Landscape Ecology **17:** 729–743, 2002.

Landscape pattern in topographically complex landscapes: issues and techniques for analysis

Brigitte Dorner*, Ken Lertzman and Joseph Fall
*School of Resource and Environmental Management, Simon Fraser University, Burnaby, V5A 1S6, British Columbia, Canada; *Author for correspondence (e-mail: bdorner@sfu.ca)*

Received 2 May 2001; accepted in revised form 18 October 2002

Key words: GIS, Landscape management, Landscape metrics, Raster analysis, Spatial statistics, Topography

Abstract

Ecological research provides ample evidence that topography can exert a significant influence on the processes shaping broad-scale landscape vegetation patterns. Studies that ignore this influence run the risk of misinterpreting observations and making inappropriate recommendations to the management community. Unfortunately, the standard methods for landscape pattern analysis are not designed to include topography as a pattern-shaping factor. In this paper, we present a set of techniques designed to incorporate the topographic mosaic into analyses of landscape pattern and dynamics. This toolbox includes adjustments to ‘classic’ landscape indices that account for non-uniform landscape topography, indices that capture associations and directionality in vegetation pattern due to topographic structure, and the application of statistical models to describe relationships between topographic characteristics and vegetation pattern. To illustrate these methods, we draw on examples from our own analysis of landscape pattern dynamics in logged and unlogged forest landscapes in southwestern British Columbia. These examples also serve to illustrate the importance of considering topography in both research and management applications.

Introduction

Landscape composition and configuration are important factors influencing ecosystem function and habitat quality (e.g., Urban et al. (1987) and Turner (1989)). In the last decade, landscape pattern analysis has received increasing attention in both the ecological research and the management community (Lehmkuhl and Ruggiero 1991; Forest Ecosystem Management Assessment Team (FEMAT) 1993; Jensen and Bourgeron 1993; Lehmkuhl et al. 1994; Voller and Harrison 1998; Cissel et al. 1999; Hessburg et al. 1999). Much theoretical research in landscape ecology has focussed on quantifying various aspects of pattern and understanding the effect of disturbance processes, both natural and human-induced, on the vegetation mosaic (see, e.g., Gardner and O’Neill (1991) and Turner et al. (1991a) for reviews). These studies generally model landscapes as a homogeneous space in which landscape dynamics arise as a consequence of free interaction between disturbance processes and vegetation dynamics. The vast majority of indices of pattern described in the literature (e.g., O’Neill et al. (1988) and Turner et al. (1991a), Riitters et al. (1995)) and compiled into landscape analysis packages such as ‘r.le’ and ‘FRAGSTATS’ (Baker and Cai 1992; McGarigal and Marks 1994) were designed to capture salient properties of pattern in such topographically ‘neutral’ landscapes.

However, even casual observation of vegetation pattern in a mountainous valley reveals that the spatio-temporal dynamics of pattern in landscapes with prominent topography can be substantially influenced by the topographic relief. Topography shapes pattern indirectly through its influence on disturbance regimes and potential successional pathways, and directly, by creating permanent natural breaks in vegetation pattern (Swanson et al. 1998; Turner 1989). Terrain analysis, or geomorphometry, the science of describing and measuring various aspects of topography is well developed (see, e.g., Florinsky (1998) for an overview). Digital datasets describing topography at various scales exist for many geographic areas, and software for manipulating topographic information has become widely available, both in form of stand-alone programs and as an integral part of many GIS packages (Pike 2000). In the ecological community, the importance of topography and topography-related variation in local site conditions for community structure, composition and successional pathways is well established (e.g., McNab (1989) and Pastor and Broschart (1990), Leduc et al. (1992), Moore et al. (1993), Hadley (1994), Wondzell et al. (1996), Ohmann and Spies (1998)). There is also an increasing body of knowledge of how topography influences the frequency, spread, extent, and distribution of natural disturbances such as fire, blowdown, pathogens, and geomorphic events across the landscape (e.g., Romme and Knight (1981) and Knight (1987), Walsh et al. (1990), Butler and Walsh (1994), Hadley (1994), Walsh et al. (1994), Costello et al. (1995), Veblen and Alaback (1996), Zhang et al. (1999), Kramer et al. (2001)). However, while some studies have integrated different aspects of ecosystem dynamics and their interactions with topography (Swanson et al. 1998, 1992; Allen and Walsh 1996; Wondzell et al. 1996), our understanding of how topography, disturbance regimes, and vegetation dynamics interact to form landscape pattern is still limited. Landscape ecological research could help to fill this gap by quantifying the effect of topography on different aspects of landscape pattern. Presence or lack of such relationships could then be used to refine or test hypotheses about the underlying landscape dynamics. Unfortunately, the theoretical framework of landscape ecology to date does not provide a well-developed methodology for analysing pattern and dynamics in landscapes with strong topography, or, more generally speaking, landscapes with a strong underlying physiographic structure. New methods are required to address research questions arising from the interplay between the physical terrain mosaic and ecosystem dynamics.

Because topographic influences can mask or exaggerate the patterns of primary concern in a given analysis, such as differences in landscape pattern due to management history, a good understanding of topographic influences on landscape dynamics is also important in research not primarily concerned with relationships between vegetation pattern and topography. This is perhaps best illustrated in the context of estimating range of natural or historic variability (RNV) as a framework and template for determining desired ecosystem and landscape conditions (Swanson et al. 1993; Landres et al. 1998, 1999). If the dynamics in a landscape are influenced by its topography, two landscapes with different topography can be expected to have a different RNV, even if they are otherwise similar with respect to vegetation and disturbance dynamics. It is often not feasible to conduct detailed studies of historic landscape dynamics for each managed area. Hence, management targets based on RNV will have to be extrapolated across space, and thus should be adjusted to account for topographic differences between studied and managed landscape.

In this paper, we present a set of methods for landscape pattern analysis that address the relationships between vegetation pattern and topography. While the studies cited above have generally addressed topographic influence by treating topographic characteristics as separate variables, here we focus primarily on integration of topography into descriptors of landscape pattern. We show how measures of landscape pattern can be corrected for the underlying topography, and develop a set of indices that measure pattern with respect to topographic gradients. Furthermore, we develop methods for factoring out topographic constraints on landscape pattern, and illustrate, how these methods can be used to compare landscape pattern between areas that differ in their topographic relief, and how RNV can be adjusted to take topographic differences between landscapes into account. Throughout the paper, rationale and development of each statistic is illustrated with examples from a study of landscape pattern in southern British Columbia, Canada. These examples also demonstrate the potential implications of not accounting for topography in a landscape analysis.

Study area and data sources

The study area from which the examples for this paper were taken consists of the Stein River and Cayoosh Creek drainage systems, located on the eastern flank of the British Columbia Coast Mountain Range, Canada, and comprising an area of approximately 200,000 ha (Figure 1a). The terrain throughout the area is mountainous, with often very steep side slopes frequently dissected by cliffs, gullies, and slide and avalanche tracks. Whereas sections of the Cayoosh Creek main valley, as well as several of its sub-drainages, have been subject to logging, the entire Stein Valley, as well as several of the watersheds in the Cayoosh Creek basin remain roadless wilderness areas. The purpose of the larger study was to obtain a description of range of natural variability for landscape pattern from the unmanaged watersheds within the study area and evaluate harvesting impacts in relation to this baseline. For the purpose of this paper, we focus on the Blowdown Creek drainage, one of the watersheds in the upper Cayoosh Creek valley, to show some of the concepts and ideas used in the broader analysis. The analyses presented here are meant as illustrations of methods only, and to demonstrate the potential implications of not accounting for topography in a landscape analysis. A complete account of the results obtained from the Stein-Cayoosh study, and discussion of their relevance and implications is presented in (Dorner 2002).

The examples used in this paper are based on an analysis of forest cover inventory maps maintained by the British Columbia Ministry of Forests, which are derived from orthophotos (approximate scale 1:20,000). Forest cover maps were provided in raster format at a resolution of 20 × 20 m. BC Ministry of Environment Terrain Resource Inventory Management data (TRIM) spotheight data were used to create a digital elevation model at a resolution of 60 × 60 m.

Approach

Depending on the research objective, topography will have to be considered at several stages of landscape analysis, from database preparation through computation of pattern descriptors, to descriptive and predictive modelling of landscape pattern dynamics. In this paper, we discuss approaches for incorporating topography into landscape analysis that roughly fall into three categories: 1) adjustment of area and distance calculations to avoid systematic biases in landscape statistics; 2) design of indices that capture characteristics of vegetation pattern in relation to topography; and 3) use of statistical models to describe broad-scale relationships between topographic characteristics and vegetation pattern. Because our aim is to present techniques that we found most useful in our own analysis, the remainder of this paper discusses both well-established methods adapted for the present context and new methods developed within the context of this study, organised by category.

The algorithms described here are designed to work with data in raster format, but most of the concepts could be easily adapted to be implemented in a vector-based system. Our spatial analyses use standard routines provided with the GRASS GIS (Westervelt et al. 1991), augmented with custom modules written in C and C++ to conform to GRASS interface specifications. Source code is available from the authors on request. All statistical analyses were performed in S-Plus (Statistical Sciences Inc. 1993).

Incorporating topography into classic indices: adjusting area and distance calculations

The predominant representation of spatial data is a 'bird's eye' view. The landscape is represented by a planar map, which depicts the projection of a non-flat surface into a two-dimensional Cartesian space. Distances and areas measured on such a planar map underestimate actual surface areas and distances. In steep terrain, the discrepancy can be considerable. When the variables of interest in a particular study are more closely correlated with actual on-the-ground area or distance than with projected measures, it is worth considering how, and to what degree, the use of projected measures might influence results or statistical power to detect treatment effects.

Example 1: relative importance of fire and logging disturbance throughout the landscape

We compare the proportion of forested area recently disturbed by fire and logging respectively in the Stein and Cayoosh drainage systems. Unlike fire, logging activity primarily occurs in areas with flat or moderate slopes (median slope is 31 degrees for fire patches and 15 degrees for logging patches). Total area in fire and logging patches is 676 ha and 2851 ha respectively when calculated on a planar map, but 851 ha and 3013 ha respectively when calculated based on actual surface area. Thus, the figures obtained from the planar map underestimate total surface area in wildfires by 20%, but total logged area by only 5%. If we had not adjusted our area calculations for topography, we would thus have underestimated the relative frequency of wildfire relative to logging and hence overestimated the relative contribution of logging to overall disturbance frequency.

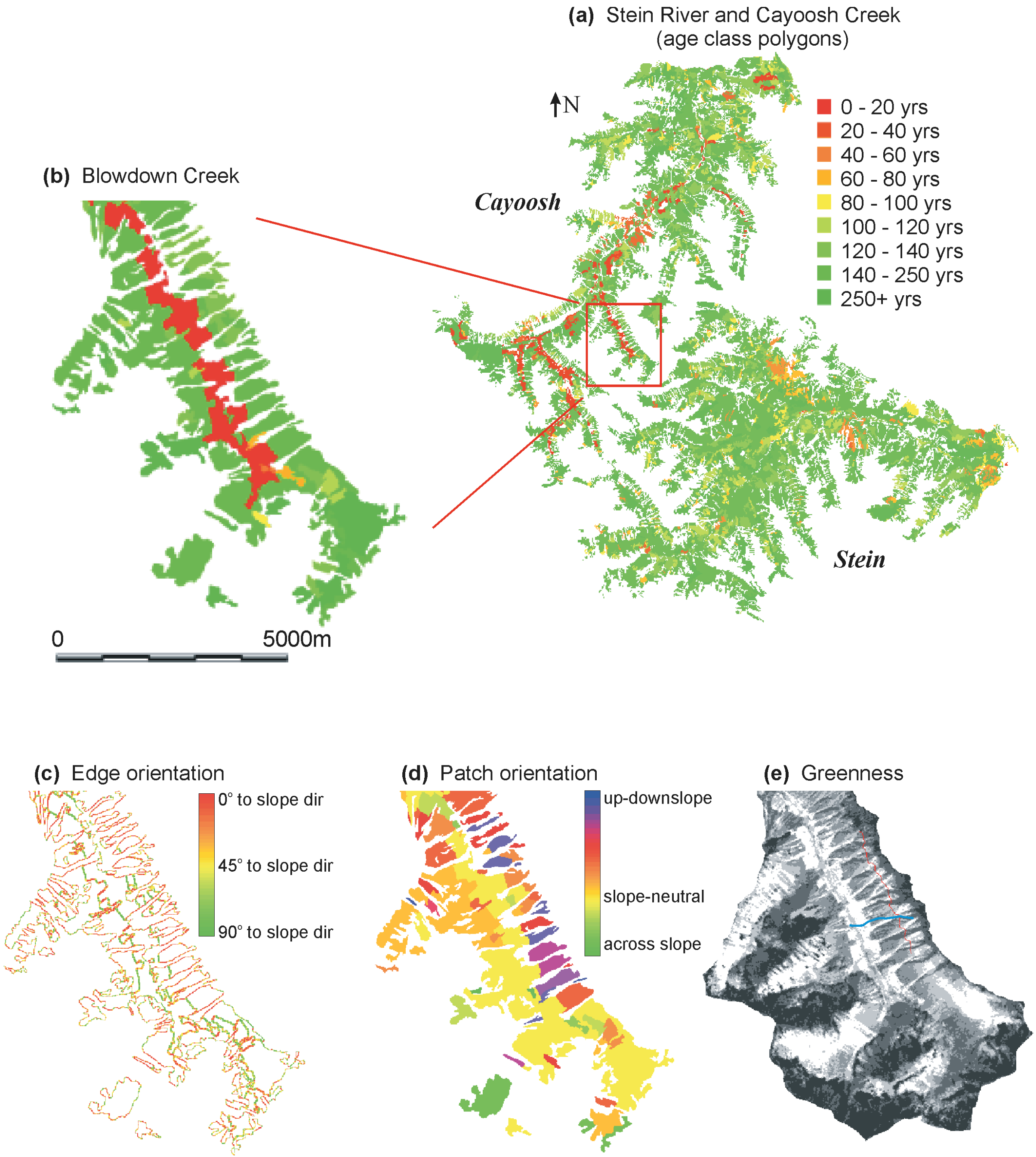

Figure 1. Forest age class mosaic for (a) Stein River and Cayoosh Creek and, within this landscape, (b) Blowdown Creek (based on 1994 BC Ministry of Forests Forest Inventory data). Blowdown Creek has not experienced major natural disturbance events within the last 40 years. The patches in the first two age classes shown in red represent recent cutblocks. Edge orientation (c), and patch orientation (d) are shown for the age-class polygons in Blowdown Creek. The red and blue lines in (e) 'Greenness' (the 2nd band of the Tasseled Cap transformation for Landsat TM data) show two samples of directional transects (See text for discussion).

Conceptually, the modifications required to incorporate true surface areas and distances into a landscape analysis framework are relatively minor. Given a digital elevation model of sufficient resolution and accuracy, true surface area can be estimated as *projected area*/cos(*slope*) for each raster cell. A precomputed raster layer containing true surface area for each cell can be used to weigh the contribution of each cell in various summary statistics. Similarly, true surface distance between centre points in adjacent cells is approximated as $\sqrt{dElev^2 + dist^2}$, where *dElev* is the difference in elevation between adjacent cells and *dist* is the Euclidean distance in the x-y plane. Since traversal distance for a cell depends on the direction in which the cell is traversed, it is unfortunately not possible to incorporate true surface distances by using precomputed weights for each cell.

It should be noted that slope-correcting areas and distances are only two of many possible adjustments researchers may apply to area and distance calculations and thus make them more relevant to their specific research question. In particular, area and distance calculations could be formulated to take into account dispersal capabilities and general behavioural characteristics to adapt standard landscape indices to a functional perspective that perceives the landscape through the 'eyes' of a particular ecological agent (Wiens 1985; Kolasa and Rollo 1991).

Indices that capture relationships between vegetation pattern and topography

Although a first elementary step for calculating metrics of spatial pattern in landscapes with a strong topographic relief, incorporating true surface area and distance into landscape index computations addresses topography only as a simple nuisance factor. A more in-depth look at the relationships between topography and vegetation pattern requires tools that can make these relationships more explicit. One such tool is provided by indices that quantify pattern in relation to underlying topographic characteristics.

Topography shapes and constrains vegetation pattern in several ways. Topography creates a range of environmental conditions that favour different ecological communities and ecosystem processes. Topography, in conjunction with geomorphic processes, also creates stable vegetation boundaries and vegetation-free areas throughout the landscape. Finally, elevational gradients impose a directionality to which ecological and physical processes respond to in shaping landscape pattern (Swanson et al. 1998, 1992; Montgomery 1999). The effects of inhomogeneity in physical landscape conditions on vegetation composition have been well-studied, and methods such as spatial correlation analysis (Legendre and Fortin 1989; Leduc et al. 1992) and electivity indices (Pastor and Broschart 1990) have been used to measure strength of spatial association between physical characteristics and vegetation pattern within a landscape analysis framework. In the remainder of this section, we focus on the other two ways in which topography may shape landscape pattern: directionality introduced by elevational gradients and constraints imposed by stable edges in the vegetation mosaic.

Measuring pattern directionality I: orientation of patches and patch edges

Direction of vegetation boundaries in relation to topographic gradients constitutes an important aspect of pattern directionality that both reflects and affects ecological flow within the landscape (Swanson et al. 1998). As a simple example, consider an avalanche track. The elongated shape, bordered by long stretches of edge following the main slope direction reflects gravity as a key driver of disturbance processes and the association of this natural disturbance type with strong elevation gradients. By dissecting the upland forest matrix, the avalanche track also changes drainage and erosion patterns and may impede or facilitate movement of animals across the mountainside, as well as providing additional variety of habitat.

To capture directionality of patches and patch edges we compute edge orientation, expressed as the angle between direction of patch edge and slope direction. We traced patch outlines and fitted a line through each two adjacent edge cells. Edge direction for each edge cell was then calculated as the average of the slope of the two lines fitted through the edge cell and its neighbours. Similarly, slope direction was calculated for each edge cell as the direction of the steepest elevation gradient in the digital elevation model. Edge orientation in relation to slope direction is then simply the angle between edge direction and slope direction. Figure 1c shows a map representing edge orientation for Blowdown Creek, one of the watersheds in the Cayoosh Creek basin (Figure 1b).

If desired, the information contained in this type of map can be summarised into a landscape index. Thus, we compute *patch orientation*, defined for each patch, as the ratio of (length of) patch edge following the slope direction (angle with slope < 30 degrees) to length of patch edge across slope (angle with slope $>$ 60 degrees). In this calculation the length of patch edge contributed by each cell is determined as the distance across the raster cell (either straight across or diagonal, depending on edge direction), adjusted for slope inclination (see previous section on adjusting area and distance calculations). Patch orientation for Blowdown creek is shown in Figure 1d. *Landscape edge orientation*, the equivalent index computed for all edges over the entire landscape, reflects the dominant layout of the vegetation mosaic in relation to topography. Landscape edge orientation index for Blowdown Creek is approximately 1.8 (i.e., 1.8 times as much edge in slope direction as across slope). Where appropriate, these indices of pattern directionality can equally be applied to physiographic gradients other than elevation, such as moisture gradients or gradients of substrate composition (Keddy 1991).

Example 2: orientation of logging vs. fire patches

Since edges following the slope direction are a visually dominant characteristic throughout most parts of the Stein and Cayoosh drainage systems, we were interested in quantifying this characteristic and in describing the effect of logging on this aspect of landscape pattern. Figure 2 shows a comparison of distributions of patch orientation indices for logging and fire patches. The two distributions differ significantly at the $\alpha = 0.05$ level (χ^2 test, $p < 0.001$). Predominant orientation of fire patches is well in accordance with the dominant upslope-downslope directionality of forest edge within the study area. Conversely, logging patches create a higher proportion of edge running perpendicular to the fall line. If harvesting replaces fire as the predominant disturbance agent in the area we may thus expect changes in the pattern of ecological flows and possibly also in terms of landscape connectivity.

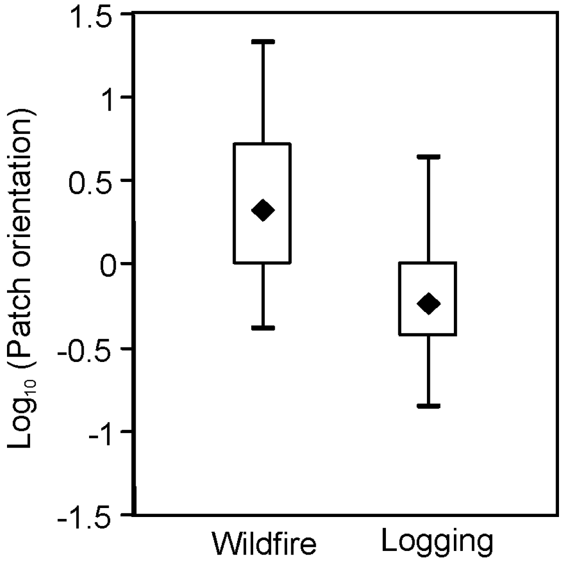

Figure 2. Distribution of patch orientation index values for early-seral patches originated after fire and logging respectively in the Stein and Cayoosh Creek drainage basins. The box in the box plots represents the central 50% of the distribution, the whiskers represent the central 90%.

Measuring pattern directionality II: pattern along transects

A somewhat different approach towards assessing pattern directionality is based on the concept of transects following gradients or isoclines. This corresponds to imposing a modified coordinate system onto the landscape, where travelling outward from a point in x direction means following the direction of maximum gradient (e.g., along the fall line) and travelling in y direction means following the isocline (e.g., along an elevational contour). Many conventional landscape indices and spatial statistics can be made to incorporate physiographic gradients this way, provided they can be applied in the one-dimensional context of transect-based analysis. The following two examples present two applications of the transect method: measuring directional forest connectivity and use of semi-variograms to derive characteristics of forest patchiness in relation to watershed topography.

Example 3: connectivity of closed canopy forest habitat in relation to watershed topography

In the Stein-Cayoosh study, we applied the concept of computing landscape statistics along and perpendicular to topographic isoclines, respectively, to derive indices that capture connectivity along the main watershed axis, as well as connectivity from upland to valley bottom areas. The statistic we compute here is travel distance across each patch of mature and late-seral forest along topographic isoclines (Figure 3a) and in up-down slope directions (Figure 3b). Thus, the value for each cell in the maps in Figure 3a and 3b indicates how connected that cell is to other mature-forest cells either across (Figure 3a) or along (Figure 3b) the elevational gradient. To produce these maps we use the edge cells of each patch as a starting point and trace along isoclines and along the fall line respectively until the other side of the patch is reached. Each cell on the traced transect is then assigned the total length of the transect. In areas with irregular topography this algorithm may leave some cells not assigned to any transect in the patch interior. Any such blank spots are filled in by interpolation from adjacent cells. A landscape connectivity index can be computed from the maps in Figure 3a and 3b by taking the (area-weighted) average connectivity value over the entire forested area. For Blowdown Creek the value of this directional connectivity index is 380 m in across-slope direction, and 357 m in up-down slope direction. Since the distance from valley bottom to ridgeline (or treeline) is typically shorter than the distance along the main watershed axis, the value obtained for connectivity in across-slope direction should be substantially larger than the value for upslope-downslope connectivity, unless connectivity is interrupted by disturbance or permanent breaks in the forest mosaic. That the two index values are very similar for Blowdown Creek thus indicates that terrain features and disturbance processes impact connectivity along the main watershed axis more than connectivity from upland to valley bottom.

Example 4: spatial scaling in relation to watershed topography derived from directional semi-variograms

A complementary perspective on scaling and fragmentation of vegetation pattern in relation to topography can be gained from directional semi-variograms (see, e.g., Legendre and Fortin (1989) or Rossi (1992) for a detailed description of variograms and similar statistics). A semi-variogram is a plot of variance in sample value against spatial distance between sample locations and can thus be interpreted as a plot of expected change in landscape characteristics as one travels outwards from a given point in the landscape. One of the strengths of semi-variograms and similar spatial statistics lies in the fact that they can be applied to continuous data and hence do not require interpretation and/or stratification of the data set. Formally, the semi-variance for distance d is given as

$$\gamma(d) = \frac{1}{2n_d} \Sigma (y_{(i+d)} - y_i)^2$$

where n is the number of samples y_i taken distance d apart. Below we use absolute difference rather than squared difference as a somewhat more robust estimator of between-sample variability.

The following analysis is based on raw Landsat TM5 satellite imagery of Blowdown Creek, coregistered to the forest cover maps and resampled to 20 m cell size using a nearest neighbourhood algorithm. The semi-variograms are computed for 'Greenness' (Figure 1e), a combination of several TM5 channels obtained through Tasseled-Cap transformation (Crist and Cicone 1984). As the name suggests, this channel combination emphasises the contrast between vegetated ('green') and non-vegetated areas. We established transects along and perpendicular to elevational isoclines by tracing outward along the fall line and isocline respectively from 200 randomly selected starting points. Semi-variance was then computed for Greenness values along these transects (Figure 4).

The variogram analysis picks up key features of natural and logging-imposed scaling that we measured in the previous example, but it also emphasises characteristics of landscape pattern in Blowdown Creek that are not immediately apparent from the timber-focussed forest inventory data. Vegetation cover within the watershed is structured in horizontal bands, interrupted at regular intervals (~500 m) by avalanche tracks. In the previous example, we noted that this aspect of landscape pattern results in an average width of 380 m in across-slope direction for mature forest patches. In the isocline transect variogram the fragmentation imposed by avalanche tracks is apparent in the initial 'hump', followed by the dip at 500 m and several minor humps and dips at larger scales which reflect harmonics of the pattern. The curve reaches its sill very early: there is no appreciable further increase in sample variation beyond the first hump, indicating no presence of additional pattern at larger spatial scales. In contrast, the variogram based on transects following the slope direction shows change in pattern characteristics across the entire spectrum of spatial scales, corresponding to the sequence of distinct horizontal cover bands. The first sill roughly reflects the scale of individual bands, one of them corresponding to the band of unharvested forest for which we measured up-down-slope connectivity as 357 m above. The pronounced dip after the second rise is largely due to the spectral similarity of early-seral forest in the valley bottom and meadow and shrub vegetation at high elevations. It would have been absent before the advent of timber harvesting.

Similar to the observations made by Swanson et al. (1998) for the H.J. Andrews Forest in Oregon, the

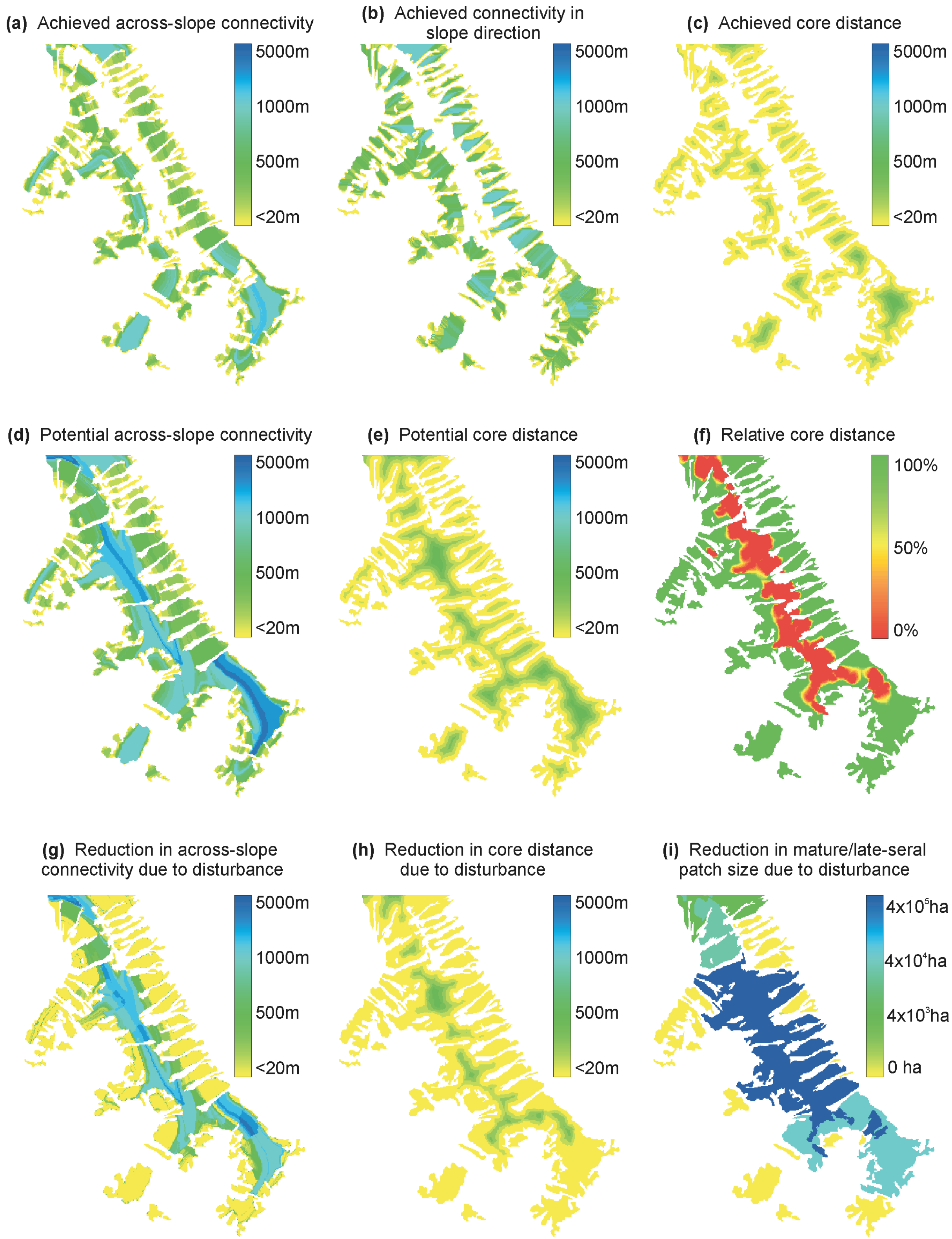

Figure 3. Maps of indices and construction of relative indices. Panels (a) to (c) show across-slope connectivity, upslope-downslope connectivity, and core distance for mature and late-seral forest in Blowdown Creek. Panels (d) and (e) show maximum potential for across-slope connectivity and core distance indices. In panel (f), achieved core distance for mature and late-seral forest is shown as a proportion of maximum obtainable values. Similarly, we calculate the effect of disturbance on index value as the difference between maximum potential and currently achieved index value. Indices measuring the reduction in index values from maximum achievable values for across-slope connectivity, core distance, and size of mature/late-seral patches are shown in panels (g) to (i). See text for further explanation on how to interpret these indices.

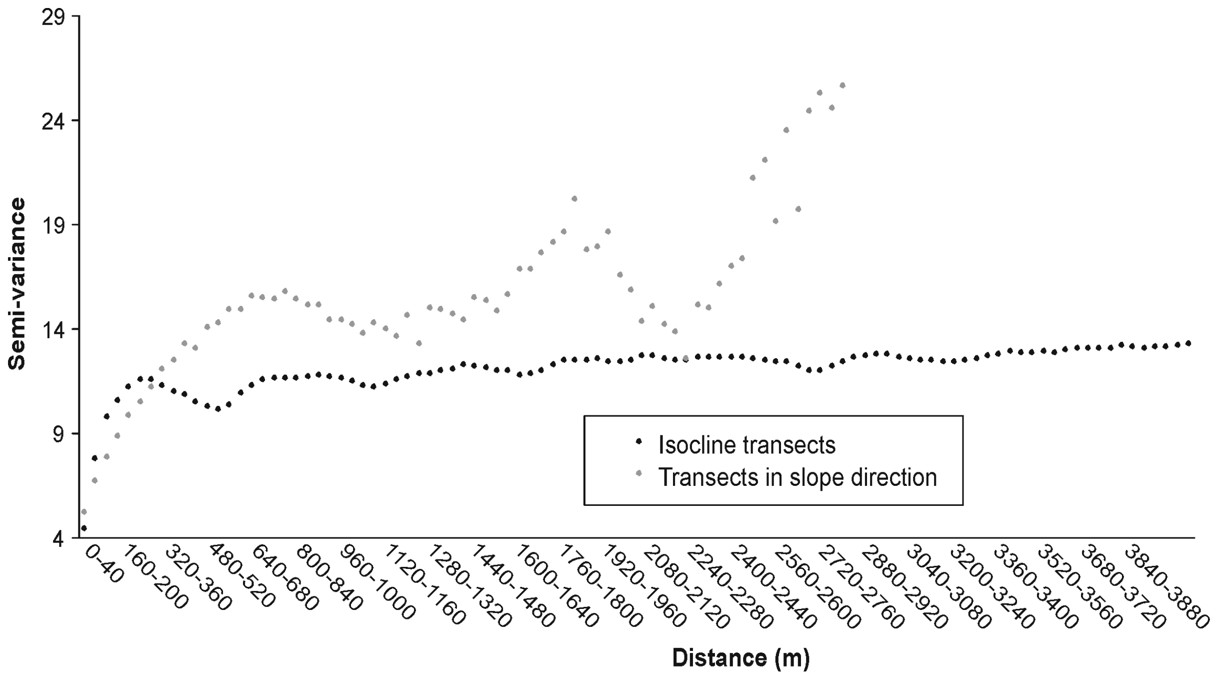

Figure 4. Directional semi-variograms for the east slope of Blowdown Creek. Distance pairs are calculated from the Tasseled Cap channel Greenness shown in Figure 1e. Graphs are based on a sample of 200 randomly placed gradient and isocline transects respectively.

variogram analysis for Blowdown Creek thus reveals both the landscape-structuring force of gravity-driven processes and the horizontal banding of ecotones resulting from elevational differences in microclimate and, in the case of Blowdown Creek, harvesting practices.

Constraints imposed by stable edges in the vegetation mosaic: maximum achievable and relative landscape indices

In the previous examples we have illustrated how avalanche tracks naturally fragment forest pattern in Blowdown Creek. Other topographic or topography-driven features, such as stream courses, cliff faces, rocky outcrops, or elevational vegetation boundaries naturally structure and fragment vegetation pattern in a similar way. Making the constraining effects of such features explicit allows us to isolate them from other pattern-shaping factors and account for them in further analyses. The first step in this process is to stratify the study area into sections that do not support vegetation, or do not support the vegetation type or types of interest in a given study, and sections that do. In our study we were primarily interested in forest. Thus, we identified a ’potential forest’ class, consisting of areas that were either currently in closed canopy forest or were currently regenerating from disturbance and likely to develop into closed-canopy stands. The remaining areas were assigned to a ’non-forest’ class, which included both areas permanently non-vegetated such as waterbodies and areas such as avalanche tracks or alpine meadows, where frequent disturbance and high snowpack accumulation will likely prevent establishment of closed-canopy forest in the near and intermediate future. This stratification process produced a binary map of ’potential forest’. Landscape index values calculated for the potential forest mosaic provide a description of the constraints the physical landscape configuration imposes on the forest mosaic.

Example 5: potential core distance, relative achieved core distance, and reduction in core distance due to disturbance in blowdown creek

Examples 3 and 4 illustrated that across-slope connectivity within the band of unharvested upslope forest is limited by a series of avalanche tracks. Using the ideas presented in the previous paragraph, it is possible to quantify the amount of natural fragmentation created by avalanche tracks and other topography-related constraints. We produced a map of potential forest for Blowdown Creek, which represents a scenario where logging and natural disturbance processes such as fire are eliminated as factors shaping the forest mosaic, leaving topography-related constraints as the only landscape-shaping factor. Figure 3d shows the result of applying the across-slope connectivity index introduced in the previous section to the potential forest map. In Blowdown creek, the valley bottom areas have the highest potential for closed-canopy forest connectivity along the main watershed axis. Consequently, a disturbance in the valley bottom has a proportionally higher impact on this type of connectivity than a disturbance of equivalent size in an isolated patch of upland forest.

Indices computed for the potential forest mosaic can also be used to calculate relative indices that measure realised pattern in relation to potential achievable values. The construction of such relative indices is exemplified in Figure 3. Panel 3 c shows distance to the nearest patch edge from within closed canopy forest (*core distance*), a measure similar to the core-area metric described in the literature (e.g., McGarigal and Marks (1994)). Core distance is calculated by growing a distance surface from patch edges towards the patch interior. Again, distances between adjacent cells are adjusted for slope inclination, and so the shortest path between two cells may not be a direct route on the plane. Thus, the spread algorithm iteratively converges on the shortest path to an edge for each cell. Starting with the edge cells, for which distance to patch edge is set to zero, the algorithm spreads to adjacent cells by propagating to them the sum of current distance to edge plus the additional distance to the cell centre. In each step, the new distance value is assigned to a cell only if it had either no distance value or had a larger distance value. The algorithm terminates when no cells change value. The area-weighted average core distance for closed-canopy patches in Blowdown Creek is 74 m. Panel 3 e shows the same calculation applied to the map of potential forest. We find that topography in Blowdown Creek constrains average core distance to 106 m. Thus, the landscape in its current state is achieving 70% (74/106) of its potential, with an average of 32 m (106-74) or 30% lost due to disturbance processes.

The concepts of relative achieved index values and reduction in core distance due to disturbance processes can also be shown in a spatially explicit fashion. To produce a map of relative achieved core distance, we calculate the ratio of achieved to potential index value for each cell in the landscape. Figure 3f shows relative core distance for Blowdown Creek. Similarly, reduction in core distance due to disturbance is calculated as the difference between local potential index value and locally achieved index value. Examples of maps showing the effect of disturbance on index values for three indices (across-slope connectivity, core distance, and size of patches of closed-canopy forest) are shown in Figure 3g, 3h, and 3i.

Maps of potential index values and relative index values are useful for visualising the relative importance of topographic constraints versus disturbance dynamics as factors driving landscape pattern. They also provide an indication of the magnitude and spatial scale of impact a disturbance of a given size and location exerts on overall landscape pattern, and might be usefully incorporated into a management decision support tool. Thus, the map of potential core distance (Figure 3e) illustrates that valley bottom areas have the highest potential for contributing to core distance in Blowdown Creek. Consequently, logging along the valley bottom reduced average core distance for Blowdown Creek much more than logging an equivalent amount of upland forest would have done. Whereas the effect of disturbance on core distance is generally confined around the actual disturbance patch (Figure 3e), disturbance impacts on other measures of mature/late-seral forest connectivity and fragmentation extend further into the surrounding landscape. For example, the impact of disturbance on patch size is pervasive throughout the watershed (Figure 3i), whereas the impact on across-slope connectivity is intermediate in its extent (Figure 3f). Thus, spatially explicit calculation of relative landscape indices can map out, how far-reaching the impact of a particular harvesting operation is for different aspects of landscape pattern, and thus for the species that respond to these aspects.

Note that relative index values should not be considered an improved version of the original index with topographic constraints factored out. Relative index values capture the dynamic potential of a particular system, given the bounds imposed by its unique topography. As such, they are useful for illustrating disturbance effects and evaluating alternative harvesting options in light of landscape-level impacts. However, 100% achieved core distance may still mean a high degree of forest fragmentation in a naturally very fragmented landscape. A neighbouring watershed that is naturally less fragmented, but has lost 50% of its core distance to disturbance processes, may provide better habitat for species dependent on large, uninterrupted tracts of mature or late-seral forest. Thus, the quantity which ecological agents ’perceive’ and respond to is likely better captured by absolute index values.

Putting it all together: statistical models of topographic influence on landscape pattern

To gain a deeper understanding of the effects of topography on vegetation pattern and dynamics it is necessary to formulate and test hypotheses and create predictive models for the topographic drivers of landscape dynamics. Depending on the data representation (numeric vs. categorical, value surfaces vs. uniform patches or polygons) there are a variety of established statistical methods which researchers can choose from that relate landscape pattern to topographic variables. Electivity indices (first described in Jenkins (1979)), correlation analysis, and regression analysis can relate pattern to a single variable. Multivariate regression techniques can be employed to build predictive models of topographic influence and estimate the degree to which pattern is determined by topography. Spatial correlograms and Mantel tests offer alternatives to classical statistical methods when spatial scaling of associations between vegetation mosaic and physical landscape is of concern (Legendre and Fortin 1989; Leduc et al. 1992). These techniques are also useful for analysing data that are characterized by slow trends and absence of sharp edges and hence not well represented by a mosaic of uniform polygons. In the remainder of this section, we present two examples that use indices presented in the previous sections in conjunction with regression analysis and simple statistical models to gain a better understanding of the relationships between landscape pattern and topography.

Example 6: RNV in landscape pattern from spatial replication: factoring out the constraints imposed by watershed topography

Range of natural, or historical variability in ecosystem conditions and processes has become an important input to forest management (Swanson et al. 1993; Attiwill 1994; Morgan et al. 1994; Lertzman et al. 1997; Landres et al. 1999), and many studies have used historic reference conditions as a baseline for describing landscape change due to intensive forest management and evaluating proposed management alternatives (e.g., Baker (1994) and Cissel et al. (1994), Mladenoff et al. (1994), Ripple (1994), Wallin et al. (1996)). One of the goals of the Stein-Cayoosh study was to derive quantitative estimates of range of natural variability in landscape pattern from spatial, rather than the more customary temporal replication. We constructed the distribution of landscape index values from a sample of unlogged watersheds to serve as a proxy of RNV for all watersheds in the study area (Figure 1a). For a given landscape metric, each watershed thus contributes one sample value, and the overall distribution of sample values can be interpreted as an estimate of RNV for that landscape metric. However, the observed variability in this distribution is a product of both stochasticity in landscape dynamics and topographic differences among sample watersheds, and it is the first of these two components that provides the spatial equivalent of range of historical variability.

In the previous examples we have shown that constraints imposed on landscape pattern by topography can be captured by computing landscape index values for the potential forest mosaic. Regressing achieved against potential index values allows us to determine, how much of the overall variability in landscape index values between watersheds can be attributed to differences in topographic constraints alone. For the core distance index (Figure 3c), achievable core distance is constrained to be smaller than the core distance value calculated for the potential forest mosaic. In a plot of achieved core distance against potential core distance the sample values obtained are therefore constrained to the area below the $y = x$ line (Figure 5). For a hypothetical landscape with a potential core distance value of zero the achieved index value must therefore also be zero, and it is reasonable to assume as a null hypothesis that range of variability in core distance should increase as maximum achievable core distance increases. This relationship between achieved and potential core distance values was incorporated into the regression analysis by forcing the intercept of the regression line to zero and by weighting the contribution of individual sample values by the inverse of their potential core distance. Similarly, the width of the RNV distribution is assumed to increase proportionally with potential index value.

The regression analysis indicates that in the unmanaged watersheds achieved core distance increases significantly with increasing potential core distance ($p < 0.001$, see Figure 5). Thus, RNV expectations should differ considerably for watersheds at the low

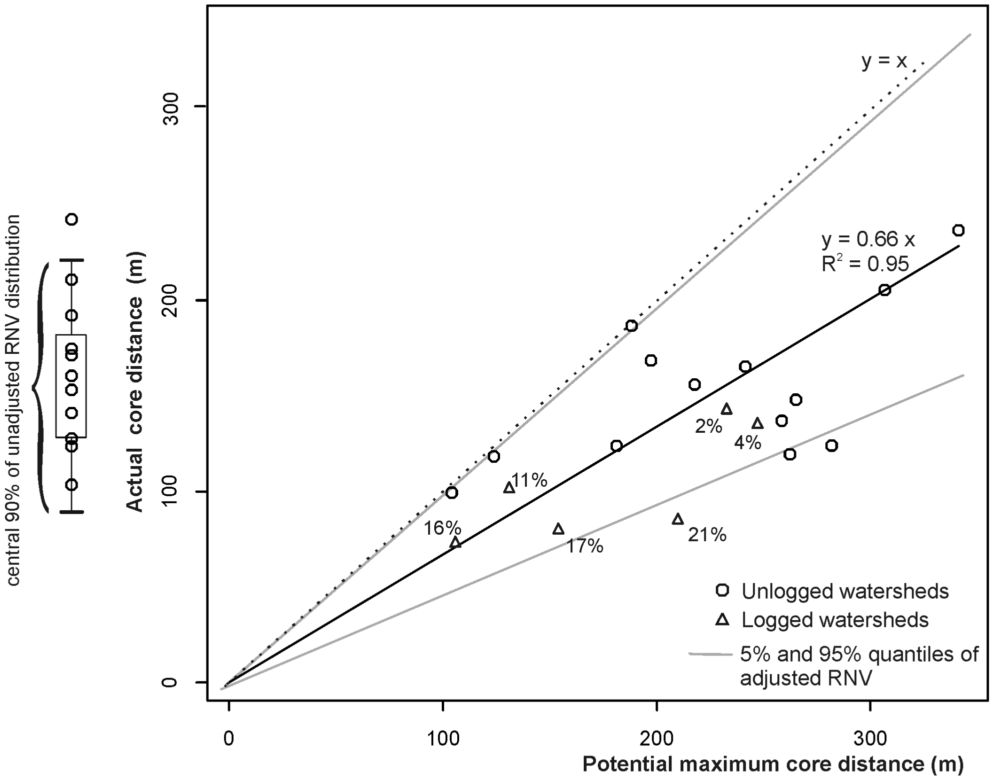

Figure 5. Landscape core distance index for a sample of 13 unlogged watersheds in the Stein and Cayoosh Creek drainage systems. The graph shows achieved vs. maximum potential index values, regression of achieved vs. maximum potential index values (solid black line) and range of natural variability (RNV) for core distance, estimated from the sample of unlogged watersheds. RNV is represented by the 5% and 95% quantiles of the distribution of index values. The marginal boxplot shows the RNV estimate for core distance *without* taking topographic constraints into account. The grey lines in the graph represent RNV for core distance as a function of potential maximum landscape core distance. For comparison, the six most heavily logged watersheds within the study area are shown (the labels give proportion of forested area logged).

and high end of the spectrum of potential core distance values. The RNV estimate obtained before adjusting for topography, which is shown to the left of the y-axis, provides a fair representation of the RNV for the mid-range of the potential core distance spectrum. However, the majority of logged watersheds within the study area also tend to have low potential core distance (Figure 5). Thus, the unadjusted RNV would be inappropriate as a quantitative guideline for management in these watersheds. A trend towards a decrease in core distance below RNV conditions in response to logging is still apparent, but the effect is not as strong as it would have appeared before taking into account the constraining influence of topography.

Example 7: orientation of patches in relation to slope position

In Examples 1 and 2 we have shown that fire and logging regimes can differ with respect to predominant location of disturbance patches within the landscape as well as with respect to patch orientation in relation to slope direction. Figure 6 presents a more in-depth representation of patch orientation in relation to slope position for both logging and wildfire patches. Again, we use quantile lines to represent the RNV estimate for patch orientation derived from fire patches. The marginal boxplots for the two distributions plotted to the left of the y-axis and below the x-axis summarise the observations from examples 1 and 2; the logging regime differs from the fire regime both with respect to patch orientation and with respect to slope position. However, the graph also illustrates that orientation of fire patches changes with slope po-

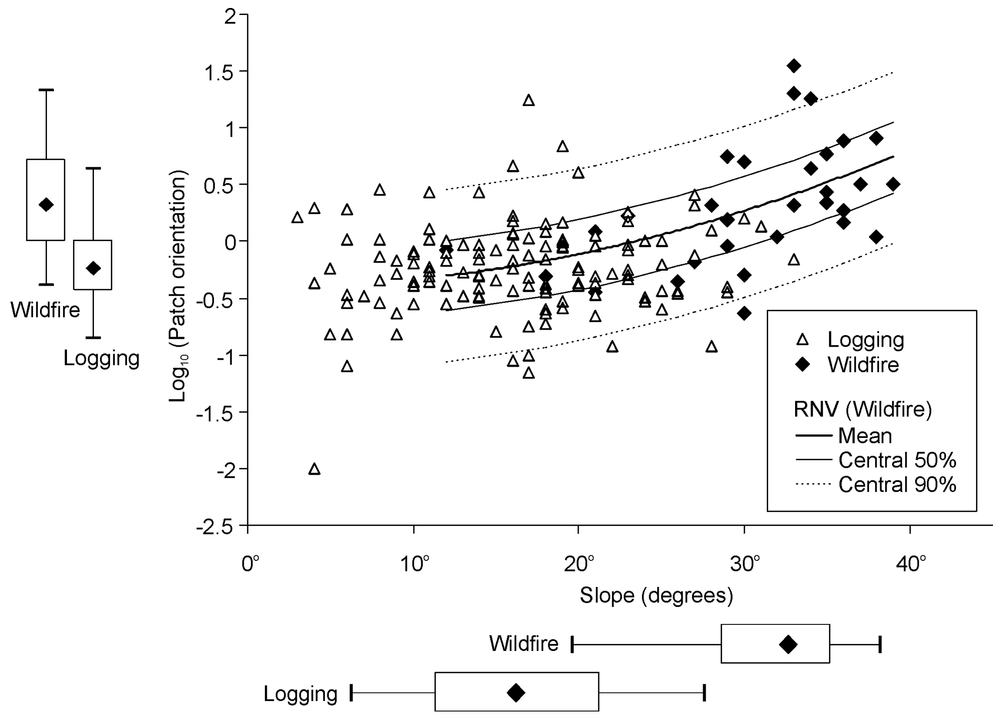

Figure 6. Patch orientation vs. median slope for wildfire and logging patches. The marginal boxplots represent the independent distributions for patch orientation and slope respectively (see also Figure 2). The graph also shows RNV for patch orientation, estimated from the fire patches. This RNV distribution is represented by central tendency and quantiles (see Figure 5). The regression lines in the figure indicate the change in RNV with median slope.

sition. For gentle slopes, the distribution of patch orientation values for logging patches is not significantly different from that of fire patches. The landscape-shaping difference between fire and logging regimes in this case is the preference of logging for valley bottom areas with gentle terrain (apart from overall higher disturbance rates in logged watersheds). Consequently, a management guideline to shape cutblocks with stronger orientation in slope direction would not necessarily serve to bring overall landscape pattern closer to RNV. From an RNV perspective, the recommendation would be to also shift logging into steeper upslope areas. Needless to say, both ecological and economic considerations would advise against adopting RNV-based guidelines in this respect.

Conclusion

In this paper, we have illustrated a set of quantitative techniques for integrating topography into pattern analysis at several levels, from adjustment of landscape indices to account for true surface area and distance metrics, through design of indices that assess pattern in relation to watershed topography, to higher-level analysis of relationships among topography, forest pattern, and forest management. Our examples demonstrate that topography can play a prominent role in structuring the vegetation mosaic. The methods described above not only helped us to gain a more complete understanding of landscape pattern within the study area; they also made it possible to quantify topographic influence on landscape pattern and help to separate out the effects of topographic constraints from those of disturbance. In studies where topographic influence is not a primary research question in itself, our methods could help researchers to gauge the importance of topography in their study area and decide, whether biases introduced by topographic effects are severe enough to warrant explicit consideration. The set of methods described in this paper is not intended as a ready-made, complete package, but rather as a set of concrete examples illustrating some novel approaches towards integrating gradients and constraints into pattern analysis. We believe that concepts and algorithms can easily be adapted to work with a variety of pattern measures, as well as different types of constraining influences and physical gradients. We hope that some of the ideas and observations outlined here will stimulate more interest in the landscape-shaping influence of the underlying physical terrain and in the development of novel approaches for revealing, assessing, and reasoning about topographic influence on landscape pattern and processes.

Acknowledgements

The authors would like to thank M.J. Fortin, H. Sandmann, A.S. Harestad, J. Franklin, and two anonymous reviewers for comments on earlier drafts of this manuscript. This research was supported by Forest Renewal BC.

References

Allen T.R. and Walsh S.J. 1996. Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. Photogrammetric Engineering & Remote Sensing 62: 1261–1268.

Attiwill P.M. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. Forest Ecology and Management 63: 247–300.

Baker W.L. 1994. Restoration of landscape structure altered by fire suppression. Conservation Biology 8: 763–769.

Baker W.L. and Cai Y. 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS GIS. Landscape Ecology 7: 291–302.

Butler D.R. and Walsh S.J. 1994. Site characteristics of debris flows and their relationship to alpine treeline. Physical Geography 15: 166–180.

Cissel J.H., Swanson F.J., McKee W.A. and Burditt A.L. 1994. Using the past to plan the future in the Pacific Northwest. Journal of Forestry 92: 30–31, 46.

Cissel J.H., Swanson F.J. and Weisberg P.J. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9: 1217–1231.

Costello J.D., Leopold D.J. and Smallidge P.J. 1995. Pathogens pattern, and processes in forest ecosystems. BioScience 45: 16–24.

Crist E.P. and Cicone R.C. 1984. Application of the Tasseled Cap concept to simulated Thematic Mapper data. Photogrammetric Engineering and Remote Sensing 50: 343–352.

Dorner B. 2002. Forest management and natural variability: the dynamics of landscape pattern in mountainous terrain. PhD Dissertation, Simon Fraser University, Burnaby, British Columbia, Canada.

Florinsky I.V. 1998. Combined analysis of digital terrain models and remotely sensed data in landscape investigations. Progress in Physical Geography 22: 33–60.

Forest Ecosystem Management Assessment Team (FEMAT) 1993. Forest ecosystem management: An ecological, Economic, and Social Assessment. U.S. Departments of Agriculture, Commerce, and the Interior; and the Environmental Protection Agency, Washington, DC, USA.

Gardner R.H. and O'Neill R.V. 1991. Pattern, process, and predictability: The use of neutral models for landscape analysis. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, New York, USA, pp. 289–307.

Hadley K.S. 1994. The role of disturbance, topography, and forest structure in the development of a montane forest landscape. Bulletin of the Torrey Botanical Club 121: 47–61.

Hessburg P.F., Smith B.G. and Salter R.B. 1999. Detecting change in forest spatial patterns from reference conditions. Ecological Applications 9: 1232–1252.

Jenkins S.H. 1979. Seasonal and year-to-year differences in food selection by beavers. Oecologia 44: 112–116.

Jensen M.E. and Bourgeron P.S. (eds) 1993. Eastside Forest Ecosystem Health Assessment. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Keddy P.A. 1991. Working with heterogeneity: an operator's guide to environmental gradients. In: Kolasa J. and Pickett S.T.A. (eds), Ecological Heterogeneity. Springer Verlag, New York, New York, USA, pp. 181–202.

Knight D.H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Turner M. (ed.), Landscape heterogeneity and disturbance. Springer Verlag, New York, New York, USA, pp. 59–83.

Kolasa J. and Rollo C.D. 1991. The heterogeneity of heterogeneity: a glossary. In: Kolasa J. and Pickett S.T.A. (eds), Ecological Heterogeneity. Springer Verlag, New York, New York, USA, pp. 1–23.

Kramer M.G.A., Hansen A.J. and Taper M.L. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology 82: 2749 – 2768.

Landres P.B., Morgan P. and Swanson F. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179–1188.

Landres P.B., White P.S., Aplet G. and Zimmermann A. 1998. Naturalness and natural variability: Definitions, concepts, and strategies for wilderness management. In: Kulhavy D.L. and Legg M.H. (eds), Wilderness & natural areas in eastern North America: research, management and planning. Center for Applied Studies, College of Forestry, Steven F. Austin University, Nacogdoches, Texas, USA, pp. 41–50.

Leduc A., Drapeau P., Bergeron Y. and Legendre P. 1992. Study of spatial components of forest cover using partial Mantel tests and path analysis. Journal of Vegetation Science 3: 69–78.

Legendre P. and Fortin M.-J. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107–138.

Lehmkuhl J.F., Hessburg P.F., Everett R.L., Huff M.H. and Ottmar R.D. 1994. Historical and current forest landscapes of eastern Oregon and Washington. General Technical Report PNW-GTR-328. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Lehmkuhl J.F. and Ruggiero L.F. 1991. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife. General Technical Report PNW-GTR-285. USDA Forest Service, Pacific Northwest Region, Portland, Oregon, USA.

Lertzman K., Spies T. and Swanson F. 1997. From ecosystem dynamics to ecosystem management. In: Schoonmaker P., von

Hagen B. and Wolf E. (eds), The Rainforests of Home: Profile of a North American Bioregion. Island Press, Washington, DC, USA, pp. 361–382.

McGarigal K. and Marks B.J. 1994. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

McNab W.H. 1989. Terrain shape index: quantifying effect of minor landforms on tree height. Forest Science 35: 91–104.

Mladenoff D.J., White M.A., Crow T.R. and Pastor J. 1994. Applying principles of landscape design and management to integrate old-growth forest enhancement and commodity use. Conservation Biology 8: 752–762.

Montgomery D.R. 1999. Process domains of the river continuum. Journal of the Water Resources Association 35: 1–14.

Moore I.D., Norton T.W. and Williams J.E. 1993. Modelling environmental heterogeneity in forested landscapes. Journal of Hydrology 150: 717–747.

Morgan P., Aplet G.H., Haufler J.B., Humphries H.C., Moore M.M. and Wilson W.D. 1994. Historical range of variability: a useful tool for evaluating ecosystem change. Journal of Sustainable Forestry 2: 87–111.

Ohmann J.L. and Spies T.A. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon. Ecological Monographs 8: 151–182.

O'Neill R.V., Krummel J.R., Gardner R.H., Sugihara G., Jackson B., DeAngelis D.L. et al. 1988. Indices of landscape pattern. Landscape Ecology 1: 153–162.

Pastor J. and Broschart M. 1990. The spatial pattern of a northern conifer-hardwood landscape. Landscape Ecology 4: 55–68.

Pike R.J. 2000. Geomorphometry – diversity in quantitative surface analysis. Progress in Physical Geography 24: 1–20.

Riitters K.H., O'Neill R.V., Hunsacker C.T., Wickham J.D., Yankee D.H., Timmins S.P. et al. 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecology 10: 23–39.

Ripple W.J. 1994. Historic spatial pattern of old-growth forests in western Oregon. Journal of Forestry 92: 45–49.

Romme W.H. and Knight D.H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62: 319–326.

Rossi R.E. 1992. Geostatistical tools for modelling and interpreting spatial dependence. Ecological Monographs 62: 277–314.

Statistical Sciences Inc. 1993. S-PLUS for Windows User's Manual, Version 3.1. Statistical Sciences, Inc., Seattle, Washington, USA.

Swanson F.J., Jones J.A., Wallin D.O. and Cissel J.H. 1993. Natural variability – implications for ecosystem management. General Technical Report PNW-GTR-318. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Swanson F.J., Kratz T.K., Caine N. and Woodmansee R.G. 1998. Landform effects on ecosystem patterns and processes. BioScience 38: 92–98.

Swanson F.J., Wondzell S.M. and Grant G.E. 1992. Landforms, disturbance, and ecotones. In: Hansen A.J. and di Castri F. (eds), Landscape boundaries: consequences for biotic diversity and ecological flows. Springer Verlag, New York, New York, USA, pp. 304–323.

Turner M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecological Systems 20: 171–197.

Turner M.G. and Dale V.H. 1991. Modeling landscape disturbance. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, New York, USA, pp. 324–351.

Turner S.J., O'Neill R.V., Conley W., Conley M.R. and Humphries H.C. 1991a. Pattern and scale: Statistics for landscape ecology. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology. Springer Verlag, New York, New York, USA, p. 536.

Urban D.L., O'Neill R.V. and Shugart H.H. 1987. Landscape ecology. BioScience 37: 119–127.

Veblen T.T. and Alaback P.B. 1996. A comparative review of forest dynamics and disturbance in the temperate rainforests of North and South America. In: Lawford R.G., Alaback P.B. and Fuentes E. (eds), High-latitude Rainforests and Associated Ecosystems of the West Coast of the Americas. Springer-Verlag, New York, New York, USA, pp. 173–213.

Voller J. and Harrison S. 1998. Conservation biology principles for forested landscapes. UBC Press, Vancouver, British Columbia, Canada.

Wallin D.O., Swanson F.J., Marks B., Cissel J.H. and Kertis J. 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. Forest Ecology and Management 85: 291–310.

Walsh S.J., Butler D.R., Allen T.R. and Malanson G.P. 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. Journal of Vegetation Science 5: 657–672.

Walsh S.J., Butler D.R., Brown D.G. and Bian L. 1990. Cartographic modeling of snow avalanche path location within Glacier National Park, Montana. Photogrammetric Engineering & Remote Sensing 56: 615–621.

Westervelt J., Shapiro M. and Goran W.D. et al. 1991. GRASS User's Reference Manual. ADP Report N-87/22. USACERL, New York, New York, USA.

Wiens J.A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. In: Pickett S.T.A. and White P.S. (eds), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, New York, USA, pp. 169–193.

Wondzell S.M., Cunningham G.L. and Bachelet D. 1996. Relationships between landforms, geomorphic processes, and plant communities on a watershed in the northern Chihuahuan Desert. Landscape Ecology 11: 351–362.

Zhang Q., Pregitzer K.S. and Reed D.D. 1999. Catastrophic disturbance in the presettlement forests of the Upper Peninsula of Michigan. Canadian Journal of Forest Research 29: 106–114.