s) and cause the subdivision of populations into separate units. The consequences of this population subdivision will be discussed later. Note, this phase may be confused or confounded with the “dissection” phase. The dissection phase, as idealized, typically occurs as a result of road-building in which the habitat is subdivided or dissected by linear features that do not result in significant reduction in habitat area. In contrast, the subdivision phase is typically characterized by concurrent habitat loss and results when the remaining habitat becomes subdivided into disjunct patches embedded within a matrix of “non-habitat.”
4. Shrinkage and Attrition.—The final stage of habitat loss and fragmentation involves the shrinkage and, in some cases, complete disappearance of the focal habitat. Here, the landscape is in a critical state with respect to the viability of the target habitat. As habitat patches are reduced in size and become more isolated from each other, the function of the landscape is seriously jeopardized for organisms associated with the target habitat. Under the island-biogeographic model, the remaining habitat fragments represent true islands in an inhospitable sea. Of course, the hostility of the matrix will depend on the organisms and how their life-history and vagility characteristics interact with landscape patterns, as discussed below.

This four-stage conceptualization of the landscape transformation represents an idealized and oversimplified view of habitat loss and fragmentation processes under the static island biogeographic model; no real landscape follows this trajectory exactly. Nevertheless, it depicts the general sequence of events characteristic of habitats undergoing reduction and fragmentation

caused by urban and/or agricultural development. Although this simple conceptual model provides a useful framework, it is important to understand that there are many alternative scenarios or patterns of habitat loss and fragmentation associated with the above landscape transformation (Fig. 4). Forman (1995) refers to such variations as “mosaic sequences.”

5. Random Model.—Habitat is lost progressively in a random pattern. Although not representative of any real-world pattern of habitat loss and fragmentation, it provides a useful null model against which to compare other scenarios.
6. Contagious Model.—Habitat is lost in a contagious (i.e., aggregated) pattern. In this case, the fragmentation of habitat is controlled by the degree of contagion in the residual habitat. Thus, under a maximum contagion scenario, the residual habitat would be aggregated into a single patch, and the habitat would not be fragmented per se.
7. Dispersed Model.—Habitat is lost in a dispersed (i.e., disaggregated) pattern. Under a maximum dispersion scenario, habitat would be perforated by dispersed ‘openings’ and would eventually be broken into discrete fragments.
8. Edge Model.—Habitat is lost progressively in a wave-like manner, beginning on one edge of the landscape and moving progressively across the landscape. In this scenario, there is no fragmentation of habitat per se, since the original habitat is not subdivided into disjunct patches, but simply reduced in size steadily over time. This process is typical of urban expansion outward from a city or some large-scale forestry operations.
9. Corridor Model.—Habitat is first bisected by corridor development (e.g., roads) and then lost progressively outward from the corridors. In this scenario, the habitat is both reduced and fragmented. This process is typical of rural and suburban residential development in many areas.
10. Nuclear Model.—Habitat is lost progressively from nuclei that may be dispersed in a random, uniform, or clumped pattern. Perforations in the habitat grow steadily in size in radial fashion until eventually the habitat is subdivided (i.e., becomes disconnected). The rate and pattern of fragmentation per se will depend on the dispersion of nuclei. This process is typical of rural development and timber harvesting.

These models represent alternative patterns by which habitat may be lost from a landscape, and although idealized and oversimplified, they illustrate the wide range of possible patterns of habitat loss. More importantly, they illustrate the quantitative differences in habitat loss and fragmentation that can result under various scenarios (Forman 1995: page 425). For example, given the same trajectory of habitat loss, the edge model maintains the largest patches of habitat in the landscape without causing fragmentation. Conversely, the dispersed model results in the quick elimination of large patches from the landscape and, at some point, causes the fragmentation of the habitat that remains.

Dynamic Landscape Mosaic Model

The second major conceptual paradigm is the dynamic landscape mosaic model. In this paradigm, landscapes are viewed as spatially complex, heterogeneous assemblages of cover types, which can't be simplified into a dichotomy of habitat and matrix (Wiens et al. 1993, With 2000; Fig. 2b). Rather, the landscape is viewed from the perspective of the organism. Habitat patches are bounded by other patches that may be more or less similar (as opposed to highly contrasting and often hostile habitats, as in the case of the island model) and the mosaic of patches itself changes through time in response to disturbance and succession processes. Connectivity is assessed by the extent to which movement is facilitated or impeded through different land cover types across the landscape. Land cover types may differ in their "viscosity" or resistance to movement, facilitating movement through certain elements of the landscape and impeding it in others. This perspective represents a more holistic view of landscapes, in that connectivity is an emergent property of landscapes resulting from the interaction of organisms with landscape structure.

The dynamic landscape mosaic paradigm derives from landscape ecology and has only recently emerged as a viable alternative to the static island biogeographic model. The major advantage of the landscape mosaic model is its more realistic representation of how organisms perceive and interact with landscape patterns. Few organisms exhibit a binary (all or none) response to habitat types, but rather use habitats proportionate to the fitness they confer. Moreover, movement among suitable habitat patches usually is a function of the character of the intervening habitats. Two suitable habitat patches separated by a large river may be effectively isolated from each other for certain organisms, regardless of the distance between them. In addition, the landscape mosaic model accounts for the dynamics in landscape structure due to the constant interplay between disturbance and succession processes. This is especially important in forested landscapes where natural disturbances and timber harvesting are the major drivers of landscape change. The major disadvantage of the landscape mosaic model is that it requires detailed understanding of how organisms interact with landscape structure; in particular, how the landscape mosaic composition and configuration affect movement patterns. Unfortunately, it is exceedingly difficult in practice to collect the needed quantitative information, rendering this model less practical. However, even in the absence of detailed information about how target organisms interact with entire landscape mosaics, it is often beneficial to characterize the landscape more realistically than as a simple binary map of habitat and matrix.

Spatial Components of Habitat Fragmentation

Whatever fragmentation paradigm one ascribes to, it is essential to understand what a given change in a landscape means physically. This requires explicit attention to the spatial components of habitat fragmentation. Although habitat fragmentation refers simply to the subdivision of habitat, given the above definition and discussion, it is clear that fragmentation is a complex process of change in multiple, and often correlated, components of landscape structure. Thus, a multivariate perspective is required and it is unreasonable to expect a single metric, or even a few metrics, to be sufficient.

Fragmentation involves changes in both landscape composition and configuration (McGarigal and Marks 1995, Cushman and McGarigal 2002). *Landscape composition* refers to the presence and amount of each habitat type within the landscape, but not the placement or location of habitat patches within the landscape mosaic. *Landscape configuration* refers to the spatial character and arrangement, position, orientation, and shape complexity of patches in the landscape. We recognize five major components of landscape composition and configuration affected by habitat loss and fragmentation, even though the distinctions among these components can be somewhat blurry at times.

1. Habitat Extent.—As noted previously, habitat loss and fragmentation are almost always confounded in real-world landscapes. Therefore, it is essential that habitat extent be considered in conjunction with any assessment of habitat fragmentation. Indeed, as described later, it is difficult, and in some cases impossible, to interpret many fragmentation metrics without accounting for habitat extent. Habitat extent represents the total areal coverage of the target habitat in the landscape and is a simple measure of landscape composition.
2. Habitat Subdivision.—Habitat fragmentation fundamentally involves the subdivision of contiguous habitat into disjunct patches, which affects the overall spatial distribution or configuration of habitat within the landscape. Subdivision explicitly refers to the degree to which the habitat has been broken up into separate patches (i.e., fragments), *not* the size, shape, relative location, or spatial arrangement of those patches. Because these latter attributes are usually affected by subdivision, it is difficult to isolate subdivision as an independent component.
3. Patch Geometry.—Habitat fragmentation alters the geometry, or spatial character, of habitat patches. Specifically, as patches are subdivided via habitat loss (Figs. 3-4), they become smaller, contain proportionately less core area (i.e., patch area after removing the area within some specified edge-influence distance), typically extend over less area, and often have modified shapes, although the nature of the change may vary depending on the anthropogenic agent (e.g., Krummel et al. 1987).
4. Habitat Isolation.—Habitat fragmentation increases habitat insularity, or isolation. That is, as habitat is lost and fragmented, residual habitat patches become more isolated from each other in space and time. Isolation deals explicitly with the spatial and temporal *context* of habitat patches, rather than the spatial character of the patches themselves. Unfortunately, isolation is a slippery concept because there are many ways to consider context. In the temporal domain, isolation can be considered as the time since the habitat was physically subdivided, but this is fraught with practical difficulties. For example, rarely do we have accurate historical data from which to determine when each patch was isolated. Moreover, given that fragmentation is an ongoing process, it can be difficult to objectively determine at what point the habitat becomes subdivided, since this is largely a function of scale. In the spatial domain, isolation can be considered in several ways, depending on how one measures the spatial context of a patch. The simplest measures of

isolation are based on Euclidean distance between nearest neighbors (McGarigal and Marks 1995) or the cumulative area of neighboring habitat patches (weighted by nearest neighbor distance) within some ecological neighborhood (Gustafson and Parker 1992). These measures adopt an island biogeographic perspective, as they treat the landscape as a binary mosaic consisting of habitat patches and uniform matrix. Thus, the context of a patch is defined by the proximity and area of neighboring habitat patches; the role of the matrix is ignored. However, these measures can be modified to take into account other habitat types in the so-called matrix and their affects on the insularity of the focal habitat. For example, simple Euclidean distance can be modified to account for functional differences among organisms. The functional distance between patches clearly depends on how each organism scales and interacts with landscape patterns (With 1999); in other words, the same gap between patches may not be perceived as a relevant disconnection for some organisms, but may be an impassable barrier for others. Similarly, the matrix can be treated as a mosaic of patch types which contribute differentially to the isolation of the focal habitat. For example, isolation can be measured by the degree of contrast (i.e., the magnitude of differences in one or more attributes between adjacent patch types) between the focal habitat and neighboring patches.

5. Connectedness.—Habitat loss and fragmentation affect the connectedness of habitat across the landscape. Connectedness integrates all of the above components and involves both a structural component (i.e., the amount and spatial distribution of habitat on the landscape; also referred to as “continuity”) and a functional component (i.e., the interaction of ecological flows with landscape pattern; also referred to as “connectivity”). Structural connectedness refers to the physical continuity of habitat across the landscape. Contiguous habitat is physically connected, but once subdivided, it becomes physically disconnected. Structural connectedness is affected by habitat extent and subdivision, but also by the spatial extensiveness of the habitat patches (Keitt et al. 1997). Specifically, as habitat patches become smaller and more compact, they extend over less space and thus provide for less physical continuity of habitat across the landscape. Structural connectedness as considered here adopts an island biogeographic perspective.

What constitutes “functional connectedness” between patches clearly depends on the organism of interest; patches that are connected for bird dispersal might not be connected for salamanders. As habitat is lost and subdivided, at what point does the landscape become functionally “disconnected?” As With (1999) notes, “what ultimately influences the connectivity of the landscape from the organism’s perspective is the scale and pattern of movement (i.e., scale at which the organism perceives the landscape) relative to the scale and pattern of patchiness (i.e., structure of the landscape); ...i.e., a species’ gap-crossing or dispersal ability relative to the gap-size distribution on the landscape” (Dale et al. 1994, With and Crist 1995, Pearson et al. 1996, With et al. 1997). Hence, functional connections might be based on: (1) strict adjacency (touching) or some threshold distance, e.g., a maximum dispersal distance); (2) some decreasing function of distance that reflects the probability of connection at a given distance; or (3) a resistance-weighted distance function, e.g., where the distance between two patches is computed as the least

cost distance on a resistance surface, where each intervening location between habitat patches is assigned a resistance value based on its permeability to movement by the focal organism. Then various indices of overall connectedness can be derived based on the pairwise connections between patches.

Biological Consequences of Habitat Fragmentation

The habitats in which organisms live are spatially structured at a number of scales, and these patterns interact with organism perception and behavior to drive the higher level processes of population dynamics and community structure (Johnson et al. 1992, Wiens et al. 1993). Anthropogenic habitat loss and fragmentation disrupts these patterns and is expected to have large, negative effects on biodiversity (Haila 2002). A disruption in landscape structure may interfere with the critical ecological processes necessary for the maintenance of biodiversity and ecosystem health (With 2000, Fahrig 2003). Specifically, habitat fragmentation creates discontinuities (i.e., patchiness) in the distribution of critical resources (e.g., food, cover, water) and environmental conditions (e.g., microclimates), and these patterns change over time in response to the fragmentation process. From the perspective of an organism, these discontinuities create variability in the distribution of suitable habitat, where suitable habitat is the combination of food, cover, water, and space necessary to sustain an individual. Ultimately, physical changes in the extent and connectivity of suitable habitat conditions affect many processes that influence the behavior and spatial habitat use patterns of individuals, and alter intra- and inter-specific interactions that influence population persistence and community structure and dynamics.

The majority of theoretical studies suggest that the effect of habitat fragmentation is weak relative to the effect of habitat loss (Collinham and Huntley 2000, Fahrig 1997, Henein et al. 1999, Flather and Bevers 2002), although some predict larger effects (Boswell et al. 1998, Burkey 1999, Hill and Caswell 1999, Urban and Keitt 2001). In addition, some theoretical studies suggest that the effects of fragmentation per se should become apparent only at low levels of habitat amount, for example below approximately 20-30% of the landscape (Fahrig 1998, Flather and Bevers 2002), although there is little empirical evidence available to test this prediction (Fahrig 2003).

The results of empirical studies of habitat fragmentation are often difficult to interpret because many studies fail to address habitat fragmentation at the landscape-level, and most do not distinguish between habitat loss and habitat fragmentation (McGarigal and Cushman 2002, Fahrig 2003). Fragmentation is a landscape-level process and its effects cannot be resolved through studies focusing on patches or those that do not separate area from configuration effects. However, empirical studies clearly suggest that habitat loss has large, consistently negative effects on biodiversity (Fahrig 2003). The effects of habitat fragmentation often are weaker, and these effects are as likely to be positive as negative (Fahrig 2003). Because the effects of habitat fragmentation per se are weaker than those of habitat loss, to reliably measure the effects of fragmentation it is necessary to experimentally or statistically control for the effects of habitat loss (McGarigal and McComb 1995, McGarigal and Cushman 2002). Below we discuss the consequences of habitat loss and fragmentation at three levels of biological organization:

individual, population, and community. Note, this reductionist and hierarchical organization is not intended to imply that fragmentation effects are distinct at each level, but is done for convenience of organization and presentation.

Individual Behavior and Habitat Use

Although there are many effects of fragmentation on individual behavior, habitat use patterns, and intra- and inter-specific interactions, they are dominated by: (1) a reduction in habitat area (area effects), (2) an increase in the proportion of edge-influenced habitat (edge effects), and (3) an increase in habitat isolation (isolation effects). Briefly, as habitat is lost from the landscape (without being fragmented), at some point there will be insufficient area of habitat to support a population and the species will be extirpated from the landscape (Flather and Bevers 2002). In addition, as habitat is lost and fragmented, the proportion of edge-influenced habitat increases. For some species, the area near the edge is avoided or provides lower habitat quality, thereby reducing the effective area of habitat available to the species. This effect is referred to as the "edge effect." For edge-sensitive species, the ultimate consequence of edge effects is to accelerate the decline of the species beyond that expected based on area relationships alone. As habitat is fragmented, individual habitat patches also become more isolated; that is, they become less connected across the landscape so that populations become subdivided and suffer the consequences of small population size (discussed later). As a result of this isolation, individuals realize fewer opportunities for intraspecific interactions (e.g., mate selection) that may be important for continued occupancy. This effect is referred to as the "isolation effect." The combination of area, edge, and isolation effects influence individuals during the fragmentation process. The following sections summarize what is known about each of these effects.

Area Effects.—Habitat loss has consistently negative effects on biodiversity (Fahrig 2003), including reductions in species richness (Findaly and Houlahan 1997, Gurd et al. 2001, Schmiegelow and Monkkonen 2002, Steffan-Dewenter et al. 2002), population declines and changes in distribution (Best et al. 2001, Gibbs 1998, Sanchez-Zapata and Calvo 1999). Habitat loss changes the distribution of resources and can affect individual behavior and spatial activity patterns, changing the ability of the organism to acquire the resources needed to survive and reproduce (Mangel and Clark 1986, Wiens et al. 1993). For example, from an energetics perspective, if food resources become more patchily distributed, it may be more costly to acquire them (Mahan and Yahner 1999). In addition, moving between disjunct resource patches to acquire food resources may involve moving through sub-optimal habitats that require higher energetic expenditures and expose individuals to higher rates of predation (Bergin et al. 2000) reduce breeding (Kurki et al. 2000), and dispersal success (Belisle et al. 2001, With and Crist 1995, With and King 1999).

Most species require at least a minimum area of habitat in order to meet all life history requirements (e.g., Robbins et al. 1989). Theoretical studies predict a threshold habitat level below which the population cannot sustain itself (Fahrig 2001, Flather and Bevers 2002, Hill and Caswell 1999, Fahrig 2003). The amount of habitat required for species persistence depends on species-specific behavioral and life-history characteristics (Gibbs 1998, Vance et al. 2003), and

the effects of habitat loss on each species will depend on the interaction of its ecological requirements and capabilities with the degree of habitat loss in the surrounding landscape (McGarigal and Cushman 2002, Schmiegelow and Monkkonen 2002, Fahrig 2003). For example, large bodied, high trophic-level species appear to be particularly vulnerable to local extinction due to habitat loss (Gibbs and Stanton 2001).

Some species require that their minimum area requirements be fulfilled in contiguous habitat patches; in other words, the individual habitat patch must be larger than the species' minimum area requirement for a species to occupy the patch. These species are sometimes referred to as "area-sensitive" species. For example, many neotropical migratory bird species display a marked area-sensitivity whereby their probability of occurrence in a forest patch increases non-linearly with the size of the patch (Lynch and Whigham 1984, Freeemark and Merriam 1986, Robbins et al. 1989, Whitcomb et al. 1981, Trzcinski et al. 1999). Some other species, however, can tolerate the subdivision of habitat patches within their home range. For example, northern spotted owls have minimum area requirements for late-seral forest that varies geographically; yet, individual spotted owls use late-seral forest that may be distributed among many patches (Lehmkuhl and Raphael 1993, Forsman et al. 1984). In either case, habitat fragmentation reduces the size of suitable habitat patches and makes it increasingly difficult for these species to meet their minimum area requirements. As the habitat undergoes fragmentation, the most area-sensitive species will be lost first. As the habitat is further fragmented, other species will drop out according to their minimum area requirements (e.g., Robbins et al. 1989, Bender and Fahrig 1998, Flather and Bevers 2002). Thus, smaller patches generally contain fewer species than larger patches (Debinski and Holt 2000), and the set of species remaining in small patches is often a predictable subset of those found in large patches in the same region (Ganzhorn and Eisenbeib 2001, Kolozsvary and Swihart 1999, Vallan 2000, Fahrig 2003).

Edge Effects.—One of the most dramatic and well-studied consequences of habitat fragmentation is an increase in the proportional abundance of edge-influenced habitat. Early wildlife management efforts were focused on maximizing edge habitat because it was believed that most species favored habitat conditions created by edges and that the juxtaposition of different habitats would increase species diversity (Leopold 1933). Indeed this concept of edge as a positive influence guided land management practices for most of the twentieth century. Recent studies, however, have suggested that changes in microclimate, vegetation, invertebrate populations, predation, brood parasitism, and competition along forest edges (i.e., edge effects) has resulted in the population declines of several vertebrate species dependent upon forest interior conditions (e.g., Strelke and Dickson 1980, Kroodsma 1982, Brittingham and Temple 1983, Wilcove 1985, Temple 1986, Noss 1988, Yahner and Scott 1988, Robbins et al. 1989, Hoover et al. 1995, Laurence et al. 2002). In fact, many of the adverse effects of forest fragmentation on organisms seem to be directly or indirectly related to these so-called edge effects. In contrast, some species appear to respond positively to edge effects (Kremsater and Bunnell 1999, Carlson and Hartman 2001, Laurance et al. 2001), emphasizing the fundamental point that the effects of habitat loss and fragmentation depend on the details of how patterns of habitat and resource availability in the landscape interact with the ecological requirements and capabilities of individual species.

Much of what we know about edge effects stems from investigations on forest edges. Hence, while the principles discussed below are valid for most habitats, the specifics pertain largely to forest edge effects.

Microclimate.—One of the primary edge effects is the alteration of microclimate within habitat patches due to changes in the physical fluxes of radiation, wind, and water (Franklin and Forman 1987, Saunders et al. 1991, Baker and Dillon 2000). Following habitat loss and conversion to developed land uses, changes in these fluxes across the newly created edges can influence the microclimate of the remnant habitat patches (Saunders et al. 1991). Air temperatures at the edge of a forest remnant, for example, can be significantly higher than those found in either the interior of the remnant or the surrounding agricultural land (Geiger 1965, Kapos 1989). Similarly, with the conversion of natural vegetation to developed land uses, the entire pattern of momentum transfer over the landscape may be altered (Saunders et al. 1991). The wind profile does not fully equilibrate with the new land cover for some distance, perhaps for a distance as much as 100-200 times the height of the vegetation under study (Monteith 1975, Grace 1983). In addition, edges may allow below-canopy winds to penetrate the patch and modify relative humidity near the edge. Conversion of natural vegetation to developed land uses alters the rates of rainfall interception and evapotranspiration, and hence changes soil moisture levels (Kapos 1989). Altered surface and subsurface flows effect the timing and magnitude of peak flows (Hornbeck 1973, Simons 1989) and the transport of soil and nutrients (Likens et al. 1970, Bormann et al. 1974). These watershed hydrological impacts influence the local moisture regimes along habitat edges.

Changes in these physical fluxes near the edge create an ecotone in microclimate (i.e., temperature, wind, and relative humidity) that extends from the edge into the patch. The magnitude of alteration in microclimate along this ecotone may be affected by latitude (Hutchinson and Matt 1976, 1977; De Walle 1983;), orientation of the edge relative to solar angle and prevailing winds (Geiger 1965, Wales 1972, Ranney et al. 1981), and the degree of structural contrast between the habitat and adjacent land cover. Although there are notable exceptions, generalizations for forest suggest that these microclimatic effects extend up to 2 to 3 tree heights (about 100 m to 150 m) inside a patch (Lehmkuhl and Ruggiero 1991). Some variables may exhibit significant changes for up to twice this distance (e.g., Chen et al. 1992). Smith (1962) reported a similar finding based on the silviculture literature. This general pattern is expected to vary with aspect; warmer aspects (usually southern and western aspects) may have two to three times the depth of edge effects as compared to northern aspects (Whitney and Runkle 1981, Ranney et al. 1981, Forman and Godron 1986, Young 1988, Matlack 1993, Young and Mitchell 1994). Depths of effects also vary with the degree of contrast between adjacent patch types (Gysel 1951, Ranney et al. 1981, Concannon 1995).

Disturbance.—One of the more obvious edge effects is increased rates of disturbance along edges, primarily as a result of increased exposure to wind (Franklin and Forman 1987, Saunders et al. 1991). Increased wind exposure at edges may result in damage to the vegetation, either through direct physical damage from pruning or windthrow (Moen 1974, Grace 1977) or by increasing evapotranspiration with reduced humidity and increased dessication (Tranquillini

1979, Lovejoy et al. 1986). Several authors have noted that edges may have more stressed, dead, and downed trees than do adjacent forests (Geiger 1965, Chen et al. 1992). This condition is conducive to insect infestations which can cause additional disturbance. Unfortunately, the depth of edge effects due to disturbance have not been quantified, but it is reasonable to assume that they do not extend any further than microclimate edge effects.

Vegetation.—One of the most important edge effects is the change in vegetation composition and structure near edges resulting from altered microclimatic conditions and disturbance regimes. Changes in light, temperature, wind, and moisture regimes affect seedling establishment, growth, and survival (Wales 1972, Bennett 1990b, Gates and Mosher 1981, Levenson 1981, Ranney et al. 1981, Laurance 1989, de Casenave et al. 1995). Some species benefit from the modified microclimate near edges, others do not (e.g., Chen et al. 1992, Zen 1995). Similarly, increased disturbance rates at edges favor certain species. Overall, the altered physical environment can exert considerable influence on the composition and structure of vegetation near edges. Plant species common at successional edges (in contrast to permanent edges caused by inherent differences between adjacent natural communities; e.g., forest-water edge) include species that benefit from disturbance, as well as shade-intolerant, mid- and early-succession vegetation and exotics (Ranney et al. 1981, Lovejoy et al. 1986, Alverson et al. 1988, Helson and Halpern 2005). Vegetation structure near edges reflects these compositional changes, and is further modified by the high rates of physical disturbance. Consequently, vegetation near edges usually consists of a diverse mixture of species and structures and is often characterized by high foliage height diversity and abundant dead wood (both snags and logs).

Because vegetation responds to microclimate and disturbance, we might expect edge effects for plants to extend inward for distances similar to the microclimatic effects (Kremsater and Bunnell 2000). In reality, observed edge effects for vegetation extend less deeply into forests than do effects on microclimate. Most researchers report effects on vegetation of less than 50 m, many are less than 25 m, but values over 100 m have been reported, depending on the vegetation variables considered (e.g., Wales 1972, Caruso 1973, Wagner 1980, Franklin et al. 1981, Gates and Mosher 1981, Ranney et al. 1981, Chen et al. 1990, Palik and Murphy 1990, Williams-Linera 1990, Agelstam 1992, Chen et al. 1992, Fraver 1994, Zen 1995). Apparently, responses of plants integrate the large variation in microclimatic influences noted above. The fact that changes in plant composition and abundance extend less far into forests than do microclimatic effects demonstrates that extreme penetrations of microclimatic effects may be unreliable indicators of biological responses (Kremsater and Bunnell 2000).

Animals.—The alteration of the abiotic and biotic environment near habitat edges can reduce the quality of the edge habitat for some animal species (and increase it for others). This reduction in habitat quality may be due to a less favorable microclimate (i.e., resulting in higher energetic costs), less favorable physical structure, fewer available food resources, adverse inter-specific interactions (e.g., increased competition, predation or parasitism), or a combination of these. Unfortunately, despite the many studies documenting trends in species abundances and distributions near edges, few studies have attempted to determine causes of the observed patterns (Kremsater and Bunnell 2000). Moreover, the vast majority of these studies have focused on

vertebrate species and forest edges. Based on the physical and biological changes near edges described above, we can predict the kinds of species that should avoid edges. Species seeking habitat interiors should include those species for which edges confer no advantage (e.g., bark gleaners). This broad group of species is loosely defined as those that have become sufficiently proficient at foraging in habitat interiors that they need not venture near dangerous edges (see discussion on predation below). A second group of interior specialists may be those that are sensitive to microclimatic conditions (e.g., amphibians) or predation risks (e.g. some neotropical migratory birds) near edges.

There is a dearth of information on invertebrate distributions near edges, and what little is known pertains to forest edges only. Moreover, the patterns are inconsistent among studies. Warmer temperatures near forest edges have positive effects on some species and negative effects on others (Kremsater and Bunnell 2000). Studies cite increased abundance of ants and ground-dwelling arthropods near edges and suggest warmer temperatures as the reason (Usher et al. 1993). Similarly, elevated light levels near edges may affect the distribution of light-loving species such as butterflies, allowing them to penetrate some distance into the forest (e.g., Pollard 1982, Warren 1985, Warren et al. 1986). Conversely, Forman (1995) cites reduced diversity and abundance of ground-dwelling arthropods near road edges and suggests reduced organic litter as the cause. Few studies have attempted to document the depth of edge effect on invertebrates, although it likely varies in response to microclimatic and vegetation edge effects.

We should expect amphibians and reptiles to exhibit opposite responses to edges - at least forest edges with pronounced temperature and moisture ecotones. Amphibians should avoid warmer and drier edge environments due to their susceptibility to dessication; conversely, reptiles should favor edges due to their preference for warmer environments. However, the increased abundance of invertebrates near many edges should benefit both groups. DeMaynadier and Hunter (1998) reported more captures of some amphibian species beyond 25 to 35 m from forest edges created by timber harvest in Maine. Plethodonid salamanders showed greater negative response to edges than did anurans, and the response was greater for high contrast edges. There is generally strong evidence that for many species habitat fragmentation and edge effects has substantial negative effects on amphibians (e.g. Rothermel and Semlitsch 2002, Marsh et al. 2004). In contrast, however, Rosenberg and Raphael (1986) reported greater amphibian richness in forest stands and landscapes characterized by greater amounts of edge, although species differed in their preference for edge environments. We are not aware of comparable empirical data on reptile distributions in relation to edge.

The distribution of game mammals (e.g., deer, elk, moose) in relation to edge was the focus of much early study (Leopold 1933). Subsequent studies confirmed the preference for edges shown by these game species (Julander and Jeffery 1964, Reynolds 1962, 1966; Harper 1969, McCaffery and Creed 1969, Willms 1972, Weger 1977). As a result, maximizing edge to enhance game populations formed the backbone of wildlife management efforts during most of the twentieth century. Comparable data for large mammalian carnivores does not exist, and the data for mid-sized predators and small mammals is scarce. Although a few mammals (e.g., fisher, martin, red-backed vole) have demonstrated a negative association with edge, most

species that have been studied either were neutral in their association or showed a preference for edge (e.g., Godfryd and Hansell 1986, Rosenberg and Raphael 1986, Buskirk and Powell 1994, Martin 1994, Mills 1995, Krusic and Neefus 1996, Erickson and West 1996, Crampton and Barclay 1996). Much of the positive response appears associated with the juxtaposition of foraging opportunities associated with the edge itself or the adjacent open areas and taller vegetation that meets other needs (e.g., cover, reproduction). This appears true of members of the deer family, and of omnivorous small mammals, predators, and bats in general (Kremsater and Bunnell 2000).

In contrast to other vertebrate groups, bird distributions in relation to edge have been extensively studied. In general, bird species richness, diversity, and overall abundance increases near edges, and the response is greater at higher contrast edges (e.g., Yahner 1983, 1984; Catt 1991; Sisk and Margules 1993), although there are notable differences among species and landscapes. Overall, about one-third of all species studied show no response to edge (Kremsater and Bunnell 2000). This includes habitat generalists as well as habitat specialist that simply show no change in abundance near edges. Of species showing a response to edge, more show a positive response. This positive response has been attributed to complex structure with shrubby vegetation (e.g., Anderson et al. 1977, Morgan and Gates 1982, Helle 1983) and well-developed foliage layers near edges (e.g., Strelke and Dickson 1980, Hansson 1983). In general, species showing a positive response to edges prefer more open, shrubby habitat, or prefer the juxtaposition of taller vegetation (e.g., to provide nest substrates or foraging perches) and open areas for foraging. Interestingly, species showing a negative response to edges are not avoiding openings per se, since most of these species use at least small openings to forage (Kremsater and Bunnell 2000). Nevertheless, most species demonstrating a preference for interior appear to prefer closed canopy conditions. Based on the data presented in Kremsater and Bunnell (2000), the differences between species preferring edges versus interiors are partially explained by differences in life history characteristics. For example, proportionately more shrub-nesting species prefer edges, owing to the more developed shrubby vegetation near edges. Similarly, proportionately more ground and understory gleaners and species that hawk from perches prefer edges, owing to the greater understory development and juxtaposition of perches and open areas near edges; whereas, most bark gleaners prefer the interior. Interestingly, while the dietary habitats of species preferring edges are quite diverse, species preferring interiors are predominantly insectivorous.

Despite the clear preference for edges or interior shown by many bird species, there is little evidence that any species are found exclusively in the edge or interior. A few species have been reported as exclusively associated with edge, but these associations do not appear consistent among regions. More importantly with respect to the adverse impacts of fragmentation, there does not appear to be strong evidence of bird species requiring only forest interior habitat (e.g., Keller and Anderson 1992, Hansson 1994, Bunnell et al. 1997, Ruefenacht and Knight 2000). Nevertheless, a minority of species do show a preference for interior conditions and it is these species that are most likely negatively impacted by fragmentation. Unfortunately, the number and type of species showing a preference for interior conditions appears to vary widely among landscapes. For example, the avoidance of edge is much more common in landscapes where

forest patches are surrounded by an agricultural or urban matrix (Marzluff and Restani 2000). The few studies conducted in forested landscapes suggest little response to forest interior conditions (e.g., Keller and Anderson 1992, Schieck et al. 1995, McGarigal and McComb 1995, Ruefenacht and Knight 2000). In addition, the majority of species with reported affinities (for edge or interior) were documented in a single study despite being evaluated in several, and roughly one-third of all "interior" species were reported as "edge" species in other studies (Kremsater and Bunnell 2000). Given the disparity in findings and inconsistent patterns for many species, it is not surprising that a wide range of depth of edge effects for birds has been documented (Kremsater and Bunnell 2000). Most studies report edge effects (variously defined) of less than 50 m for birds, similar to those reported for vegetation (Gates and Gysel 1978, Haila et al. 1980, Gates and Mosher 1981, Hansson 1983, Helle 1983, Vickholm 1983, Helle 1986, Fuller and Whittington 1987, Fuller 1988, Fuller and Warren 1991, Klenner and Huggard 1997). Given the variability in edge response, further generalizations are not warranted.

Parasitism and Predation.—One of the more well-documented edge effects involves increased parasitism and predation near edges. Most of this research has focused on birds (e.g., Yahner 1988, Terborgh 1992, Paton 1994). Parasitism of nests by brown-headed cowbirds may have a significant impact in areas where wooded habitats are surrounded by agricultural areas or fields. In eastern North America, where such conditions are relatively common, cowbird density has been inversely related to distance from open habitats (Brittingham and Temple 1983, Gates and Gysel 1978). Cowbirds typically feed in grasslands or agricultural fields and venture into forests to parasitize broods of other species. In an early study, Brittingham and Temple (1983) documented high levels of brood parasitism by brown-headed cowbirds near forest openings and stimulated much concern about negative edge effects on neotropical migrants. Since then, there have been several similar studies and the results have been inconclusive and inconsistent (Paton 1994, Kremsater and Bunnell 2000). First, increased parasitism near edges is shown in only one-third of the studies. In some cases, parasitism was more closely associated with proximity to human settlement than the presence of edges (Trail and Baptista 1993, Cooker and Capen 1995). There appear to be significant regional differences as well. In the Pacific Northwest, for example, there is little indication of increased parasitism by cowbirds near forest edges, presumably due to the relatively rarity of cowbirds in the region (McGarigal and McComb 1995, Schieck et al. 1995). Thus, while it is clear that parasitism can have a significant impact on some species under certain regional landscape conditions, it should not be assumed that it plays a significant role in all cases.

In contrast to the evidence for parasitism, there is increasing and consistent evidence in the eastern United States and Europe that generalist predators can negatively impact forest birds near edges (Bider 1968, Robbins 1979, Gates and Mosher 1981, Whitcomb et al. 1981, Chasko and Gates 1982, Ambuel and Temple 1983, Andren et al. 1985, Haila 1986, Janzen 1986, Johnson and Temple 1986, Laudenslayer 1986, McLellen et al. 1986, Temple and Carey 1988, Yahner and Scott 1988, Csuti 1991, O'Conner and Faaborg 1992, Santos and Telleria 1992). Corvids (jays, crows, and ravens) are reportedly the primary avian predator of nests near edges (Moller 1989, Andren 1992), but many smaller mammals also prey on bird nests and may be under-represented in study results (Leimgruber et al. 1994, Hernandez et al. 1997, Marzluff and

Restani 2000). Based on a comprehensive review of published studies, Paton (1994) and Kremsater and Bunnell (2000) conclude that the majority of these studies (60%) convincingly show elevated depredation rates within 50 m of an edge. They further conclude that patches must be <10 ha to produce elevated depredation rates. Similar edge effects have not been reported in largely forested landscapes where timber harvesting is the primary anthropogenic disturbance (Rudnicki and Hunter 1993, Schieck et al. 1995, King et al. 1996, Vander Haegan and DeGraaf 1996, Bayne and Hobson 1997, Marzluff and Restani 2000, Ruefenacht and Knight 2000). Here, edges are transient and may not attract the same suite of generalist edge predators characteristic of woodland-field edges.

Roads and Human Activities.—Edges tend to concentrate and funnel human activities such as littering, drift of fertilizers, trampling from domestic animals, grazing, escaping fires, hunting, poaching, and excessive human disturbance. For example, due to the preference for edge by most game species, hunting is often concentrated along edges. Roads are linear landscape features that produce a disproportionately large amount of edge for their area and provide human access and a source of disturbance (Bennett 1990, Baker and Knight 2000). Roads provide access for hunters, so hunting is often concentrated along road edges. Road edges can be a source of exotic plants that invade adjacent habitat (Tyser and Worley 1992). Additional edge effects around roads result from disturbance by traffic (e.g., noise) as well as direct mortality (vehicle collisions). Some species (e.g., deer and elk) have apparently responded by avoiding road edges (Pedersen et al. 1979, Rost and Bailey 1979, Lyon 1976, 1983; Witmer and deCalesta 1983, Huggard 1993, Cole et al. 1997). These edge effects can extend for considerable distances. Deer have been reported to use areas 300 to 400 m from the road three times more often than they use areas within 100 m of the road (Rost and Bailey 1979). Similarly, elk have been reported avoiding areas within 500 m of paved roads (Witmer and deCalesta 1983) and possibly suffering higher mortality rates within 1 km of a highway because of collisions with vehicles. Similar avoidance of roads and human disturbance have been reported for bears (Archibald et al. 1987, Garner and Vaughan 1987, Brody and Pelton 1989, McLellan 1990, Mattson 1990, Kasworm and Manley 1990). Amphibians appear particularly vulnerable to fragmentation of habitat by roads (Cushman submitted). The high vulnerability of amphibians to fragmentation by roads is due to their relatively low vagilities, which amplifies the effects of habitat fragmentation (Gibbs 1998, deMaynadier and Hunter 2000, Bowne and Bowers 2004), and their high vulnerability to death in moving across roads and through inhospitable terrain, which depresses population growth rates (Fahrig et al. 1995, Carr et al. 2000, Carr and Fahrig 2001).

Isolation Effects.—One of the more immediate consequences of habitat fragmentation is the disruption of movement patterns and the resulting isolation of individuals and local populations. As habitat is fragmented, it is broken up into remnants that are isolated to varying degrees. Because remnant habitat patches are relatively small and therefore support fewer individuals, there will be fewer local (within-patch) opportunities for intra-specific interactions. This may not present a problem for individuals (and the persistence of the population) if movement among patches is largely unimpeded by intervening habitats in the matrix and connectivity across the landscape can be maintained. However, if movement among habitat patches is significantly impeded, then individuals (and local populations) in remnant habitat patches may become

functionally isolated (McCoy and Mushinsky 1999, Rukke 2000, Virgos 2001, Bender et al. 2003, Tischendorf et al. 2003). The degree of isolation for any fragmented habitat distribution will vary among species depending on how they perceive and interact with landscape patterns (Dale et al. 1994, With and Crist 1995, Pearson et al. 1996, With et al. 1997, With 2000); less vagile species with very restrictive habitat requirements and limited gap-crossing ability will likely be most sensitive to isolation effects (e.g. Marsh and Trenham 2001, Rothermel and Semlitsch 2002).

Habitat patches can become functionally isolated in several ways. First, the patch edge may act as a filter or barrier that impedes or prevents movement, thereby disrupting emigration and dispersal from the patch (Wiens et al. 1985). Some evidence for this exists for small mammals (e.g., Wegner and Merriam 1979, Chasko and Gates 1982, Yahner 1986), but the data are scarce for other vertebrates. Whether edges themselves can limit movement presumably depends on what species are trying to cross the edge and on the structure of the edge habitat (Kremsater and Bunnell 2000). Second, the distance from remnant habitat patches to other neighboring habitat patches may influence the likelihood of successful movement of individuals among habitat patches. Again, the distance at which movement rates significantly decline will vary among species depending on how they scale the environment. In general, larger organisms can travel longer distances. Therefore, a 100 m-wide agricultural field may be a complete barrier to dispersal for small organisms such as invertebrates (e.g., Mader 1984) or amphibians (Rothermel and Semlitsch 2002, Marsh et al. 2004), yet be quite permeable for larger and more vagile organisms such as birds. Lastly, the composition and structure of the intervening landscape mosaic may determine the permeability of the landscape to movements. Recall that under the island biogeographic perspective, habitat patches exist in a uniform sea that is hostile to both survival and dispersal. In this case, the matrix is presumed to contain no meaningful structure and isolation is influenced largely by the distance among favorable habitat patches. However, under the landscape mosaic perspective, habitat patches are bounded by other patches that may be more or less similar (as opposed to highly contrasting and hostile) and connectivity is assessed by the extent to which movement is facilitated or impeded through different habitat types across the landscape. Each habitat may differ in its "viscosity" or resistance to movement, facilitating movement through certain elements of the landscape and impeding it in others (e.g. Cushman et al Submitted, Cushman et al. in prep). Again, the degree to which a given landscape structure facilitates or impedes movement will vary among organisms. Regardless of how habitat patches become isolated, whether it be due to properties of the edges themselves, the distance between patches, or properties of the intervening matrix, the end result is the same-fewer individual movements among habitat patches.

Population Structure and Viability

Both theoretical analyses (Bascompte et al. 2002), and empirical studies (Donovan and Flather 2002) suggest negative effects of habitat loss on population growth. At the level of the population, patchiness in the distribution of resources (and suitable habitat conditions) caused by habitat fragmentation may ultimately affect population viability. Specifically, the subdivision and isolation of populations caused by fragmentation can lead to reduced dispersal success and

patch colonization rates which may result in a decline in the persistence of local populations and an enhanced probability of regional extinction for the entire population across the landscape (e.g., Lande 1987, With and King 1999, With 2000). Habitat fragmentation by roads and other barriers can decrease dispersal success (Gibbs 1998, deMaynadier and Hunter 2000), increase mortality (Fahrig et al. 1995, Carr and Fahrig 2001) and reduce genetic diversity (Reh and Seitz 1990). Increased population isolation increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande 1988, Schoener and Spiller 1992, Sjogren-Gulve 1994). However, in other cases, habitat fragmentation may benefit populations. For example, Bowman et al. (2002) argued that fragmentation can increase immigration success for certain species, if immigration is a function of the linear dimension of a habitat patch rather than the area of the patch. Furthermore, many species require more than one kind of habitat (Law and Dickman 1998) and increasing fragmentation could result in higher availability of complementary resources (Dunning et al. 1992). For the same amount of habitat, a more fragmented landscape will have a higher interdigitation of different habitat types (Fahrig 2003), which could increase landscape complementation, positively affecting biodiversity (Law and Dickman 1998, Tscharntke et al. 2002). For example, Pope et al. (2000) showed that the proximity of feeding habitat to breeding ponds was related to the abundance of leopard frog populations and Pedlar et al. (1997) found that raccoon abundance highest in landscapes with intermediate amounts of forest. Clearly, the effects of habitat loss and fragmentation on population persistence depend fundamentally on the ecological capabilities and requirements of the species involved and details of the amount and pattern of habitats across the landscape.

Spatially-structured populations are often referred to as metapopulations (after Levin 1974). In order to understand the metapopulation consequences of habitat fragmentation, a brief summary of metapopulation theory is required (see Hanski and Gilpin 1991). Metapopulations are literally populations of populations. For example, a metapopulation may consist of the populations existing in discrete habitat patches remaining following the fragmentation of intact habitat. The theory holds that within each patch the population has a finite probability of extinction, and likewise each patch has a particular colonization rate based on the number of occupied patches in the metapopulation. Populations in particular patches continually go extinct, but the metapopulation as a whole persists so long as colonization rate is equal to extinction rate. Metapopulations subject to high extinction rates, but with correspondingly high rates of recolonization, have high population turnover, but persist as long as the opposing rates are equal. The theory was formalized in a number of models. The first generation of metapopulation models were not spatially explicit; each patch was identical to all others and all patches were equally accessible. Later models included explicit consideration of patch differences and the influences of their arrangement and dispersion. These models had tremendous influence on community and conservation biology theory. They provided a number of major insights about the influence of fragmentation on the probability of population persistence.

Harrison (1991, 1994) and Harrison and Taylor (1997) reviewed metapopulations and described several variations on the metapopulation theme. Note, these are all the same basic

model: they all consist of spatially-structured populations, but vary in the degree of among?patch dispersal.

- Mainland/Island (Core/Satellite) Populations.--A direct analogy to island-biogeographic cases, the mainland (or core) population is resistant to extinction while some subset of island (or satellite) populations tend to go extinct repeatedly and be recolonized by dispersal from the mainland source. Note that because the mainland is persistent by definition, the metapopulation is as well.
- Source/Sink Populations.--In source/sink systems (Pulliam 1988), a source has a positive local recruitment rate in the absence of immigration, and thus provides a net surplus of emigrants. A sink has negative local recruitment and so would not persist in the absence of a dispersal subsidy from elsewhere. The source population is resistant to extinction while some subset of sink populations tend to go extinct repeatedly and be recolonized by dispersal from the source. In Pulliam's model and most examples, the sources and sinks are defined by habitat quality (productivity). A key result is that a large proportion of a metapopulation can exist in sink habitats if the source patches are sufficiently productive to subsidize the sinks. These source/sink systems can also be defined in the time domain: source patches act as persistent refugia, from which populations expand outward during good times (though often to sink habitats), and contracting back during less favorable times.
- Patchy Populations.--Patchy populations are metapopulations that are so well mixed and interconnected by dispersal that they function essentially as a single population. Local extinctions are recolonized immediately, and a single individual might live in multiple patches during its lifetime. Many "r-selected" species form patchy populations because they exploit patchy or ephemeral habitats.
- Non-equilibrium Metapopulations.--In some systems local extinctions are symptomatic of a general decline of the metapopulation; local extinctions go largely unanswered by recolonization. This is typical of "relaxing" island-system populations, and increasingly, of landscapes subject to broadscale habitat reduction such as forest clearing. Presumably, such a system will ultimately re-equilibrate to a functioning metapopulation, although some local populations might be lost permanently.
- The Classic Metapopulation.--The idealized system comprises multiple patches whose populations are reciprocally linked by dispersal, with extinction and recolonization (turnover) measured on time scales of more than one but less than several generations. Ironically enough, it seems that these are the ones that are hardest to find in nature.

Metapopulation dynamics reflect the rates of local extinctions and recolonizations as determined by inter-patch movement, and factors affecting these processes. Individual movement between patches is perhaps the most important defining feature of a metapopulation. For example, variations on the metapopulation theme described above largely differ in the rate of

individual movement among habitat patches. Furthermore, how fast and how far organisms move imposes a scale on the environment; highly vagile animals integrate heterogeneity over broader scales than do sessile individuals and therefore perceive the environment with a coarser filter or "grain" (Wiens 1997). Several factors affect movement within and between patches. Patch characteristics such as size and shape influence the likelihood that a dispersing individual or an individual moving within its home range will encounter the patch boundary during a specified time interval. Whether or not an individual will cross a patch boundary upon encountering it is a function both of features of the boundary itself (i.e., boundary permeability) and of the characteristics of the adjoining patch (i.e., patch context). Movements of individuals within and between patches must be extended to the scale of the population rather than individual patches to be relevant to metapopulation dynamics. This involves shifting the scale from that of movements and patches defined by individual home ranges to the broader-scale movements of populations (i.e., dispersal) and the scale of patchiness represented by interactions within and among local populations.

There are three proximate agents of local extinction: demographic stochasticity, genetic stochasticity, and environmental stochasticity. Demographic stochasticity refers to random fluctuations in demographic rates (e.g., natality and mortality) that cause the population to fluctuate in size and is important for populations that fall below a certain threshold size. In these cases, the order of demographic processes becomes critical. For example, it might make a lot of difference if an individual dies before it reproduces or reproduces before it dies. The order of reproduction and death matters, as does the proportion of sexes among the offspring. In small populations unbalanced sex ratios can arise by chance, and reduce the effective population number. Genetic stochasticity refers to random fluctuations in the genome leading to deleterious effects; for example, the loss of heterozygosity or loss of fitness due to inbreeding in very small populations. Environmental stochasticity refers to random fluctuations in environmental conditions; for example, vagaries of the weather that result in fluctuations in food supply or habitat quality, or result in direct mortality. Such extrinsic fluctuations might act in a density-dependent manner to reduce a local population. Environmental stochasticity of an extreme form that affects the entire metapopulation, causing local extinctions in a density-independent manner, are often denoted as catastrophes, separating these events from "normal" environmental fluctuations. Habitat loss and fragmentation acts to decrease patch size and thereby increase local extinction rates which, if not balanced by increased colonization rates, can lead to metapopulation extinction.

Because recolonization depends on the successful establishment of new recruits in a habitat patch, the factors influencing recolonization reflect the interplay between life-history traits that affect the vagility of the organism and the connectivity of the habitat as perceived by that organism. For plants, seed size and viability (often related to size), dispersal vector (wind, water, animal), and habitat (seedbed) requirements are important factors. For animals, simple distance from other habitat patches, "resistance" of intervening habitats, dispersal behavior (preference or avoidance of some habitats, search and orientation during dispersal, use of stepping stones or corridors), and mortality rates during dispersal itself (including agents of this mortality such as predation) are important factors. Habitat fragmentation acts to increase isolation of habitat

patches and thereby decrease local recolonization rates which, if not balanced by decreased extinction rates, can lead to metapopulation extinction.

Metapopulations are logistically confounding subjects for study. A metapopulation is defined by dispersal events that need occur only once every generation or so, and so it stands to reason that these events are unlikely to be witnessed in the field. Thus, theoretical models have been widely used to investigate the relationship between habitat fragmentation and population persistence. Many theoretical models predict that the local and regional persistence of some species depends on both the total amount and configuration of habitats in the landscape (Pulliam and Danielson 1991, Pulliam et al. 1992, Flather and Bevers 2002, Fahrig 2003). The probability of patch occupancy for some species may be a function of both patch size and isolation (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988). Some models indicate that the effects of habitat fragmentation on a population can be nonlinear and appear suddenly and catastrophically after a large portion of the habitat has been removed with little or no observed effect; i.e., that there will be thresholds of habitat fragmentation below which the population will quickly crash to extinction (Tilman 1990, Kareiva and Wennergren 1995, Fahrig 1997, Flather and Bevers 2002). For example, generalist predators may often increase with moderate fragmentation of large expanses of originally continuous habitat (Andren et al. 1985, Andren and Angelstam 1988, Small and Hunter 1988, Andren 1994), but then may crash when critical thresholds of landscape composition are exceeded (Gilpin and Hanski 1991, Kareiva and Wennergren 1995, Kurki et al 1998).

The logistical difficulty in defining metapopulations with field observations places an appreciable strain on the theory, which otherwise is well developed. Given the difficulty in observing dispersal directly, empirical evidence for metapopulations has been slow to accumulate. Empirical studies of metapopulations have proceeded in a variety of ways (Kareiva 1990). Most empirical studies have dealt with short-lived species, often insects, for which short generation times and fine-scale patterns of habitat use make it a bit easier to observe metapopulation processes. For larger organisms, the processes are inferred from long-term presence/absence (or abundance) data but that doesn't tell you where colonists came from. Harrison (1991, 1994) and Harrison and Taylor (1997) reviewed the empirical evidence in support of metapopulations, and suggest that while there are a few cases that are sufficiently well documented to support the theory, in more cases the evidence is simply not strong enough to demonstrate metapopulation dynamics are occurring. Despite these difficulties and the lack of irrefutable empirical evidence, it is clear that many populations in heterogeneous environments exhibit marked spatial structure (Kareiva 1990). Even though most populations probably do not exhibit classic metapopulation dynamics, the processes involved in metapopulation dynamics-local colonization and extinction affected by inter-patch movements-are likely involved to varying degrees in all spatially structured populations. Habitat fragmentation, which affects these critical processes, often has major consequences for population (or metapopulation) persistence (Flather and Bevers 2002, Fahrig 2003). Ultimately the impact of habitat fragmentation (positive, negative, or neutral) on a species will depend on the interaction of its life-history and behavioral characteristics with the scale and pattern of habitat change (Laurence 1990, Fahrig 2003).

Interspecific Interactions

At the level of the community, patchiness in the distribution of resources caused by habitat fragmentation can affect a range of interspecific interactions and strongly influence community structure and stability. For example, habitat loss has been shown to reduce trophic chain length (Komonen et al. 2000), and to alter species a range of species interactions (e.g. Taylor and Merriam 1995). Habitat loss and fragmentation can have strong influences on predator-prey and competitive interactions (Nee and May 1992, Ives 1995). Under some conditions, habitat fragmentation can allow for predator-prey coexistence (Huffaker 1958, Vandermeer 1973, Hastings 1977, Caswell 1978, Jansen 1995, Holyoak 2000), lead to eruptions of the prey population (Kareiva 1987, Oksanen et al. 1992) or result in the elimination or depression of the prey species (Holt 1984, May and Robinson 1985). Furthermore, depending on the circumstances, habitat fragmentation can either moderate competition and allow coexistence, or increase the intensity of competition and lead to competitive exclusion. For example, a number of theoretical studies have demonstrated that in certain cases habitat subdivision can stabilize interspecific competition and allow for the coexistence of similar species (Tilman 1994, Chesson and Case 1986, Holyoak and Lawler 1996, Jansen 1995). Habitat fragmentation can increase the stability of two-species competition (Levin 1974, Shimda and Eller 1984, Slatkin 1974). Similarly, in an empirical study, Atkinson and Shorrocks (1981) found that coexistence of two competing species could be prolonged by dividing the habitat into smaller patches. In these cases coexistence results from a tradeoff between dispersal rate and competitive ability (Chesson 1985, Fahrig 2003). Tilman (1994), for example, showed that coexistence of competitors in spatially structured habitats can result from interspecific tradeoffs in colonization ability, competitive ability, and longevity. In contrast, Danielson (1991) predicted that interactions between competitors are very sensitive to the structure of the landscape, and that as fragmentation increases, competition may increase in severity until one of the species is eliminated.

For single species systems, fragmentation of required habitat into discrete patches may lead to higher extinction rates within each patch, and ultimately to meta-population extinction. In contrast, in some situations habitat subdivision by asynchronous local disturbances can stabilize single-species population dynamics by reducing the probability of simultaneous extinction (den Boer 1981). Furthermore, in a multi-species system with predator-prey or competitive interactions, local extinctions and recolonizations at the patch level may lead to coexistence of species that would not coexist in a homogeneous environment (Hassell and May 1973, Vandermeer 1973, Levin and Paine 1974, Hastings 1977, Sabelis and Diekmann 1988, Taylor 1990, Pacala 1990, Johnson et al. 1992). For example, predation risk may alter the foraging behavior of sympatric species with different vulnerabilities to predation, leading to habitat partitioning and allowing coexistence (Caswell 1978, Hanski 1983, Hughes et al 1994). These and other mathematical models and experimental studies have shown that fundamental properties of multi-species communities can be changed whenever spatial heterogeneity is important in interspecific interactions (Kareiva 1987). The prime message to emerge is that in many systems predation and competition may interact with the spatial pattern and temporal dynamics of landscapes to structure animal communities (Kotlar and Holt 1989). Fragmentation affects predatory prey interactions by creating temporary refuges for prey or barriers for predators, and

affects competitive exclusion by creating heterogeneous mosaics in which post-disturbance colonization and competitive superiority change across space and through time. The key factors in each case will be the interactions of the behavioral and life-history characteristics of particular species with the scales and patterns of heterogeneity of the landscapes in which they live.

When is Habitat Fragmentation Important?

The bulk of empirical and theoretical evidence to date suggests that the effects of habitat loss are generally much greater than those of habitat fragmentation (Fahrig 2003). Breaking apart of habitat, independent of habitat loss, has generally weaker effects on biodiversity that are as likely to be positive as negative. Our ability to accurately predict when and to what degree individuals, populations, and communities will be affected by habitat loss and fragmentation is still imprecise. Much of the apparent lack of predictive power stems from a failure to properly consider habitat fragmentation from the perspective of the organism or process of interest. Specifically, human activities often lead to changes in the spatial extent and configuration of land cover types, but whether these changes result in the loss and fragmentation of suitable habitat for a particular organism depends on the scale and nature of those changes in relation to how that organism perceives and interacts with landscape patterns. For example, changes in the size and isolation of mature forest patches may have little or no detectable impact on species that select habitat on the basis of other environmental variables (e.g., shrub cover, litter depth) or species that utilize a broad range of habitats (i.e., generalist or multi-habitat species). Likewise, studies that fail to match the scale of observation to the scale of the organism will fail to identify meaningful relationships between pattern and process. For example, if the entire extent over which habitat loss and fragmentation are measured is less than the home range of a single individual, then it is certain that population impacts will not be observed. Ultimately, the scale and pattern of habitat fragmentation must coincide with how the focal organism scales and perceives habitat at either the individual or population level. Reconciling these issues remains the single greatest challenge to fragmentation research.

Consequently, the scientific debate on fragmentation recently has focused on the question: when does fragmentation of habitat become important? Or, conversely, how much habitat and in what configuration is required to maintain viable populations of target species? Much of the theoretical debate in this arena has centered on identifying and describing thresholds in organism responses to fragmentation. In this context, a critical threshold is an abrupt, nonlinear change that occurs in an organism response (e.g., dispersal success, productivity, patch occupancy, etc.) across a small range of habitat loss and fragmentation (With and King 1999). Both empirical data (Koopowitz et al. 1994, Carlson and Stenberg 1995, Doncaster et al. 1996, Jansson and Angelstam 1999) and theoretical models predict critical thresholds of habitat where ecological relationships change abruptly (Turner and Gardner 1991, O'Neil et al. 1988, With and Crist 1995, Bascompte and Sole 1996, Flather and Bevers 2002). For example, neutral landscape models, derived from percolation theory as applied in the field of landscape ecology (Gardner and O'Neil 1991, With 1997, With and King 1997), have been used to characterize habitat fragmentation as a threshold phenomenon (With and King 1999). Above the so-called percolation threshold, habitat loss results in a simple additive loss of habitat. At the threshold, a

qualitative change in landscape structure occurs. A small additional loss of habitat at this point produces a fragmented landscape in which habitat is subdivided into many small isolated patches. Further habitat loss leads to further fragmentation. The threshold at which habitat becomes physically fragmented depends on the initial configuration of habitat. In a simple model of homogeneous habitat with random loss, this threshold corresponds to the point at which habitat continuity across the landscape is disrupted (i.e., the percolation threshold).

Nearly all research on threshold relationships in animal populations has been limited to habitat area effects. Some theoretical and empirical work suggests that major population declines will occur due to habitat loss when habitat area drops below 10-30% (With and Crist 1995, Hill and Caswell 1999, Jansson and Angelstam 1999, Fahrig 2001, Flather and Bevers 2002). In addition, theoretical studies suggest that habitat fragmentation per se can affect where the extinction threshold occurs on the habitat amount axis. Also, effects of habitat fragmentation are predicted to increase below some level of habitat loss. Some theoretical studies suggest that the effects of fragmentation per se should become apparent only when habitat area drops below approximately 20-30% of the landscape (Fahrig 1998, Flather and Bevers 2002, Fahrig 2003). Threshold studies considering only a single factor at a single scale are limited in their applicability to real-world systems, because habitat loss and fragmentation in real landscapes typically involve multiple factors operating at several scales. Some recent work has attempted to describe the interaction of several factors on threshold behaviour. Jansson and Angelstam (1999) studied threshold levels for the presence of the long-tailed tit. Their study is one of the few that has explicitly quantified the interaction between habitat area and isolation. They found that thresholds of habitat occupancy changed dramatically at certain combinations of habitat area and isolation. Specifically, the probability of habitat occupancy rose from 10 to 80% if gap distances decreased from 500m to 100m in landscapes with 5% habitat cover. Interestingly, occupancy rose equally if gap distance declined from 900m to 500m in landscapes with 15% habitat cover. These results suggest that threshold studies based only on a single factor and not controlling for the effects of others may give equivocal results. Thus it is important to consider the interaction of multiple factors on threshold behavior. The point at which habitat becomes functionally disconnected depends not only on the pattern of habitat distribution but on the life history characteristics (e.g., dispersal capabilities) of the target organism (With and Crist 1995, Pearson et al. 1996, With 1997, With et al. 1997).

Currently there is insufficient knowledge to predict with precision when habitat fragmentation will be ecologically consequential to many organisms. Clearly, as habitat is reduced in extent and subdivided, at some point it becomes structurally disconnected. Percolation theory predicts that this will occur abruptly when habitat is reduced to 40-60% of the landscape, depending on how the physical connections are defined (e.g., Gardner et al. 1987, Gardner et al. 1989, Gardner and O'Neill 1991, Pearson and Gardner 1997, With 1997, With and King 1997). Depending on the characteristics of the target organisms, at some point the habitat will become functionally disconnected as well. The evidence suggests that population declines above the threshold will be linear functions of amount of habitat. However, beyond the threshold, population declines are exacerbated by edge, isolation and other fragmentation effects and become nonlinear and often precipitous. Initial theoretical and empirical work suggest that

these negative impacts are likely to become significant when habitat is reduced to 10-30% of the landscape and that the configuration of habitat may have a substantial effect on this relationship. In particular, important population processes may be retained if the remaining habitat is highly aggregated or contagious in its distribution. These guidelines should be viewed as hypotheses and any management activities designed to implement these guidelines should be viewed as experiments within an adaptive management framework.

Implications for National Forest Management

The empirical evidence collected to date suggests that the effects of fragmentation per se on biodiversity are generally weaker than the effects of habitat loss. In addition, the effects of fragmentation are as likely to be positive as negative, and depend fundamentally on the interaction between habitat patterns and the ecological requirements and capabilities of the organism. This makes prediction of fragmentation effects much more challenging than prediction of the effects of habitat loss. These understandings suggest several directions for natural resources research and management. The Protocol described in the final section of this document presents a series of concepts, questions and procedures for designing research to measure the effects of habitat loss and fragmentation, and ways to incorporate these understandings into management decisions. Below are some general statements regarding the implications of current knowledge for National Forest Management. The Protocol that follows provides a detailed roadmap for addressing these issues.

Implications for Natural Resources Research

Given the paramount importance of habitat amount to species persistence, a fundamental emphasis must be placed on accurately describing habitat quality. Habitat relationships must be quantified for species of interest, and these understandings applied to map habitat quality across space, and through time based on empirical models. This capacity is currently woefully under developed.

Reliable habitat capability models will exhibit several important characteristics. First, they should be developed individually for species of interest. Each species has unique relationships with environmental gradients across a range of scales. Coarse-filter, or GAP-type models are insufficient for reliably predicting habitat quality for individual species. Second, they should be developed using large and representative samples of species presence or abundance across broad combinations of environmental gradients. Grid-based sampling designs such as the National Vegetation Pilot (Cushman and McKelvey in prep) or the FIA grid are ideal frameworks for gathering large, representative samples of species distribution and abundance and the necessary data on multiple environmental gradients. Third, the models must utilize appropriate statistical approaches. Specifically, as species habitat capability is theoretically an n-dimensional hypervolume in an environmental gradient space (Hutchinson 1957, 1965; Whittaker 1967), approaches such as gradient modeling (Cushman and McGarigal 2002, Cushman and McGarigal 2004) which explicitly describe species niches as zones of tolerance in environmental gradient space should be utilized. Fourth, models must account for multiple-scale species-environmental

interactions. Species will respond to environmental variability individually according to their ecological requirements and capabilities. Many species will simultaneously respond to variation from several spatial scales or levels of organization (Cushman and McGarigal 2002). It is essential to utilize gradient modeling approaches that can integrate and partition the influences of environmental factors from a range of spatial scales (e.g., Cushman and Wallin 2002, Grand and Cushman 2003, Cushman and McGarigal 2004). Fifth, it is essential to map expected habitat quality at a fine spatial scale across large extents. Methods such as gradient imputation (Ohmann and Gregory 2002) offer a means of applying hierarchical habitat models to create maps of expected habitat capability across space for each species. Sixth, habitat quality will change over time due to succession, natural disturbances (e.g., wildfire), forest management, road building, urbanization and climate change. It is important to be able to predict the expected future extent and pattern of habitat under a range of management alternatives. Linking dynamic landscape models to the gradient habitat capability models will allow quantitative prediction of expected future areas and patterns of habitat under a range of potential scenarios of management, fire regime and climate change (Cushman et al. in prep.). Seventh, wildlife habitat is not the only resource of importance in National Forest management, and attention should be given to other resources and processes such as vegetation, aquatic ecosystems, fuels, fire and climate change. Multi-scale gradient modeling is well suited to predicting and mapping vegetation, fuels, and other resources, and can be used in conjunction with other methods to assess the interaction of biophysical gradients, fire regimes and climate change (Cushman et al. in prep.).

Spatial predictions of expected habitat capability alone will not be sufficient. Capable habitat does not always equate to occupied habitat. There are many reasons that an organism may not be present in habitat that is suitable. Indeed, for many species of highest conservation concern, such as forest carnivores, there may be large areas of potentially capable habitat that are not occupied due to past eliminations of local populations due to hunting, trapping and poisoning, for example. Thus, it is essential to conduct large scale, grid-based, representative surveys to document the distribution and range of species of concern. Grid-based monitoring efforts such as the National Wildlife Pilot (Cushman and McKelvey in prep), and FIA provide the framework for such monitoring efforts, as well as the data to develop the habitat relationships models described above. It is essential to document both expected habitat quality and actual patterns of habitat occupancy to guide forest management.

Expected habitat quality and occupancy provide a means predict to distribution and abundance. However, these predictions may not be sufficient to infer population-level implications. For example, occupied habitat does not provide a perfect surrogate for habitat quality. Organisms may be present in habitats in which they have negative vital rates (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991), and it is important to quantify the relationships between habitat characteristics at a range of scales and demographic parameters such as survivorship and reproduction. To reliably understand relationships between habitat area and fragmentation it is essential to quantify demographic responses as well as distributions along gradients of environmental structure. Thus, it is also important to invest in research that can measure vital rates on large grid-based sampling regimes.

While habitat area tends to be more important than habitat fragmentation, the specific relationships between organisms and their environment will depend on specifics of life history and ecological requirements. It would be erroneous and dangerous to ignore habitat patterns entirely and focus exclusively on habitat amounts. Habitat structure at a range of spatial scales can have large influences on organism distribution (Cushman and McGarigal 2004), movements (Gambel et al. submitted, Cushman et al. submitted), gene flow (Coulon et al. 2004, Cushman et al. in prep) and a range of other phenomena (Levin 1992, Cushman et al. in prep.). Much further research is needed to investigate the interactions between habitat area, configuration and ecological processes. Importantly, reliable maps of habitat quality and species distributions are essential for meaningful spatial analysis of habitat area and configuration. Once reliable spatial predictions of species habitat, distributions, vegetation condition, old growth and other resources of interest are available, informative spatial analyses will be possible. However, sophisticated spatial analysis of an inaccurate map is not meaningful. A central focus must be given to accurate, multi-scale modeling and mapping of forest resources. Once reliable spatial predictions are available, spatial analysis to associate extent and pattern of habitat, vegetation, and other forest resources should follow the steps outlined in the protocol below to evaluate landscape patterns with respect to historic ranges of variability and with respect to influences on species distributions and abundances, vegetation structure and key ecological processes such as fire regimes and climate change (Cushman et al. in prep.).

Implications for Natural Resources Management

Currently, adequate knowledge of habitat requirements, distributions and sensitivity to habitat fragmentation is lacking for most species of management concern. In the absence of reliable information, it would be wise for managers to adopt a conservative approach in which habitat conditions are maintained well within their ranges of natural variability across broad landscapes (Swanson et al. 1990). In the absence of reliable diagnostic models it would be prudent to err on the side of caution with regard to habitat area and connectivity. To paraphrase Leopold (1949), the first rule to intelligent management in the face of uncertainty is to maintain flexibility. Land management often imparts a legacy of habitat loss and fragmentation that can take centuries to erase (Wallin et al. 1996). Thus, adaptive management will require treatments that are reversible in terms of their impacts on habitat areas and configurations within reasonably short planning horizons. Great care must be given to ensure that current and future management actions do not impair the flexibility of ecological systems to respond to changes in management as improved knowledge of species-habitat relationships becomes available.

The predominant importance of habitat area and the lesser importance of habitat fragmentation and connectivity for most species suggest that management targeted at maintaining or enhancing biodiversity should first focus on preserving and expanding habitat core areas or increasing the number of habitat core areas. These have well-documented positive benefits in all cases, if habitat is adequately defined with respect to the species of concern. It would be very questionable to attempt to mitigate for habitat loss through efforts to increase connectivity (Fahrig 2003). Fragmentation and connectivity can be important and should be considered. But, attempts to use putative corridors or linkage zones to mitigate the effects of

habitat loss are unlikely to be successful. Methods are currently under development to quantify species-specific relationships between habitat patterns and population connectivity (e.g. Cushman et al. submitted, Compton et al. in prep., Cushman et al. in prep.). However, until the interactions between habitat area, pattern and population connectivity are understood for species of concern, focus should remain firmly on protecting remaining habitats, expanding core habitats, and restoring degraded habitat areas (Fahrig 2003).

As improved knowledge of species-environment relationships becomes available, managers should adopt quantitative approaches to predict, map and future habitat quality under a range of scenarios. A two part program, composed of large scale grid-based monitoring and multi-scale gradient modeling of species-environment relationships, such as being implemented in the National Wildlife Pilot (Cushman and McKelvey in prep), would provide managers the means to integrate the best available science into timely, fine-scale management applications. Linking these multi-scale empirical models with landscape simulations of the influences of alternative future scenarios on the extent and pattern of habitat will provide a means for managers to proactively investigate the potential effects of management alternatives and their interaction with natural disturbance regimes and climatic change (Cushman et al. in prep.).

ISSUES IN THE QUANTITATIVE ANALYSIS OF HABITAT LOSS AND FRAGMENTATION

The Primer in the previous section clearly illustrates that habitat loss and fragmentation is a complex, multidimensional process. Consequently, the quantitative analysis of habitat loss and fragmentation is fraught with numerous difficult issues. In this section, we review some of the most critical of these issues and emphasize those with practical implications with regards to how one actually measures fragmentation. Specifically, we address the issues of deciding on an appropriate model of landscape structure, scale of analysis, and spatiotemporal context for assessing habitat loss and fragmentation, and we describe a parsimonious suite of measures of habitat loss and fragmentation?

What is the Appropriate Model of Landscape Structure?

As noted in the Primer, there are many ways to model or represent landscape structure corresponding to different perspectives on habitat fragmentation. For example, in the *island biogeographic* model the landscape is represented as a simple binary landscape consisting of habitat patches and a background matrix. In this case, habitat is represented as occurring in discrete patches distributed in an ecologically neutral (or at least homogeneous) matrix. In contrast, in the *landscape mosaic* model the landscape is represented as a complex and spatially heterogeneous mosaic of patches, some of which represent habitat patches--but of varying degrees of suitability (or quality), others of which represent patches that confer varying degrees of resistance to the target organism. The difference between these or other models of landscape structure centers on the notion that habitat fragmentation occurs only in reference to a specific habitat as perceived by one or more target organisms. Thus, the appropriate model of landscape

structure depends on the target organism(s) under consideration. The same landscape can be modeled or represented, and subsequently analyzed, in many different ways. It is incumbent on the investigator or manager to select a model that adequately represents the landscape in a manner and scale relevant to the focal organism(s) under consideration.

For example, on the San Juan National Forest in southwest Colorado, the same high elevation landscape can be represented in different ways and at different resolutions of classification (Fig. 5). We might define late-seral spruce-fir forest as habitat for suite of target organisms and consider all other land cover as ecologically neutral, as in the island biogeographic perspective (Fig. 5a). Alternatively, for most organisms associated with late-seral spruce-fir forest, it is probably more realistic to consider other forest cover types and/or seral stages as providing habitat of varying degrees of suitability and perhaps contributing differentially to the functional isolation (or connectedness) of the late-seral spruce-fir patches, as in the landscape mosaic perspective (Fig. 5b). In addition, while some organisms may perceive and respond to changes in the amount and distribution of late-seral spruce-fir forest, other organisms may exhibit more general associations with late-seral *conifer* forest of any composition. In this case, it may be more meaningful to represent the landscape with more broadly defined patches, for example where late-seral spruce-fir forest is aggregated with other conifer forest types (e.g., mixed-conifer) into a late-seral conifer condition (Fig. 5c-d). Or for some organisms it might be more meaningful to consider all late-seral forest, including both deciduous (e.g., aspen) and coniferous forest, or perhaps all forest as a single comprehensive class (Fig. 5e-f). In all of these examples, the landscape has been classified into patches based on properties of the vegetation cover. This may be very meaningful for some organisms but not for others. For example, soil organisms are likely to be more sensitive to soil characteristics (e.g., depth, texture, wetness, organic matter, pH, etc.) than to above-ground vegetation. For these organisms, the landscape might be better modeled as a mosaic of soil patches. There are in fact many other legitimate frameworks for classifying the landscape. The key point here is that there are many ways to “slice” the landscape. The correct model of landscape structure ultimately depends on the organism(s) under consideration.

Unfortunately, in most applications we are interested in many species, not just a single species. Given that each species perceives and scales habitat differently, it is impossible to choose a single classification scheme at a single resolution and simultaneously model the landscape in a way that is equally relevant to all species. Does this mean that the landscape must be analyzed separately for each species—a daunting and impractical task to say the least? Ideally, with perfect knowledge of every species' habitat requirements, we would develop a species-specific model of landscape structure and analyze each species separately. However, we do not know enough about most organisms to accurately define their habitat requirements. In addition, many organisms have similar habitat associations and can be treated collectively, e.g., as a guild. Thus, in practice it is necessary to apply a combination coarse- and fine-filter approach to the analysis of habitat fragmentation. In the *coarse filter*, the landscape is classified and analyzed at one or more resolutions, with the understanding that the habitat patches being represented are generally important to many organisms and ecological processes. Here, the landscape is classified using criteria known to be important to many organisms and processes.

For example, vegetation structure and floristics are widely accepted to be important factors influencing vertebrate communities. Therefore, a classification of land cover types (patches) using these factors will likely be important and relevant to many organisms, but not perfect for any organism. In the *fine filter*, the landscape is classified and analyzed separately for select species of special interest and where their habitat requirements are well understood. The combination coarse- and fine-filter approach can provide a reasonably comprehensive assessment of habitat loss and fragmentation.

Regarding models of landscape structure, it is important to recognize that there are different data formats for digitally representing any model of the landscape, and there are practical implications to the choice of formats. Vector and raster data formats are both commonly used in landscape ecological investigations (Fig. 6). In a vector format, each patch is represented as a polygon, where the boundaries of the polygon conform to the actual boundaries of the patch in the real world. In a raster format, the landscape is represented as a lattice of grid cells, in which each cell is assigned a value corresponding to the patch type or class comprising the majority of the cell. Patches are created by outlining contiguous cells of the same patch type. The choice between formats is largely a technical one and hinges upon available data and computer software (e.g., GIS), but there are practical implications. For example, because vector and raster formats represent lines differently, metrics involving edge or perimeter will be affected by the choice of formats (Fig. 6). Edge lengths will be biased upward in raster data because of the stair-step outline, and the magnitude of this bias will vary in relation to the grain or resolution of the image. The key point here is that many landscape metrics used to assess habitat fragmentation (see below) are not invariant to the data format, and some metrics are defined only for vector or raster formats. In this regard, the raster format has gained popularity over the vector format because of the ease of conducting complex spatial computations on grids.

What is the Appropriate Scale of Analysis?

The ability to detect pattern is a function of scale, and the spatial scale of ecological data encompasses both extent and grain (Forman and Godron 1986, Turner et al. 1989, Wiens 1989a). *Extent* is the overall area encompassed by an investigation or the area included within the landscape boundary. From a statistical perspective, the spatial extent of an investigation is the area defining the population (in a statistical sense) we wish to sample. *Grain* is the size of the individual units of observation. For example, a fine-grained map might structure information into 1-ha units, whereas a map with an order of magnitude coarser resolution would have information structured into 10-ha units (Turner et al. 1989). Extent and grain define the upper and lower limits of resolution of a study, respectively, and any inferences about scale-dependency in a system are constrained by the extent and grain of investigation (Wiens 1989a). From a statistical perspective, we cannot extrapolate beyond the population sampled, nor can we infer differences among objects smaller than the experimental units. Likewise, in the assessment of landscape structure, we cannot generalize beyond the extent of the investigation or landscape and we cannot detect pattern below the resolution of the grain (Wiens 1989a).

In practice, extent and grain are often dictated by the scale of the imagery (e.g., aerial photos, Landsat images) being used or the technical capabilities of the computing environment. However, it may be more ecologically meaningful to define scale from the perspective of the organism or ecological phenomenon under consideration. For example, from an organism-centered perspective, grain and extent may be defined as the degree of acuity of a stationary organism with respect to short- and long-range perceptual ability (Kolasa and Rollo 1991). Thus, grain is the finest component of the environment that can be differentiated up close by the organism, and extent is the range at which a relevant object can be distinguished from a fixed vantage point by the organism (Kolasa and Rollo 1991). While this is ecologically an ideal way to define scale, it is not very pragmatic.

It is critical that extent and grain be defined for a particular study and represent, to the greatest possible degree, the ecological phenomenon or organism under study; otherwise, the landscape patterns detected will have little meaning and there is a good chance of reaching erroneous conclusions. For example, it would be meaningless to define grain as 1-ha units when the organism under consideration perceives and responds to habitat patches at a resolution of 1-m². A strong landscape pattern at the 1-ha resolution may have no significance to the organism under study. Similarly, it would be meaningless to define the landscape extent as 1-km² when the organism under consideration has a home range size several times that size. Typically, however, we do not know what the appropriate resolution should be. In this case, it is much safer to choose a finer grain than is believed to be important because the grain sets the minimum resolution of investigation. Once set, we can always resample to a coarser grain. In addition, we can always specify a minimum mapping unit that is coarser than the grain. That is, we can specify the minimum patch size to be represented in a landscape, and this can easily be manipulated above the grain size. Indeed, it may be useful to reanalyze the same landscape using progressively coarser minimum patch sizes to better assess landscape heterogeneity across a range of potentially relevant scales. Thompson and McGarigal (2002) used this approach successfully to define the “best” scale (grain and extent) for representing bald eagle habitat along the Hudson River, New York.

It is important to recognize the practical implications of the choice of grain and extent for a particular application. Many of the landscape metrics used to quantify habitat fragmentation (see below) are particularly sensitive to grain. Metrics involving edge or perimeter will be affected; edge lengths will be biased upwards in proportion to the grain size—larger grains result in greater bias. Edge lengths can vary by as much as 25-50% over vector calculations depending on grain size. Metrics based on cell adjacency information such as the contagion index of Li and Reynolds (1993) will be affected as well, because grain size effects the proportional distribution of adjacencies. In this case, as resolution is increased (grain size reduced), the proportional abundance of like adjacencies (cells of the same class) increases, and the measured contagion increases (Fig. 7). Similarly, the measured degree of habitat fragmentation may vary with extent, especially if the habitat is not uniformly distributed throughout the entire study area (Fig. 8). Intuitively this makes sense, because as the landscape extent increases, new patch types may be encountered and habitat configurations may change in response to underlying environmental or land use gradients.

The ratio of grain to extent for a particular analysis warrants consideration as well. If the ratio is very small (i.e., a coarse-grained map), then the landscape dynamics are likely to be dominated by boundary effects, analogous to the bias associated with small sample size in statistics (Fig. 9). Moreover the boundary of the landscape can have a profound influence on the value of certain metrics. Landscape metrics are computed solely from patches contained within the landscape boundary. If the landscape extent is small relative to the scale of the organism or ecological process under consideration and the landscape is an “open” system relative to that organism or process, then any metric will have questionable meaning. Metrics based on nearest neighbor distance or employing a search radius can be particularly misleading. Consider, for example, a local population of a bird species occupying a patch near the boundary of a somewhat arbitrarily defined landscape. The nearest neighbor within the landscape boundary might be quite far away; yet, in reality, the closest patch might be very close but just outside the designated landscape boundary. In addition, those metrics that employ a search radius (e.g., proximity index) will be biased for patches near the landscape boundary because the searchable area will be much less than a patch in the interior of the landscape. In general, boundary effects will increase as the landscape extent decreases relative to the patchiness or heterogeneity of the landscape (Fig. 9). The key point is that some landscape metrics are likely to be very sensitive to this ratio (e.g., those based on nearest-neighbor distances such as the mean proximity index, Gustafson and Parker 1992 and 1994).

Information may be available at a variety of scales and it may be necessary to extrapolate information from one scale to another. In addition, it may be necessary to integrate data represented at different spatial scales. It has been suggested that information can be transferred across scales if both grain and extent are specified (Allen et al. 1987), yet it is unclear how observed landscape patterns vary in response to changes in grain and extent. The limited work on this topic suggests that qualitative and quantitative changes in measurements across spatial scales will differ depending on how scale is defined (Turner et al. 1989) and that metrics vary markedly in their sensitivity to scale and the nature of the scaling relationships (Wickham and Riitters 1995, O'Neill et al. 1996, Saura and Martinez-Millan 2001, Saura 2002, Wu et al. 2002). In investigations of landscape structure, until more is learned, any attempts to compare landscapes measured at different scales should be done cautiously.

The key point here is that any model of landscape structure requires an explicit identification of scale. Unfortunately, in many applications, scale is selected arbitrarily or defined by technical considerations and the ecological significance of the scale-imposed limitations are dismissed or not recognized. In any landscape structural analysis, it is incumbent upon the investigator or manager to select a scale (i.e., extent, grain, minimum mapping unit) that is appropriate to the phenomenon under consideration, because any interpretation of landscape structure is ultimately constrained by the scale. In addition, any observed patterns or relationships should be described relative to the limitations imposed by the scale of the investigation. For these reasons, in most applications a multi-scale assessment of habitat loss and fragmentation is recommended, in which a relevant landscape model is established across a broad range of scales (i.e., grain and extent).

What is the Relevant Spatiotemporal Context for Assessing Habitat Loss and Fragmentation?

Landscapes do not exist in isolation. Landscapes are nested within larger landscapes, that are nested within larger landscapes, and so on. In other words, each landscape has a context or regional setting, regardless of scale and how the landscape is defined. The landscape context may constrain processes operating within the landscape. Landscapes are "open" systems; energy, materials, and organisms move into and out of the landscape. This is especially true in practice, where landscapes are often somewhat arbitrarily delineated. That broad-scale processes act to constrain or influence finer-scale phenomena is one of the key principles of hierarchy theory (Allen and Star 1982) and 'supply-side' ecology (Roughgarden et al. 1987). The importance of the landscape context is dependent on the phenomenon of interest, but typically varies as a function of the "openness" of the landscape. The "openness" of the landscape depends not only on the phenomenon under consideration, but on the basis used for delineating the landscape boundary. For example, from a geomorphological or hydrological perspective, the watershed forms a natural landscape, and a landscape defined in this manner might be considered relatively "closed". Of course, energy and materials flow out of this landscape and the landscape context influences the input of energy and materials by affecting climate and so forth, but the system is nevertheless relatively closed. Conversely, from the perspective of a bird population, topographic boundaries may have little ecological relevance, and the landscape defined on the basis of watershed boundaries might be considered a relatively "open" system. Local bird abundance patterns may be produced not only by local processes or events operating within the designated landscape, but also by the dynamics of regional populations or events elsewhere in the species' range (Wiens 1981, 1989b, Vaisanen et al. 1986, Haila et al. 1987, Ricklefs 1987).

Fragmentation metrics quantify the amount and configuration of habitat within the designated landscape boundary only. Consequently, the interpretation of these metrics and their ecological significance requires an acute awareness of the landscape context and the openness of the landscape relative to the extent of the landscape and the organism(s) under consideration. In particular, the focal habitat may be quite rare and fragmented in distribution at one landscape extent, but form a highly connected matrix at a broader or finer extent (Fig. 10). Moreover, the ecological consequences of the measured habitat fragmentation may vary depending on the landscape extent in relation to the character of the landscape context. For example, a fragmented habitat distribution at one scale nested within a regional landscape context in which that habitat is abundant and highly connected may function differently than if that habitat is similarly rare and fragmented within the regional context as well (e.g., McGarigal and McComb 1995; Fig. 10a). Likewise, an abundant and unfragmented habitat distribution at the focal scale may not function as expected if the habitat is rare and highly fragmented within the broader context (Fig. 10b). Hence, any assessment of habitat loss and fragmentation should include at least a qualitative assessment of habitat conditions within the broader regional context.

The interpretation of fragmentation metrics at any scale is further plagued by the lack of a proper temporal reference framework. Fragmentation metrics quantify the pattern of habitat at a snapshot in time. Yet it is often difficult, if not impossible, to determine the ecological

significance of the computed value without understanding the range of natural variation in habitat pattern. For example, in disturbance-dominated landscapes, habitat patterns may fluctuate widely over time in response to the interplay between disturbance and succession processes (e.g., Wallin et al. 1996, He and Mladenoff 1999, Haydon et al. 2000, Wimberly et al. 2000, McGarigal et al. 2001). It is logical, therefore, that landscape metrics should exhibit statistical distributions that reflect the natural spatial and temporal dynamics of the landscape. By comparison to this distribution, a more meaningful interpretation can be assigned to any computed value. Despite widespread recognition that landscapes are dynamic, there are few studies quantifying the range of natural variation in landscape pattern metrics (Neel et al. 2004). This remains one of the greatest challenges confronting landscape pattern analysis.

For example, high elevation landscapes in the San Juan Mountains of southwestern Colorado are spatially and temporally dynamic as a result of disturbance and succession processes (e.g., Romme and Despain 1989, Bessie and Johnson 1995, Weir et al. 1995, Schmid and Mata 1996, Roworth et al. submitted). The natural disturbance regime is dominated by relatively infrequent, large-scale fires that, in large part, control the coarse-grained mosaic of vegetation types and seral stages (Romme et al. 2000). Using a stochastic fire simulation model (RMLANDS), we simulated changes in landscape patterns over hundreds of years under a range of natural disturbance regimes (Roworth et al. submitted) and modeled changes in habitat for several species (Crist et al. submitted). Not surprisingly, the amount and fragmentation of habitats varied over time in response to the interplay between disturbance and succession processes. Figure 11 depicts the expected change in the abundance and configuration (measured here with the clumpiness index) of late-seral conifer forests (Fig. 11a-b) and the corresponding change in suitable American marten (*Martes americana*) habitat (Fig. 11c-d) over a 600-year period under the current climate disturbance regime. These results illustrate the dynamic nature of habitats. More importantly, these results provide a temporal framework for interpreting habitat fragmentation.

What are the Best Measures of Habitat Loss and Fragmentation?

Clearly, given the number and variety of components of landscape structure affected by habitat loss and fragmentation (see Primer), it is unreasonable to expect a single metric, or even a few metrics, to be sufficient (Neel et al. in prep.). Therefore, a truly multivariate approach is warranted in most applications. Unfortunately, the selection of a suite of fragmentation metrics is constrained by the lack of a proper theoretical understanding of metric behavior. The proper interpretation of a landscape metric is contingent upon having an adequate understanding of how it responds to variation in landscape patterns (e.g., Gustafson and Parker 1992, Hargis et al. 1998, Jaeger 2000, Neel et al. 2004). Failure to understand the theoretical behavior of the metric can lead to erroneous interpretations (e.g., Jaeger 2000). Neutral models (Gardner et al. 1987, Gardner and O'Neill 1991, With 1997) provide an excellent way to examine metric behavior under controlled conditions because they control the process generating the pattern, allowing unconfounded links between variation in pattern and the behavior of the index (Gustafson 1998). Unfortunately, neutral models of fragmentation under various forms of fragmentation (e.g., random, contagious, disperse, corridor, edge, and nuclear; see Primer) have not been used in a

comprehensive manner to evaluate a broad array of metrics. Therefore, it is not possible to reliably identify the "best" measures of habitat loss and fragmentation. Rather, the measures described below provide a comprehensive, yet parsimonious, suite of metrics for quantifying habitat loss and fragmentation, and are recommended until such time as a more thorough investigation of metric behavior is completed.

As described in the Primer, there are five major spatial components to habitat loss and fragmentation: (1) habitat extent, (2) habitat subdivision, (3) patch geometry, (4) habitat isolation, and (5) habitat connectedness (see the Primer for a complete discussion of these components). Numerous landscape metrics have been developed for each of these components (e.g., Baker and Cai 1992; McGarigal and Marks 1995; Jaeger 2000, McGarigal et al. 2002). However, these categories are not discrete and many landscape metrics measure properties that relate to several components. Thus, a simple classification of metrics into these categories is not straightforward. Nevertheless, this classification has practical utility because it ensures that a comprehensive suite of metrics is selected. In the sections below, we identify and describe a parsimonious suite of metrics for measuring habitat loss and fragmentation (Table 1). It is important to note that the specific metrics included here do not represent a comprehensive list of useful fragmentation metrics and do not necessarily include the "best" metrics as considered from any one perspective. Rather, given the overwhelming number and variety of available metrics, it was our intent to suggest a parsimonious suite of metrics that measure different aspects of habitat loss and fragmentation and that when taken together may provide a comprehensive assessment of habitat loss and fragmentation in most applications.

Habitat Extent.—Habitat extent represents the total areal coverage of the target habitat in the landscape and is a simple measure of landscape composition, represented by the following metric:

- **Percentage of Landscape.**—A straightforward and intuitive metric that measures habitat extent in relative terms is the *percentage of the landscape* (PLAND) comprised of the target habitat (Fig. 12), defined as follows:

$$\text{PLAND} = P_i = \frac{\sum_{j=1}^n a_{ij}}{A} (100)$$

where P_i equals the proportion of the landscape occupied by the i^{th} patch type (the focal habitat); a_{ij} is the area (m^2) of the j^{th} patch; and A is the total landscape area (m^2). PLAND approaches 0 when the corresponding patch type (class) becomes increasingly rare in the landscape. PLAND equals 100 when the entire landscape is comprised of the focal patch type; that is, when the entire image is comprised of a single patch. PLAND is a relative measure, as opposed to total class area, and therefore may be used for comparing among landscapes of varying sizes. PLAND is not affected in any way by the spatial distribution or configuration of habitat patches.

Habitat Subdivision.—Habitat subdivision deals explicitly with the degree to which the habitat has been broken up into separate patches (i.e., fragments), *not* the size, shape, relative location, or spatial arrangement of those patches. Because these latter attributes are usually affected by subdivision, it is difficult to isolate subdivision as an independent component. Subdivision can be measured in a variety of ways, but it is perhaps best defined by the absolute or relative number of patches, the degree of habitat aggregation or clumpiness, and the degree of subdivision derived from a geometric view based on the cumulative distribution of patch sizes, as represented by the following metrics:

- **Number of Patches or Patch Density.**—A simple and direct measure of habitat subdivision is given by the *number of patches* (NP) or, alternatively, *patch density* (PD)(Fig. 13). Unfortunately, both of these measures are difficult to interpret by themselves without also considering habitat area. Nevertheless, regardless of habitat area, as the number of habitat patches increases, technically the habitat becomes more fragmented (subdivided into disjunct patches). For this reason, this metric is often reported as a basic descriptor of habitat subdivision. The choice between NP or PD largely depends on the application. If more than one landscape is involved and they are different sizes, then PD is the more logical formulation because patch number is standardized to a per unit area. However, if a single landscape or multiple landscapes of equal extent are involved, the two formulations are equivalent and the choice becomes one of personal preference.
- **Clumpiness.**—A useful measure of habitat subdivision is given by the *clumpiness index* (CLUMPY) which measures the degree to which the focal habitat is aggregated or clumped given its total area (Fig. 13). CLUMPY is calculated from the adjacency matrix, which shows the frequency with which different pairs of patch types (including like adjacencies between the same patch type) appear side-by-side on the map. CLUMPY is scaled to account for the fact that the proportion of like adjacencies (G_i) will equal P_i for a completely random distribution (Gardner and O'Neill 1991), and is defined as follows:

$$\text{Given } G_i = \left(\frac{g_{ii}}{\left(\sum_{k=1}^n g_{ik} \right) - n e_i} \right)$$

$$\text{CLUMPY} = \left[\begin{array}{l} \frac{G_i - P_i}{P_i} \text{ for } G_i < P_i \text{ \& } P_i < .5, \text{ else} \\ \frac{G_i - P_i}{1 - P_i} \end{array} \right]$$

where g_{ii} is the number of like adjacencies (joins) between pixels of patch type (class) i ,
 g_{ik} is the number of adjacencies (joins) between pixels of patch types (classes) i and k ,

min e_i = minimum perimeter (in number of cell surfaces) of patch type (class) i for a maximally clumped class, and P_i is the proportion of the landscape occupied by patch type (class) i . The formula is contingent upon G_i and P_i because the minimum value of G_i has two forms which depend on P_i . Specifically, when $P_i \leq 0.5$, $G_i = 0$ when the class is maximally disaggregated (i.e., subdivided into one cell patches) and approaches 1 when the class is maximally clumped. However, when $P_i \geq 0.5$, $G_i = 2P_i - 1$ when the class is maximally disaggregated and approaches 1 when the class is maximally clumped. Given any P_i , CLUMPY equals -1 when the focal patch type is maximally disaggregated; CLUMPY equals 0 when the focal patch type is distributed randomly, and approaches 1 when the patch type is maximally aggregated. Thus, CLUMPY has a straightforward and intuitive interpretation that indicates whether the focal habitat is more or less clumped than expected by chance alone. Note, because CLUMPY is based on “cell” adjacencies, it is sensitive to the grain size or resolution of the landscape. As the grain size is reduced (i.e., the landscape is mapped at a finer resolution), the proportion of like adjacencies will increase and the landscape will appear to be more clumped. Thus, this metric, like most others, must be interpreted in reference to the resolution of the map and is perhaps best used as a comparative index for comparing among different landscapes or the same landscape over time.

- **Degree of Landscape Division.**--Jaeger (2000) presented a new suite of indices that measure habitat subdivision from a geometric point of view and are calculated from the cumulative distribution function of the habitat patch sizes. *Degree of landscape division* (DIVISION) equals the probability that two randomly chosen places in the landscape under investigation are not situated in the same contiguous habitat patch (Fig. 13). Thus, as the habitat becomes increasingly subdivided into smaller patches, the probability increases that two randomly chosen locations will belong to separate patches. DIVISION is defined as follows:

$$\text{DIVISION} = \left[1 - \sum_{j=1}^n \left(\frac{a_{ij}}{A} \right)^2 \right] \quad (100)$$

where a_{ij} is the area (m^2) of patch ij and A is the total landscape area (m^2). DIVISION equals 0 when the landscape consists of a single patch, and approaches 100 as the proportion of the landscape comprised of the focal patch type decreases and as those patches decrease in size. DIVISION is maximum when the focal patch type consists of single one-cell patches. Conceptually, DIVISION and its related metrics (the splitting index and effective mesh size, not described here) are similar to simple measures of number of patches and average patch size, but they possess desirable mathematical properties that make them superior to the simpler measures. In particular, they have low sensitivity to very small patches, behave monotonically to the various fragmentation phases, and are sensitive to structural differences in the landscape mosaic (Jaeger 2000). DIVISION is closely related and effectively redundant with the area-weighted mean size of focal habitat patches, which explains its insensitivity to very small patches (i.e., small patches are given very little weight). Note, unlike CLUMPY, DIVISION (at the class

level) is effected by both habitat extent and subdivision, thus confounding these two components. Consequently, this metric must be interpreted in conjunction with PLAND and is perhaps best used as a comparative index for comparing among different landscapes with the same habitat extent.

Patch Geometry.—Patch geometry deals explicitly with the spatial character of habitat patches. Given the myriad aspects of patch geometry, there exists a wide variety of patch geometry metrics. Here we focus exclusively on “core area” because it integrates several aspects of patch geometry relevant to habitat fragmentation. Core area is defined as the area within a patch beyond some specified depth-of-edge effect distance. Holding patch area constant, as a patch becomes more convoluted and complex in shape, core area decreases because less of the patch is greater than the specified depth-of-edge distance from the perimeter. Core area measures are particularly sensitive to habitat subdivision because, as just noted, they are sensitive to basic perimeter-area relationships. For example, holding the total area of habitat constant, the subdivision of habitat automatically decreases core area because of the increase in the ratio of habitat perimeter to area. Concomitant habitat loss and subdivision results in an even greater decrease in core area. Although there are many alternative ways to index core area, they all measure the same basic integrated aspect of patch geometry and are therefore largely redundant. Consequently, a single metric is sufficient, as follows:

- **Core Area Index.**—The *core area index* (CAI) is basically an edge-to-interior ratio like many shape indices (McGarigal et al 2002), the main difference being that the core area index treats edge as an area of varying width and not as a line (perimeter) around each patch (Fig. 14). CAI is computed at the patch level, as follows:

$$CAI = \frac{a_{ij}^c}{a_{ij}} (100)$$

where a_{ij}^c is the core area (m^2) of patch ij based on specified depth-of-edge distances (m), and a_{ij} is the area (m^2) of patch ij . In other words, CAI equals the percentage of a patch that is core area. CAI can be averaged across all patches of the focal habitat (weighted by patch area) to provide a suitable class-level metric, or an equivalent *total core area index* (TCAI) can be calculated directly, as follows:

$$TCAI = \frac{\sum_{j=1}^n a_{ij}^c}{\sum_{j=1}^n a_{ij}} (100)$$

TCAI is equivalent to the *area-weighted mean core area index* (CAI_AM) reported in FRAGSTATS (McGarigal et al. 2002). TCAI equals 0 when there is no core area (i.e., every location within the focal habitat is within the specified edge influence distance from the habitat edge); that is, when the habitat contains no core area. TCAI approaches 100 when the habitat, because of patch size, shape, and edge width, contains mostly core

area. TCAI is a relative index; it does not reflect patch size, class area, or total landscape area; it merely quantifies the percentage of available area, regardless of whether it is 10 ha or 1,000 ha, comprised of core. Consequently, this index does not confound area and configuration; rather, it isolates the configuration effect. For this reason, the core area index is probably best interpreted in conjunction with total habitat area, or its relativized equivalent – PLAND.

Habitat Isolation.—Habitat isolation deals explicitly with the spatial and temporal *context* of habitat patches, rather than the spatial character of the patches themselves. Unfortunately, isolation is a difficult thing to capture in a single measure because there are many ways to quantify context. Isolation can be measured in the spatial dimension in several ways, depending on how one views the concept of isolation. Here, we focus exclusively on a measure of neighborhood similarity, or, conversely, contrast, within a specified ecological neighborhood surrounding each habitat patch. Isolation is measured by the degree of contrast (i.e., the magnitude of differences in one or more attributes between adjacent patch types) between the focal habitat and neighboring patches.

- **Similarity Index.**—The *similarity index* (SIMILAR) is a patch-level measure of neighborhood similarity (McGarigal et al. 2002). It considers the size and proximity of all patches, regardless of class, whose edges are within a specified search radius of the focal patch (Fig. 15). SIMILAR is computed at the patch level, as follows:

$$\text{SIMILAR} = s_{ij} = \sum_{s=1}^n \frac{a_{ijs} * d_{ik}}{h_{ijs}^2}$$

where a_{ijs} is the area (m^2) of patch ijs within the specified neighborhood (m) of the focal patch; d_{ik} is the similarity (coefficient between 0-1) between the focal patch (type i) and the k^{th} patch within the specified neighborhood; and h_{ijs} is the distance (m) between the focal patch and each neighboring patch ijs , based on patch edge-to-edge distance. SIMILAR can be averaged across all patches of the focal class (weighted by patch area) to provide a suitable class-level metric, as follows:

$$\text{SIMILAR_AM} = \sum_{j=1}^n \left[s_{ij} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$$

SIMILAR_AM equals 0 if all the patches surrounding the focal habitat patches have a zero similarity coefficient (i.e., maximum contrast). SIMILAR_AM increases as the habitat patches are increasingly surrounded by patches with greater similarity coefficients and as those similar patches become closer and more contiguous in distribution. The similarity index quantifies the spatial context of a (habitat) patch in relation to its neighbors of the same or similar class; specifically, the index distinguishes sparse distributions of small and insular habitat patches from configurations where the habitat forms a complex cluster of larger, hospitable (i.e., similar) patches. Note, in a binary

landscape consisting of the focal habitat class and a non-habitat matrix, as might be represented under an island biogeographic perspective on landscape structure (see Primer), the similarity index reduces to the proximity index given in FRAGSTATS [see also Gustafson and Parker (1992) and Whitcomb et al. (1981)], which considers only patches of the focal class. Note, the similarity index must be interpreted carefully in relation to habitat extent. Specifically, because it is computed at the patch level and considers only the composition of the landscape surrounding each habitat patch, not the area of the patch itself, it can exhibit erroneous behavior under certain circumstances. For example, when the focal habitat comprises most (or all) of the landscape and is connected into a single matrix-forming patch, SIMILAR_AM equals 0 because there are no other (similar) habitat patches in the neighborhood, implying isolation when in fact the habitat is both abundant and highly connected. Thus, SIMILAR_AM is best interpreted in conjunction with PLAND and its use should probably be limited to landscapes in which the focal habitat is not matrix forming (i.e., typically say PLAND < 30-40%) and consists of multiple patches.

Connectedness.—Connectedness integrates all of the above components and involves both a structural component (continuity) and a functional component (connectivity)[see Primer for a detailed discussion]. As noted previously, it is difficult to isolate connectedness in a metric owing to the myriad constituent components. Consequently, the range of available connectedness metrics is somewhat limited; although, this is an area of active development in landscape pattern analysis so new measures will likely become available in the future. Here we focus on a single continuity metric and a single connectivity metric. Note, however, that there is considerable redundancy between these metrics and the suggested isolation and subdivision metrics.

- **Correlation length.**—A useful measure of the continuity or structural connectedness of habitat is the *correlation length index* (CLI)(Keitt et al. 1997), which is derived from the patch *radius of gyration* (GYRATE), as follows:

$$\text{GYRATE} = g_{ij} = \sum_{r=1}^z \frac{h_{ijr}}{z}$$

where h_{ijr} is the distance (m) between cell ijr [located within patch ij] and the centroid of patch ij (the average location), based on cell center-to-cell center distance; and z is the number of cells in patch ij . GYRATE equals the mean distance (m) between each cell in the patch and the patch centroid and represents the average distance an organism can move and stay within the patch boundary. The correlation length index (CLI) is computed as the *area-weighted average patch radius of gyration* (GYRATE_AM), as follows:

$$\text{CLI} = \text{GYRATE_AM} = \sum_{j=1}^n \left[g_{ij} \left(\frac{a_{ij}}{\sum_{j=1}^n a_{ij}} \right) \right]$$

where a_{ij} is the area of patch ij . CLI equals 0 when the habitat consists of single-cell patches and increases as the patches increase in extensiveness (Fig. 16). Correlation length is intuitively appealing, because as patches become smaller and more compact, they extend over less space and therefore provide for less physical continuity of the habitat across the landscape. Large and elongated patches extend over greater space and provide for greater connectedness of the habitat. Thus, holding habitat area constant, as the habitat becomes more subdivided during fragmentation, correlation length decreases. Correlation length can be interpreted as the average distance an organism might traverse the map, on average, from a random starting point and moving in a random direction, i.e., it is the expected traversability of the map (Keitt et al. 1997).

- **Traversability Index.**—A useful measure of the functional connectivity of habitat is given by the *traversability index* (TRAVERSE) based on the idea of ecological resistance (McGarigal et al. 2002). The premise is that a hypothetical organism dispersing from a focal habitat cell in a highly traversable neighborhood can reach a large area with minimal crossing of “hostile” cells. This metric uses a resistance surface to determine the area that can be reached from each cell in the focal habitat. The focal cell gets an organism-specific “bank account,” which represents, say, an energy budget available to the organism for dispersal from the focal cell. The size of the account is selected to reflect the organism’s dispersal or movement ability. Each patch type (including the focal patch type) is assigned a cost based on a user-specified resistance matrix. Specifically, relative to a each focal patch type, each patch type is assigned a resistance coefficient in the form of weights ranging from 1 (minimum resistance, usually associated with the focal patch type) to any higher number that reflects the relative increase in resistance associated with each patch type. The metric is computed by simulating movement away from the focal cell in all directions, where there is a cost to move through every cell. Under the best circumstances (i.e., minimum resistance), there will exist a maximum dispersal area based on the specified account or energy budget. Note that assigning a (small) cost for traveling through the focal community (typically a cost of 1) results in a linearly decaying function. Moving through more resistant cells costs more and drains the account faster. Thus, depending on the resistance of the actual landscape in the vicinity of the focal cell, there will be a certain area that a dispersing organism can access. This area represents the least-cost hull around the focal cell, or the maximum distance that can be moved from the cell in all directions until the “bank account” is depleted (Fig. 17). This dispersal area, given as a percentage of the maximum dispersal area under conditions of minimum resistance, provides a measure of the relative traversability of the landscape in the vicinity of the focal cell. Averaging this index across cells of the focal habitat provides a class-level index of traversability, computed as follows.

$$\text{TRAVERSE} = \left[\frac{\left(\frac{\sum_{r=1}^z t_{ir}}{z_i} \right)}{t_{\max}} \right] \quad (100)$$

where t_{ijr} is the least cost hull area around the r^{th} cell in the focal patch type (i); z_i is the total number of cells in the focal patch type (i); and t_{max} is the maximum least cost hull area around a cell of the focal patch type (i) given minimum resistance. TRAVERSE equals 0 when the focal habitat consists of one or more single-cell patches surrounded by hostile patch types that prevent any movement (i.e., function as barriers). This is achieved when the resistance coefficient for the neighboring patch type(s) is greater than the user-specified bank account for the focal cell. TRAVERSE equals 100 when the focal habitat is surrounded by minimally resistant patch types. TRAVERSE is computed at the cell level and then averaged across cells in the focal patch. As a result, this metric requires substantial computations and may take considerable time to compute for a large landscape. In addition, this metric requires the user to specify an appropriate resistance matrix containing coefficients for each pairwise combination of patch types, as well as a scaling factor that governs the size of the maximum least cost hull; that is, the size of the area surrounding the focal cell that is accessible given minimum resistance.

A PROTOCOL FOR ASSESSING HABITAT LOSS AND FRAGMENTATION

It should be clear from the previous sections that assessing habitat loss and fragmentation is a complex process involving many components. Some of the issues are conceptual and involve establishing clear objectives and perspectives on the fragmentation process. Other issues are technical and have significant implications for the computation and interpretation of selected fragmentation metrics. A thorough understanding of these issues is prerequisite to the effective application of the protocol that follows. In this section, we present a five-step protocol for quantifying habitat loss and fragmentation (Fig. 18). The protocol presented is not a cookbook with precise step-by-step instructions. Rather, it is a general process outlining broad steps and important considerations. The details of the analysis; that is, the decisions made at each step in the process, must be tailored to the specific context of the application.

Illustrated Example

To illustrate the general application of the protocol, we present a multi-faceted example from the San Juan National Forest in southwestern Colorado. Note, it is impractical to provide an illustrated example that covers all possible analytical contexts. Each application is unique; the specific decisions made in our example are not necessarily transferable to other applications, but the general approach is. What follows is a detailed description of the project area. This information provides useful background for our specific application of the assessment protocol; however, this section can be skipped if you desire a more cursory understanding of the example.

The project area encompasses roughly 40,000 ha of the Pagosa Ranger District on the San Juan National Forest and lies within the South Central Highlands Section of the southern Rocky Mountains Province in southwestern Colorado (Blair 1996; Fig. 19). The area comprises the Piedra River watershed and encompasses a portion of the Weminuche Wilderness area west of the continental divide. Elevation ranges from 2,400 m in the valley bottoms to over 4,200 m mountain peaks along the continental divide. The geology of the area is quite complex. Parent materials date from ancient Precambrian rocks to recent alluvial deposits (Ellingson 1996a, Campbell and Brew 1996). Current landforms were created by a variety of geomorphological processes, including plate tectonics, volcanism, glaciation, and erosion (Brew 1996, Ellingson 1996b, Blair 1996). The climate varies significantly in relation to the pronounced elevational and topographic gradients. Temperatures range from an average high of 73 degrees (c) in July to an average low of -1 degrees (c) in January. Precipitation ranges from a mean of more than 60 in (cm) on the highest peaks to less than 20 in (cm) in the lower reaches of the study area and usually falls in late summer (July and August) and winter (January through March), although there may be significant local variation (Keen 1996). Overall, the project area is typical of the South Central Highlands Section with respect to physiographic variation and landscape patterns.

The Greater San Juan Mountain Area, which includes the project area, supports some 507 native vertebrate species (Povilitis 1993), as well as biotic communities representative of eleven potential natural vegetation types (sensu Kuchler 1964). Thirty-two species of vascular plants

and 40 species of vertebrates are listed as endangered, threatened, or species of special concern at the state or federal level. Seven major vegetation types of ecological and economic significance occur within the project area. Each of these types has a unique ecological setting and history (Romme et al. 1992, Spencer and Romme 1996, Floyd-Hanna et al. 1996, Jamieson et al. 1996, Sommers et al. 1996), as well as distinctive human impacts and changes since Euro-American settlement. At the lowest elevations, the vegetation is dominated by pinon-juniper woodlands (primarily *Pinus edulis* and *Juniperus osteosperma*) and various kinds of grasslands. At the foothills and on tops of broad plateaus and mesas, the vegetation ranges into Ponderosa Pine (*Pinus ponderosa*) forest interspersed with shrub-dominated stands (Petran chaparral dominated by *Quercus gambelii*). The middle slopes are covered by a mosaic of mixed conifers (*Pinus ponderosa*, *Psuedotsuga menziesii*, *Abies concolor*, *Picea pungens*) and quaking aspen stands (*Populus tremuloides*), broken by occasional meadows. The highest elevations contain extensive spruce-fir forests (primarily *Picea engelmannii* and *Abies lasiocarpa*), subalpine meadows, and treeless alpine communities on the highest peaks. Running through all these types are riparian woodlands and meadows along the borders of perennial rivers and streams.

The San Juan Mountain country has never been static; there have been continual changes in the climate, geomorphology, vegetation, and human influences at least since the end of the Pleistocene ice age some 14,000 years ago. Rapid and substantial global warming around 14,000 years ago brought about the end of the ice age and caused dramatic readjustments in the distribution and abundance of the biota. Since the end of the Pleistocene, however, the regional climate has been comparatively stable, although there have been important periods of smaller-scale variability—such as the warmer and drier conditions of the altithermal (ca 4,000 years ago), the prolonged droughts that coincided with Anasazi abandonment of the region around 1300 AD, and the Little Ice Age that lasted from about 1600 A.D. until the early 1800s. However, general vegetational zonation and species composition apparently have remained roughly the same throughout the latter half of the Holocene period (Peterson 1981, Betancourt 1990).

Humans have been present in the South Central Highlands for at least 8,000 years, and have influenced ecosystems and landscape patterns throughout the time of their occupancy (Dike 1995, 1996). The extent and magnitude of human influences on local ecosystems during the Paleoindian and Archaic periods (ca 8,000 B.C. to 1 A.D.) is poorly understood, but people probably had comparatively minor impact during that early period of low population densities than they had in later periods. There was a dramatic change in the extent, magnitude, and kinds of human impacts during the Anasazi period in southwestern Colorado and northwestern New Mexico (ca 1 A.D. to 1300 A.D.), when human population densities reached levels comparable to those of today and agricultural and subsistence activities affected large areas. Following Anasazi abandonment of the region around 1300 A.D., human populations apparently fell to relatively low levels and remained comparatively low during this period of indigenous settlement until the arrival of large numbers of Euro-American settlers in the mid to late 1800's.

Under the pre-European settlement disturbance regime, landscape dynamics were driven primarily by the patterns of wildfire. The historical fire disturbance regime varied dramatically within the project area. The median fire interval was only 10-20 years in the lower elevation

ponderosa pine type; 20-30 years in the dry mixed conifer type; 60-80 years in the aspen type; and 200-300 years in the spruce-fir type (Romme et al. 2002). Many individual stands escaped fire for far longer than the median return interval and some burned at shorter intervals, creating a complex vegetation mosaic at the landscape scale. Although stand replacement fires initiate stand development and maintain a coarse-grain mosaic of successional stages and cover types across the landscape, other disturbance processes, such as landslides, floods, windthrow, insects and disease also play a role on a finer scale. In particular, the disturbance regime of individual stands in the later stages of development is dominated by chronic, fine-scale processes that kill individual trees or small groups of trees (Veblen et al. 1989, Lertzman and Krebs 1991, Veblen et al. 1991, Roovers and Rebertus 1993).

With the exception of the period of Anasazi occupation between 1-1300 A.D., anthropogenic disturbances probably had a relatively minor effect on landscape structure prior to the early 1900's. Although logging by Euro-American settlers began as early as 1875, the scale and impact of logging increased dramatically in the late 1800's with the advent of railroad logging. Most of the activity was confined to the pine forest at lower elevations. By 1950, essentially all of the old-growth ponderosa pine forests of this region had been exploited and profoundly altered. In contrast, extensive logging at the higher elevations generally began much later in the twentieth century. The first large-scale spruce logging operation began in 1946. Logging in spruce-fir and mixed conifer forests was accelerated dramatically in the 1950s and reached a peak in the 1960s and 1970s. Logging was carried out using clearcutting and a variety of partial cutting methods. Clearcutting was discontinued by 1980 in all but aspen forests because of problems in regenerating clearcut stands. The aggressive road-building and logging programs of the 1950s-1980s led to profound changes in the landscape structure of some high elevation areas (McGarigal et al. 2001).

Step 1: Establish Analysis Objectives

- *Identify and define focal habitats for species or communities of concern*
- *Identify the causes of habitat loss and fragmentation*

Ultimately, the analysis must be guided by well-formulated objectives. Thus, the first step is to establish analysis objectives to answer these basic questions: fragmentation of what, why does it matter, and what is causing it?

Given the variety of organisms, and the equally many ways to define habitat, the first question that must be addressed is what constitutes the focal habitat of concern. Inevitably, this will involve selecting target species and/or communities—usually those of special conservation concern either because of documented declining populations (species), loss of integrity (communities), or sensitivity to proposed land management activities. In addition, the habitat of the target species and/or communities must be clearly defined. This is essential in order to effectively model the landscape structure in step 2. Ideally, the species and/or communities selected should exhibit somewhat discrete habitat associations so that habitat patches can be clearly delineated in step 2. This step may involve adopting a combination coarse- and fine-filter

strategy. In the coarse filter, one or more target habitat types (e.g., ecosystems, natural communities) may be selected because they are themselves the target of conservation concerns or because they represent habitats for many species of concern. In the fine filter, one or more target species and their associated habitats may be selected either because their habitat needs are not addressed by the coarse filter or because they are of special concern.

In addition to defining the focal habitat, it is important to identify the causes of habitat loss and fragmentation for the target species/communities. This is necessary in order to discriminate between natural disturbance and succession processes operating to fragment habitat, and anthropogenic activities that may be causing the system to move outside its natural range of variation. Distinguishing between these causes is important if management is going to be proposed as a solution.

Illustrated Example

The goal of this example is to evaluate the effects of alternative land management scenarios on the extent and fragmentation (i.e., condition) of habitat for species associated with high elevation late-seral coniferous forests. The specific objective is to quantitatively compare the extent and fragmentation of the focal habitat and its variation over time under a natural disturbance regime and several alternative timber harvest regimes. Here, we will consider two focal habitats: (1) late-seral, mixed-coniferous and spruce-fir forest (hereafter simply referred to as late-seral coniferous forest), and (2) pine marten (*Martes americana*) habitat.

Late-seral coniferous forest.--Late-seral coniferous forest habitat is broadly defined on the basis of overstory composition and structure and includes habitats for a wide range of species; it represents a coarse-filtered habitat evaluation because there is no reference to any particular species. The condition of late-seral coniferous forest is deemed important to the maintenance of biodiversity in this landscape. Due to the prevalence of timber harvesting in the higher elevations over the past 50 years, there is increasing concern over the impact of current and proposed land management activities on species associated with this habitat (including pine marten, see below). It is important to note that catastrophic (i.e., stand-replacing) fires are a natural disturbance process in this landscape and function to alter the extent and spatial configuration of forest cover types and seral stages over time. Thus, this landscape is not static; rather, it is characterized by the dynamic interplay between disturbance and succession. The range of variation in landscape structure under these dynamic conditions provides a reference against which to compare various land management scenarios. In this case, the anthropogenic agent of habitat loss and fragmentation under consideration is timber harvesting. Indeed, timber harvest is the primary anthropogenic disturbance in the high-elevation portion of this landscape.

Pine marten habitat.--Pine marten habitat is narrowly defined from the perspective of a single species; it represents a fine-filtered habitat evaluation. We chose the pine marten because it is a species of conservation concern and it is considered an “indicator” of interior, late-seral, high-elevation coniferous forest. Pine marten habitat can be viewed as a subset of the coarse filter habitat type; it includes only the larger patches of late-seral coniferous forest containing interior

environment. Specifically, pine marten are strongly associated with interior portions of late-seral spruce-fir forests for foraging and denning (Buskirk and Powell 1994). Marten appear to use structural components of mature forests to avoid predators (Drew 1996), to gain access to prey in winter (Hargis and McCullough 1984, Corn and Raphael 1992, Sherburne and Bisonette 1994) and to gain thermal advantages, especially while resting (Buskirk et al. 1989, Taylor 1993, Raphael and Jones 1997). Marten generally avoid habitats that lack overhead cover and avoid traveling >23 meters from forest edges, especially in winter (Koehler et al. 1990, Ruggerio et al. 1994). Marten also appear to respond negatively to habitat fragmentation and may require a certain proportion of forest interior within their home ranges. Hargis et al. (1999) found that marten were nearly absent from landscapes having > 25% non-forest cover, even though forest connectivity was still present. In this study, marten were sensitive not only to loss of habitat area, but also to the size and proximity of open areas (Hargis et al. 1999). However, marten sensitivity to forest edges is somewhat equivocal. Buskirk and Powell (1994) concluded that marten use of forest edges may depend on the vegetation composition and structure on either side. In California, marten actually preferred edges that bordered mesic meadows (Simon 1980, Spencer et al. 1983). In Maine, edge between residual conifer forests and regenerating clearcuts was used in proportion to availability (Chapin 1995, Chapin et al. 1998). Nevertheless, most of the literature and all of the wildlife experts we surveyed indicated that pine marten have a strong preference for interior conditions of late-seral conifer forest.

The size of marten home ranges is influenced by such factors as the abundance of food, population density, and the physiological condition of individual martens (Marshall 1951, Weckwerth and Hawley 1962, Soutiere 1979). Typically, male home ranges (2-15 km in diameter) are two to three times greater than female home ranges (0.8-8.4 km in diameter) (Lofroth and Banci 1991). Adult martens tend to be solitary, somewhat territorial, and males often have home ranges that overlap two to six adult female home ranges (Clark 1984, Powell 1994). The maximum reported density is 2 individuals per km² (Thompson and Colgan 1994). The marten's preferred prey is the red-backed vole (*Clethrionomys* spp.), which also inhabits late-seral interior conifer forests (Nurdyke and Buskirk 1991).

Effects of natural and anthropogenic disturbances on marten habitat vary with the extent and severity of disturbances (e.g., Koehler and Hornocker 1977, Spencer et al. 1983, Koehler et al. 1990). In general, high severity disturbance returns late-seral forest to early-seral conditions, which are not preferred by marten. Pine marten are permanent residents in our study area, and are listed regionally as a sensitive species due to recent loss of habitat and apparent decline in their populations.

Step 2: Define the Landscape

- *Delineate the landscape boundary (i.e., establish the extent of analysis)*
- *Establish a model of the landscape structure (i.e., what constitutes the patches, corridors, and matrix)*
- *Establish a relevant grain of analysis and data model*

Once the analysis objectives have been established and the focal habitat(s) has been determined, the next step is to define the landscape in a manner that is relevant to the target species/communities. This involves establishing the spatial extent of the analysis (i.e., delineate landscape boundary), establishing a model of the landscape structure, and establishing a relevant spatial grain and data model for the analysis.

Delineate the landscape boundary.—The first step in defining the landscape is to delineate the landscape boundary. This is often a difficult task because the relevant ecological boundaries often do not correspond to the superimposed administrative and/or analysis boundaries. To the extent possible, the extent of the landscape should be meaningful ecologically given the scale at which the target populations/communities operate. For example, the local range of the focal species or of the local population or metapopulation, or the range of the focal community within an ecoregion may be suitable as the basis for delineating the landscape. In many cases, however, there will be other practical considerations that must be taken into account. For example, the landscape extent may have to correspond to a specific project planning area (e.g., timber sale area), a timber or wildlife management unit, a watershed, or an administrative unit (e.g., ranger district or national forest). At a minimum, the scope and limitations of the analysis given these scaling considerations should be made explicit.

Establish a model of the landscape structure.—The second step is to establish a digital model of the landscape structure. Here, it is likely that the patch-corridor-matrix model of landscape structure will provide the best means of representing the landscape—and in a manner that lends itself to pattern analysis given the current state-of-the-art and available analytical tools (but note that this may change in the future as new pattern analysis approaches are developed). Specifically, a patch classification scheme should be established for each target species/community, where the patches either represent the focal habitat type under consideration, or other patch types that the target species/community may perceive and respond to differentially. In some cases, it may be appropriate to designate a matrix patch type consisting of an abundant and highly connected background land cover within which focal habitat patches exist.

Establish a relevant grain of analysis and data model.—The last step in defining the landscape is to define a relevant grain (or minimum mapping unit) and digital data model. In some cases, these decisions will be guided by technical considerations owing to the source of the data and the data processing software available. In most cases, a raster data model will be desirable because the software for analyzing landscape patterns (see below) is primarily geared to raster formats. Additionally, the grain of the data should represent a balance between the desire for accurate calculations of landscape pattern, computational efficiency, and the desire to scale patterns appropriately for the chosen landscape extent. On the one hand, the grain should be kept as fine as possible to ensure that small and narrow, yet meaningful, features of the landscape are preserved in the data model. On the other hand, the grain should be increased in relation to the extent so that unnecessary detail is not confounded with the important coarse-scale patterns over large spatial extents.

Illustrated Example

Delineate the landscape boundary.--We selected a representative 4th-order watershed (40,000 ha) on the Pagosa Ranger District of the San Juan National Forest for this illustrated example. The choice of this landscape extent was based on several factors. First, 40,000 ha is sufficiently large to potentially encompass the home ranges of many individuals of most species of concern (i.e., those associated with late-seral coniferous forest). Thus, it is likely that most populations are potentially sustainable within the extent of this landscape. As such, it is likely that habitat changes (in either extent or fragmentation) will have both individual- and population-level implications. And given the overarching management goal of maintaining viable populations of all species, we are most concerned with the impacts of human activities at a scale that affects population processes. Second, the extent of this landscape is sufficiently large to incorporate the largest natural disturbances (i.e., catastrophic fires), at least based on our best understanding of historic fire sizes. Thus, the landscape is capable of operating within a dynamic equilibrium that can be characterized. Third, this particular landscape is representative of the broader surrounding landscape in terms of land cover patterns. Thus, the results obtained from this experiment should be generalizable to the broader regional landscape. Finally, the choice of a 4th-order watershed was based in part on the increasing use of watersheds of this magnitude as the basis for land management and planning.

Establish a model of the landscape structure.--Given our primary interest in the extent and configuration of late-seral coniferous forest and pine marten habitat, it was necessary to classify the landscape on the basis of both seral stage and plant community and in a manner appropriate to the assessment of pine marten habitat suitability. Although the details of this classification are not presented here, briefly, we classified the landscape into broad cover types (plant communities) representing the major vegetation types corresponding to the strong elevation gradient in plant communities (Table 2, Fig. 20). Although the non-coniferous forest cover types are not a focus in this analysis, they warrant equal attention because they comprise the ecological neighborhood of all coniferous forest patches and will therefore affect some of the habitat configuration metrics (e.g., similarity index, traversability index). All forest cover types were further classified into four seral stages according to well-established functional stages of even-age stand development (Oliver and Larson 1990, Spies 1997): (1) stand initiation, (2) stem exclusion, (3) understory reinitiation, and (4) old-growth, shifting mosaic. Forest stands undergo this successional sequence following catastrophic, stand-replacing disturbance (i.e., fire or clearcutting), but the age at which a stand transitions from one stage to another varies among cover types. Thus, there is an element of chance in the rate at which a stand succeeds from one stage to another. In summary, the landscape was classified into a variety of well-established cover types and seral stages which provided a useful initial model of landscape structure sufficient for assessing fragmentation of the two focal habitats.

In addition, although we do not explicitly distinguish a matrix from patches and corridors, it is possible to do so. At one level of resolution, the coniferous forest forms the matrix within which nonforested and deciduous forest patches and road and stream corridors exist. However, given the dynamic nature of the forest (i.e., constantly changing seral stage distribution), and the

importance of seral stage to most species, we have chosen not to designate a matrix. Instead, we consider each cover-seral stage as a patch within the landscape mosaic. We can consider streams, riparian zones, and roads as corridors because of their linear form and context, as well as their effects on landscape function; however, because this habitat fragmentation analysis is largely a “structural” analysis, as opposed to explicitly assessing landscape function, it is mute whether we call these features corridors or patches (which happen to be linear in form).

All data for this example were derived from the National Resources Information System (NRIS) database developed and maintained by the USDA Forest Service for the San Juan National Forest. This database contains geographic information on a wide variety of landscape characteristics. We derived our land cover map from a combination of data layers, including the Common Vegetation Unit (CVU) polygon coverage and the Roads and Streams line coverages. The CVU layer itself was developed by the Forest Service from a combination of information sources and processes, including the existing NRIS polygon boundaries, aerial photo interpretation (1993, 1:24,000 natural color), digital image analysis of Landsat Thematic Mapper imagery, and logic written into a C program to delineate and attribute polygons. Attributes for each polygon included species, percent crown cover and tree size class, among others. We used information on species composition, size class and stand age to assign each polygon to a cover type and seral stage class. Stand age was either determined directly from stand exams or estimated based on empirically-derived relationships between age and size class of the dominant vegetation for each cover type. Roads and streams of various size classes were superimposed on this CVU-derived cover map to obtain our final cover map.

Based on this initial land cover characterization, and subject to the limitations of the available spatial data in the NRIS database, we subsequently defined late-seral coniferous forest as all mixed-conifer (warm, dry and cool, moist) and spruce-fir cover types, with and without aspen, in the understory reinitiation or old-growth, shifting mosaic stages of development. Thus, for purposes of this habitat analysis, we combined several cover types and seral stages into a single focal class (patch type) and aggregated the remaining cover types and seral stages into three separate classes deemed broadly important for assessing the ecological neighborhood of late-seral coniferous forest patches (Table 3, Fig. 21). Note, in the context of the simulation experiments described below (step 3), we reclassified the landscape in this manner for each time step (10-year snapshots of the landscape). Thus, the simulation operated on the initial landscape definition and was unaffected by this reclassification, only the output landscapes (snapshots) were reclassified for purposes of this habitat analysis. This highlights that in most habitat analyses the landscape will have to be reclassified prior to the analysis, since rarely will the database have been established with reference to a particular habitat definition.

Similarly, we defined pine marten habitat as the unique combination of conditions that provide the resources needed by an individual pine marten to fulfill its life history requirements. Specifically, we applied a habitat capability model to assign a habitat capability index (HCI) value to each grid cell. Although the details of the HCI model are not presented here (see Crist et al. Submitted for details), each cell was assigned a value between 0 (low value) and 1 (high value) based on the local composition (e.g., cover type, seral stage) and context (e.g., distance

from edge) of each grid cell and the amount and spatial configuration (i.e., fragmentation) of high-quality local habitat within a window scaled to the average home range size of the species (250 ha). Thus, each cell was given a habitat capability score that indicated its likelihood of supporting a pine marten. We classified these HCI scores into two classes representing habitat ($HCI \geq .7$) and non-habitat ($HCI < .7$) (Fig. 22). Here, we are interested in analyzing the extent and fragmentation of capable habitat. As before, the habitat capability classification was done after the simulation on each of the output landscapes.

Establish a relevant grain of analysis and data model.—For our initial landscape characterization, we chose a grain (cell) size of 25 m, which allowed us to depict patches as small as 0.0625 ha (1 cell). We chose this grain size in part owing to the resolution of some of the source data (e.g., 30 m resolution of Landsat imagery), but it also reflected a compromise between our desire to accurately represent relevant linear landscape elements such as roads and streams that potentially serve as fragmenting features, on the one hand, and our desire to emphasize coarse vegetation patterns in a computationally efficient manner on the other. In addition, a 25 m cell size allowed us to represent depth-of-edge distances at a resolution of 25 m, which we felt gave us sufficient flexibility in quantifying potential edge effects. Overall, a 25 m cell size seemed a reasonable compromise given these considerations, while at the same time it seemed sufficient to our task of assessing fragmentation of late-seral conifer forest and pine marten habitat at an ecologically relevant scale.

Thus, while a grain size of 25 m was deemed effective for our initial landscape characterization, we believed that 0.0625-ha patches were probably too small to be relevant for most organisms associated with late-seral coniferous forest. More importantly, we recognized that many fragmentation metrics are sensitive to the grain of the data and are particularly affected by the number of patches. In the context of the simulation experiments described below (step 3), we recognized a priori that many extremely small patches would be created by the simulated disturbance processes and that this would have a significant impact on the computed metrics. Thus, we decided to eliminate very small patches less than 0.5 ha in the final land cover and habitat capability maps before computing the fragmentation metrics. Note, given the uncertainty in the impact of different grain sizes on the computed metrics and the uncertainty in the ecological implications of eliminating small patches below an arbitrary minimum patch size, we recognized that an ideal approach would be to resample the final land cover and habitat capability maps at a range of resolutions, bracketing what we believe to be meaningful upper and lower resolutions given our analysis objectives; for the purpose of this exercise, we did not do this.

A final consideration in defining the landscape is choosing a digital data model. Here, although the original source data was in vector format, consisting of both polygon and line coverages, we elected to convert the land cover maps to a raster (grid) format to facilitate computation of the fragmentation metrics in step 4 below.

Step 3: Establish a Spatio-Temporal Reference Framework

- *Define the spatial and temporal context of the current landscape (i.e., the broader landscape context and the historical factors that shaped the current landscape)*
- *Establish reference conditions for interpreting current and future landscape patterns*

Perhaps the most challenging step in this protocol is to establish an appropriate reference framework for evaluating habitat fragmentation for the target organisms/communities. The difficulty is rooted in the philosophical issue of what constitutes an appropriate reference framework. Under one perspective, the historic range of natural variability is deemed an appropriate reference framework. Unfortunately, there is often little agreement over what constitutes the appropriate period in history to reference. Often it is argued that the period immediately preceding Euro-American inhabitation is best; however, it is argued in opposition that native Americans were present and impacting landscape patterns and processes for thousands of years prior to Euro-American settlement. The contention is rooted in the philosophical issue of what constitutes “natural”, and whether natural is even desirable.

Despite these philosophical issues, it is widely accepted that some reference framework is better than none. Therefore, the purpose of this step is to establish some meaningful basis for placing the current and potential future landscape conditions into context. This reference framework may be qualitative or quantitative in nature. For example, it may be sufficient to simply describe in narrative terms the “natural” patterns of variation in habitat conditions over time and space for the landscape under consideration. Where possible, a more quantitative approach is desirable. This may involve the use of retrospective studies of past landscape conditions (e.g., historical reconstructions of landscape patterns and dynamics) or the use of computer simulation models to simulate landscape changes based on the best understanding of the processes that drive landscape change.

In addition to a temporal reference framework (i.e., how habitat conditions vary over time), a spatial reference framework should be established as well. Ideally, this should involve a qualitative or quantitative assessment of habitat conditions over a much broader spatial extent than the landscape under consideration. In other words, what is the broader regional context of the focal landscape. In order to understand the biological consequences of habitat fragmentation, it is necessary to understand whether or not the habitat is both locally and regionally rare and fragmented. Large regional source populations, for example, may offset any local fragmentation impacts. Another strategy is to establish a reference landscape; that is, another landscape that somehow represents a suitable benchmark to compare against the focal landscape. Of course, finding a suitable reference landscape is fraught with difficulty, because at the scale of most landscapes under consideration here there are often too many other confounding sources of variation to warrant direct comparison.

Illustrated Example

Temporal context.--As noted previously, this landscape is dynamic--constantly changing in structure as a result of the dynamic interplay between disturbance and succession. The range of variation in landscape structure under these dynamic conditions provides a reference against

which to compare habitat fragmentation impacts under various land management scenarios. In this case, the anthropogenic agent of habitat loss and fragmentation under consideration is timber harvesting, which is the primary anthropogenic disturbance in the high-elevation portion of this landscape. Thus, to provide a spatio-temporal framework for understanding the impacts of anthropogenic habitat fragmentation, we conducted a simulation experiment using the Rocky Mountain Landscape Simulator (RMLANDS). Specifically, we simulated the following five different disturbance scenarios:

1. Wildfire regime.—In this scenario, the frequency, size and variability of fires represented our best estimate of the fire disturbance regime for pre-Euro-American settlement conditions (circa 1610-1850). The details of this wildfire scenario were described by Roworth et al. (submitted). Briefly, the mean fire return interval or disturbance rotation period varied from approximately 20 yrs in the low elevation ponderosa pine forest to 300 years in the high elevation spruce-fir forests. The disturbance regime consisted of relatively frequent, small fires in the low elevations and infrequent, large fires in the high elevations. For the purpose of this experiment, we simulated only catastrophic, stand-replacing (i.e., high severity) fires.
2. Long rotation, dispersed cutting.—In this scenario, 100% of the mixed-conifer and spruce-fir cover was available for harvest on a 300-year rotation period. Maximum harvest unit size was 18 ha (40 acres) and a 400 m buffer was established around each harvest unit within which timber harvest was prohibited for 10 years. In addition, harvest units were maximally dispersed across the landscape in a staggered setting fashion.
3. Long rotation, aggregated cutting.—In this scenario, 100% of the mixed-conifer and spruce-fir cover was available for harvest on a 300-year rotation period. Maximum harvest unit size was 18 ha (40 acres) and NO buffer was established around each harvest unit. In addition, harvest units were maximally aggregated. The combination of no buffer and maximum aggregation causes harvest units to merge together (by chance) into larger harvest blocks.
4. Short rotation, dispersed cutting.—Same as scenario 2, but with a 200-year rotation period. Hence, this scenario represents a higher intensity of timber harvesting.
5. Short rotation, aggregated cutting.—Same as scenario 3, but with a 200-year rotation period. Again, this scenario represents a higher intensity of timber harvesting, but differs from 4 in the dispersion of harvest units.

Each simulation consisted of a 200-300 year period of disturbance and succession, depending on the rotation period of the scenario, and was replicated 10 times. The details of the simulation model are too complex to present here and are not essential for our purpose. Suffice it to say that under each scenario, disturbances and succession were implemented as constrained stochastic processes in an attempt to mimic real-world patterns of disturbance and succession, while at the same time incorporating an element of chance. The model operates with a 10-year time step and

produces an output of the landscape condition (i.e., distribution of cover types and seral stages) at each step.

In all timber harvest scenarios, we used clearcutting exclusively as the silvicultural system. In reality, a variety of other silvicultural systems (e.g., individual tree selection, group selection, shelterwood) are employed, but the use of a single system serves to better illustrate habitat fragmentation differences among scenarios. In addition, in all timber harvest scenarios, we restricted harvesting to the mixed-conifer and spruce-fir cover types. This simplified the simulations and facilitated comparisons among scenarios. Clearly, these simulated conditions are not entirely realistic. First, much of the area subject to timber harvesting in the simulations is actually administratively protected in wilderness or research natural areas and therefore has been taken out of the suitable timberland base. Second, we did not allow any wildfire during the timber harvest simulations, despite the fact that wildfires would certainly occur in this landscape regardless of management activities. Thus, while these scenarios are not entirely realistic, they serve to highlight and exacerbate the differences in habitat loss and fragmentation patterns resulting independently from these disturbance agents.

There are two important points regarding the simulation modeling approach for generating a reference framework. First, the simulation approach involves using a model to project potential future landscape trajectories based on our current understanding of disturbance and succession processes. This has certain advantages and disadvantages. On the positive side, this approach allows us to quantify landscape conditions accurately and precisely over long periods of time, thereby allowing us to quantitatively describe the range of variation in habitat conditions over meaningful periods of time. This is especially useful because in most landscapes it is not possible to reconstruct historic landscape patterns accurately and over sufficiently long periods of time. On the downside, a model is just that, a simplified “model” of the real world. As such, it is only as good as the data used in the model. More importantly, incorrect specification of model parameters can lead to spurious results and erroneous conclusions. Nevertheless, if interpreted in the proper context and with these limitations in mind, the simulation approach can provide a useful reference framework.

Second, and perhaps more importantly, this approach provides a reference framework that explicitly considers habitat conditions as dynamic. Habitat is not static in any real landscape. Thus, it is inappropriate to use a single snapshot of a landscape as a reference framework, except under special circumstances. Habitat conditions change over time as the landscape undergoes disturbance and succession. Thus, it is more realistic to represent habitat as a range of conditions, as we have done here.

Spatial context.--The project area does not exist in isolation; it has a spatial context, and this broader regional landscape context has an important influence on the function of the landscape. In particular, populations of species associated with the focal habitat (late-seral coniferous forest), including pine marten populations, do not honor the watershed boundary selected for this analysis. In many respects, the watershed is an open system with respect to the flow of the focal organisms. Consequently, it is important to consider the uniqueness of the project area and its

potential interaction with the surrounding landscape context. Note, the spatial context of the focal landscape does not affect the structural analysis of habitat conditions within the focal landscape; that is, the measured extent and fragmentation of habitat within the focal landscape is not affected by the character of the surrounding landscape. Rather, the spatial context can affect how we interpret our findings; that is, the ecological implications of particular habitat conditions. In our case, the selected watershed is representative of the broader regional landscape conditions in terms of land cover patterns and disturbance processes. Therefore, it is likely that the habitat patterns we quantify will represent other similarly-sized watersheds within the region.

Step 4: Quantify Habitat Fragmentation

- *Select relevant landscape metrics*
- *Compute selected landscape metrics*
- *Interpret landscape metrics*

The next step is to quantify habitat fragmentation for the landscape under consideration. This entails selecting a relevant suite of fragmentation metrics that offers a comprehensive, yet parsimonious description of habitat conditions (see Table 1). Computing the selected metrics is made relatively simple due to the availability of computer software such as FRAGSTATS (McGarigal et al. 2002). Once computed, the metrics must be interpreted properly. From a technical standpoint, this requires both a theoretical understanding of the metrics as well as intimate knowledge of the data model used in the analysis. Otherwise, the interpretation of the metrics is constrained only by their expected behavior under the reference conditions (Step 3).

Illustrated Example

Select and compute landscape metrics.--We selected a parsimonious yet comprehensive suite of fragmentation metrics for use in this analysis (Table 1). We used FRAGSTATS (McGarigal et al. 2002) to compute these metrics for each landscape snapshot under each simulated disturbance scenario (Step 3). Specifically, under each disturbance scenario, we reclassified the landscape at each time step (10-year intervals over 200-300 year period, replicated 10 times) according to the two focal habitat schemes: (1) each landscape was reclassified into four classes, including the late-seral coniferous forest class, and (2) each landscape was reclassified into habitat and nonhabitat classes using the pine marten HCI model. We ran FRAGSTATS on each of the reclassified landscapes and computed the class metrics listed in Table 1, except for the traversability index which was not available in FRAGSTATS at the time of this analysis.

Some of the computed fragmentation metrics required additional parameterization. The *core area index* required that we specify depth-of-edge effects – the depth at which adverse edge effects penetrate into a patch from its perimeter. Although reported depth-of-edge effects vary widely (see Primer), we selected a constant 100 m as an appropriate depth for the coarse-filter community-based assessment. Recall that for the late-seral coniferous forest habitat, we are interested in all organisms associated with this cover type. Given that each organism may exhibit a unique response to edge, it is impossible to specify a single depth-of-edge effect that will be

equally relevant to all species under consideration. Indeed, the majority of species may not even exhibit a significant edge effect. However, the core area index is designed to be meaningful for those species adversely effected by edges. Thus, it is reasonable to select a relatively large distance, since we are trying to emphasize the most interior-sensitive species. In addition, the choice of edge-influence distance is not particularly important when using this metric solely as a measure of patch geometry, since in this manner it is simply a perimeter-area ratio of shape complexity. For pine marten habitat, the choice of edge-influence distance is somewhat trivial because edge effects have already been explicitly incorporated into the HCI model. The important thing is that the edge-influence distance be held constant across all scenarios.

The *similarity index* required that we specify a search radius (or analysis window size) representing the ecological neighborhood of each patch. Unfortunately, there is no single ecological neighborhood size appropriate for all organisms under consideration, nor is there a single rationale for choosing a specific distance for any single species. These difficulties are complicated because many different ecological processes are affected by ecological neighborhoods (sensu Addicott et al. 1987). Often, dispersal is deemed the most relevant process for considering patch isolation; consequently, the mean maximum dispersal distance of the focal species, or say the 95th percentile of recorded dispersal distances, could be considered a reasonable basis for the search radius. In the absence of empirical data on dispersal distance, the search radius is sometimes defined as several times the diameter of the average home range of the focal species. Unfortunately, when conducting a coarse-filter community-based habitat analysis, even this rule of thumb doesn't help much given the wide variety of organisms associated with the focal community. Thus, for our analysis, we established a single search radius based on pine marten home range size. Specifically, we used a radius equal to roughly 2.5 times the diameter of the average pine marten home range (2000 m). In addition, the similarity index required that we specify similarity coefficients for each patch type. In the analysis of late-seral coniferous forest habitat, we specified coefficients based on the similarity in vegetation composition and structure with the focal habitat (Table 4). In the analysis of pine marten habitat, the specification was much simpler because we were dealing with only two classes (i.e., habitat and nonhabitat).

Interpret landscape metrics.—It is beyond the scope of this document (and not essential to our main purpose) to present in full the detailed results of our analysis. Instead, below we discuss the major differences among land management scenarios and the wildfire scenario with respect to the five major components of habitat loss and fragmentation (Table 1) for each of the focal habitats: late-seral coniferous forest and pine marten habitat (Figs. 23 and 24, respectively). Because pine marten habitat is essentially a subset of the late-seral coniferous forest, many of the differences among scenarios for the landscape metrics are quite similar for the two habitat definitions. Therefore, we discuss late-seral coniferous forest in greater detail and highlight only the major patterns and important differences for pine marten habitat.

(1) Late-seral Coniferous Forest:

- Habitat extent.—As expected, short-rotation timber harvest scenarios resulted in greater habitat loss than long-rotation scenarios, while there were no differences between harvest unit dispersion patterns (aggregated vs. dispersed) for each rotation length (Fig. 23a). Interestingly, under the long-rotation scenarios habitat extent actually increased for a period of about 60 years before eventually declining. This time lag was due to the large cohort of mid-seral stage forest in the current landscape that succeeded to the late-seral stage at a rate that exceeded harvesting in the short term. All harvest scenarios eventually reached a constant equilibrium in PLAND that fell within the 90% range of variation of the wildfire scenario; however, the short-rotation scenarios stabilized at a much lower PLAND than the long-rotation scenarios. Interestingly, all scenarios, including wildfire, resulted in a loss of late-seral coniferous forest over time, suggesting that either the current landscape contains more late-seral coniferous forest than during the reference period (represented here by the wildfire scenario) or that our simulation included too much wildfire. Finally, note that habitat extent under the wildfire scenario fluctuated over time between roughly 7% and 28% of the landscape, reflecting the dynamic shifting mosaic pattern of habitat resulting from the stochastic interplay of disturbance and succession. In contrast, the timber harvest scenarios (as implemented here) resulted in the complete regulation of forest disturbance and succession, which eventually transformed the landscape into one characterized by a constancy in habitat area. Note, however, that these differences are the result of our simulation of timber harvest scenarios without concurrent wildfires which occur stochastically and maintain the landscape in a constant state of flux.
- Habitat subdivision.—Although the basic patterns of habitat subdivision under the various scenarios were consistent with our expectations, there were some interesting differences among the three subdivision metrics that revealed subtle differences among scenarios and among the metrics--and highlighted the multi-faceted nature of subdivision as a component of habitat fragmentation (Fig. 23b-d). As expected, NP and CLUMPY both revealed that dispersed cutting under either a short- or long-rotation regime resulted in greater habitat subdivision than aggregated cutting. Specifically, the short-rotation, dispersed cutting resulted in substantially greater NP than the other scenarios, while the long-rotation, aggregated cutting resulted in the least NP. Interestingly, NP was comparable for the short-rotation, aggregated cutting and long-rotation, dispersed cutting scenarios. NP increased gradually over time under all timber harvest scenarios despite the decrease in habitat area, indicating that concomitant habitat loss and subdivision was a universal outcome of all timber harvesting scenarios. NP was well outside and below the range of variation for the wildfire scenario, suggesting that fires caused substantially greater habitat subdivision than timber harvesting. The increased NP under the wildfire scenario was caused by heterogeneous spread of simulated wildfires compared to homogeneous spread of timber harvest units, but it was also a direct consequence of our choice of minimum patch size in the output land cover maps. This highlights the implications of the choices we made in defining the landscape in Step 2. We could have just as easily increased the minimum patch size and decreased the range of variation in NP under the wildfire scenario.

CLUMPY revealed the same basic patterns as NP, but with some interesting additional interpretations (Fig. 23c). First, the values of CLUMPY (0.85-0.95) indicate that the habitat under all scenarios was more aggregated (i.e., less subdivided) than expected under a spatially random distribution. This is not too surprising as we generally expect vegetation patterns to exhibit some degree of contagion (i.e., aggregation). However, this is also a function of the scale of the data. Recall that as the cell size (i.e., grain) decreases relative to the actual grain of the patch mosaic (i.e., average patch size), the proportion of like adjacencies among cells increases and indicates a greater degree of spatial aggregation. Thus, the measured degree of aggregation can be altered by simply changing the grain of the data without any real-world change in the land cover patterns. This highlights the need to consider this metric (and most other metrics) as comparative measures. Second, in contrast to NP, the CLUMPY trajectories under the timber harvest scenarios largely fall within the range of variation in the wildfire scenario, suggesting that perhaps the most important impact of timber harvesting is not on the level of habitat subdivision but on its temporal dynamic. Specifically, timber harvesting (as simulated) minimized the variation in subdivision over time, whereas wildfire maintained the landscape in dynamic equilibrium.

DIVISION largely mirrored the patterns in PLAND, and thus did a relatively poor job of differentiating dispersed from aggregated cutting patterns (Fig. 23d). The long-rotation timber harvest scenarios resulted in a temporary decrease in DIVISION, corresponding to the increase in PLAND, followed by a gradual increase in DIVISION until reaching equilibrium at a very high level of division. The values of DIVISION (0.88-0.99) under all scenarios indicate that there was a very high probability that two randomly chosen places in the landscape were not situated in the same contiguous habitat patch. Thus, we can conclude that late-seral, coniferous forest naturally exhibits a high degree of subdivision.

- Patch geometry.—As expected, the spatial character of habitat patches was effected by both the intensity of timber harvesting and the pattern of harvest units (Fig. 23e). All timber harvest scenarios resulted in a decrease in TCAI, although only the short-rotation, dispersed cutting scenario caused TCAI to drop below the range of variation estimated for the wildfire regime. Interestingly, the differences between long-rotation scenarios were not discernable for the first 120 years of the simulation, after which TCAI decreased more rapidly for the dispersed cutting scenario. The long-rotation, aggregated cutting scenario maintained the highest TCAI over the duration of the simulation. The long-rotation, dispersed cutting scenario and short-rotation, aggregated cutting scenario had similar effects on TCAI after reaching equilibrium, similar to the patterns observed for NP and CLUMPY.
- Habitat isolation.—As expected, the isolation of habitat patches was affected dramatically by the total amount of habitat in the landscape (PLAND). In general, as PLAND increases, there is an increasing likelihood that a habitat patch will contain more habitat

within its neighborhood--and therefore be less isolated. Thus, SIMILAR largely mirrored the patterns in PLAND, with some notable differences (Fig. 23f). First, due to the pulse of mid-seral, conifer forest succeeding to the late-seral condition during the first 60 years of the simulation, SIMILAR exhibited a two-fold increase for 60 years under the long-rotation scenarios before steadily declining to an equilibrium condition similar to the mean condition under the wildfire scenario. Second, SIMILAR was higher under the dispersed cutting scenarios than the corresponding aggregated cutting scenarios for a considerable portion of the simulation, and this difference was especially pronounced under the short-rotation scenarios. Why did dispersed cutting result in less habitat isolation (i.e., greater neighborhood similarity) than aggregated cutting, a seemingly counterintuitive result? The answer (below) lies in the basis of this particular metric and nicely illustrates why a thorough understanding of each metric is necessary before ecological interpretations can be made.

SIMILAR is a patch-based metric; that is, each patch is evaluated separately, and then (in this case) the area-weighted mean across all patches is taken as the overall landscape metric. For each habitat patch, SIMILAR is computed by summing the area of every other patch within the specified ecological neighborhood (in this case we used 2000 m), where the neighboring patches are weighted by class (i.e., higher weights are given to patches that are more “similar” to the focal habitat patch, see Table 4) and by distance from the focal habitat patch. Thus, a large habitat patch surrounded by dissimilar patches will receive a very low score, whereas a small habitat patch surrounded by several other habitat patches will receive a much higher score. Consequently, as the focal habitat is initially subdivided into disjunct patches, as is the case in the short-rotation, dispersed cutting scenario, as long as the disjunct habitat patches are relatively close together (i.e., within the specified neighborhood distance), the similarity index may actually increase over the case of the more contiguous (undivided) habitat. Hence, while the habitat patches are, in effect, less isolated from other habitat patches, it may be misleading to conclude that habitat isolation overall is less under the dispersed cutting scenarios. Note, this is not a deficiency of this metric, as it is designed to represent the isolation of habitat “patches” from other “patches” of the same or similar class, but rather it illustrates why this particular metric is perhaps best used under certain circumstances, namely, when the habitat is relatively rare (say 0-30% of the landscape) and subdivided into many patches. Under these conditions, SIMILAR will effectively discern clumped distributions of habitat (i.e., where habitat patches are relatively close to each other) from highly dispersed distributions (i.e., where habitat patches are relatively isolated from each in space). These conditions are not reached until 100 (short-rotation) or 200 (long-rotation) years into the simulation.

- Habitat connectedness.—As expected, like habitat isolation, the physical continuity of habitat was affected dramatically by the total amount of habitat in the landscape (PLAND). In general, as PLAND increases, there is an increasing likelihood that habitat patches will coalesce into larger, more extensive patches that physically span more of the landscape. Thus, correlation length (GYRATE_AMN) largely mirrored the patterns in

PLAND (Fig. 23g). Long-rotation scenarios maintained a relatively high correlation length during the first 100-200 years of the simulation, but eventually declined to an equilibrium level almost identical to the mean correlation length under the wildfire scenario. Short-rotation scenarios maintained correlation length at current levels for roughly 60 years before declining dramatically and then stabilizing at a relatively low level. Differences between short- and long-rotation scenarios were rather dramatic throughout most of the simulation, indicating that the average distance one might traverse the map and remain within a habitat patch was substantially less under the short-rotation scenarios. In addition, the relationship between dispersed and aggregated cutting patterns was similar to that described above for SIMILAR. Specifically, the dispersed cutting pattern resulted in greater correlation length (i.e., greater habitat continuity) than the aggregated cutting pattern during the early portion of the simulation before the relationship reversed itself. This happened because under the dispersed cutting scenario, initial harvest units were more likely to perforate large, contiguous patches of habitat and therefore not change overall habitat extensiveness; whereas, under the aggregated cutting scenario, initial harvest units were more likely to eliminate large blocks of habitat and thus reduce overall habitat extensiveness.

(2) Pine Marten Habitat:

- Habitat extent.—Pine marten habitat decreased in area under all scenarios, although the trajectory of change differed in relation to rotation length and cutting pattern (Fig. 24a). Short-rotations resulted in immediate and dramatic decreases in habitat, and the decrease was more rapid in the dispersed cutting scenario. Indeed, pine marten habitat was eliminated completely after 100 years under the dispersed scenario. Interestingly, pine marten habitat actually increased slightly for several decades before declining under the long-rotations, reflecting the pulse of mid-seral coniferous forest succeeding to late-seral forest during the initial few decades of the simulation. The difference between dispersed and aggregated cutting under the long-rotation scenarios did not emerge until 120 years, after which dispersed cutting caused pine marten habitat to decline precipitously. At equilibrium, the long-rotation, aggregated cutting maintained the greatest habitat area, and at a level similar to the mean level maintained under the wildfire scenario. Interestingly, the long-rotation, dispersed cutting scenario and short-rotation, aggregated cutting scenario equilibrated at similar levels of habitat, indicating an interaction between cutting intensity and cutting pattern that has important management implications; i.e., that aggregating cutting units may compensate, at least partially, for increased harvest intensity for interior sensitive species like the pine marten. All timber harvest scenarios, except the short-rotation, dispersed cutting regime, ultimately maintained habitat extent within the 90% range of variation under the wildfire scenario.

It is instructive to note the differences between late-seral, coniferous forest (Fig. 23a) and pine marten (Fig. 24a) habitat extent with respect to the effect of timber harvest cutting patterns (dispersed vs. aggregated). Specifically, cutting patterns had no effect on late-seral, coniferous forest extent, but had a substantial impact on pine marten habitat

extent owing to their sensitivity to edge effects (i.e., preference for interior late-seral, coniferous forest).

- Habitat subdivision.—As expected, pine marten habitat subdivision was effected by both timber harvesting intensity and cutting patterns, but the relationships were complex and varied among subdivision metrics (Fig. 24b-d). NP increased rapidly for several decades under the short-rotation, dispersed cutting scenario before rapidly declining to zero. The initial increase was due to the subdivision of large blocks of interior, late-seral, coniferous forest as harvest units perforated the forest matrix. However, continued perforation and loss of large blocks of interior forest eventually caused the decline and complete attrition of habitat patches. The other three timber harvest scenarios resulted in similar values of NP for 100 years before differentiating. The differences between short- and long-rotation scenarios illustrates the difficulty of interpreting NP independently from other metrics. Based on NP alone, the long-rotation scenarios resulted in greater habitat subdivision (fragmentation), yet the total area of habitat maintained was much greater than under the short-rotation scenarios (Fig. 24a). This begs the question: Is it better to have more habitat distributed among many smaller patches or less habitat distributed among fewer larger patches? As noted in the Primer, most theoretical and empirical studies indicate that habitat area is generally far more important than habitat configuration.

CLUMPY revealed the same basic patterns as NP, but with some noteworthy differences (Fig. 24c). First, CLUMPY consistently discriminated between dispersed and aggregated cutting patterns under both rotation periods; CLUMPY was consistently greater under aggregated cutting patterns. Second, in contrast to dispersed cutting patterns, aggregated cutting patterns maintained CLUMPY within the 90% range of variation of the wildfire scenario. Third, CLUMPY demonstrated erratic behavior under the short-rotation, dispersed cutting scenario late in the scenario, reflecting the difficulty of measuring habitat aggregation (with any metric) when PLAND is near zero.

DIVISION largely mirrored the patterns in PLAND, and thus offered little unique interpretive value in this application (Fig. 24d).

- Patch geometry.—As expected, the spatial character of habitat patches was effected by both the intensity of timber harvesting and the pattern of harvest units, although the differences were not pronounced until late in the simulation (Fig. 24e). For a given rotation length, the dispersed cutting scenario resulted in lower TCAI than the aggregated cutting scenario. Only the short-rotation, dispersed cutting scenario caused TCAI to drop and stay below the range of variation estimated for the wildfire regime. Interestingly, the differences between long-rotation scenarios were not discernable for the first 120 years of the simulation, after which TCAI decreased more rapidly for the dispersed cutting scenario.

- Habitat isolation.—As expected, the isolation of habitat patches was affected dramatically by the total amount of habitat in the landscape (PLAND). In general, as PLAND increases, there is an increasing likelihood that a habitat patch will contain more habitat within its neighborhood—and therefore be less isolated. Thus, SIMILAR largely mirrored the patterns in PLAND, with some notable differences (Fig. 24f). First, due to the pulse of mid-seral, conifer forest succeeding to the late-seral condition during the first 60 years of the simulation, SIMILAR exhibited a two-fold increase for 60 years under the long-rotation scenarios before steadily declining to an equilibrium condition similar to the mean condition under the wildfire scenario. Second, for the same reasons discussed above for late-seral coniferous forest, SIMILAR was higher under the dispersed cutting scenarios than the corresponding aggregated cutting scenarios for a considerable portion of the simulation, and this difference was especially pronounced under the short-rotation scenarios.
- Habitat connectedness.—As expected, the physical continuity of pine marten habitat was affected dramatically by the total amount of habitat in the landscape (PLAND). Correlation length (GYRATE_AMN) largely mirrored the patterns in PLAND (Fig. 24g). Long-rotation scenarios maintained a relatively high correlation length during the first 80 years of the simulation before correlation length eventually declined. Short-rotation scenarios resulted in an immediate decline in correlation length before eventually stabilizing at a relatively low level. Overall, differences in correlation length among timber harvest scenarios were quite pronounced, especially at equilibrium, indicating that pine marten habitat continuity was substantially affected by both the intensity of timber harvesting and the pattern of harvest units. Interestingly, the long-rotation, aggregated cutting scenario generated a correlation length at equilibrium very similar to the mean correlation length achieved under the wildfire scenario.

Step 5: Characterize the Landscape Relative to Analysis Objectives

- *Characterize the condition of the landscape relative to analysis objectives*
- *Interpret findings within the scope and limitations of the analysis*

The final step is to characterize the landscape relative to the objectives of the analysis. Ultimately, this is the most important step because it allows you to apply the knowledge gained from the analysis to improve management. Here the intent is to use the results of the analysis to guide land management decisions. In addition, here the conclusions should be tempered with an explicit discussion of the scope and limitations of the analysis. In particular, the scale of the analysis in relation to the scale of the ecological system (e.g., populations and communities) should be addressed. In addition, the definition of the landscape in terms of the patch classification scheme or schemes employed and the target organisms and/or communities should be discussed. Limitations in the quality of data used to model landscape patterns should be acknowledged as well. Here the intent is not to undermine the results of the analysis, but to provide an honest context for interpreting the reliability of the results.

Illustrated Example

The goal of our analysis was to evaluate the effects of alternative land management scenarios on the extent and fragmentation of habitat for species associated with late-seral, coniferous forests. Our specific objective was to compare the extent and fragmentation of late-seral, coniferous forest (coarse filter, community-based assessment) and pine marten habitat (fine filter, species-based assessment) under a wildfire disturbance regime and several alternative timber harvest regimes. Our results have several important implications for the management of the Piedra River watershed:

1. Late-seral, coniferous forest and pine marten habitats were heterogeneously distributed across the landscape and fluctuated substantially over time in both extent and configuration under a wildfire scenario. These focal habitats were perhaps best characterized as dynamic shifting mosaics under the wildfire regime. Timber harvesting in the absence of wildfire principally affected the dynamic behavior of the landscape by reducing the amount of fluctuations in habitat extent and configuration.
2. All scenarios, including the wildfire scenario, resulted in substantial habitat loss over time, indicating either that the current landscape contains more habitat than existed during the reference period or that our estimate of the wildfire rotation period was too low.
3. As expected, under timber harvest scenarios, short-rotation periods resulted in greater loss of habitat than long-rotation periods. Interestingly, habitat area increased for several decades under the long-rotation periods before eventually declining and reaching an equilibrium much lower than starting conditions.
4. Many of the metrics exhibited the confounding of habitat loss and fragmentation. Specifically, several of the metrics designed to measure habitat ‘fragmentation’ mirrored the changes in habitat ‘area’ (PLAND), making it difficult to isolate the changes due to habitat area versus habitat configuration.
5. Both focal habitats exhibited a high degree of subdivision under all scenarios reflecting the fact that these habitats are naturally quite subdivided. The differences among scenarios were as expected; namely, habitat was more subdivided under the dispersed cutting scenarios than the aggregated cutting scenarios.
6. Habitat fragmentation, in terms of subdivision and geometry, was similar under the long-rotation, dispersed scenario and short-rotation, aggregated scenario (at least at equilibrium), revealing an interesting interaction between harvest intensity and harvest unit dispersion. These results suggest that there may be alternative management strategies to achieve the same end. Specifically, a reduction in habitat area (e.g., due to increased timber harvesting intensity) may be compensated for (at least partially) by maintaining aggregated blocks of residual habitat.

7. Several metrics revealed interesting time lag effects. For example, the differences among timber harvest scenarios in TCAI were not evident until 120 years after implementing treatments. This has important management implications. First, the full effects of management actions may not be revealed until many years or decades later, making adaptive management challenging. Second, landscape trajectories contain a certain “momentum” for change, which can partially or completely compensate in the short-term for drivers of change to the existing trajectory.

In summary, our findings suggest that a long-rotation, aggregated cutting scenario will likely maintain the two focal habitats within their historic range of variation and result in the least loss and fragmentation of habitat in the long term. However, given the current landscape momentum, i.e., increasing succession to late-seral coniferous forest, a short-term departure from this strategy may be warranted if the aim is to maintain the landscape within its historic range of variation. Of course, these recommendations must be interpreted within the scope and limitations of this study. In particular, while we believe that our study area is representative of the broader regional landscape, it is clear that populations of species associated with late-seral coniferous forest (e.g., pine marten) extend far beyond the boundaries of our landscape. Thus, our findings must be interpreted in the context of anticipated changes in the surrounding landscape. In addition, for the purpose of illustrating the fragmentation protocol our analysis focused on two habitats: late-seral coniferous forest and pine marten habitat. Clearly, in a real-world application, a comprehensive suite of habitats and focal species should be identified and assessed in the same manner.

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Table 1. Parsimonious suite of metrics for measuring habitat loss and fragmentation. See text for a detailed description of each metric. Note, there are many other fragmentation metrics and failure to be included here does not imply inferiority.

Habitat Component	Metric	Description
Extent	Percent of landscape	The <i>percentage of the landscape</i> (PLAND) comprised of the target habitat.
Subdivision	Number of patches	The <i>number of patches</i> (NP) of the focal habitat or, alternatively, <i>patch density</i> (PD).
	Clumpiness	The <i>clumpiness index</i> (CLUMPY) measures the extent to which habitat is aggregated or clumped.
	Landscape division	<i>Degree of landscape division</i> (DIVISION) equals the probability that two randomly chosen places in the landscape under investigation are not situated in the same contiguous habitat patch, and is closely related to the area-weighted mean patch size.
Geometry	Core area index	The <i>core area index</i> (CAI) is basically an edge-to-interior ratio like many shape indices, the main difference being that the core area index treats edge as an area of varying width and not as a line (perimeter) around each patch. CAI can be averaged across all patches of the focal habitat (weighted by patch area) to provide a suitable class-level metric, or an equivalent <i>total core area index</i> (TCAI).
Isolation	Similarity index	The <i>similarity index</i> (SIMILAR) is a patch-level measure of neighborhood similarity. It considers the size and proximity of all like and unlike patches whose edges are within a specified search radius of the focal patch. SIMILAR can be averaged across all patches of the focal class (weighted by patch area) to provide a suitable class-level metric (SIMILAR_AM).

Connectedness	Correlation length	The <i>correlation length index</i> (CLI) is a measure of the structural continuity or connectedness of the focal habitat based on a measure of the extensiveness of each patch as measured by the <i>radius of gyration</i> (GYRATE). CLI is equivalent to the area-weighted mean radius of gyration (GYRATE_AM).
	Traversability	The <i>traversability index</i> (TRAVERSE) is a functional measure of connectivity based on the idea of ecological resistance. This metric uses a resistance surface to determine the area that can be reached from each cell in the focal habitat

Table 2. Description of the cover types used to characterize vegetation patches on the Pagosa Ranger District of the San Juan National Forest, Colorado. Cover types were derived from the life form and species mix data in the Common Vegetation Unit (CVU) data layer in the US Forest Service National Resources Inventory System (NRIS) data base.

Cover Type	Description
Other forest	Primarily ponderosa pine (<i>Pinus ponderosa</i>) but may include pinyon pine (<i>Pinus edulis</i>) or juniper species (<i>Juniperus osteosperma</i> or <i>J. scopulorum</i>) as secondary or tertiary species.
Warm, dry mixed-conifer	Mixed conifer stands that may have ponderosa pine (<i>Pinus ponderosa</i>) listed as the primary or secondary species, with douglas-fir (<i>Psuedotsuga menziesii</i>) or white-fir (<i>Abies lasiocarpa</i>) in abundance. In addition, species such as blue spruce (<i>Picea pungens</i>), englemann spruce (<i>Picea engelmannii</i>), and others may be abundant. Restricted to south facing slopes.
Warm, dry mixed-conifer with aspen	Same as for warm, dry mixed-conifer except that aspen (<i>Populus tremuloides</i>) is also present.
Cool, moist mixed-conifer	Mixed conifer stands that may list douglas-fir (<i>Psuedotsuga menziesii</i>), white-fir (<i>Abies lasiocarpa</i>), or blue spruce (<i>Picea pungens</i>) as the primary or secondary species. Mixed throughout may be species such as englemann Spruce (<i>Picea engelmannii</i>), white-fir (<i>Abies lasiocarpa</i>), Rocky Mountain white pine (<i>Pinus flexilis</i>), and southwestern white pine (<i>Pinus strobiformis</i>). Restricted to north facing slopes. Ponderosa pine (<i>Pinus ponderosa</i>) absent.
Cool, moist mixed-conifer with aspen	Same as Cool-Mixed Conifer except that aspen (<i>Populus tremuloides</i>) is also present.
Aspen	Aspen (<i>Populus tremuloides</i>) present with no other species, except that pinyon pine (<i>Pinus edulis</i>) or junipers may be present as secondary or tertiary species.
Spruce-fir	Stands dominated by englemann spruce (<i>Picea engelmannii</i>), white-fir (<i>Abies lasiocarpa</i>), or Arizona Rocky Mountain fir (<i>Abies lasiocarpa</i> var <i>arizonica</i>).
Spruce-fir with aspen	Same as spruce-fir except that aspen (<i>Populus tremuloides</i>) is also present.
Grassland (non-	Treeless areas dominated by various forms of flowering and non-

forest)	flowering plant species, herbs, forbs, and legumes.
Riparian	Areas dominated by hydrophilic plant and tree species.
Shrubland	Lower elevation areas dominated by gamble oak (<i>Quercus gambelii</i>) and petran chaparral.
Bare rock	Areas with bare rock such as boulder fields, cliff-faces, and outcroppings.
Water	All rivers, streams, ponds and reservoirs.

Table 3. Reclassification of original cover types used to characterize vegetation patches on the Pagosa Ranger District of the San Juan National Forest, Colorado (see Table 2) into four aggregate classes for the purpose of assessing fragmentation of late-seral coniferous forest.

Cover Type	Description
Late-seral coniferous forest	Warm, dry mixed-conifer (with and without aspen); Cool, moist mixed-conifer (with and without aspen); and Spruce-fir forest (with and without aspen); all in the <i>understory reinitiation</i> or <i>shifting mosaic, old-growth</i> stage of stand development.
Mid-seral coniferous forest	Same cover types as above, but in the <i>stem exclusion</i> stage of stand development.
Early-seral coniferous forest & Aspen	Same cover types as above, but in the <i>stand initiation</i> stage of stand development, plus Aspen stands in any stage of development.
Nonforested & low elevation forest	All other cover types, including Other forest, Grassland, Riparian, Shrubland, Bare rock, and Water.

Table 4. Similarity coefficients used in the similarity index (SIMILAR) for the analysis of late-seral coniferous forest isolation. See text for a description of the similarity index and its use in this exercise. Coefficient of 1 equals maximum similarity to the focal habitat - in this case, late-seral coniferous forest.

Focal cover type	Nonforested & low elevation forests	Early-seral coniferous forest & aspen	Mid-seral coniferous forest	Late-seral coniferous forest
Late-seral coniferous forest	0	0.1	0.3	1

FIGURE CAPTIONS

1. Schematic illustration of the *patch* versus *landscape* perspectives on habitat fragmentation. In the patch perspective, a patch can be reduced in size (area effect) or become more isolated (isolation effect) from nearby patches, but these effects are relative to a focal patch. In the landscape perspective, a contiguous habitat distribution or suite of habitat patches can be reduced in areal extent (area effect) and subdivided into disjunct patches (fragmentation effect), and these effects are relative to the entire landscape.
2. Schematic illustration of the *island biogeographic* versus *landscape mosaic* perspectives on habitat fragmentation. In the island biogeographic perspective habitat fragments are viewed as analogues of oceanic islands in an inhospitable sea or ecologically neutral matrix. In the landscape mosaic perspective, landscapes are viewed as spatially complex, heterogeneous assemblages of patches of differing types, which can't be simplified into a dichotomy of habitat and matrix.
3. Idealized phases of the habitat loss and fragmentation process, beginning with (A) dissection of the habitat (often by roads); followed by (B) perforation, usually associated with habitat conversion (e.g., development, timber harvest, etc.); ultimately resulting in (C) subdivision of contiguous habitat into disjunct habitat fragments; and culminating in (D) shrinkage and attrition as habitat is reduced to scattered fragments or eventually eliminated altogether.
4. Idealized alternative models of habitat loss and fragmentation, including (A) habitat lost in a random fashion, (B) habitat lost in a contagious (i.e., aggregated) manner, (C) habitat lost in a dispersed (i.e., disaggregated) pattern, (D) habitat lost progressively in a wave-like manner along an edge, (E) habitat first bisected by corridor development (e.g., roads) and then lost progressively outward from the corridors, and (F) habitat lost progressively from nuclei that may be dispersed in a random, uniform, or clumped pattern. In these examples, habitat is progressively altered by disturbance over three time periods. Disturbed areas slowly recover over time following disturbance, as in a dynamic forested landscape. Black represents the original, unaltered habitat; white represents recently disturbed areas, and the two shades of gray represent increasing stages of recovery following disturbance. Note, these models could also be represented by progressive loss and fragmentation of habitat without recovery following disturbance, as in a landscape undergoing transformation due to urban and/or agricultural development.
5. Alternative landscape definitions for an arbitrary area on the San Juan National Forest in southwest Colorado. The island biogeographic perspective (see Fig. 2) depicts the focal habitat against an ecologically neutral matrix, whereas the landscape mosaic perspective (see Fig. 2) depicts the focal habitat in a mosaic of other patch types. The focal habitat is defined at three levels of measurement resolution: (A-B) old-growth spruce-fir forest, (C-D) old-growth conifer forest, and (E-F) all forest.

6. Vector versus raster data models for an arbitrary landscape. In the vector model, patches are represented as polygons; whereas, in the raster model, patches are represented as contiguous like-valued cells in a square grid lattice.
7. Effects of changing spatial grain from 25 m (high resolution) to 100 m (low resolution) on four representative landscape metrics for an arbitrary landscape: (1) Simpson's diversity, a measure of overall landscape diversity reflecting the variety and relative abundance of patch types; (2) contagion, a measure of overall clumpiness of patch types, (3) patch density, a simple measure of the number of patches per unit area, and (4) edge density, a simple measure of the length of edges between patches per unit area.
8. Effects of changing spatial extent from a relatively small landscape to a relatively large landscape on four representative landscape metrics (see figure 7 caption for a description) for an arbitrary landscape.
9. Boundary effects vary as a function of the internal heterogeneity of the landscape. In relatively fine-grained landscapes, the boundary of the landscape represents proportionately less of the total edge and therefore has less effect (bias) on the computed value of the metric. In relatively coarse-grained landscapes, however, the boundary of the landscape has a proportionately greater effect.
10. Landscape spatial context (i.e., the broader regional context) of the project area has an important impact on the biological consequences of habitat loss and fragmentation at the local landscape scale. For example, areas of highly fragmented habitat (shown in dark) within a matrix of continuous habitat may not suffer adverse fragmentation effects due to the buffering effect of the broader habitat matrix; whereas, areas of unfragmented habitat within a highly fragmented matrix may suffer significant fragmentation effects for the opposite reasons.
11. Trajectories of change in habitat extent (PLAND) and configuration (represented here by the clumpiness index, CLUMPY) for late-seral coniferous forest habitat (A-B) and pine marten habitat (C-D) under a simulated wildfire disturbance regime representing an historic reference period on the San Juan National Forest in southwest Colorado. These trajectories illustrate the dynamic nature of habitat resulting from the interplay between disturbance and succession processes.
12. Arbitrary landscapes illustrating differences in habitat (shown in dark) extent, as measured by the percentage of the landscape (PLAND). Habitat is illustrated here using an island biogeographic model (see Fig. 2) of landscape structure for simplicity.
13. Arbitrary landscapes illustrating differences in habitat (shown in dark) subdivision, as measured by the number of patches (NP), clumpiness index (CLUMPY) and landscape division index (DIVISION). Habitat is illustrated here using an island biogeographic model (see Fig. 2) of landscape structure for simplicity. Habitat extent (PLAND) is held constant among landscapes to highlight the independent effect of habitat subdivision.

14. Arbitrary landscapes illustrating differences in habitat (shown in dark) geometry, as measured by the total core area index (TCAI). Habitat is illustrated here using an island biogeographic model (see Fig. 2) of landscape structure for simplicity. Habitat extent (PLAND) is held constant among landscapes to highlight the independent effect of habitat subdivision.
15. Arbitrary landscapes illustrating differences in habitat (shown in dark) isolation, as measured by the similarity index (SIMILAR_AM) based on an arbitrary search radius and logical similarity coefficients. Focal habitat extent (PLAND) is held constant among landscapes while the overall landscape composition and configuration varies to highlight the independent effect of habitat isolation.
16. Arbitrary landscapes illustrating differences in the structural or physical continuity (i.e., connectedness) of habitat (shown in dark) as measured by the correlation length index (CLI; also referred to as the area-weighted mean patch radius of gyration, GYRATE_AM). Habitat is illustrated here using an island biogeographic model (see Fig. 2) of landscape structure for simplicity. Habitat extent (PLAND) is held constant among landscapes to highlight the independent effect of habitat connectedness.
17. Arbitrary landscapes illustrating differences in the functional connectivity (i.e., connectedness) of two locations as measured by the traversability index (TRAVERSE). The landscape are illustrated here using a landscape mosaic model of landscape structure where each land cover type is assigned a different level of resistance (e.g., corresponding to the difficulty of the focal organism(s) successfully traversing a unit length of that cover type, say during dispersal) relative to the focal cover type (shown in gold). The least cost hull (i.e., the maximum traversable area) is depicted by the solid dark line, with contours spreading outward from the focal cell. The traversability value shown is for the corresponding focal cell; however, the traversability index (not shown) is computed as the average traversability across all cells of the focal habitat.
18. Outline of the major steps in the habitat loss and fragmentation assessment protocol.
19. Project area location on the Pagosa Ranger District of the San Juan National Forest in southwestern Colorado, U.S.A. The project area comprises the 40,000 ha Piedra River watershed.
20. Land cover map of the project area on the Pagosa Ranger District of the San Juan National Forest in southwestern Colorado, U.S.A. Land cover types represent combinations of the major vegetation types and seral stages of forest stand development (see Table 2 for a description of each cover type).
21. Reclassified land cover map of the project area on the Pagosa Ranger District of the San Juan National Forest in southwestern Colorado, U.S.A. All high-elevation coniferous forest types (spruce-fir, cool-moist mixed-conifer, and warm-dry mixed-conifer, each with and without

aspen) in the understory reinitiation and old-growth, shifting mosaic seral stages were combined into a single “late-seral coniferous forest” class (see Table 3 for details). Map on left shows the original land cover map (as in Fig. 20) and the map on the right is the reclassified landscape.

22. Pine marten habitat capability map for the project area on the Pagosa Ranger District of the San Juan National Forest, Colorado. The map represents one snapshot of habitat conditions during a 600-year landscape simulation under the wildfire scenario (see text for details). Black represents habitat and the various shades of grey represent non-habitat.
23. Late-seral coniferous forest habitat trajectories of change over 200-300 years under four timber harvest scenarios: (1) long-rotation (300 yrs), aggregated cutting pattern; (2) long-rotation, dispersed cutting pattern; (3) short-rotation (200 yrs), aggregated cutting pattern; and (4) short-rotation, dispersed cutting pattern (see text for details). The mean and 90% range of variation (5-95th percentile) under the reference conditions, simulated here as a wildfire scenario, is shown in the dashed (mean) and solid light lines. Sub-figures represent different landscape metrics: (A) percentage of the landscape, PLAND; (B) number of patches, NP; (C) clumpiness index, CLUMPY; (D) landscape division index, DIVISION; (E) total core area index, TCAI; (F) similarity index, SIMILAR_AM; and (G) correlation length, or the area-weighted mean patch radius of gyration, GYRATE_AM (see Table 1 for descriptions of metrics).
24. Pine marten habitat trajectories of change over 200-300 years under four timber harvest scenarios (see figure 23) and the mean and 90% range of variation (5-95th percentile) under the reference conditions, simulated here as a wildfire scenario, is shown in the dashed (mean) and light lines. Pine marten habitat was defined as cells with habitat capability values > 0.7 computed from a habitat capability model. Subfigures represent different landscape metrics: (A) percentage of the landscape, PLAND; (B) number of patches, NP; (C) clumpiness index, CLUMPY; (D) landscape division index, DIVISION; (E) total core area index, TCAI; (F) similarity index, SIMILAR_AM; and (G) correlation length, or the area-weighted mean patch radius of gyration, GYRATE_AM.