Evaluation of Landscape Metrics for Quantifying Fragmentation in the Morice & Lakes IFPA Area

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Summary

The IFPA Ecosystem Technical Advisory Committee is charged with evaluating the potential impacts of alternative land use plans on landscape-level biodiversity and on selected wildlife species. Towards this end, they have asked us to provide them with an analysis and interpretation of selected fragmentation indices.

Total habitat abundance, patch size, patch spacing and edge area emerge from the scientific literature as general, ecologically-relevant landscape properties. Edge area was not considered in this study because it does not greatly affect connectivity (our focus). Based on our study and for the purpose of assessing connectivity, we recommend three metrics:

Habitat abundance. Habitat abundance should be the first metric examined because habitat abundance constrains pattern. Theoretical models show that patch size and spacing depend on abundance. The territory-dispersal model and most of the metrics examined in our study were strongly influenced by abundance. In addition, habitat abundance has the clearest ecological links, is obviously sensitive to management and is easy to understand.

Patch size distribution. Patch size distribution should be the second metric examined. Patch size distributions can distinguish between fire and logging disturbance, both simulated (this report) and real (Eng 2002). This capability is particularly important in the context of ecosystem-based management. Under certain conditions, patch size distributions also provide information about patch spacing, because spacing correlates with size and abundance. Patch size distributions are relatively easy to understand and communicate. The area in each patch class provides more ecologically relevant information than the number of patches in each class.

Centroid connectivity index (CCE). Finally, to examine patch spacing, Total CCE should possibly be the third metric examined. CCE measures the interaction among all patch pairs, accounting for both patch size and spacing. CCE is one of the few metrics that combines patch size and patch spacing in a relatively understandable way, however, as a single-number metric, it confounds the effects of size and spacing. Unfortunately, we cannot strongly recommend CCE, because Mean CCE and Max CCE did not distinguish fire from logging in our simulations. We expect Total CCE may be a better metric than Mean or Max CCE because it has better mathematical properties, but Total CCE was not evaluated in this study and requires further testing.

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Introduction

Loss of natural forests, and the fragmentation of remaining areas into progressively smaller patches isolated by lands converted to other uses (e.g., plantations, agriculture or industrial/urban development), is a significant global trend (Harris 1984) and has received considerable attention in the ecological literature. Studies have identified the composition (abundance of different vegetation types) and configuration (pattern of different vegetation types) of landscapes as important factors influencing ecosystem function and habitat quality (Turner 1989). Prompted by island biogeography theory (MacArthur and Wilson 1967), analysis of landscape patterns has received considerable attention from both the ecological research and management communities (Dorner et al. 2002 and references cited therein). In the last decade, numerous metrics have been developed to quantify landscape pattern (McGarigal and Marks 1994; Riitters et al. 1995). Selecting metrics that are appropriate for a given application has become a confusing task.

Assessing the ecological merits of alternative land use plans requires the selection and comparison of indicators (a class which includes landscape metrics) of ecological condition. This task is particularly challenging if one is searching for a general metric to describe biodiversity. One typical approach uses a metric that describes impacts on indicator species. Another approach uses metrics that describe impacts on features that have general ecological relevance. For example, a variety of species prefer a specific forest age class. Here we adopt the latter approach.

Selection of indicators for assessing ecological impacts has received considerable attention in the forest management literature. Features of a good indicator include

1. ecological relevance;
2. sensitivity to management actions (and insensitivity to other forces);
3. ease of interpretation/communication; and
4. mathematical soundness.

The first two criteria are typically used to assess the quality and appropriateness of indicators (Beasely and Wright 2001). To these, we add ease of interpretation/communication, which is particularly important in a planning context, and mathematical soundness, a potential concern with some landscape metrics. The balance between these criteria depend in part on intended use. Planning indicators should be distinguished from monitoring indicators (Yamasaki et al. 2001). Planning indicators need to be relatively simple in order to facilitate scenario modelling, multiple comparisons and communication to a non-specialist audience.

The sections below provide some background on the ecological relevance of landscape composition (abundance of different vegetation types) and configuration (pattern of different vegetation types). The ecological effects of abundance are difficult to separate from those of pattern. Forest fragments are almost always created by habitat removal and the effects of removing habitat and creating smaller pieces are difficult to separate.

Ecological effects of habitat abundance

The ecological effects of habitat abundance are well documented. Both population size (Fahrig 2002) and species richness (Preston 1962) decrease as habitat abundance decreases. Habitat loss is generally regarded as the biggest single threat to biodiversity (Erhlich 1988). This relationship is most clear when one habitat type is being replaced by a significantly different one (e.g., forest being replaced by agriculture or urban development; Bunnell 1999). A null hypothesis in landscape ecology is that the ecological integrity of a landscape, for a given species, declines linearly with amount of habitat. The degree to which integrity declines non-linearly is an indication of the role that pattern and non-habitat areas play in maintaining or impeding population persistence. A non-linearity at approximately 30% (Andren 1994) suggests that pattern effects may be more important when habitat abundance drops below this threshold.

Habitat abundance also exerts considerable control over landscape pattern. Consider a landscape (raster maps) with one of two habitat classes (one habitat, one non-habitat) assigned randomly to each raster cell. As habitat proportion decreases, patch size decreases and the distance between patches increases (Andren 1994) in a predictable manner until a percolation threshold (where one patch connects all four map corners) is reached at about 60% habitat (Stauffer and Aharony 1992). When specific patch sizes are randomly assigned, the same trends occur, but percolation values differ (Gardner and O'Neill 1991). When patches are uniformly spaced on a grid, the ratio of patch size to patch spacing varies with habitat abundance in a predictable manner (Daust 1994). This implies the obvious: at a given habitat abundance, artificial landscapes can have a few widely spaced patches or many small patches that are closer together (or some combination). The extent to which this implication holds on real landscapes is not well documented.

Ecological effects of pattern

The effects of ecological patterns are also well documented in some ecosystems. The classic work on island biogeography (McArthur and Wilson 1967) identifies two ecologically relevant aspects of pattern (summarised in Bunnell 1999):

> "*Area*: larger islands contain more species than do small islands. This occurs because small islands experience more extinctions (small populations are more vulnerable to chance events) and receive fewer immigrants (species wandering from the mainland to nearby islands are not as likely to encounter them—a kind of "target size" effect).
>
> *Distance*: equivalent-sized islands more remote from the mainland or source population will have fewer species because the extinction rate is the same but the immigration rate is lower (fewer immigrants reach the island)."

Other lines of investigation corroborate the importance of area and distance effects. Meta-population theory supports the importance of patch size and isolation on extinction and colonization processes (Levins 1969, 1970, Hanski 1994). Theory on minimum viable populations suggest that species persistence is greatly compromised when habitats support less than 50 individuals (Shaffer 1981). Larger species may have trouble finding habitat in sufficient density to support a home range in heavily fragmented forests (e.g., Chapin et al. 1998).

Area (of a patch) and distance (between patches) effects, however, are poorly documented in forested settings (Bunnell 1999). Some of the studies that have found effects have not controlled for habitat abundance. Many studies that have controlled for abundance have not been able to demonstrate a strong affinity of species to pattern (Bunnell 1999). Bunnell (1999) suggests that findings in managed forests differ from Island Biogeography theory because forest fragments are not true islands and because the non-habitat matrix is not a true sea: in the forest, "islands" share species with the "sea". While many vertebrate species prefer natural old forest, they can often inhabit young forest, particularly young forest with natural structure. This may be less true of other taxa, such as some epiphytic lichens that are correlated with old stands and oldgrowth structure (Price and Hochachka. 2001). When intervening habitat is hostile to both survival and movement, the importance of connectivity is well established (Bunnell 1999). In managed forests, more movement occurs inside of than outside of corridors, suggesting that clearcuts may be somewhat hostile to some species. The blurring of differences between habitat and matrix presents a challenge to researchers to identify the appropriate scales and indicators to assess issues of pattern.

Despite the differences between forest and island settings, some studies (e.g., Jansson and Angelstam 1999, Laurance and Bierregaard 1996) have found effects consistent with Island Biogeography theory. In addition, species-specific simulation models also predict pattern effects (Fahrig 2002).

In addition to area and distance effects, studies have identified a third ecological effect of pattern: edge effects. Edges are places where plant communities meet, or where successional stages or vegetation conditions within plant communities come together (Kremsater and Bunnell 1999). Edge effects include changes in microclimate and consequently in plant distributions; animal distributions also respond to edge for a variety of reasons (Kremsater and Bunnell 1999). Microclimatic effects extend from 100 to 150 m from the edge; the most important effects on biological organisms (e.g., predation) extend 50 m, however, the effects of roads can extend 400 m (Kremsater and Bunnell 1999). Some animals prefer edges, others avoid it. While negative edge effects are well documented where forest patches are isolated by agriculture, they are less well documented along forest to clearcut edges (Kremsater and Bunnell 1999).

Other aspects of pattern such as shape and fractal dimension appear to have less ecological relevance, although some examples of ecological linkages exist (Hamazaki 1996). Future research may provide new information.

In summary, the influence of habitat abundance on biodiversity is clear in general, but less clear when habitats are somewhat similar, as is the case with different forest age classes. Similarly, the importance of pattern on biodiversity is clear in general, but less clear in forested ecosystems. Habitat abundance should probably be the focus of analysis because it has strong ecological linkages and because it constrains pattern. Three aspects of pattern with strong ecological connections also seem worthy of attention: patch area, patch spacing and edge.

Landscape metrics

The common usage of the term "landscape metrics' refers to indices developed for categorical (polygon) maps (McGarigal 2002). Landscape metrics characterize the geometric and spatial properties of mapped patterns at a single scale, using patches as the basic unit of analysis (McGarigal 2002).

Patches represent discrete areas of relatively homogenous environmental conditions at a particular scale (McGarigal 2002). Patch boundaries are distinguished by abrupt discontinuities in relevant environmental conditions (Kotliar and Wiens 1990). Defining an ecologically relevant patch is one of the most challenging aspects of landscape analysis, particularly if the patch should relate to a broad concept like biodiversity. Changes in structure and vegetation that occur with stand age are not always abrupt and patch definitions based on age class involve subjectivity.

In addition, the resolution and representation of data influence patch connectivity. As resolution decreases (on a raster grid), small patches disappear and larger patches coalesce as non-habitat fragments disappear.

Landscape metrics are commonly divided into three different levels of organization (McGarigal 2002):

- Patch-level metrics describe individual patches;
- Class-level metrics describe a "population" of patches belonging to a particular class. They integrate patch level metrics (e.g., mean patch size) or may describe properties that occur only at the class level (e.g., contagion); and
- Landscape-level metrics integrate information from all classes that occur on a landscape.

Landscape metrics can be further divided into those that describe composition (e.g., number of different classes) and those that describe pattern (configuration of habitat into patches of different size and shape, and the spacing between patches). While there are numerous pattern metrics, they derive mainly from some primary measures: patch perimeter, patch size and patch spacing (see Li et al. 1993 and McGarigal 2002 for classification of metrics). Patch size and spacing together determine the number of patches on the landscape and patch density (patch area / sample area).

Landscape metrics can also be classified by whether or not they directly consider ecological function (McGarigal 2002). Structural metrics measure the composition and pattern defined by the classification and geometry of the map in a generic manner; they leave ecological interpretation for later (although ecological information should certainly have been involved in the original definition of a patch or habitat). Functional metrics directly address process issues relevant to specific organisms when measuring landscape pattern (which is a motivation for use of dispersal or individual based models that attempt to model relevant aspects of the process). Functional metrics include, for example, information about the depth of edge influence, sometimes as a function of the type of adjacent land class (e.g., contrast between classes). They may also include minimum patch sizes to consider and may assess connectivity in terms of different movement processes and dispersal distances; dispersal may vary with each land class traversed. Note that the term connectivity assesses patch spacing (or inter-patch distance or isolation) from a species- or process-specific perspective and scale.

This study focuses on class-level metrics that describe pattern. Patch-level metrics have little relevance at the strategic planning scale because they include too many details. Landscape-level metrics confound information about the different patch classes. We assume that all relevant patch classes are worthy of being analysed separately.

This study searches for metrics that are ecologically relevant, sensitive to management, easy to understand and mathematically well-behaved. It contains two parts. In the first, we filter metrics for ecological relevance, ease of communication and mathematical behaviour using a set of subjective criteria. In the second, we assess ecological relevance and sensitivity to management in a simulation experiment.

Part 1. Subjective evaluation

Methods

We selected 46 metrics from the literature that have been used relatively frequently or that have appeared recently and show interesting properties (Appendix 1). Most metrics (43) are a single number, but we also evaluate patch size distribution, mean cluster size and expected cluster size (x, y graphs). We developed a set of criteria with which to evaluate metrics:

1. *Ecological relevance*. In the context of this study, we consider metrics based on patch size and/or spacing to be ecologically relevant. Although edge is another ecologically relevant aspect of pattern, it is beyond the scope of this study. Ecological relevance is further investigated in part 2.

2. *Ease of interpretation/communication*. Metrics should be easy to interpret and convey. We prefer metrics that focus on a single aspect of pattern rather than ones that confound different aspects of pattern. We prefer commonly used statistics (e.g., means and standard deviations) over uncommon indices.

3. *Mathematical behaviour*. We make some observations on the mathematical behaviour of the different metrics.

Results

Of the 43 single-number metrics evaluated, we identified 19 metrics as being ecologically relevant (Table 1). Five metrics are based on patch size: largest patch index (LPI), largest patch (LargestPatch), mean patch size (MPS), patch size standard deviation (PSSD) and patch size coefficient of variation (PSCV). We did not include the smallest patch, even though it is based on patch size, because we could think of no ecological reasons for knowing the size of the smallest patch and additionally, the smallest patch usually obtains the value of the grid cell size used in the analysis. Nine metrics are based on spacing: mean nearest neighbour (MNN), maximum nearest neighbour (MaxNN), nearest neighbour standard deviation (NNSD), nearest neighbour coefficient of variation (NNCV), mean minimum spanning tree (MeanMST), total minimum spanning tree (tMST), mean minimum planar graph (MeanMPG), total minimum planar graph (tMPG) and mean centroid distance (MeanCD). Number of patches (NP) and patch density (PD) also depend largely on spacing, but also on patch size and landscape extent. Thus, NP and PD are difficult to interpret without reference to patch size. Two metrics, mean centroid connectivity Index (CCE) and maximum centroid connectivity index (MaxCCE), are based on both size and spacing. We retained contagion (CONTAG2; defined as the relative probability that two cells of the same class will be adjacent), because it depends partly on patch size and spacing.

All three multiple-number metrics are ecologically relevant. Patch size distribution is based on patch size. Mean and expected cluster size are based on patch size and spacing.

Twelve single-number metrics were rated as easy to understand and communicate. Seven metrics were rated as moderate to difficult: CCE and MaxCCE confound the effects of size and spacing; tMST, MeanMST, tMPG and MeanMPG evaluate all the connections on the landscape at one time rather than summarising a population of inter-patch distances; contagion does not relate directly to size or spacing. Although patch size distribution includes more numbers, it is still relatively easy to interpret. Graphs based on mean or expected cluster size are difficult to interpret.

We noted several mathematical concerns that apply to these metrics. First, several metrics are mathematically related to other metrics (Table 1), providing similar information. Second, a single number does a poor job of describing the interaction of two variables. Metrics based on size do not describe spacing, Metrics based on spacing do not describe size. Third, a single number does a poor job of capturing the heterogeneity of patterns. For example, a landscape with patches in only one corner can have the same value for NND as a landscape with the same pattern of patches spread over the entire landscape. In the case of MPS, this problem can be somewhat offset by considering standard deviation, however, the assumption that the distribution is normal is unrealistic. Fourth, mean is a poor statistic for describing ecological values, particularly if the distribution contains many small elements. Means give equal weights to small and large elements. In ecology, we know that ecological weight should be related to the area contained in a unit (area weighted patch size or "expected patch size; Box 1). Mean patch size can be greatly reduced in value by many small patches and thus is particularly sensitive to the scale of analysis and errors associated with the raster grid.

Consider a landscape with a 1 ha patch and a 99 ha patch:

Mean patch size = 1 + 99 / 2 = 50 ha
Expected patch size (= area weighted patch size) = (1 x 1) + (99 x 99) / 100 = 98 ha

Box 1. Example comparing mean patch size to expected patch size.

Table 1. Performance of single-number metrics against evaluation criteria.

Name or acronym	Ecological basis	Interpretation	Mathematical similarity
LPI	patch size	easy	
LargestPatch	patch size	easy	
MPS	patch size	easy	
PSSD	patch size	easy	
PSCV	patch size	easy	
MNN	spacing	easy	≈ MeanMST & MeanMPG
MaxNN	spacing	easy	
NNSD	spacing	easy	
NNCV	spacing	easy	
MeanCD	spacing	easy	
MeanMST	spacing	mod. to difficult	≈ MNN & MeanMPG
tMST	spacing	mod. to difficult	≈ tMPG
MeanMPG	spacing	mod. to difficult	≈ MNN & MeanMST
tMPG	spacing	mod. to difficult	≈t MST
NP	(spacing)	easy	≈ PD
PD	(spacing)	easy	≈ NP
CCE	size, spacing	mod. to difficult	
MaxCCE	size, spacing	mod. to difficult	
CONTAG2	(spacing)	mod. to difficult	

Part 2. Performance on simulated landscapes

Methods

Several studies have used principle components analysis in an effort to find a suite of metrics that capture the variation generated by all the metrics (e.g., Riitters et al. 1995). These studies identify metrics that are good at distinguishing the range of landscape patterns examined. In this study we do not just wish to distinguish landscapes based on differences in all aspects of pattern, we wish to distinguish landscapes based on differences in their ecological value, that is, we are searching for ecologically relevant metrics. In order to assess the ecological relevance of a metric, ecological assumptions must be stated clearly:

1. patch size and spacing are the most relevant aspects of pattern (edge is beyond the scope of this study);
2. natural landscape patterns differ from typical anthropogenic patterns in ecological value;
3. habitat abundance constrains pattern;
4. pattern becomes more important at habitat abundances of less than 30%; and
5. landscapes that allow animals to move more readily (at territory and dispersal scales) are better connected, ecologically.

To address the first assumption, we only assess metrics that measure patch size or spacing. To address the second assumption, we assess the ability of metrics to distinguish patterns created by simulated natural (fire) and anthropogenic (logging) disturbances. This assessment also identifies metrics that are sensitive to management actions. To address the third and fourth assumptions, we control for abundance by creating and assessing patterns at different abundance levels and focus on patterns where abundance is below 30%. To address the fifth assumption, we simulate territory occupancy and dispersal and compare patterns in metrics to patterns in simulated connectivity. In summary, metrics are evaluated against two criteria:

- ability to distinguish fire-induced from logging-induced patterns.
- ability to match results (i.e., follow same trends) of the territory/dispersal model

Generating landscapes

We generated 72 maps of landscape pattern at nine different levels of habitat abundance (Table 2), simulated territory use and dispersal on selected maps, calculated a suite of landscape metrics for each map and evaluated metrics against the criteria discussed above. We used SELES to generate landscape patterns and calculate patch metrics. We used PATCH (Schumaker 1998) to simulate territory formation and dispersal.

Table 2. Combinations of variables used to generate landscape patterns

Base Landscape	Disturbance Models	Habitat Abundance*	Replicates	Total
Square	Fire	9 levels	2	18
	Logging	9 levels	2	18
Morice	Fire	9 levels	2	18
	Logging	9 levels	2	18
				72

* 1, 5, 10,15, 20, 30, 40, 60, 80%

Landscape patterns were generated with a simple fire model and two simple logging models on two different landscapes. A square landscape consisted of a 500 cell x 500 cell raster grid that was completely forested. The Morice landscape consisted of an approximately 1.1 million ha area within an over 3 million ha rectangular grid. It is divided into forest and non-forest (e.g., lakes, alpine, urban) cover classes. The Morice landscape lies in central British Columbia in an area subject to frequent stand replacing natural disturbances, mainly from fire and insects. Forest age was set to 300 years before simulations to remove the influence of recent history and to highlight the effects of the simulated disturbance regime. Both areas were modelled using one hectare raster cells.

The fire model burned patches in the landscape each year, based on a specified fire return interval and mean fire size. It modelled stand ageing. The number of fires per year was calculated from the return interval and mean fire size. Each year, the number of fires and fire size were modelled stochastically using a negative exponential distribution. Mean fire size was set to 500 ha on the square landscape and 100 ha on the Morice landscape. Fire return interval was varied from 27 to 562 years in order to approximately generate a specified proportion of oldgrowth (>250 yrs). Constraints were added so the model left the precise proportion of oldgrowth.

Like the fire model, the logging models logged patches and modelled stand ageing. Both logging models included green-up rules that disallowed harvesting adjacent to recent cutblocks (< 20 yr old). The width of the adjacency buffer was approximately equal to the width of the cutblock. Both models had a higher probability of logging stands next to greened-up cutblocks. The Morice model included a higher probability of logging close to the mill. The square model included a higher probability of logging next to roads, but over the course of the simulation, the entire area became roaded so the rule had little influence. Block size was selected stochastically from a uniform distribution ranging from 10 to 60 ha. Annual allowable harvest was set to 1% per year. Constraints were added to the model to leave the desired proportion of oldgrowth.

Defining habitat patches

We translated selected age class maps resulting from the model runs into binary (habitat / non-habitat) maps. Age class 250+ was classified as habitat. The rest of the landscape was classified as non-habitat.

Modelling territory formation and dispersal

Only maps generated on the square landscape were used because of software limitations in PATCH. SELES maps were converted into bitmaps and loaded into PATCH where we modelled territory formation and dispersal at three spatial scales (following the approach used by Richard et al 2002). We specified maximum territory sizes at each scale: 15 ha, 100 ha and 1000 ha and indicated that territories must be comprised of at least 70% habitat. Together these specifications lead to minimum territory sizes of 10, 70 and 700 ha. PATCH then identified possible territories on the landscape; no overlapping territories were permitted. We randomly seeded half of the territories with “breeders”, each of which produced one disperser, and then simulated the first year of dispersal assuming that dispersers take a “directed walk”. In a "directed walk" dispersers generally follow a straight trajectory when traveling through non-breeding habitat, but when they hit suitable habitat they tend to stay in it searching before moving off again through non-habitat. We only simulated the first year of dispersal because we wished to focus on connectivity, rather than on demographics. We replicated the seeding and dispersal 100 times. Dispersal was set to 40 x the linear dimension of average home range size (Bowman et al. 2002). We assumed there was no mortality associated with the dispersal process. We recorded the number of territories formed, the number of territories as a proportion of number of territories if all potential habitat was in territories (the habitat dilution effect) and the proportion of dispersers that found a vacant territory (an index of connectivity).

Calculating and evaluating metrics

For each landscape pattern (Table 2), we calculated patch size and spacing statistics. We determined patch size and nearest neighbour for each patch in each map (recording values for each patch allows for a more detailed analysis). We plotted the ratio of mean nearest neighbour distance to the square root of mean patch size to test the hypothesis that this ratio does not vary with disturbance process or starting landscape. We calculated the number of patches in different size classes (1-10, 11-100, 101-1000, 1001-10000 and 1000+) and multiplied the number of patches in each size class by the class midpoint to estimate the area in each size class. We visually compared patch size distributions to see if they differed and to see if they matched the results of the territory/dispersal model.

For each landscape pattern (Table 2), we used SELES to calculate a suite of single-number metrics (Table 1) for each patch map. For each metric, we plotted values for different disturbance types on the Square and Morice landscapes against habitat abundance. We examined graphs visually to determine whether metrics could distinguish between burned and logged landscapes, particularly at habitat abundances of less than 30%. Then we compared each metric to the results from the territory/dispersal model.

One of the more complicated metrics based on cluster size required additional steps (see Fall and Beasley 2002 for a description of cluster size calculations). SELES aggregated patches into clusters if they were less than a specified distance (referred to as the *correlation distance*) from their neighbouring patch. It calculated the number of clusters, the mean cluster size (MCS) and the expected cluster size (area-weighted mean; ECS) at each correlation distance. Correlation distance ranged from 0 to 10,000 m in increments of 100 m. For each patch map, we plotted MCS and ECS against correlation distance. Typically, these graphs showed two stable states (many small clusters or few large clusters), with a rapid transition between states over a short range of correlation distances. After inspecting several graphs, we chose the smallest correlation distance at which cluster size exceeds 10% of habitat abundance as the beginning of the transition between states. Each landscape map has one transition point based on MPS and one based on EPS. We plotted transition points against habitat abundance and disturbance type. We also plotted the minimum correlation distances that produced 10, 100 and 1000 ha clusters. We examined graphs visually to determine whether metrics could distinguish between fire-disturbed and logged landscapes, particularly at habitat abundances of less than 30%. Then we compared them to the results from the territory/dispersal model.

Results

Territory abundance and dispersal

Territory abundance and dispersal success varies with habitat abundance and with the disturbance regime modelled. Territory abundance increases with habitat abundance at all spatial scales (Figure 1). Small territories increase in proportion to habitat abundance and do not differ with disturbance regime. Medium territories increase in proportion to habitat abundance for fire disturbance; with logging disturbance, relatively fewer territories occur at 10, 20 and 40% abundance levels than with fire disturbance. Large territories do not form until habitat abundance exceeds 10% on fire disturbed landscapes and 40% on logged landscapes. The difference in habitat use (measured as number of territories formed as a proportion of the maximum number that could be formed given the area of habitat) between fire-disturbed and logging landscapes peaks at about 40% habitat abundance (Figure 2).

Dispersal success increases as habitat abundance increases up to 60% (Figure 3). Relative to fire-disturbed landscapes, logged landscapes have lower dispersal success from small and medium territories until 40% habitat abundance. Successful dispersal from medium territories begins at 10% and 20% habitat abundance on fire-disturbed and logged landscapes respectively. Successful dispersal from large territories begins at 20% and 60% habitat abundance on fire-disturbed and logged landscapes respectively.

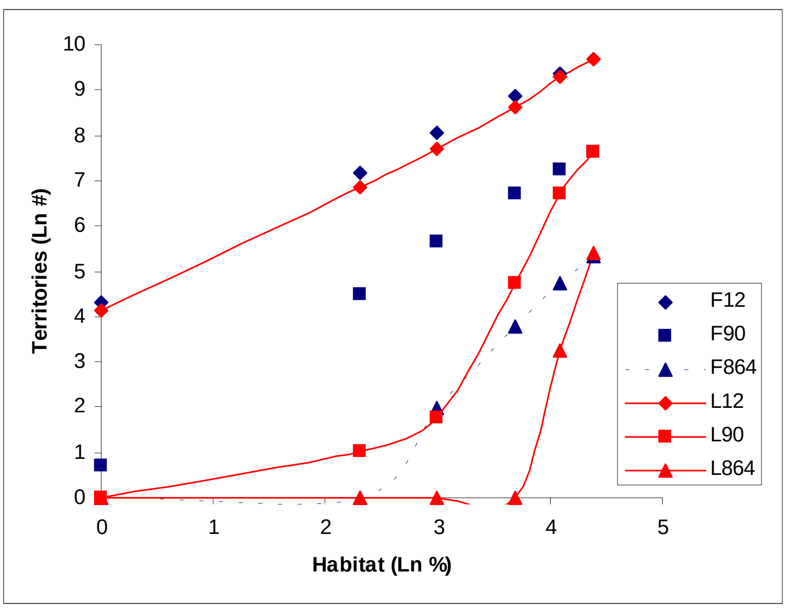

Figure 1. Natural log of number of territories formed vs. natural log of habitat abundance.

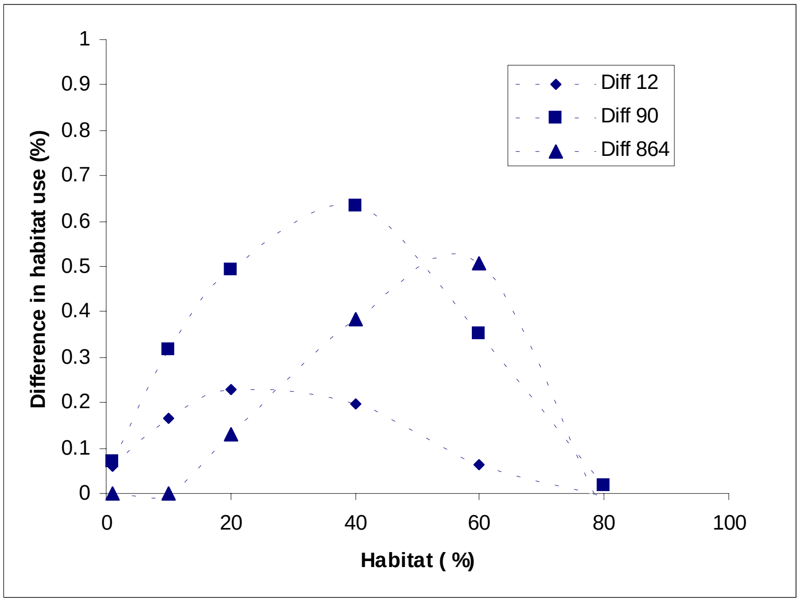

Figure 2. Difference in habitat use (%) versus habitat abundance (%). Habitat use is the number of territories created divided by the maximum number that could be created with the habitat available. The difference equals use on fire-disturbed minus use on logged landscapes (Square only).

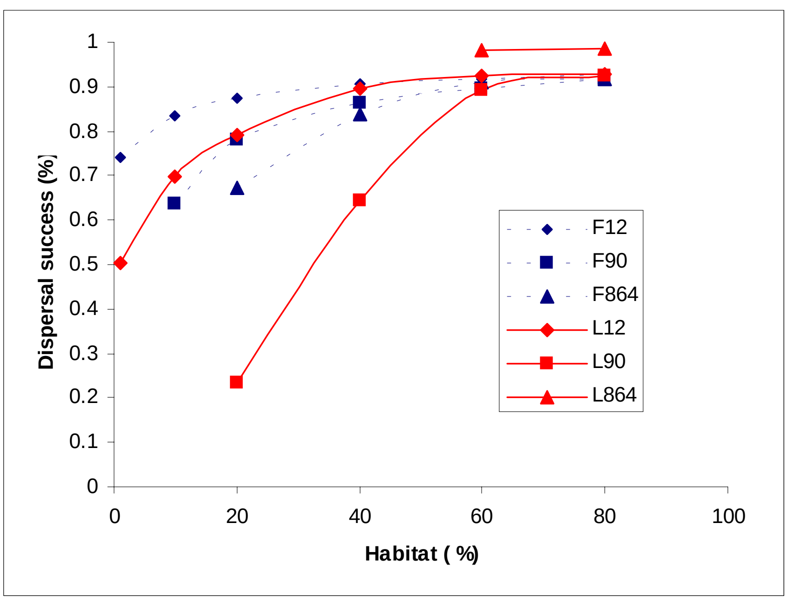

Figure 3. Dispersal success versus habitat abundance. Dispersal success is the percentage of randomly seeded dispersers finding suitable territories.

In general, considering territory abundance and dispersal success, logged and fire-disturbed landscapes are most similar at very low habitat abundance (1%) and at higher abundances (> 80%).

Patch size and spacing

Mean patch size (MPS) increases exponentially with increasing habitat abundance, but increases more rapidly on logged landscapes (Figure 4). Mean nearest neighbour distance (NND) decreases exponentially with increasing habitat abundance, but decreases more rapidly on fire-disturbed landscapes (Figure 5). The ratio of NND to the square root of MPS does not vary by landscape (Figure 6). That is, relative to fire-disturbed landscapes, logged landscapes tend to have larger patches that are farther apart, but the ratio of patch spacing to patch width is the same. Ratios generated with the disturbance models were smaller than those predicted using a regular grid (Figure 6).

Patch size distributions can distinguish fire from logging, but do not match the results of the territory/dispersal model well. The number of patches in each size class tends to follow a negative exponential distribution on fire-disturbed landscapes. On logged landscapes, the beginning of the distribution is relatively flat and the end is truncated. Logged landscapes have relatively more area in two patch size classes than do fire-disturbed landscapes: 11-100 and 101-1000 (Figure 7). On logged landscapes, large patches emerge at higher habitat abundances than they do on fire-disturbed landscapes (Figures 8 and 9). These results suggest that large territories may be difficult to create, but do not intuitively suggest a problem creating 100 ha territories.

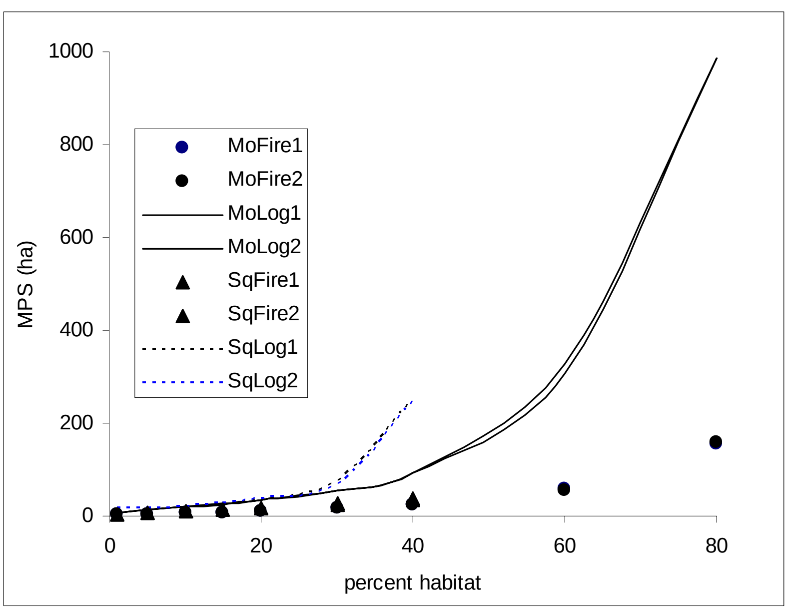

Figure 4. Mean patch size versus habitat abundance on the Square and Morice landscapes with fire-disturbed and logging models (results for replicate 1 only).

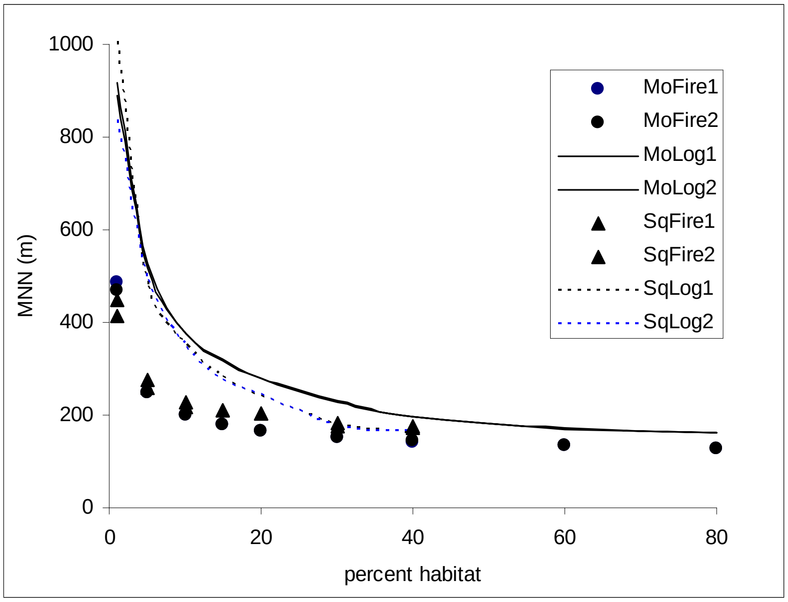

Figure 5. Mean nearest neighbour distance versus habitat abundance on the Square and Morice landscapes with fire-disturbed and logging models (results for replicate 1 only).

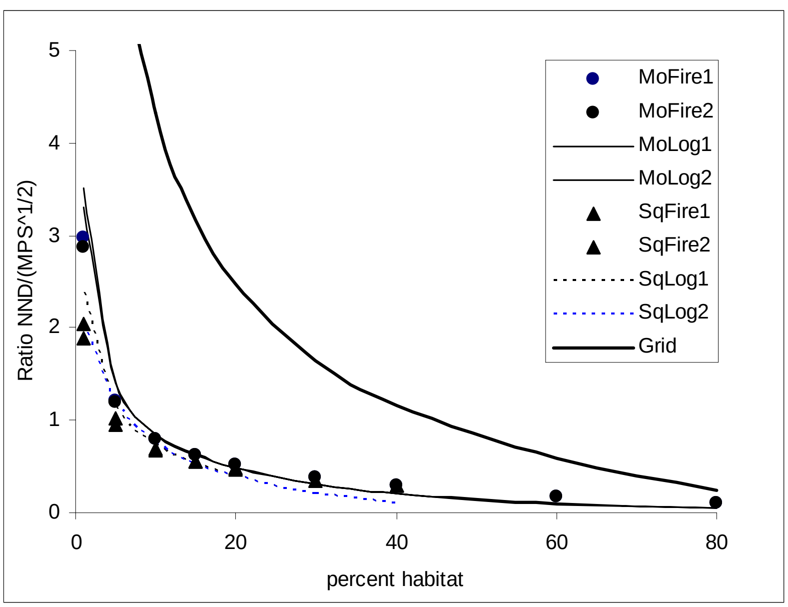

Figure 6. Ratio of mean nearest neighbour distance to root mean patch size versus habitat abundance on the Square and Morice landscapes with fire-disturbed and logging models (results for replicate 1 only).

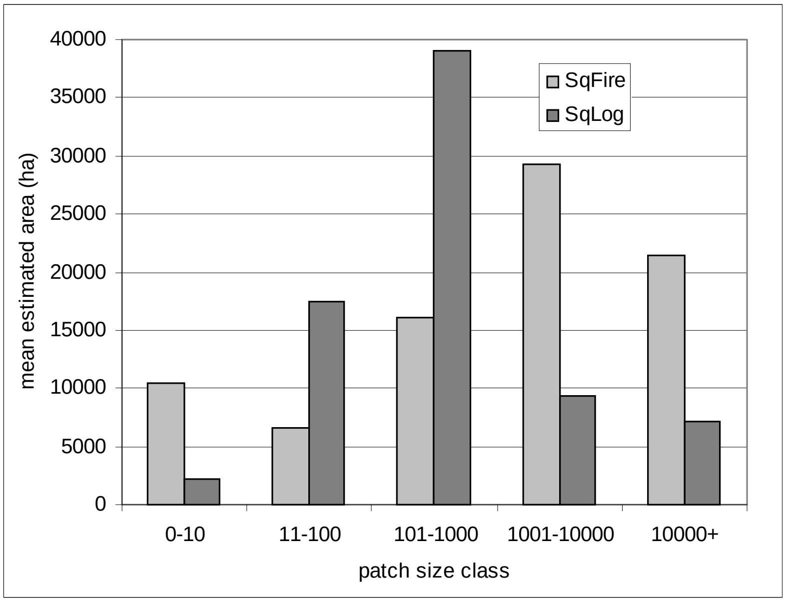

Figure 7. Mean estimated area by patch size class for fire and logging disturbances on the Square landscape. Means cover all habitat abundance levels.

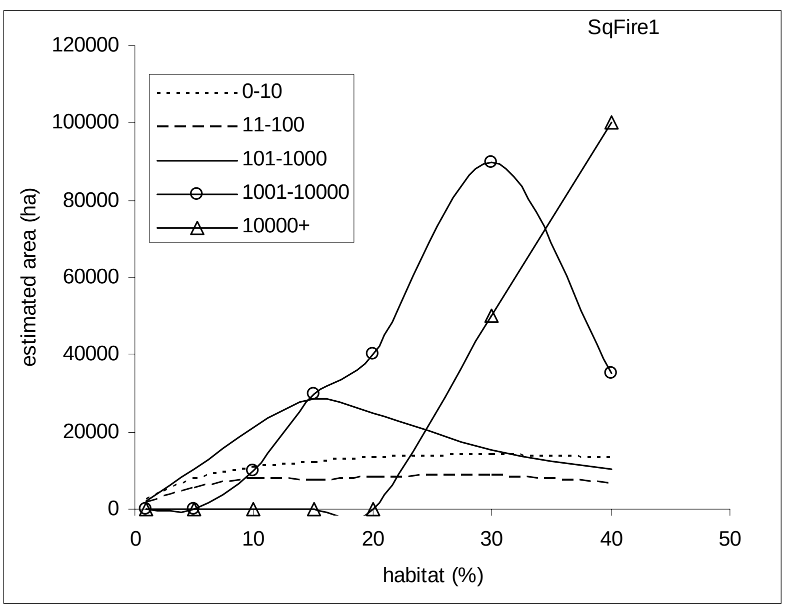

Figure 8. Estimated area in each patch size class versus habitat abundance for fire disturbance on the Square landscape.

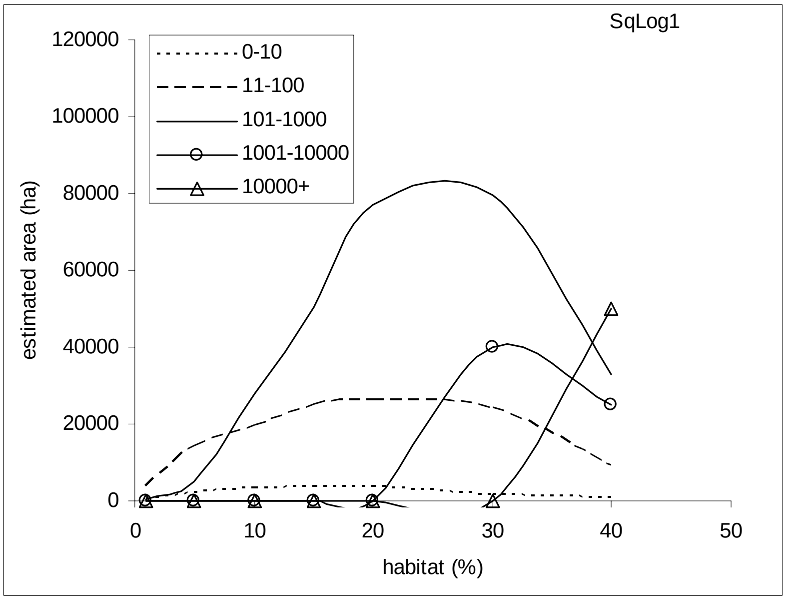

Figure 9. Estimated area in each patch size class versus habitat abundance for logging disturbance on the Square landscape.

Cluster size metrics

Graphs of mean cluster size and expected cluster size produce different results. Transitions from many small to few large clusters occur at smaller correlation distances as habitat abundance increases (Figure 10). At a given habitat abundance, transitions occur at lower correlation distances on logged landscapes, based on mean cluster size (Figure 10), but at higher distances based on expected cluster size (Figure 11). Correlation distances required to produce a specified cluster size decrease as habitat abundance increases (Figure 12). Fire and logging both produce the same mean cluster sizes at the same correlation distance (Figure 12). Logging produces 100 and 1000 ha expected cluster sizes at higher correlation distances than fire (Figure 13). Ten hectare patches occurred at zero correlation distance with both disturbance types. Correlation distances required to produce 100 and 1000 ha ECS values show the largest difference between logging and fire of all the cluster-based graphs, but do not match the results of the territory/dispersal simulation.

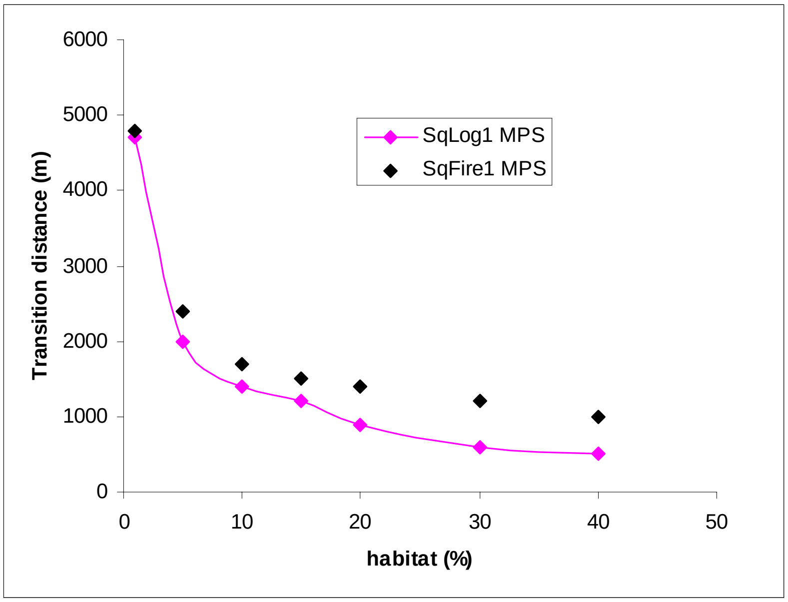

Figure 10. Correlation distance where connectivity increases rapidly versus habitat abundance for fire and logging disturbances on the Square landscape (based on mean cluster size)

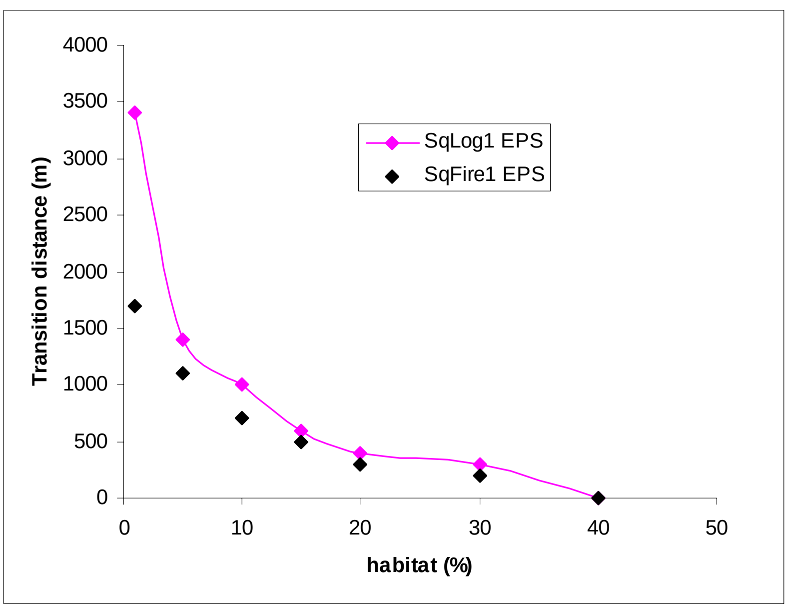

Figure 11. Correlation distance where connectivity increases rapidly versus habitat abundance for fire and logging disturbances on the Square landscape (based on expected cluster size)

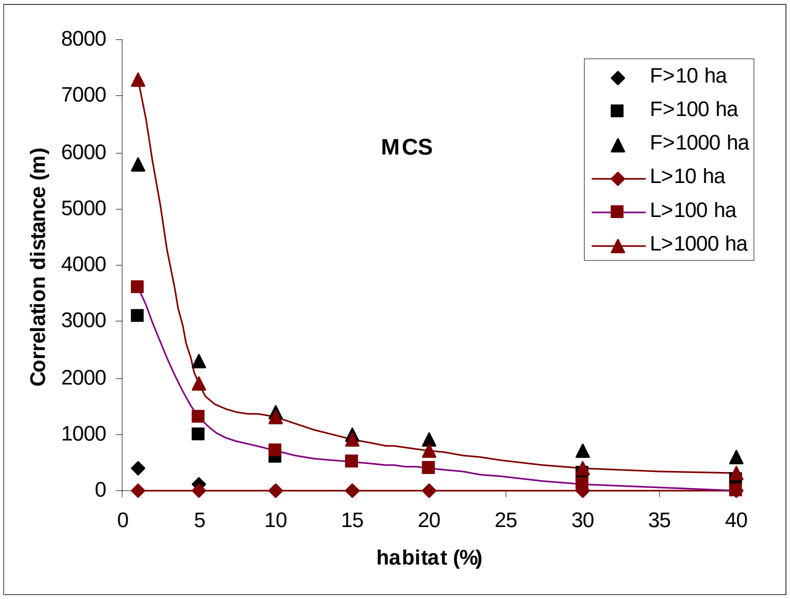

Figure 12. Correlation distance where mean cluster size exceeds 10, 100 and 1,000 ha versus habitat abundance for fire and logging disturbances on the Square landscape

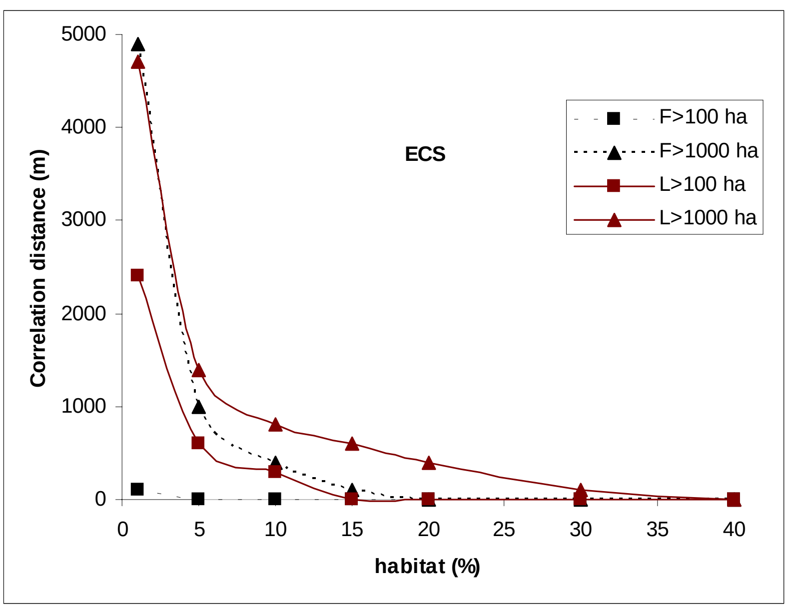

Figure 13. Correlation distance where expected cluster size exceeds 10, 100 and 1,000 ha versus habitat abundance for fire and logging disturbances on the Square landscape

Single-number metrics

Patch density (PD) emerges as a relatively good metric. It strongly distinguishes logging from fire and shows differences that generally match results of the territory/dispersal model (less difference at low and high habitat abundance).

Two metrics distinguish between fire-disturbed and logged landscapes at habitat abundances of less than 30% on both the Morice and the Square landscapes: PD and MNN (Appendix 2, Figure 1 and 2). Another five distinguish disturbances on the Morice but not on the square landscape: MeanMST, MeanMPG, tMST, tMPG and NNCV (Appendix 2. Figure 3 to 7). Note that NNSD and MeanCD do not distinguish fire from logging but do distinguish the square from the Morice (Appendix 2. Figure 8 and 9). Other metrics show less obvious patterns (Appendix 2).

Only one metric—PD—matches the pattern shown by the territory/dispersal model, showing the greatest differences between fire-disturbed and logged landscapes between 10% and 60% habitat abundance (Appendix 2, Figure 1).

Discussion

Several challenges complicate the selection and application of landscape metrics:

- There are an overwhelming number (hundreds) of metrics to choose from (McGarigal 2002).
- Many metrics are redundant or partially redundant because they derive from the same primary measures of pattern (McGarigal 2002, Li et al. 1993).
- Definitions of land classes can significantly influence metric values (imagine defining oldgrowth as older than 250 vs. older than 140), but often receive inadequate attention.
- Some metrics are difficult to interpret because they combine and confound primary measures of pattern (e.g., perimeter-area ratios reflect size and edge), or because they express class-level metrics in a non-intuitive way (i.e., not as a mean or a standard deviation; Rogers 1993).
- Summarizing metrics to the class level can hide important variation. For example mean patch size does not distinguish two 500 ha patches from one 999 ha patch and one 1 ha patch.
- Metric values can vary with data type (raster vs. vector) and scale (grain and extent) of data (McGarigal 2002). Some metrics are overly sensitivity to measurement scale and accuracy (e.g., grid cell size, or effect of misclassifying small areas of the landscape), or are tied too closely to grid resolution (i.e. they cannot be scaled to a resolution other than the grid, even though the target organism may perceive the landscape at a different scale than the grid).
- Most metrics do not adequately describe the spatial distribution of patches (Hargis et al. 1998). For example, nearest neighbour distance does not distinguish a landscape with all patches clumped

from one with widely dispersed pairs of patches, even when mean and standard deviation are considered (Rogers 1993).

- Some metrics lack demonstrated ecological relevance. For example, fractal dimension has little known relevance to connectivity. Furthermore, to understand the ecological relevance, the values taken on by a metric under a range of natural conditions must first be explored (McGarigal 2002)
- Some metrics require parameters that are difficult to estimate (e.g., depth of edge effect).
- Metrics may not be responsive to the range of patterns considered. For example, nearest neighbour distance provides little useful information when disturbance exceeded 20% (Hargis et al. 1998).
- Some metrics are difficult to understand or communicate.

The desire to have a small set of metrics to quantify effects of management on biodiversity is particularly challenging because different species view the landscape from different perspectives. Different species use different land classes as habitat and may use, avoid or ignore edges. Species have different home ranges and dispersal abilities, that may or may not depend on variation in the non-habitat classes traversed. We have made several perhaps bold ecological generalisations in this study in order to reduce complexity and these should be seen as oversimplifications.

In order to detect ecological patterns, it is usually necessary to simplify complexity. Too much information obscures ecological patterns because it is incomprehensible; however, so does too little information, because it is incomplete. Part of the challenge, then, involves extracting useful bits of information while ignoring “noise”. We have focused on metrics based on patch size and spacing because we believe these are ecologically useful. Efficient metrics incorporate a relatively high amount of information at a given level of comprehension. Habitat abundance is an efficient metric, informative and easily understood. Patch size distribution is probably more efficient than expected cluster size because it adds information without losing much in comprehension.

Visually, landscapes generated by the fire model differ from those generated by logging models. Several metrics and a simulation of territory formation and dispersal success highlight these differences. Logged landscapes have fewer territories and poorer dispersal success. These results surprised us because although we thought logging patterns would differ from dispersal patterns, we did not explicitly predict higher territory formation and dispersal success on fire generated landscapes.

In this study, we searched for metrics that were

- ecologically relevant;
- sensitive to management;
- easy to understand; and
- mathematically well-behaved.

Although abundance was not formally evaluated, abundance has the clearest ecological links, it is obviously sensitive to management and it is easy to understand. Past studies have shown that pattern depends on abundance. The territory/dispersal model and most of the metrics examined in this study were strongly influenced by abundance.

Patch size and spacing are two ecologically important aspects of landscape pattern. The ratio of patch spacing to patch width varied with habitat abundance but not with disturbance process or landscape considered. This implies, for example, that at a given habitat abundance, a landscape can have either small patches, close together, or large patches, farther apart (or some combination). In order to move large patches closer together, habitat abundance must increase. The consistency of the ratio across disturbance processes suggests that under certain conditions one may be able to measure patch size and simply infer spacing (at a given habitat abundance). Habitat abundance constrains the possible range of patterns. Measurements of patch size or patch spacing identify the scales at which the pattern occurs.

Patch size distributions differ markedly between logged and fire-disturbed landscapes in our simulations and on real landscapes (Eng 2002). Logged landscapes had a higher proportion of habitat sitting in intermediate size classes than did fire-disturbed landscapes. They lacked area in small and large size classes. These differences correlate only partly with the differences between logging and fire shown in the territory/dispersal model. Likely, logging leaves single, isolated blocks (10 to 60 ha) at lower habitat abundances and connected groups of blocks at higher habitat abundances, accounting for the high proportion of habitat falling in 11 to 1000 ha patches on logged landscapes.

Patch density (PD) was able to distinguish logging-induced from fire-induced patterns, and matched results from the territory / dispersal simulation. However, it has a somewhat weak ecological linkage, because it does not directly describe patch size or spacing.

Several studies have attempted to find a parsimonious set of landscape metrics. These studies focus on the ability of metrics to distinguish landscapes. Likely, they do not apply directly to the IFPA landscape (different regions have different disturbance patterns) and they do not consider ecological relevance, but they highlight metrics that can differentiate pattern.

> Cumming and Vernier (2002) examined all pair-wise comparisons of the 29 class-level variables in Fragstats (McGarigal and Marks 1994). In a principle components analysis, they found that metrics based on core area, nearest neighbour distance and an interspersion and juxtaposition index explained about 75% of the variation. Cumming and Vernier (2002) also found that they were able to explain about 75% of the variation in the first principal component variables (which accounted for 50% of the total variation) using only three variables: total habitat area, mean patch size and patch size standard deviation.

> Using 85 land cover maps, Riitters et al. (1995) reduced 55 metrics to six general measures of pattern and structure: average perimeter-area ratio, contagion, standardized patch shape, patch perimeter-area scaling, number of attribute classes and large-patch density area scaling. Hargis et al. (1998) suggest that some measure of nearest neighbour distance be added. They also suggest that perimeter-area fractal dimension is not useful when averaged at the class level and that mass fractal dimension is highly correlated with disturbance and is unable to distinguish clumped and dispersed patches.
>
> Cushman et al. (draft) identified edge contrast, patch shape complexity, aggregation, nearest neighbour distance, patch dispersion, large patch dominance and neighbourhood similarity as important measures.

In summary, for a given class of habitat, metrics describing patch size, patch spacing and edge (or its corollary: core), among others, emerge as useful for distinguishing landscapes. Because core area is largely influenced by patch size, core area may be able to capture effects on patch size and edge habitat simultaneously. Patch shape also appears to be useful for distinction, but lacks ecological relevance for our purposes.

This study assumed that the composition (different vegetation classes) of the landscape has been studied and those classes that serve as good indicators of biodiversity have been selected. Defining vegetation classes is a crucial step because it can greatly influence the abundance of habitat on the landscape, which in turn constrains pattern.

Alternatives to promote connectivity include corridor and matrix management (see Bunnell 1999). Whether habitat is allocated to corridors or additional patches are left behind to reduce patch spacing, more habitat must be retained to increase connectivity while maintaining average patch size.

Limitations

This study did not evaluate all possible metrics, partly because searching for obscure metrics is a large task. While we may have missed some interesting metrics, most metrics tend to be related because they are based on the same fundamental elements of pattern. We feel we have covered a good range of metrics that address patch size and spacing.

This study did not address metrics of edge. Core area and edge habitat area can be calculated directly and probably are the most easily understood measurements of edge. The difficult part with evaluating edge is not selecting a metric, but rather defining the depth of the edge effect and the types of adjacent habitats that cause edge effects.

The simulations of fire and logging were relatively simple: however, the aim of the simulations was to generate the relatively random patterns associated with natural disturbance and the relatively homogenous patterns associated with anthropogenic disturbance. The simulations did not aim to model actual current logging practices.

The territory formation and dispersal simulations were also simple. The aim was to examine territory formation and dispersal at different spatial scales and in relation to a general habitat type rather than to model the habitat requirements and movement patterns of a specific species.

Future work

Patch density was one of the best single-number metrics for distinguishing fire-disturbed from logged landscapes, however, it does not provide some seemingly important information about patch size. Information contained in patch density is partly described by patch size distribution. For a given habitat abundance, landscapes with many small patches will have a higher density. Measurements of patch density at different scales and in different regions should be evaluated in future research.

The usefulness of cluster size distribution versus correlation distance (a three dimensional graph) should be examined in future research. Cluster size distribution includes information about abundance, patch size and spacing. It could be very informative, but may push the limits of comprehension.

Recommendations

For the purposes of the planning (scenario evaluation), we recommend first that the definition of patch type be considered carefully. Then, we suggest that three metrics be used.

- *Abundance*: as well as having a strong ecological link, the abundance of habitat constrains the range of patterns that can be created.
- *Patch size distribution*: this set of numbers provides more information than can be conveyed by a single number and is still relatively easy to understand and communicate. It can identify differences in simulated and real disturbance processes. When considered in conjunction with abundance and under certain conditions, it may reduce the need to consider patch spacing (i.e., patch spacing can correlate with patch size and abundance). If a single metric is desired to describe patch size, expected patch size provides more ecologically relevant information than mean patch size.
- *Centroid Connectivity Index (CCE)* is one of the few metrics that combines patch size and patch spacing in a single number and may be a good complement to abundance and patch size distribution. Total CCE should be used rather than Mean CCE, however, because Mean CCE suffers from problems associated with means (see part 1 results).

For the purposes of subsequent monitoring, where a more detailed analysis of pattern by ecological specialists may be warranted, we suggest that graphs of expected cluster size versus correlation distance be examined. While complicated to interpret, these graphs provide a comprehensive look at both patch size and spacing.

While the above metrics evaluate ecologically relevant aspects of pattern, there is no context-independent way of assigning specific ecological value to a particular metric value. In several recent ecological analyses, metrics calculated from naturally disturbed landscapes are used as benchmarks for comparison. We recommend that deviations from the "natural values" of metrics be used to compare scenarios.

In addition, metrics describing edge (or core) habitat should also be used. Metrics based on the abundance (of core or edge) should be preferred over those based on pattern (of core or edge).

Acknowledgements

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Appendix 1: Description of metrics

Name or Acronym	Description
Aan	This is the Apack analog to MSI, and is the square of the inverse of MSI. That is, the per-patch value is patch area divided by the square of patch perimeter / 4. The overall value is the mean across patches.
ap	mean perimeter per patch (m)
AWMSI	area-weighted mean shape index. Same as MSI, but instead of dividing by the number of patches to get the mean, the sum of per-patch shape values is divided by the total area covered by the class.
CACV1	patch core area coefficient of variation (%)
CACV2	(disjunct) core area coefficient of deviation
CAD	core area density (number/100ha)
CASD1	patch core area standard deviation (ha)
CASD2	(disjunct) core area standard deviation
CCE	centroid connectivity index (mean interaction between patch pairs where interaction is defined as the product of patch size divided by the square of the distance between them)
CONTAG2	contagion index (%). Only applicable to cases with more than one patch class.
CPCTLAND	core percent of landscape (ha/ha): total core area divided by landscape area
ED	edge density (m/ha): total edge divided by landscape area
EDA	edge area density (ha/ha): total edge divided by landscape area
Expected Cluster size	a graph for each landscape of area-weighted mean cluster size versus correlation distance
LargestPatch	largest patch (hectares)
LPI	largest patch index (% of landscape occupied by larges patch)
LSI	landscape shape index: amount of edge relative to amount of edge if class was a single square patch. Computed as total perimeter / 4 divided by the square root of the total area. If a patch is square, the value will be 1.
MaxCCE	maximum centroid connectivity index (maximum interaction)
MaxNN	maximum nearest neighbour distance (measured from patch edges)
MCA1	mean core area per patch (ha)

MCA2	mean (disjunct) core area size (ha)
MCAI	mean core area index (mean percent of each patch in core area)
MeanCD	mean centroid distance (mean distance between patch centroids in m)
Mean Cluster Size	a graph for each landscape of mean cluster size versus correlation distance
MeanMPG	mean minimum planar graph (connects patches to several close neighbours)
MeanMST	mean minimum spanning tree (connects all patches to nearest neighbours)
MNN	mean nearest neighbour distance (measured from patch edges)
MPS	mean patch size (ha)
MSI	mean shape index: amount of edge relative to amount of edge if each patch in the class was a square patch. Computed for each patch as: patch perimeter / 4 divided by the square root of the patch area. If all patches are square, the value will be 1.
NCA	number of core areas (one patch may have more than one core area—referred to as disjunct cores—if it has a constriction).
NNCV	nearest neighbour distance coefficient of variation
NNSD	nearest neighbour distance standard deviation
NP	number of patches on landscape
NumSameNeighbs	number of neighbours between a cell of this class and other cells of this class
OPOE	ratio of edge area per patch to total edge
Patch Size Distribution	a graph for each map showing number or area of patches by size classes
PD	patch density (number of patches divided by landscape area times 100)
PSSD	patch size standard deviation (ha)
PSCV	patch size coefficient of variation (%)
SmallestPatch	smallest patch (hectares)
TCA	total core area (ha): a core cell is not an edge cell
TCAI	total core area index (percent of class that is in core area)
TE	total edge (metres): length of cell edges between two different types of cell
TEA	total edge area (ha): area of a one cell wide buffer along edges
tMPG	total minimum planar graph (connects patches to several close neighbours)
tMST	total minimum spanning tree (connects all patches to nearest neighbours)

Appendix 2: Graphs of single-number metrics

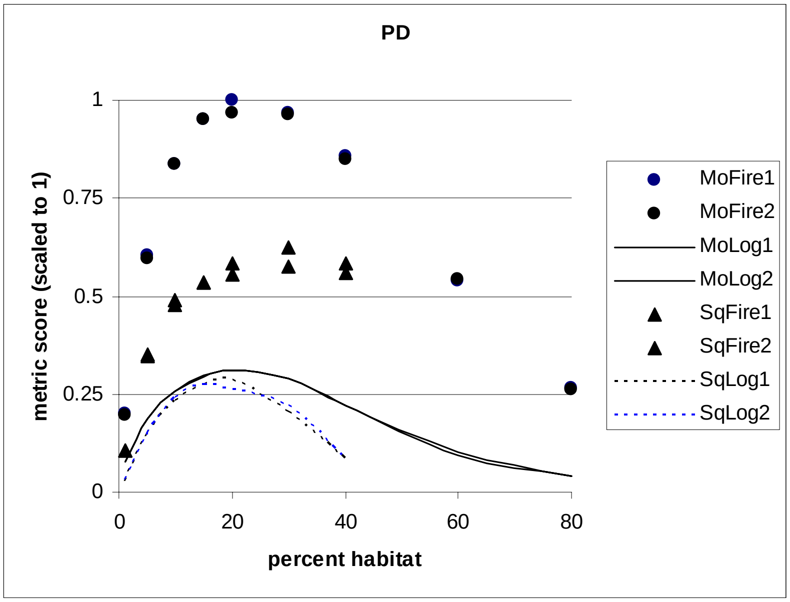

Figure 1. Patch density versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

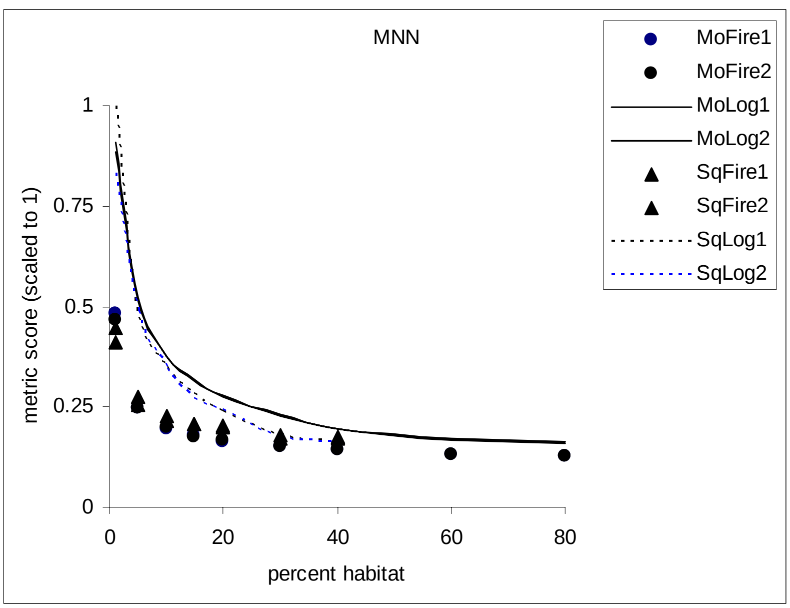

Figure 2. Mean nearest neighbour distance versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

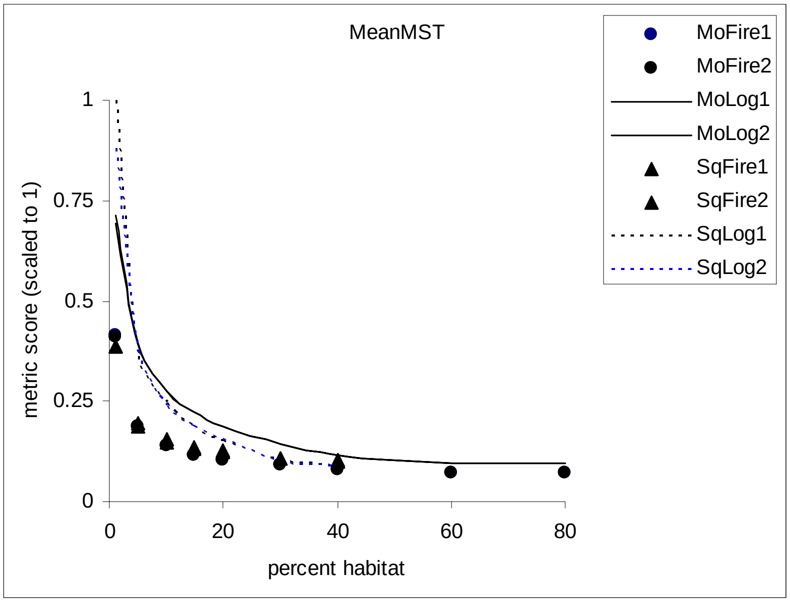

Figure 3. Mean minimum spanning tree versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

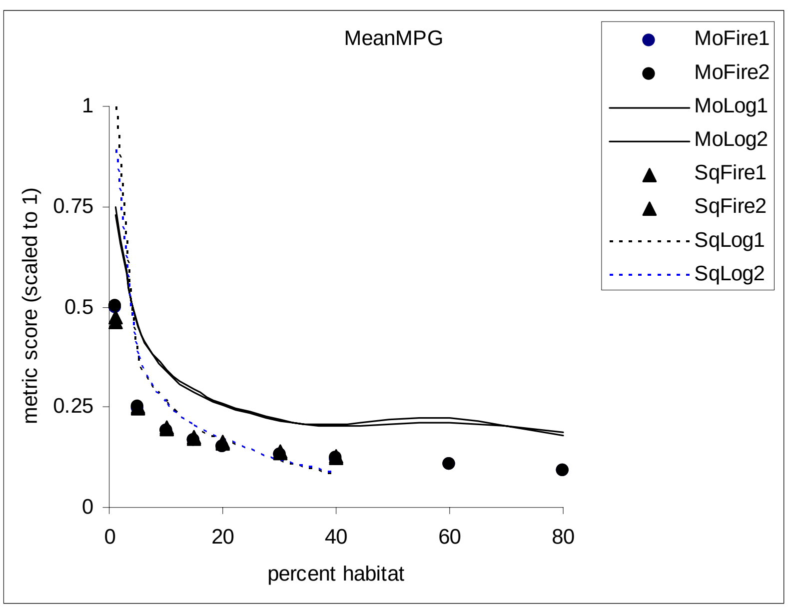

Figure 4. Mean minimum planar graph versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

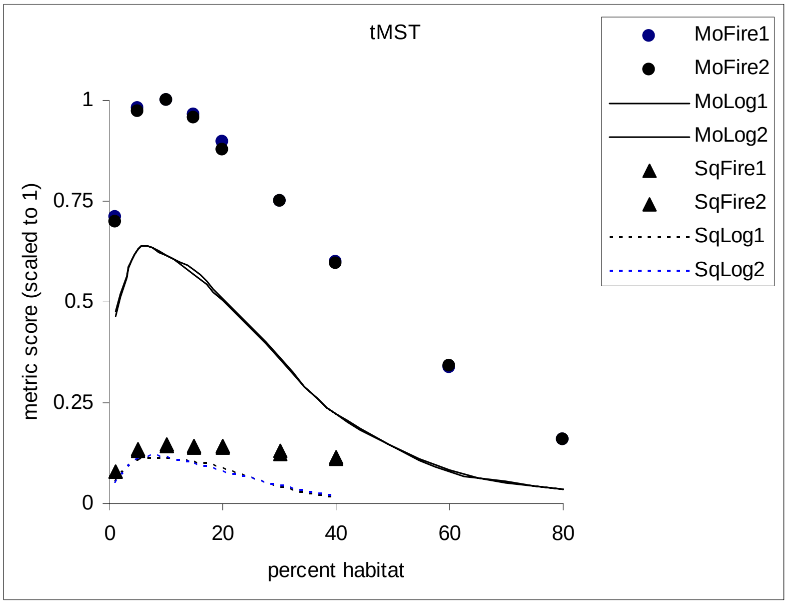

Figure 5. Total minimum spanning tree versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

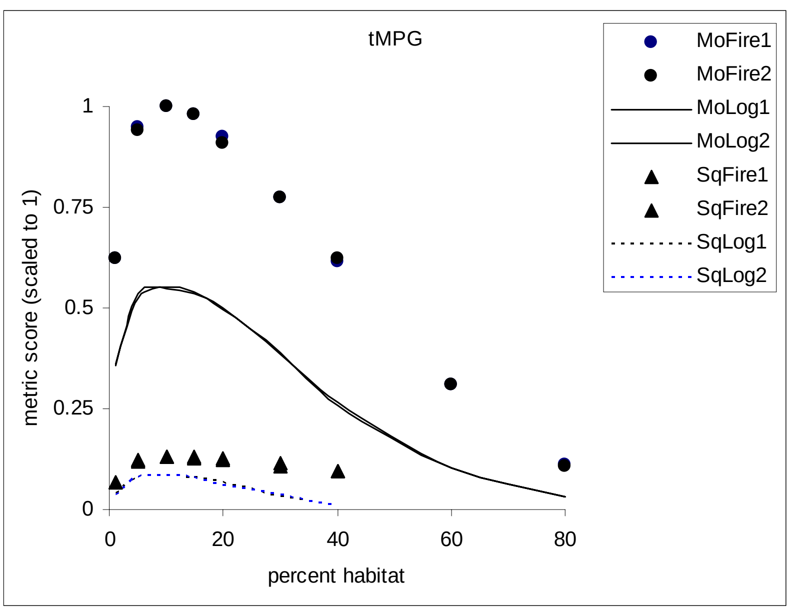

Figure 6. Total minimum planar graph versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

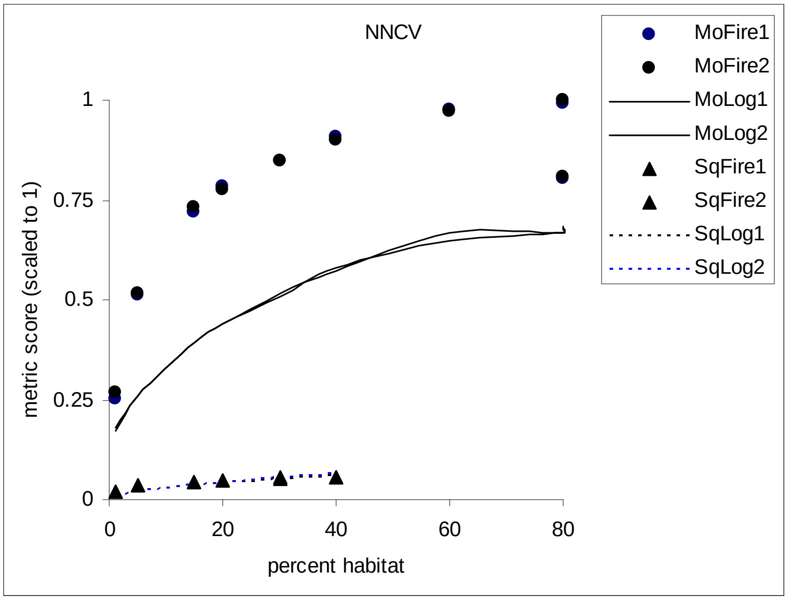

Figure 7. Nearest neighbour coefficient of variation versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

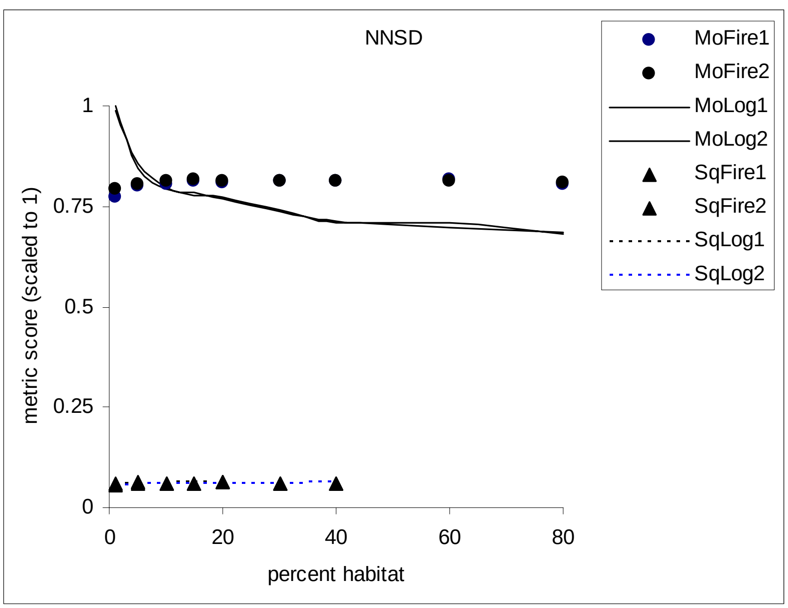

Figure 8. Nearest neighbour standard deviation versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

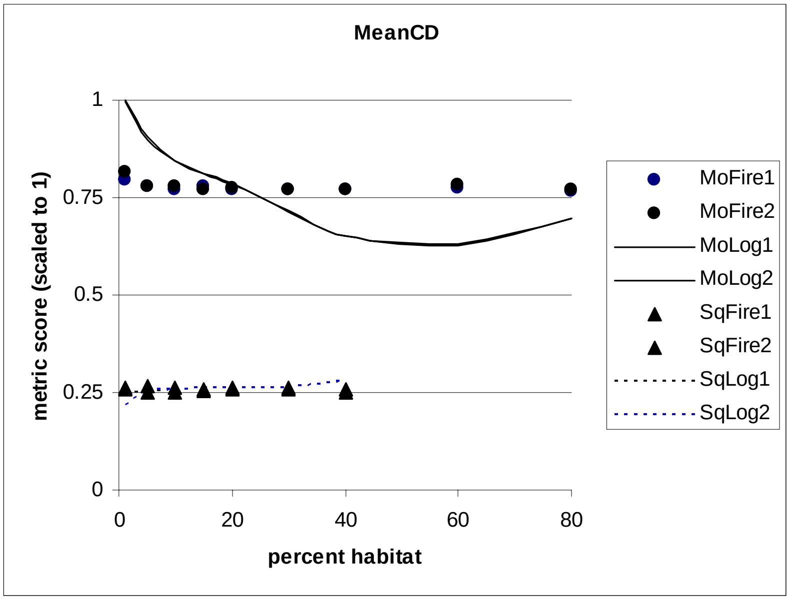

Figure 9. Mean centroid to centroid distance versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

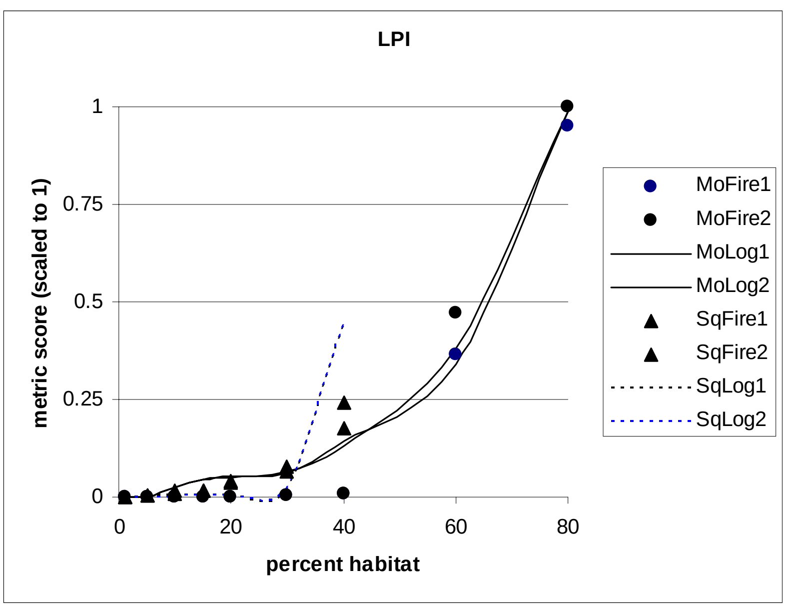

Figure 10. Largest patch index versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

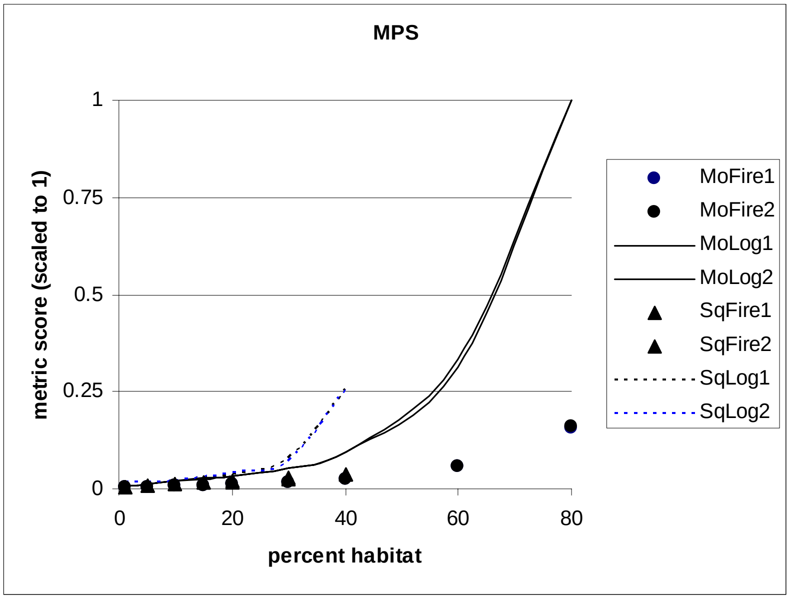

Figure 11. Mean patch size versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

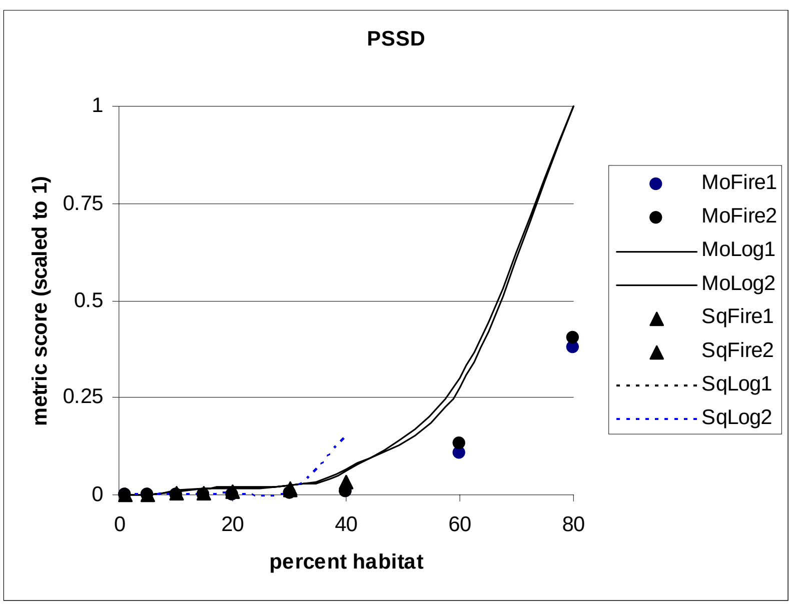

Figure 12. Patch size standard deviation versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

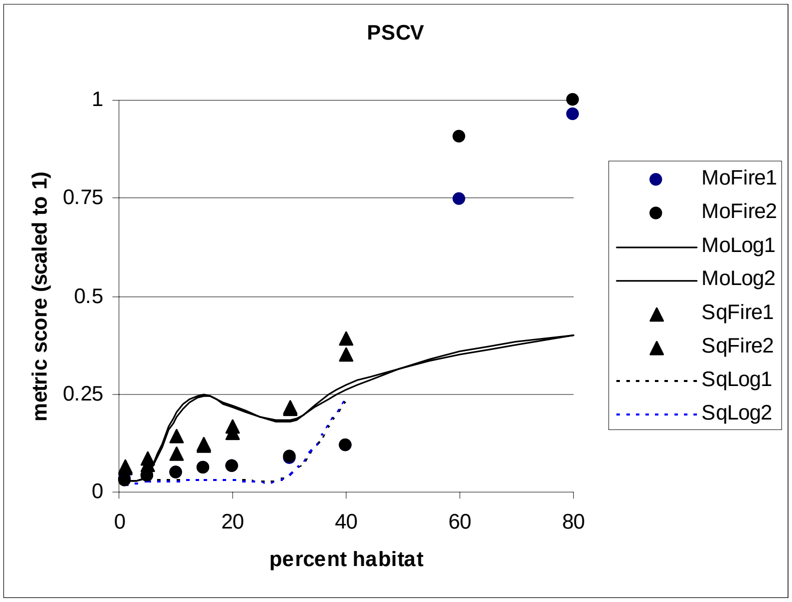

Figure 13. Patch size coefficient of variation versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

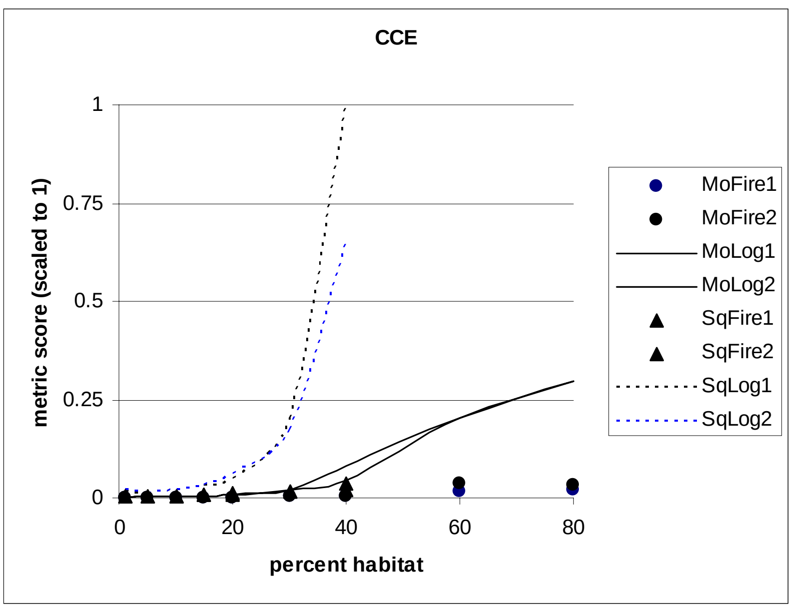

Figure 14. Mean interaction between patch pairs (connectivity of centroids) versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

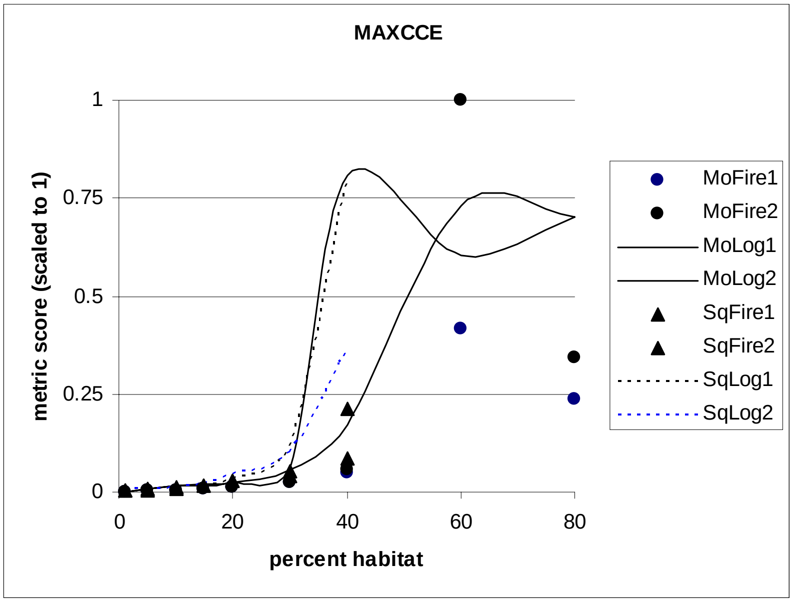

Figure 15. Maximum connectivity between centroids versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

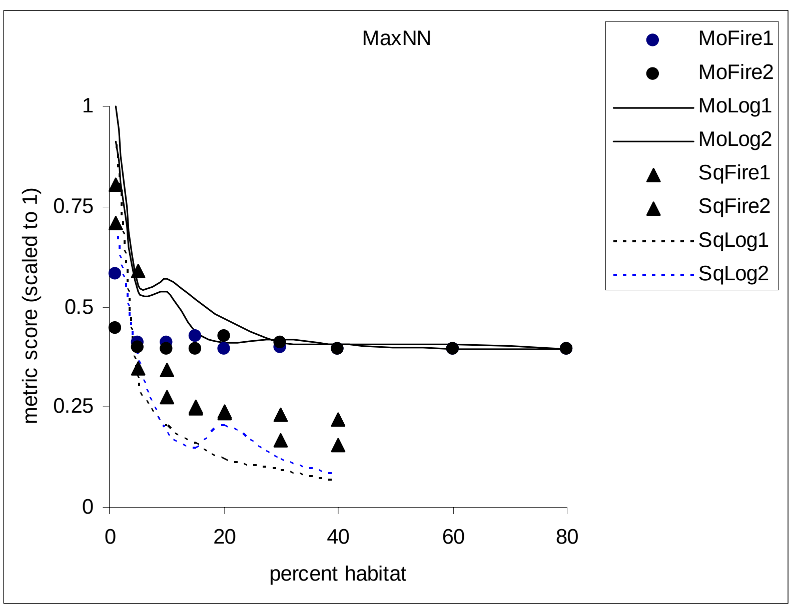

Figure 16. Maximum nearest neighbour distance versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.

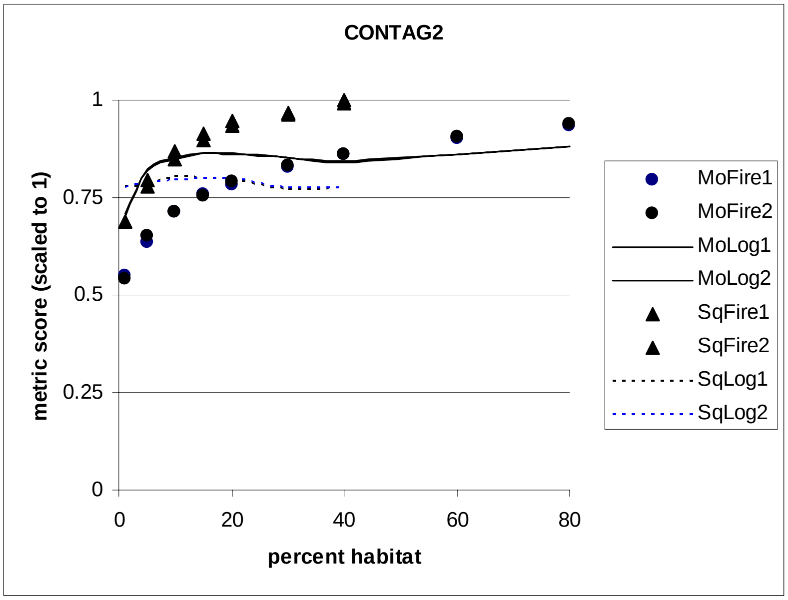

Figure 17. Contagion index versus habitat abundance on the Morice and Square landscapes with logging and fire-disturbance.