

Remote sensing derived edge location, magnitude, and class transitions for ecological studies

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Abstract. Regionally intensive human activities related to resource extraction (i.e., harvesting, oil and gas extraction) are increasing the occurrence of edges found in some forested landscapes. Edges between different land cover types represent important transition zones for abiotic and biotic processes. However, boundary detection methods often identify edges solely in areas of high contrast, such as transitions between forest and non-forest areas, and are insensitive to the relative contrast and orientation of different transitions. Edge contrast and orientation can determine the magnitude and even the occurrence of ecological edge effects and should be measured to provide information on landscape condition and habitat potential. Wombling was applied to the wetness component of a tasselled cap transformation (TCT) of a Landsat scene acquired over a portion of the eastern slopes of the Rocky Mountains in Alberta, Canada. By incorporating wombled edge contrast and orientation, and edge class transition type obtained from a land cover dataset, the nature of all transitions between land cover classes within the image was characterized and quantified. The consistency between edges identified by wombling and other common methods of edge delineation (such as spatial clustering) and methods of edge quantification (such as landscape pattern indices, or LPIs) was also assessed. Land cover transitions showed a broad range of edge contrast. Comparisons of edge contrast and the LPI edge density showed a positive correlation ($r^2 = 0.33$); however, the strength of this relationship varied with the dominant land cover type (e.g., $r^2 = 0.016$ for broadleaf open forest to $r^2 = 0.48$ for dense coniferous forest). Stratifying edge contrast to higher values (i.e., >1 standard deviation) increased agreement with edge density, indicating that the LPI is preferentially relating high contrast edges. This study demonstrates how unique edge characteristics may be generated from a remotely sensed continuous variable (TCT wetness). This knowledge of the location, magnitude, and class transitions found at edges provides insights into the nature of the edge effects and enables the development and testing of hypotheses informing wildlife habitat use and selection.

Résumé. Les activités humaines intensives au plan régional associées à l'extraction des ressources naturelles (c.-à-d. les coupes forestières et l'extraction de pétrole et de gaz) font augmenter la fréquence des contours rencontrés dans certains paysages forestiers. Les contours entre les différents types de couvert représentent des zones de transition importantes pour les processus abiotiques et biotiques. Cependant, les méthodes de détection de frontières ne permettent souvent d'identifier des contours que dans des zones de fort contraste, comme les transitions entre les zones forestières et non forestières, et celles-ci sont insensibles au contraste et à l'orientation relatifs des différentes transitions. Le contraste et l'orientation des contours peuvent déterminer l'importance et même l'occurrence des effets de contour écologique et devraient être mesurés pour fournir une information sur l'état du paysage et le potentiel des habitats. La technique d'estimation de frontières par la méthode de Womble a été appliquée à la composante humidité de l'espace indiciel transformé (tasseled cap transformation-TCT) d'une image Landsat acquise au-dessus d'une portion des versants est des montagnes Rocheuses en Alberta, au Canada. En incorporant, d'une part, le contraste et l'orientation des contours obtenus à l'aide de l'estimation de frontières par la méthode de Womble et, d'autre part, le type de transition de classe de contour obtenu à partir de l'ensemble des données du couvert, il a été possible de caractériser et de quantifier la nature de toutes les transitions entre les classes de couvert à l'intérieur de l'image. On a également évalué la cohérence entre les contours identifiés à l'aide de l'estimation de frontières par la méthode de Womble et les autres méthodes conventionnelles de délimitation de contours (comme le groupement spatial) et les méthodes de quantification de contours (comme les

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indices de patrons d'organisation spatiale du paysage, LPI). Les transitions du couvert ont affiché une grande diversité de contrastes de contour. Des comparaisons entre le contraste de contour et la densité de contour LPI ont montré une corrélation positive ($r^2 = 0,33$); toutefois, l'intensité de cette relation variait avec le type de couvert dominant (p. ex., de $r^2 = 0,016$ pour les forêts claires de feuillus à $r^2 = 0,48$ pour les forêts denses de conifères). La stratification du contraste de contour à des valeurs plus élevées (c.-à-d. écart-type >1) a accru la concordance avec la densité de contour suggérant que le LPI relie plutôt des contours de fort contraste. L'étude a démontré comment des caractéristiques inédites peuvent être générées à partir d'une variable continue (humidité dérivée de TCT). Cette connaissance de la localisation, de l'intensité et de la classe des transitions rencontrées à la limite des contours fournit des informations sur la nature des effets de contour et permet de développer et de tester des hypothèses sur l'utilisation et la sélection des habitats fauniques. [Traduit par la Rédaction]

Introduction

Edges, or the boundaries separating distinct habitat patches (Ries et al., 2004), are inherent features of a landscape and play an important role in ecosystem dynamics (Fortin and Edwards, 2001). Edges are identified, either qualitatively or quantitatively, as transitions between spatially adjacent locations where a key variable (e.g., photosynthetically active radiation, vegetation structure, community composition) shows high levels of contrast (Fortin et al., 1996; 2000; Kotliar and Wiens, 1990). Anthropogenic activities have increased the prevalence of edges as a by-product of the increasing fragmentation of habitats (Cadenasso et al., 2003a; Fagan et al., 1999; Fortin and Edwards, 2001). Both the amount and types of edges in a landscape are being altered by land cover – land use changes (Fagan et al., 1999).

Alteration of edges across a landscape is of concern because of the wide impacts of edges on local physical characteristics, flora, and fauna. Edges can dramatically affect species behaviour. For example, edges can act as landmarks for individual animals determining home range limits (Fortin and Edwards, 2001; Kent et al., 2006) or influence the movement patterns of wildlife, such as the flight selection of eastern bluebirds with preferential flight paths parallel to forest edges (Levey et al., 2005). Species abundances also change in relation to edges, although the direction of the response is species specific (Malcolm, 1994; Ries et al., 2004; Schultz and Crone, 2001). Organisms are predicted to increase in abundance near an edge when able to gain access to resources from adjacent habitats (Fletcher et al., 2007; Rand et al., 2006). Grizzly bears, for example, use edges between intermediate-aged harvest units and forests because of the juxtaposition of rich food resources within the regrowth of a harvested area and, potentially, the security of the nearby forest (Nielsen et al., 2004a; 2004b). This pattern is also seen in Alaska moose at forest–meadow edges (Molvar and Bowyer, 1994). Other species require core habitat (i.e., habitat that is not influenced by edge effects) due to reduced quality of the adjacent habitat and the habitat edge or to increased risk of predation or parasitism at edges (Fagan et al., 1999; Paton, 1994).

To complement and augment knowledge of edge location, both edge orientation and contrast help inform edge characteristics, determining (i) whether or not an edge

effect occurs, (ii) the magnitude of the edge effect, and (iii) the distance to which an edge modifies habitat characteristics and species responses (Ries et al., 2004). Edge contrast provides information regarding the dissimilarity of neighbouring pixel values and determines edge permeability to energy, material, and species (Cadenasso et al., 2003b), for example, affecting forest regeneration success via impacts on microclimate, seed dispersal, and seed predation (López-Barrera et al., 2006; 2007). Edge contrast has been shown to influence the abundance, diversity, and species composition of ants (Dauber and Wolters, 2004; Debuse et al., 2007), insects (Duelli et al., 1990), amphibians (DeMaynadier and Hunter, 1998), and birds (Reino et al., 2009). Edge contrast also influences butterfly flight patterns; edge-sensitive species tend to avoid edges, and edge-tolerant species react only to the strongest edges (Ries and Debinski, 2001). As with edge effects in general, the effects of edge contrast observed in the aforementioned studies are largely species or functional-group specific. Interestingly, the effects of edge contrast are not always consistent with edginess or between different habitat uses or response variables for a given species, underscoring the importance of considering the contrast in addition to the presence–absence of edges. Mule deer home range size was found to be negatively affected by the density of all edges but was positively related to mean edge contrast within analysis units (Kie et al., 2002). Siberian flying squirrels are more strongly associated with high-contrast edges when moving than when nesting (Desrochers et al., 2003). Marbled murrelets preferentially breed along high-contrast edges but have greater breeding success on lower contrast edges or within forest interiors (Malt and Lank, 2007; Zharikov et al., 2007).

Edge orientation has seen little scientific study, but it has clear effects on microclimate (Chen et al., 1993), with consequent impacts on the risk of biological invasion (Honnay et al., 2002), windthrow (Mitchell et al., 2001), moss growth (Hylander, 2005), butterfly energetics (Meyer and Sisk, 2001), herb layer richness (Gignac and Dale, 2007), and epiphytic lichens (Johansson, 2008).

Edge contrast is often developed qualitatively, with categorical class transition labels; semiquantitatively, with subjectively assigned indexes; or with field measurements of underlying variables, such as photosynthetically active radiation. Edge orientation is also often assessed manually,

either in the field or from land cover maps, and to our knowledge has only been studied for high-contrast forest–non-forest edges. To have a more thorough understanding of edge effects, including the mediating influences of edge contrast and orientation, and to rigorously include such effects in landscape models, species distribution models, and habitat selection functions, improved, automated methods are needed to completely characterize edges spatially and over broad extents.

Edges are typically detected through four distinct methods, namely moving split window, spatial clustering, wombling, and fuzzy set modeling (see **Table 1** for further descriptions). The two methods predominately used in ecological edge detection are spatial clustering and wombling. Spatial clustering forms homogeneous clusters (i.e., the patches of a land cover classification) in which contiguity constraints may be applied (Fortin, 1994), with edges extracted as transitions between clusters. As a result, spatial clustering can only detect strong, contiguous boundaries and is therefore more appropriate when boundaries are abrupt (Fortin and Edwards, 2001). The second method, wombling, calculates the magnitude of edge contrast and edge orientation from the first partial derivative of an environmental variable over the x and y spatial dimensions of a 2×2 kernel moved across the dataset. This creates continuous surfaces of edge contrast and orientation; boundaries are then demarcated in contiguous regions of high contrast and similar orientation (Fortin, 1994; Fortin and Drapeau, 1995; Jacquez et al., 2000). Wombling is well suited for detecting both strong and gradual boundaries that are found between and within landscape patches (Fortin and Edwards, 2001).

Alternatively, the edginess of a landscape may be summarized over multipixel aggregates using a landscape pattern index (LPI) (Hargis et al., 1998; Wulder et al., 2008a). LPIs can be used to characterize the structural characteristics of a landscape, providing important variables for ecological studies (Wu, 2004). Edge density is an LPI that characterizes the amount of edge in a landscape as the total length of edge per unit area within each landscape. Edge density has been used to examine changes in habitat edge resulting from fragmentation (Hargis et al., 1998; McGarigal and Marks, 1995). LPIs, such as edge density, are useful metrics for measuring landscape-level fragmentation but are for a number of reasons limited in measuring local fragmentation. First, data need to be classified, often to a few categorical classes (e.g., forest–non-forest–other) (Wulder et al., 2008a). This reduces the inherent heterogeneity of the data and leads to the simplification of complex ecological phenomena. Second, LPIs are dependent on scale, with the results being a function of both grain (spatial resolution of source data) and extent (size of the unit over which the metrics are computed). Although LPIs are useful tools in the exploration of landscape fragmentation (Gergel, 2007), we hope to supplement this information through local measures of edge contrast.

This study expands on traditional land cover map based edge detection to analyze how edge contrast and orientation, as calculated through wombling, can provide additional information not readily available in spatial clustering and LPIs. Wombling was adapted and applied to capture important information contained within the less severe edge transitions and transitions that may be ignored when data are clustered or classified. These edges can be as important

Table 1. Summary of selected methods used to generate edges at grain scales.

Description	Advantage	Disadvantage	Reference
Moving split window			
A window, divided into two equal halves, is slid along a transect; edges are located in areas of maximum dissimilarity between halves	Relatively simple to implement	Restricted to one-dimensional transects and cannot be used with spatial data	Jacquez et al., 2000
Spatial clustering			
Groups samples into spatial clusters based on similar characteristics in the variables; boundaries are created as a by-product between clusters	Completely divides the study area into patches	Delineates only sharp boundaries, which may not accurately represent the study area	Fortin and Drapeau, 1995; Jacquez et al., 2000
Wombling			
Kernel used to calculate magnitude of change (often using first partial derivative) for a sampling unit; boundaries are identified as the areas with the highest rates of change (highest slope values)	Determines a range of boundary contrasts	Boundaries are often arbitrarily determined to be the top 10% of the available rates of change	Fortin and Drapeau, 1995; Jacquez et al., 2000
Fuzzy set			
Boundaries have an associated relative degree of edge certainty	More natural and flexible boundaries	Edges are represented as zones as opposed to lines	Jacquez et al., 2000

to microclimate and flora and fauna as the strong edges detected by other methods (Schultz and Crone, 2001; Fagan et al., 2003). Furthermore, wombling is the only existing algorithm that provides objective and automated measures of edge contrast and orientation, both important controls of ecological edge effects. The goal of this study is to characterize, quantify, and attribute the magnitude of edge contrast and orientation of all transitions over a continuous raster grid using wombling and to assess these products with respect to conventionally derived edges and edge metrics.

Background

Wombling

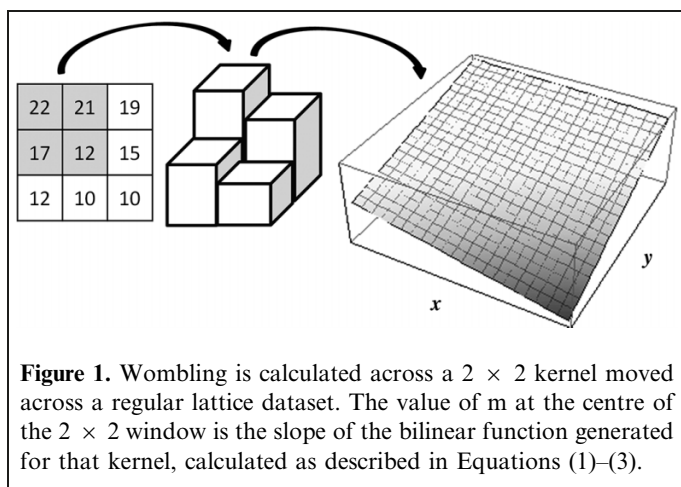
Wombling was first proposed by Womble (1951) as a method of measuring rates of change (termed contrast from here on) across a regular lattice. A 2×2 kernel is moved across the dataset, and a bilinear equation (Equation 1) is created for the kernel to interpolate between the values at the four corners (Z_a , Z_b , Z_c , and Z_d). The x and y coordinates are scaled to run from 0 to 1, and wombling calculates edge contrast based on the slope (m) of the bilinear function at $x = y = 0.5$, and edge direction as the orientation of that slope (θ) (see **Figure 1**):

$$f(x, y) = Z_a(1-x)(1-y) + Z_b(x)(1-y) + Z_c(x)(y) + Z_d(1-x)(y) \quad (1)$$

The slope of the function is calculated from the partial derivatives of the kernel's bilinear function as shown in Equation (2), and the angle calculation is shown in Equation (3):

$$m = \sqrt{\left[\frac{\partial f(x, y)}{\partial x}\right]^2 + \left[\frac{\partial f(x, y)}{\partial y}\right]^2} \quad (2)$$

$$\theta = \arctan \left[\frac{\partial f(x, y) / \partial y}{\partial f(x, y) / \partial x} \right] + \Delta \quad (3)$$



where $\Delta = 0^\circ$ if $\partial f(x, y) / \partial x > 0$ and $\Delta = 180^\circ$ if $\partial f(x, y) / \partial y < 0$. The results of the wombling operation are two matrices, one of edge contrast and one of edge direction over the entire image. Both matrices represent the slope and orientation at the centre of a cell with a resolution twice that of the input lattice data, although the output resolution is the same as the input resolution because an overlapping moving window is used. However, the coordinates of the output matrices have been shifted by half a pixel from those of the original.

Discrete edges can be extracted from these continuous wombling surfaces. Cells constituting boundaries are referred to as boundary elements (Jacquez et al., 2000) and are defined as collections of cells with high slope magnitudes (i.e., high edge contrasts, typically in the upper 5th–10th percentile) in similar orientations (e.g., $\pm 30^\circ$) (Barbujani et al., 1989; Fortin and Drapeau, 1995; Jacquez et al., 2000). It is also possible to test the significance of boundary elements using a binomial test (e.g., Crida and Manel, 2007). However, this was not done here to allow flexibility and the selection of boundary elements over a range of edge contrasts. Lastly, the significance of the spatial patterning of an entire landscape, as indicated by the boundary elements identified, can be tested with subgraph statistics and constrained randomization tests (Fortin, 1994). Since the goal of the present study is to spatially describe all the edges in a landscape (and thus the organization of that landscape) rather than to determine if the landscape has nonrandom organization in general, such metrics were not computed here.

Study area and data

Study area

The study area is located in west-central Alberta, Canada, along the eastern slope of the Rocky Mountains (53.1°N , 116.3°W ; **Figure 2**). The $\sim 34\,000\text{ km}^2$ area supports a diverse array of human activities, including national parks, urban areas, managed forests, mining, and oil and gas development (Linke et al., 2009). Elevation ranges markedly from 600 m to >3500 m. Habitats within the study area include glaciers, mountains, alpine and subalpine meadows, wet meadows, and forests dominated by coniferous and mixed life forms (Achuff, 1994).

Data

Landsat-7 ETM+ image data (path 45, row 23) of the study area were acquired on 19 October 1999 and converted to top-of-atmosphere reflectance (Han et al., 2007). To extract edges, wombling was performed on the wetness component of a tasselled cap transformation (TCT) (Kauth and Thomas, 1976). TCT for Landsat data is often used in mapping changes in land cover because of its capacity to detect changes in vegetation (Healey et al., 2005; Jin and

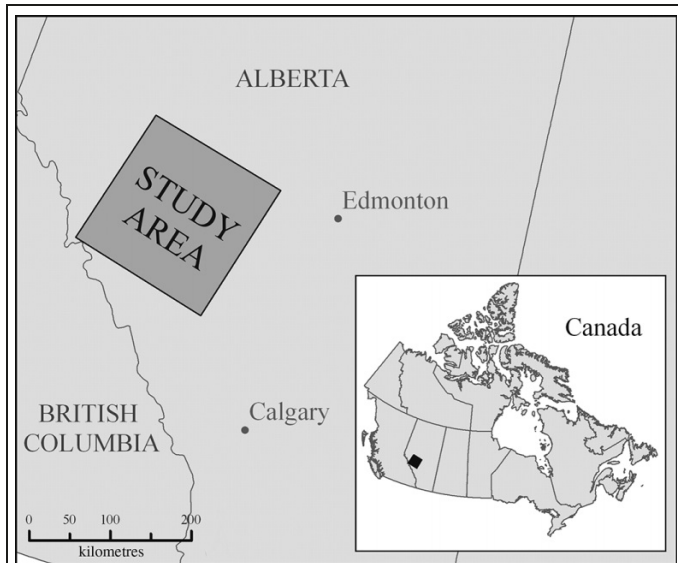


Figure 2. Location of the study area in the foothills of the Rocky Mountains of south-central Alberta, Canada. Inset of Landsat-7 Enhanced Thematic Mapper Plus (ETM+) image, path 44 and row 23, centred at 53.1°N, 116.3°W.

Sader, 2005). The TCT wetness component was selected for wombling because of its relationship to soil and plant moisture (Crist and Cicone, 1984) and vegetation structure (Cohen et al., 1995). Changes in the structure and maturity of closed canopy forest stands can therefore be identified using the TCT wetness component (Cohen et al., 1995). The study area is rather heterogeneous. The continuous nature of the TCT wetness is expected to allow for the detection of sharp edges between distinct features as well as more subtle edges within broad land cover classes without requiring any prior class-based stratification of the land base.

Edges identified in a land cover classification were also investigated to compare our continuous wombling measures with those derived from spatial clustering. The Earth Observation for Sustainable Development of Forests product (EOSD) is a 25 m resolution land cover map of the entire forested area of Canada representing circa year 2000 conditions (Wulder et al., 2008b). The EOSD follows a closed hierarchical legend of up to 23 classes, which can be simplified to a number of levels. This land cover product was used to provide a classification from which to compute indices of landscape pattern (Wulder et al., 2008a) and to investigate the links between edge contrast and the land cover classes present. Two thematic resolutions of the classification were used, described as levels 4 and 2 in **Table 2**. Hereafter, classification level 2 is indicative of general land cover class (i.e., forest–non-forest), and level 4 relates a more detailed cover-type level characterization (e.g., water, shrub, conifer).

Table 2. Reclassification of EOSD into forest, non-forest, and other.

Level 4	Level 2
Shadow	Other
Cloud	Other
No data	Other
Water	Other
Snow–ice	Other
Rock–rubble	Other
Exposed land	Non-forest
Wetland shrub	Non-forest
Wetland herb	Non-forest
Wetland treed	Forest
Conifer	Forest
Broadleaf	Forest
Mixed wood	Forest
Shrub	Non-forest
Herb	Non-forest
Bryoid	Non-forest

Methods

Wombling was performed on the wetness component of a TCT of a Landsat-7 ETM+ image. To align the wombling products with the original imagery, the image data were resampled from 30 m cells to 15 m cells using cubic convolution. As the wombling outputs are shifted by half a pixel in the x and y direction, this resampling facilitates comparison between the wombling output and land cover derived edges. The resulting raster datasets of edge contrast and orientation were then resampled back to the original input resolution of 30 m using the same methods. Boundary elements were identified by separating the wombling contrast values into deciles. The top four deciles were investigated, rather than the top-most decile, to characterize weak as well as strong edges (hereafter, these are referred to as high-, medium-, medium–low-, and low-contrast edges). Although all deciles could have been summarized, the results from analysis of the lower deciles proved inconsequential and were subsequently removed. Following Barbujani et al. (1989), boundary elements were identified as edges if the cell's edge contrast was in one of the top four deciles, and if a surrounding cell had equal or higher wombling contrast and was oriented in the same direction, plus or minus 30°. The result of this processing is an output lattice with a resolution equal to that of the input lattice, with four classes of edge contrast. The wombling outputs were thus raster datasets of edge contrast and edge orientation and a raster image describing the location and class of boundary elements. The edge-contrast and orientation rasters were used to attribute transitions in the EOSD product, and both image-wide edge contrast and boundary elements were compared with landscape pattern indices.

Prior to extracting edges from the EOSD classification product, the land cover product was resampled from 25 m to 30 m using a nearest neighbour algorithm to match the

resolution of the wombling datasets. Wombled edge contrast and orientation values were extracted from the pixels at transitions between EOSD land cover classes to evaluate the relationship between edge contrast and edge type. Each cell in the input EOSD dataset was given a transition value based on the surrounding cells in a 3×3 moving window. A Rook's case window was used, where neighbouring cells with a full shared edge with the central cell were considered, and those on the diagonals were ignored (see grey cells in **Figure 3**). If the kernel contained homogeneous values, the transition retained its original land cover value. If there was heterogeneity, a transition value was given listing the unique values inside the window. Only transitions containing two land cover classes were retained because of the complex ecological nature of higher transitions. Such higher order transitions were extremely rare; see **Table 3** for a breakdown of all transitions in the study area. For instance, over 60% of the image is homogeneous within a 3×3 kernel, and nearly 30% of the image contains transitions between two classes. Transitions between three classes occur in only 6% of the kernels. The results of the transition extraction are a series of categorical transitions labelling the EOSD classes that adjoin within the window. Level 4 (analogous to cover type; **Table 2**) (see Wulder and Nelson, 2003) of the EOSD classification was used to label transitions.

For each EOSD land cover transition, the underlying wombling contrast and orientation values were extracted and summary statistics (mean and standard deviation (sd)) were calculated. Values were extracted by masking edge contrast and orientation using all four levels of boundary elements. For each EOSD transition, edge contrast and orientation were extracted from directly underneath the transition; the same was done for homogeneous areas.

The LPI edge density was calculated over $990 \text{ m} \times 990 \text{ m}$ ($33 \text{ cells} \times 33 \text{ cells}$) extents using the level 2 EOSD classification (**Table 2**) for comparison with wombling

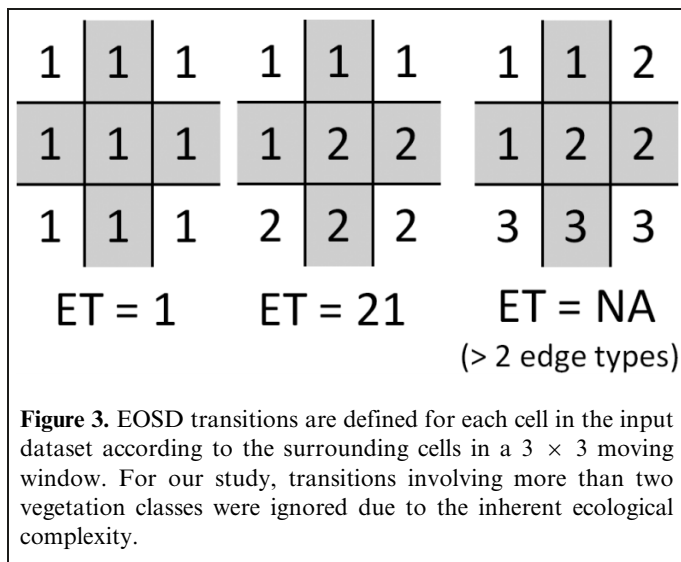


Table 3. Transition occurrence, noting the frequency over the study area of differing class juxtapositions.

	Transition count	Frequency over study area (%)
Homogeneous	47 956 087	63.23
Two classes	12 301 410	30.58
Three classes	2 387 961	5.94
Four classes	102 936	0.26
Five classes	267	0.00

values. This extent was chosen because it approximates the 1 km extents used in previous studies investigating forest fragmentation, is similar to the 1 km products produced nationally in Canada (Wulder et al., 2008a), and enables capture of landscape conditions. The minimum, maximum, mean, and coefficient of variation of wombling edge contrast were calculated, as well as boundary element density, for each $990 \text{ m} \times 990 \text{ m}$ LPI landscape and correlated with the LPI edge density. Landscapes were stratified by dominant land cover to investigate whether wombling performed better or worse depending on land cover.

Results

The classes present in the EOSD classification at two levels of categorical detail are presented in **Table 2**, with the greater class detail (level 4) used to show class transitions and a hierarchically aggregated level 2 that is used as an input to generate the LPI edge density. The frequency of class transitions is shown in **Table 3**; over 60% of the pixels in the study area were in homogeneous locations, that is, with like-class neighbours. Two-class transitions were found for approximately 30% of the pixels, and the remaining 7% contained juxtapositions of three or more classes within a Rook's case kernel. Additional detail on the transitions present and the edge contrast at these locations is presented in **Table 4**. The most frequent transitions were with the conifer class (e.g., 25% of transitions were between coniferous forests and wetlands, and 20% between coniferous and broadleaf forests) due to its overall prevalence within the study area. This land cover class also exhibited some of the strongest transitions in terms of edge contrast: two of the three highest mean contrast values found with this class were for conifer to herb and shrub classes. The standard deviation of edge contrast values is also shown in **Table 4**, revealing high variability of contrast values for given class transition pairs. Additional detail regarding the contrast of wetness values for given class pairs is presented in **Figure 4**, where conifer to broadleaf transitions are shown to have had a low contrast and a relatively limited variance in values. Alternately, the contrast between exposed land and herb classes was of variable strength with a high standard deviation.

As a complement to the edge contrast values, edge orientation results are presented in **Figure 5**. Edge orientations were highly variable within transition types, and there

Table 4. Mean wombling contrast and percent of transitions.

	Exposed	Shrubs	Wetland	Herbs	Conifer	Broadleaf
Exposed	10.990 ± 10.350	0.84%	0.20%	3.51%	1.51%	0.17%
Shrubs	9.312 ± 8.075	5.347 ± 4.556	1.03%	5.16%	7.47%	1.96%
Wetland	5.657 ± 5.122	5.133 ± 3.956	3.572 ± 2.945	4.67%	25.20%	7.83%
Herbs	9.259 ± 8.668	6.541 ± 5.503	5.773 ± 4.288	4.580 ± 4.400	5.59%	8.23%
Conifer	4.990 ± 5.936	4.847 ± 4.434	3.840 ± 3.246	5.626 ± 4.968	2.403 ± 2.496	20.21%
Broadleaf	6.058 ± 5.038	5.045 ± 3.774	4.380 ± 3.178	5.432 ± 3.926	3.792 ± 3.113	3.969 ± 2.896

Note: Values above the diagonal represent transition occurrence values, values below the diagonal indicate wombling contrast ± sd, and diagonal values represent mean contrast for homogeneous areas. The totals do not sum to 100 because the no-data and water classes are excluded.

were no clear differences in edge orientation between transitions. However, there was a tendency for edges to have a northerly direction.

Comparisons were made between LPI edge density and wombling contrast and boundary element density in 990 m × 990 m landscapes (Table 5). The correlation between high-contrast boundary element density and LPI edge density was $r^2 = 0.173$ across the study area; however, correlation values increased with the inclusion of the weaker boundary elements (up to $r^2 = 0.27$ with the inclusion of all boundary elements) and decreased to a low $r^2 = 0.118$ when edge contrast from all pixels was considered (Table 5). Stratifying by land cover (Table 6) caused some of the

relationships between wombled edge contrast and edge density to increase in strength, up to an $r^2 = 0.48$ for the coniferous dense class.

Edge and boundary element densities were also generalized into “high” and “low” edginess classes (density greater or less than 1 sd from the mean, respectively) for these 990 m × 990 m landscapes. A confusion matrix was generated to measure agreement between edge density and wombling boundary element density and to identify areas where the two metrics were different; see Table 7 for the matrix and Figure 7 for a map of the resulting classification. There was strong agreement (76%) between the two methods at identifying landscapes with high and low edge densities.

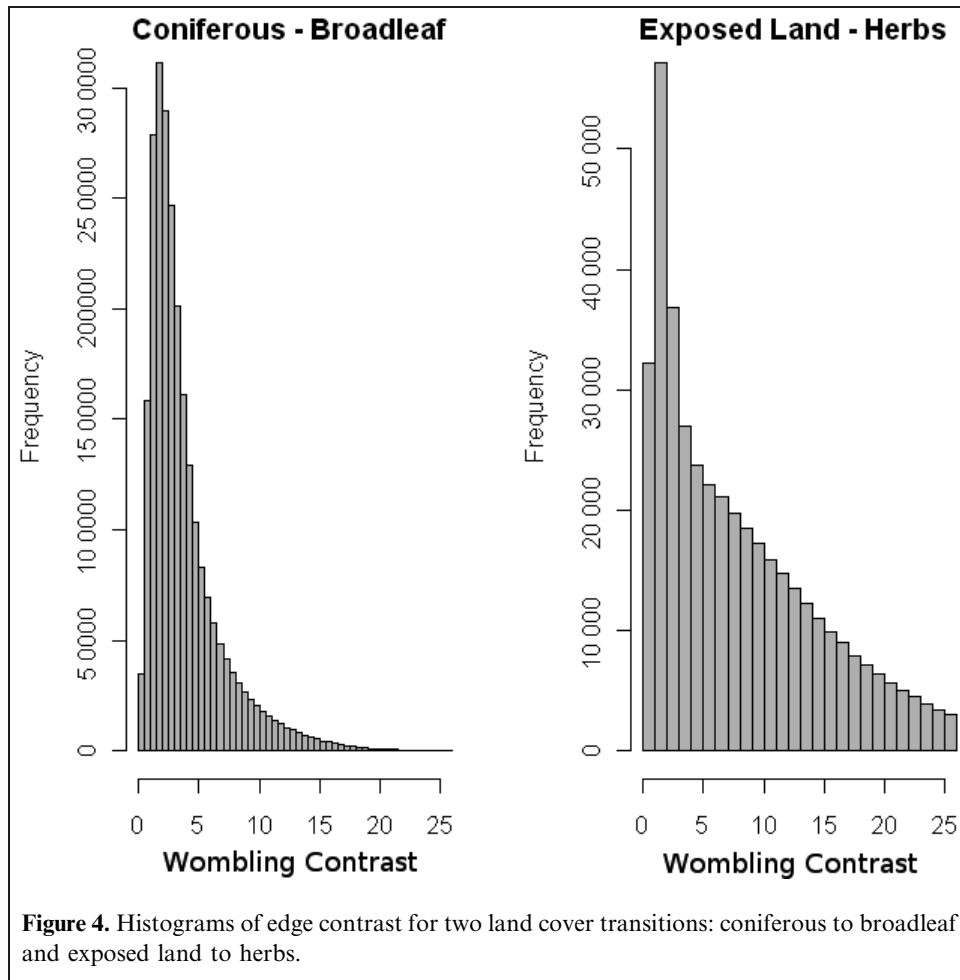


Figure 4. Histograms of edge contrast for two land cover transitions: coniferous to broadleaf and exposed land to herbs.

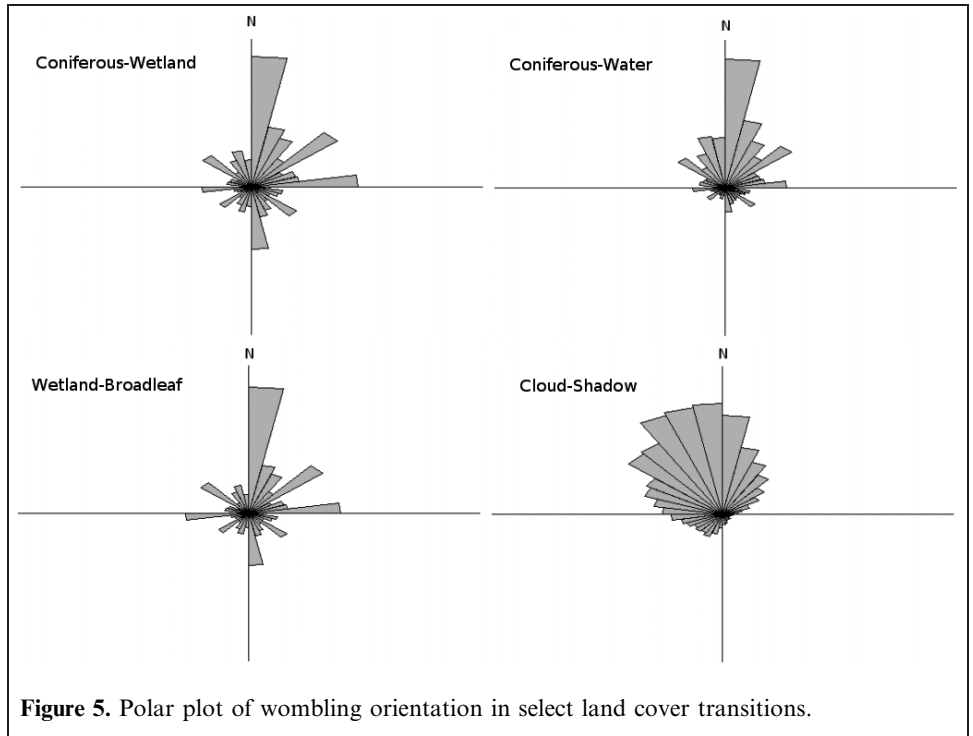


Figure 5. Polar plot of wombling orientation in select land cover transitions.

Table 5. Correlations (r^2) between LPI edge density and wombling contrast values.

	Mean wombling	High contrast	High and medium contrast	High, medium, and medium-low contrast	All four boundary element contrasts
Edge density	0.117688	0.173487	0.251371	0.266576	0.274901

Discussion

Transitions between land cover classes within the EOSD dataset were attributed with wombled edge contrast and orientation to assess the between- and within-transition class variation (see Table 4 for a breakdown of transition occurrence and edge contrast). Recall that low contrast values indicate weak land cover transitions, and high contrast values indicate strong transitions. Each transition shows heterogeneous contrasts and orientations, highlighting the variability of edges within the EOSD transitions. If

Table 6. Correlation between edge density from LPI and average wombling contrast across 990 m landscapes, stratified by dominant land cover class.

EOSD land cover	Correlation, r^2	p
Coniferous dense	0.482	<0.001
Rock-rubble	0.208	<0.001
Shrub tall	0.390	<0.001
Herbs	0.237	<0.001
Wetland shrub	0.318	<0.001
Shrub low	0.027	0.004
Broadleaf dense	0.298	0.417
Broadleaf open	0.016	0.818

we look at the contrast values, we can see that the transition between coniferous and deciduous forests, a common transition that accounted for 20% of all the transitions within the study area, had one of the lowest edge contrasts, namely 3.792 ± 3.113 (mean \pm sd). This is to be expected, given the spectral variable from which edge contrast was computed and the relative subtlety of a transition from coniferous to broadleaf forest. Compare this to the transition between exposed land and herbs, which represented 3.5% of all transitions and had mean \pm sd edge contrast of 9.259 ± 8.668 . Again, this is to be expected.

Table 7. Confusion matrix comparing edge density and wombling boundary element (BE) density.

	Edge density		Row-wise % disagreement
	High	Low	
Wombling BE density			
High	1466	974	0.399
Low	371	2802	0.116
Column-wise % disagreement	0.202	0.258	
Overall agreement	0.760		

Note: High values are those greater than 1 sd, and low values are those less than -1 sd.

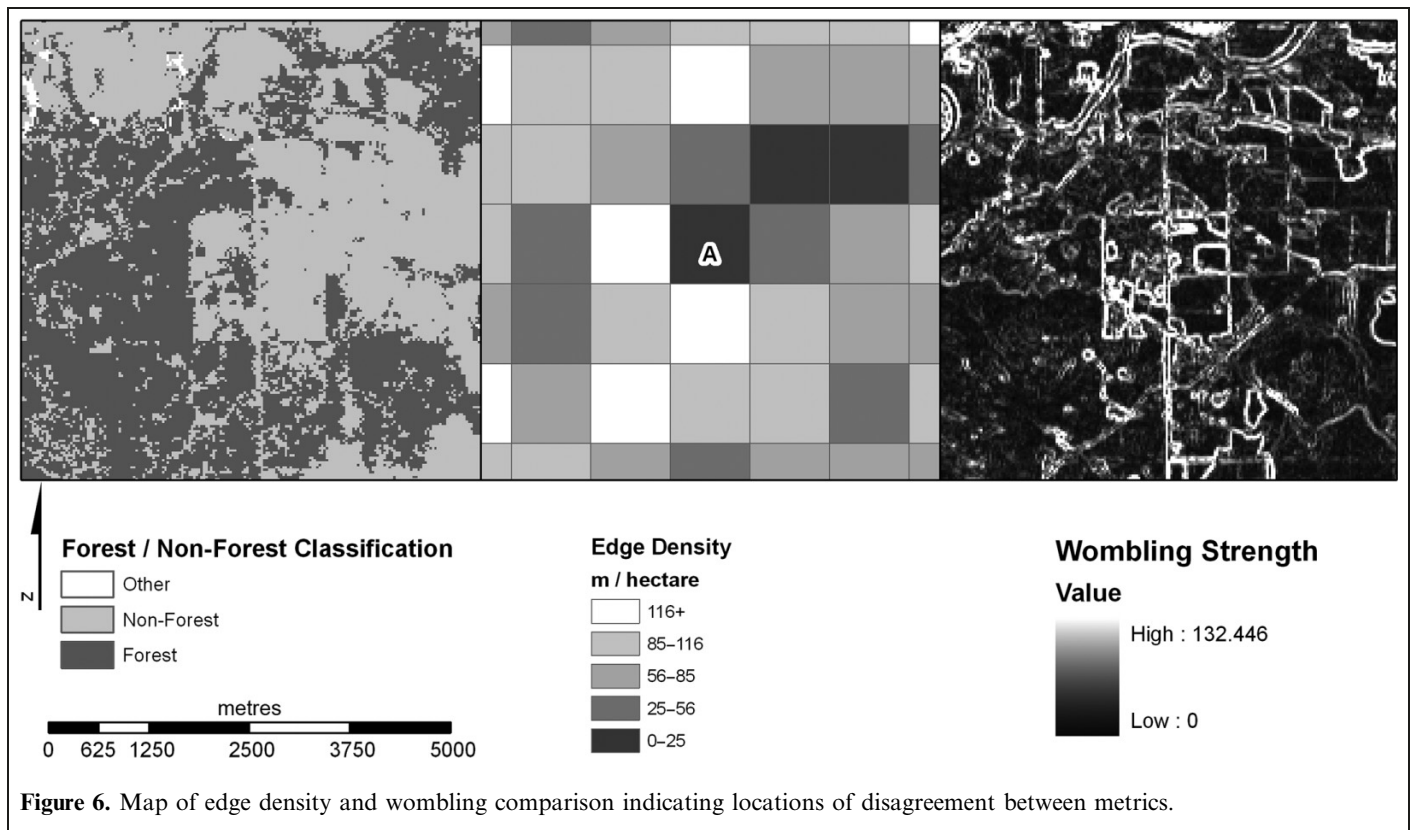


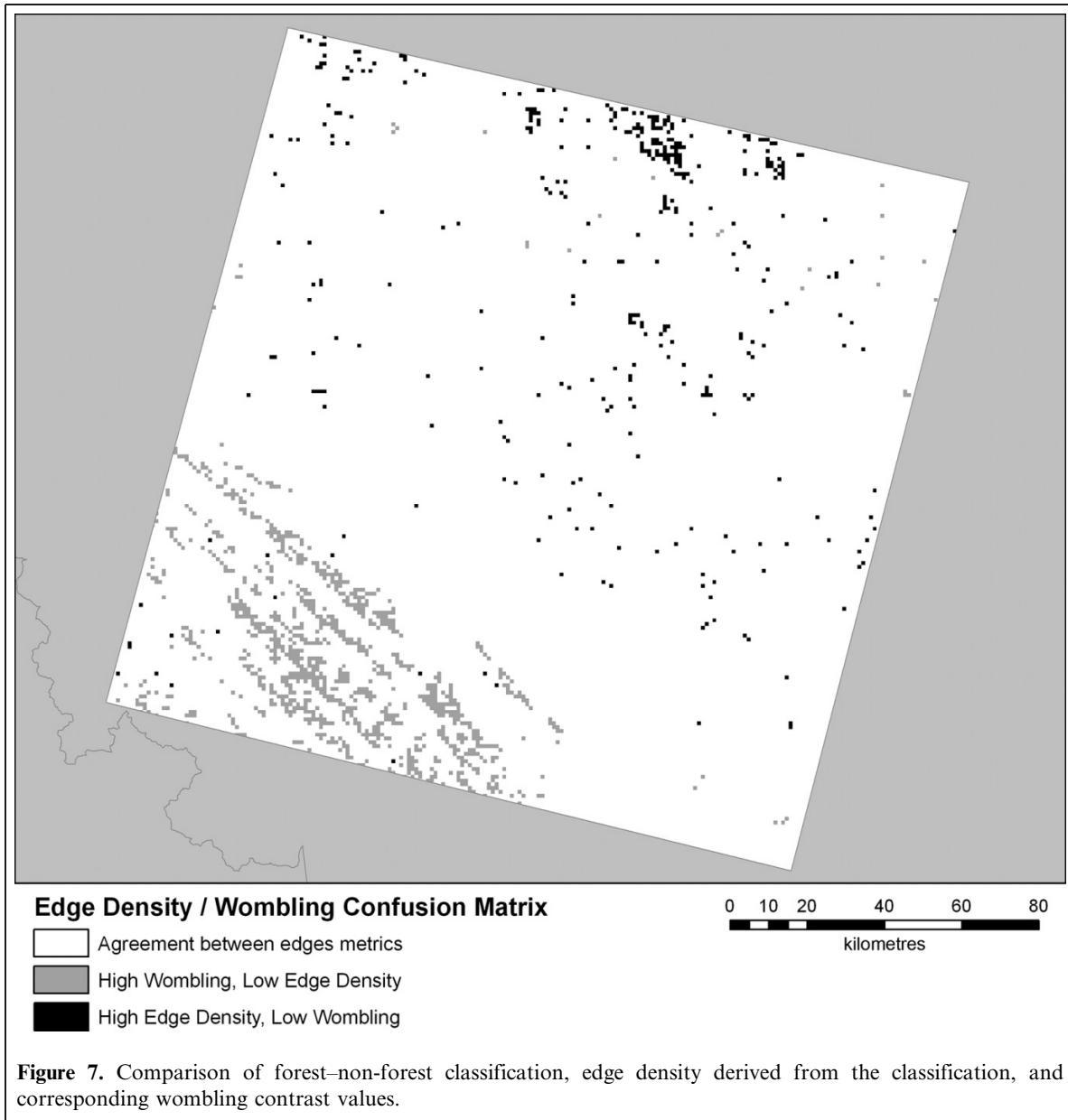
Figure 6. Map of edge density and wombling comparison indicating locations of disagreement between metrics.

Exposed land is much drier and thus much brighter in the mid-infrared (MIR), yielding much lower wetness values than those from vegetated pixels. However, edge contrasts for this transition were highly variable, which may be due to subpixel mixing with bare ground, species composition and associated spectral differences, differences in microclimate, topographic position, and soil type leading to differences in foliar moisture, degree of plant senescence, etc. Histograms of edge contrast for these two transitions are presented in **Figure 4**. These specific examples, as well as all of the transition-edge contrast information presented in **Table 4**, highlight the dramatic differences in edge contrast between the EOSD transitions and the variation within both individual transition types and homogeneously classified areas.

As with edge contrast, the wombling edge orientation attribute was highly variable. Although no significant trends were found, the variability in the orientation of transitions is important, as it shows the heterogeneous nature of the edges detected through wombling (see **Figure 5** for the range of orientations observed in representative transitions). For example, the cloud to shadow transition showed a strong tendency for northeast-oriented edges, as would be driven by sun-surface-sensor geometry. The capture of the directionality of cloud to shadow transitions with a physically based tendency builds confidence in the robustness of the orientation values generated. In other study areas where topographic or wind regimes impact pattern, stronger directional trends are anticipated.

The variation in wombling values for the EOSD transitions indicates that wombling can be used as a local measure of edge, providing a complete, spatial product of edge contrast and orientation for every location within a landscape; however, it is not limited to local analyses. Wombling can be used to generate landscape measures of fragmentation, such as mean edge contrast or boundary element density within a landscape, that are commensurate with traditional landscape pattern indexes such as edge densities derived from land cover classifications. LPI edge density was more strongly related to mean edge contrast when considering only boundary elements (those continuous edges with edge strength in the top 40th percentile) rather than all pixels within a landscape. The agreement between high-contrast edge strengths at the landscape scale and edge density illustrates that stronger edges are captured preferentially with the LPI and that a greater range of conditions are captured with wombling. When stratified by dominant land cover class (**Table 6**), correlation values increased substantially for certain land covers.

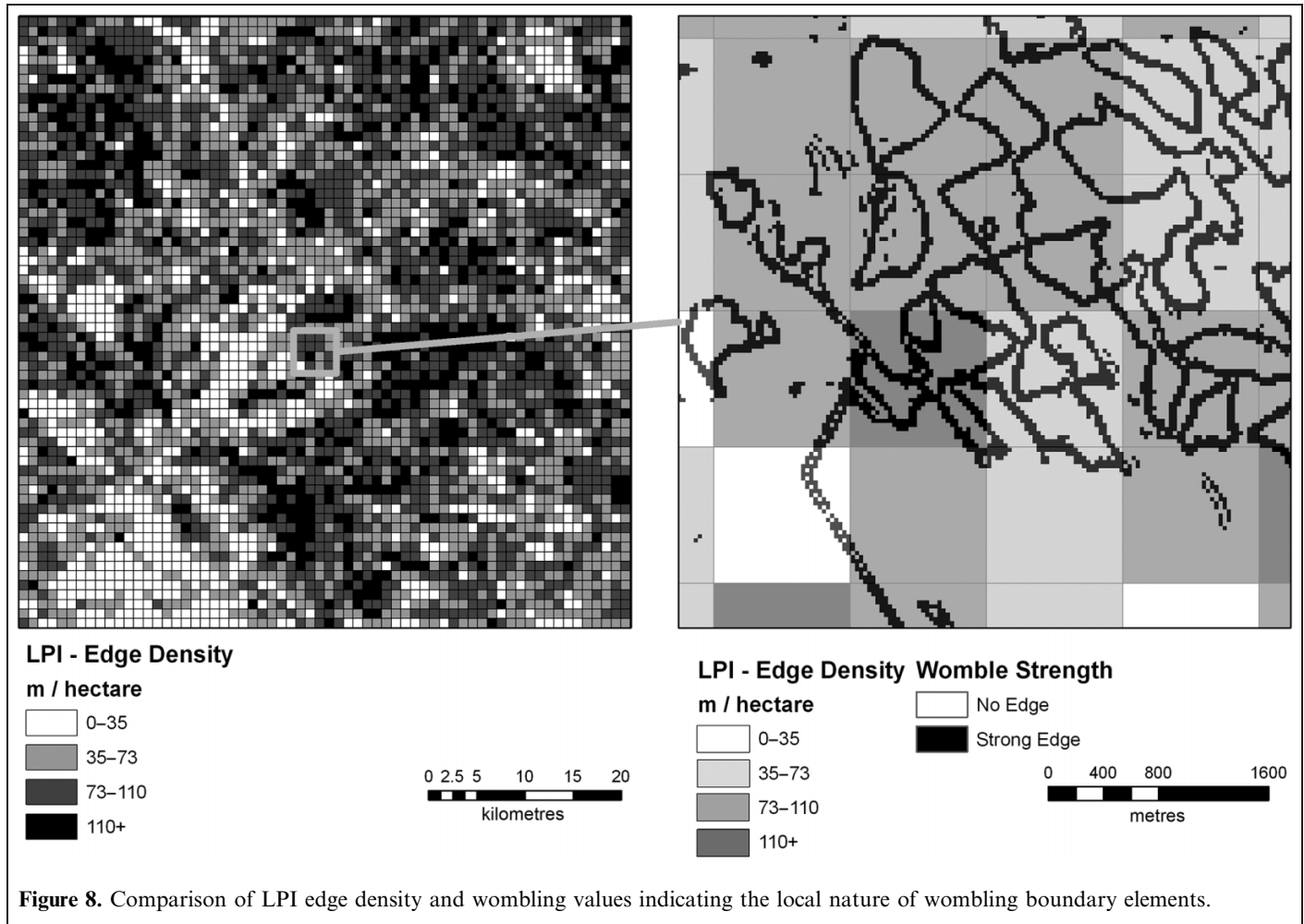
One might expect to observe a correlation between boundary elements and edge density, since both TCT wetness and the forest-non-forest classification from which edge density was calculated are sensitive to the presence-absence of forest. However, wombling of the TCT wetness component will also detect edges that are concealed within the broad forest-non-forest classes. Conversely, wombling may identify weak edges in areas of high edge density if there are many forest-shrub or forest-herb boundaries.



These will be noted as strong, abrupt edges in the land cover map but may only be moderate-contrast edges on the basis of the TCT wetness component because they are all transitions between types of green vegetation. **Figure 6** provides an example, where location A (marked on the edge density map) appears homogeneous in the binary forest–non-forest classification, has a low edge density, and includes high wombling values. When represented with binary data, the variability provided by the wombling approach is lost.

There was strong agreement between edge density and boundary element density when aggregating both measures into broad classes (i.e., high versus low). Situations where the two methods fail to agree are instructive. For example, the mountains in the southwest corner of the study area

(**Figure 7**) are classified as high wombling but low edge density. This occurs due to the reflectance differences between snow–ice, which is dark in the MIR and thus has high TCT wetness, and barren rock, which has high MIR reflectance and low TCT wetness; this combination causes notable differences in reflectance values, which lead to high wombling values. Conversely, the forest–non-forest classification identifies almost all of this as non-forest, leading to low LPI edge density. Less common are areas with low densities of strong, wombling-derived boundary elements but high edge densities from the forest–non-forest classification. This can occur when adjacent forest and non-forest areas are spectrally similar. Alternatively, wombling will produce false negatives where image values produce saddle points. The first partial derivative is zero at saddle



points, indicating no edge, despite heterogeneity in the values within the 2×2 kernel. Strictly speaking, this will only occur when the pixel values in opposite corners are equivalent (i.e., in Equation (1), $Z_a = Z_c \neq Z_b = Z_d$, which is especially problematic when Z_a and Z_c are dramatically different from Z_b and Z_d) and is thus expected to be relatively rare in an image of continuous values. However, near-saddle points may occur in highly heterogeneous areas (i.e., $Z_a \approx Z_c$ and is very different from $Z_b \approx Z_d$), giving low wombling strengths that fail to be classified as boundary elements. The frequency of such situations bears further investigation.

Another consideration is that while wombling was performed on the wetness component of the TCT, the land cover classification used to delineate spatially clustered edges was derived using all six of the Landsat optical bands and a texture index (Wulder et al., 2008b). The two edge detection methods will thus necessarily be sensitive to different properties and may consequently detect different edges. A single index will never adequately capture all of the information present in a multiband image. The wetness component was chosen here because it is physically based, interpretable, and sensitive to edges of interest (e.g., those

along forest harvest blocks). Wombling has recently been extended to the multivariate domain (Crida and Manel, 2007). Multivariate wombling may provide a more complete description of all edges and edge types within a landscape and should be applied to multiple spectral bands or image products.

The comparison of wombling and the LPI edge density has identified that, although there may be areas where these two metrics vary, by and large they consistently identify areas of edge in the broad sense. Both methods generally agree on areas of “high” and “low” edginess, despite having relatively low correlations when continuous comparisons were performed. However, lost in these comparisons is the local aspect of wombling. As LPI edge density was calculated on $990 \text{ m} \times 990 \text{ m}$ landscapes, there are 1089 (33×33) individual wombling values in each landscape (see **Figure 8** for a visual comparison). In this way, wombling can provide local measures of individual edges and can be aggregated into landscape-level edge metrics, thereby providing a complement to current edge detection methodologies. Aggregating wombling values could be used as a measure of edge variability in areas appearing homogeneous when represented with binary forest–non-forest values.

Investigating comparisons against other edge detection techniques was considered; however, creating a system where multiple techniques of edge detection were compared was not our goal in this paper. Rather, the focus was on what additional details can be gained from a novel application of wombling to remotely sensed data. In doing so, a test, to some extent, of wombling against edge detection by spatial clustering is presented. Extreme variation in wombled edge strengths was found not only for any given transition type (i.e., at spatial clustered edges), but also within areas that the land cover classification designates as homogeneous (i.e., at areas not identified as edges by spatial clustering) (**Table 4**). Further, **Table 4** reveals that, in large part, edge contrast values are similar between patch edges and patch interiors from spatial clustering, suggesting that spatial clustering and wombling are not likely to agree on the location of edges. If it is true that edge location is highly dependent on the method used to delineate edges, it is most appropriate to use multiple techniques in concert, to supplement and inform upon each other, as undertaken in this paper. Furthermore, the comparisons of edge density with wombled edge contrast (**Tables 5 and 6**) and boundary element density (**Table 7**) show (albeit a spatially at the level of the 990 m landscapes) that, although wombling and spatial clustering do broadly agree about regions of high and low edginess, there is considerable scatter in the relationship, again pointing out that wombling and spatial clustering provide different views of a landscape.

Conclusion

Edges play an important role in many ecological systems and are becoming increasingly important as anthropogenic and natural disturbances alter natural environments. Traditional edge detection (spatial clustering) and quantification techniques (landscape pattern indices) are beneficial in identifying areas of fragmentation; however, local detail is missed and only the presence–absence or abundance of edges is characterized, ignoring important edge characteristics such as contrast and orientation. Extension of edge effects to landscape models has been limited to date, in part because of a lack of simple, spatial, quantitative measures of edge contrast and orientation.

Once edges are identified, the addition of unique and novel information, such as edge contrast and orientation, can be derived. For example, all transition types in our study were shown to have a large distribution of contrast values, indicating there is potential to further stratify edges by additional characteristics. As well, areas were found that have high edge density from landscape pattern indices calculated on a forest–non-forest classification but low wombling contrast values. This indicates that wombling values could be used to inform on the degree of contrast between forest and non-forest classes, providing useful ecological information.

Wombling is not a replacement for spatial clustering edge detection, rather wombling provides useful, complementary information. For example, edge type and edge contrast can and should be used together to drive ecological studies. Most extant studies of edge contrast confound contrast with edge type (e.g., hard and soft edges are formed by different land cover types). However, the wide range of wombling edge contrast values obtained here between particular edge types shows that this is not necessarily the case. Land cover maps and wombled edge contrasts can be used in concert to sample edge type and edge contrast, eliminating this possible shortcoming and allowing the separation of effects of adjoining habitat quality (edge type) and edge contrast.

The methods described in this paper document that quantitative measures of edge contrast and orientation can be generated with straightforward, objective, automated procedures and used to augment traditional edge detection methods, providing additional insight into what is becoming an increasingly important area of study. By characterizing the contrast of a number of land cover transitions and identifying areas in which wombling provides new and different information from that of other edge detection methods, we have identified a number of key areas where wombling can be fundamental in classifying and modeling ecological processes.

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References

- Achuff, P.L. 1994. *Natural regions, subregions and natural history themes of Alberta: A classification for protected areas management*. Alberta Environmental Protection, Edmonton, Alta. 72 pp.
- Barbujani, G., Oden, N.L., and Sokal, R.R. 1989. Detecting regions of abrupt change in maps of biological variables. *Systematic Zoology*, Vol. 38, pp. 376–389.
- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Bell, S.S., Benning, T.L., Carreiro, M.M., and Dawson, T.E. 2003a. An interdisciplinary and synthetic approach to ecological boundaries. *BioScience*, Vol. 53, pp. 717–722.
- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., and Jones, C.G. 2003b. A framework for a theory of ecological boundaries. *Bioscience*, Vol. 53, pp. 750–758.

- Chen, J.Q., Franklin, J.F., and Spies, T.A. 1993. Contrasting microclimates among clear-cut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, Vol. 63, pp. 219–237.
- Cohen, W.B., Spies, T.A., and Fiorella, M. 1995. Estimating the age and structure of forests in a multi-ownership landscape of western Oregon, USA. *International Journal of Remote Sensing*, Vol. 16, pp. 721–746.
- Crida, A., and Manel, S. 2007. WOMBOSOFT: an R package that implements the Wombling method to identify genetic boundaries. *Molecular Ecology Notes*, Vol. 7, pp. 588–591.
- Crist, E.P., and Cicone, R.C. 1984. Application of the tasseled cap concept to simulated Thematic Mapper data. *Photogrammetric Engineering & Remote Sensing*, Vol. 50, pp. 343–352.
- Dauber, J., and Wolters, V. 2004. Edge effects on ant community structure and species richness in an agricultural landscape. *Biodiversity and Conservation*, Vol. 13, pp. 901–915.
- Demaynadier, P.G., and Hunter, M.L. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology*, Vol. 12, pp. 340–352.
- Debusse, V.J., King, J., and House, A.P.N. 2007. Effect of fragmentation, habitat loss and within-patch habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia. *Landscape Ecology*, Vol. 22, pp. 731–745.
- Desrochers, A., Hanski, I.K., and Selonen, V. 2003. Siberian flying squirrel responses to high- and low-contrast forest edges. *Landscape Ecology*, Vol. 18, pp. 543–552.
- Duell, P., Studer, M., Marchand, I., and Jakob, S. 1990. Population-movements of arthropods between natural and cultivated areas. *Biological Conservation*, Vol. 54, pp. 193–207.
- Fagan, W.F., Cantrell, R.S., and Cosner, C. 1999. How habitat edges change species interactions. *The American Naturalist*, Vol. 153, pp. 165–182.
- Fagan, W.F., Fortin, M.-J., and Soykan, C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. *BioScience*, Vol. 53, pp. 730–738.
- Fletcher, R.J., Ries, L.J., Battin, J., and Chalfoun, A.D. 2007. The role of habitat area and edge in fragmented landscapes: definitively distinct or inevitably intertwined. *Canadian Journal of Zoology*, Vol. 85, pp. 1017–1030.
- Fortin, M.-J. 1994. Edge detection algorithms for two-dimensional ecological data. *Ecology*, Vol. 75, pp. 956–965.
- Fortin, M.-J., and Drapeau, P. 1995. Delineation of ecological boundaries: Comparison of approaches and significance tests. *Oikos*, Vol. 72, pp. 323–332.
- Fortin, M.-J., and Edwards, G. 2001. Delineation and analysis of vegetation boundaries. In *Spatial uncertainty in ecology: implications for remote sensing and GIS applications*. Edited by C.T. Hunsaker, M.F. Goodchild, M.A. Friedl, and T.J. Case. Springer, New York. pp. 158–174.
- Fortin, M.-J., Drapeau, P., and Jacquez, G. 1996. Quantification of the spatial co-occurrences of ecological boundaries. *Oikos*, Vol. 71, pp. 51–60.
- Fortin, M.-J., Olson, R.J., Ferson, S., Iverson, L., Hunsaker, C.T., Edwards, G., Levine, D., Butera, K., and Klemas, V. 2000. Issues related to the detection of boundaries. *Landscape Ecology*, Vol. 15, pp. 453–466.
- Gergel, S. 2007. New directions in landscape pattern analysis and linkages with remote sensing. In *Understanding forest disturbance and spatial pattern: remote sensing and GIS approaches*. Edited by M.A. Wulder and S.E. Franklin. Taylor and Francis, Boca Raton, Fla. pp. 173–208.
- Gignac, L.D., and Dale, M.R.T. 2007. Effects of size, shape, and edge on vegetation in remnants of the upland boreal mixed-wood forest in agro-environments of Alberta, Canada. *Canadian Journal of Botany*, Vol. 85, pp. 273–284.
- Han, T., Wulder, M.A., White, J.C., Coops, N.C., Alvarez, M.F., and Butson, C. 2007. An efficient protocol to process Landsat images for change detection with tasseled cap transformation. *Geoscience and Remote Sensing Letters*, Vol. 4, No. 1, pp. 147–151.
- Hargis, C.D., Bissonette, J.A., and David, J.L. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology*, Vol. 13, pp. 167–186.
- Healey, S.P., Cohen, W.B., Yang, Z.Q., and Krankina, O.N. 2005. Comparison of Tasseled Cap-based Landsat data structures for use in forest disturbance detection. *Remote Sensing of Environment*, Vol. 97, pp. 301–310.
- Honnay, O., Verheyen, K., and Hermy, M. 2002. Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management*, Vol. 161, pp. 109–122.
- Hylander, K. 2005. Aspect modifies the magnitude of edge effects on bryophyte growth in boreal forests. *Journal of Applied Ecology*, Vol. 42, pp. 518–525.
- Jacquez, G., Maruca, S., and Fortin, M.-J. 2000. From fields to objects: A review of geographic boundary analysis. *Journal of Geographical Systems*, Vol. 3, pp. 221–241.
- Jin, S.M., and Sader, S.A. 2005. Comparison of time series tasseled cap wetness and the normalized difference moisture index in detecting forest disturbances. *Remote Sensing of Environment*, Vol. 94, pp. 364–372.
- Johansson, P. 2008. Consequences of disturbance on epiphytic lichens in boreal and near boreal forests. *Biological Conservation*, Vol. 141, pp. 1933–1944.
- Kauth, R.J., and Thomas, G.S. 1976. The tasseled cap — A graphical description of the spectral-temporal development of agricultural crops as seen by LANDSAT. In *Proceedings of the Symposium on Machine Processing of Remotely Sensed Data*, 29 June – 1 July 1976, Purdue University, West Lafayette, Ind. IEEE, New York. pp. 41–51.
- Kent, M., Moyeed, R.A., Reid, C.L., Pakeman, R., and Weaver, R. 2006. Geostatistics, spatial rate of change analysis and boundary detection in plant ecology and biogeography. *Progress in Physical Geography*, Vol. 30, pp. 201–231.
- Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B., and Loft, E.R. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology*, Vol. 83, pp. 530–544.
- Kotliar, N.B., and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, Vol. 59, pp. 253–260.
- Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S., and Haddad, N.M. 2005. Effects of landscape corridors on seed dispersal by birds. *Science (Washington, D.C.)*, Vol. 309, pp. 146–148.
- Linke, J., McDerimid, G.J., Laskin, D.N., McLane, A.J., Pape, A.D., Cranston, J., Hall-Beyer, M., and Franklin, S.E. 2009. A disturbance-inventory framework for flexible and reliable landscape monitoring.

- Photogrammetric Engineering & Remote Sensing*, Vol. 75, No. 8, pp. 981–996.
- López-Barrera, F., Manson, R.H., González-Espinosa, M., and Newton, A.C. 2006. Effects of the type of montane forest edge on oak seedling establishment along forest-edge-exterior gradients. *Forest Ecology and Management*, Vol. 225, pp. 234–244.
- López-Barrera, F., Manson, R.H., González-Espinosa, M., and Newton, A.C. 2007. Effects of varying forest edge permeability on seed dispersal in a neotropical montane forest. *Landscape Ecology*, Vol. 22, pp. 189–203.
- Malcolm, J.R. 1994. Edge effects in Central Amazonian forest fragments. *Ecology*, Vol. 75, No. 8, pp. 2438–2445.
- Malt, J., and Lank, D. 2007. Temporal dynamics of edge effects on nest predation risk for the marbled murrelet. *Biological Conservation*, Vol. 140, pp. 160–173.
- McGarigal, K., and Marks, B.J. 1995. *FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure*. USDA Forest Service, General Technical Report PNW-351.
- Meyer, C.L., and Sisk, T.D. 2001. Butterfly response to microclimatic conditions following ponderosa pine restoration. *Restoration Ecology*, Vol. 9, pp. 453–461.
- Mitchell, S.J., Hailemariam, T., and Kulis, Y. 2001. Empirical modeling of cutblock edge windthrow risk on Vancouver Island, Canada, using stand level information. *Forest Ecology and Management*, Vol. 154, pp. 117–130.
- Molvar, E.M., and Bowyer, R.T. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan Moose. *Journal of Mammalogy*, Vol. 75, pp. 621–630.
- Nielsen, S.E., Boyce, M.S., and Stenhouse, G.B. 2004a. Grizzly bears and forestry: I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada. *Forest Ecology and Management*, Vol. 199, No. 1, pp. 51–65.
- Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., and Boyce, M.S. 2004b. Grizzly bears and forestry: II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. *Forest Ecology and Management*, Vol. 199, No. 1, pp. 67–82.
- Paton, P.W.C. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology*, Vol. 8, pp. 17–26.
- Rand, T.A., Tylanakis, J.M., and Tschardtke, T. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecological Letters*, Vol. 9, pp. 603–614.
- Reino, L., Beja, P., Osborne, P.E., Morgado, R., Fabião, A., and Rotenberry, J.T. 2009. Distance to edges, edge contrast and landscape fragmentation: interactions affecting farmland birds around forest plantations. *Biological Conservation*, Vol. 142, pp. 824–838.
- Ries, L., and Debinski, D.M. 2001. Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. *Journal of Animal Ecology*, Vol. 70, pp. 840–852.
- Ries, L., Fletcher, R.J., Battin, J., and Sisk, T. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecological Systems*, Vol. 35, pp. 491–522.
- Schultz, C.B., and Crone, E.E. 2001. Edge-mediated dispersal behaviour in a Prairie butterfly. *Ecology*, Vol. 82, pp. 1879–1892.
- Womble, W.H. 1951. Differential systematics. *Science (Washington, D.C.)*, Vol. 114, No. 2961, pp. 315–322.
- Wu, J. 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology*, Vol. 19, pp. 125–138.
- Wulder, M.A., and Nelson, T. 2003. *EOSD land cover classification legend report: Version 2*. Pacific Forestry Centre, Canadian Forest Service, Natural Resources Canada, Victoria, B.C. 83 pp. Available from www.pfc.forestry.ca/eosd/cover/EOSD_Legend_Report-v2.pdf [accessed 13 January 2003].
- Wulder, M.A., White, J.C., Han, T., Coops, N.C., Cardille, J.A., Holland, T., and Grills, D. 2008a. Monitoring Canada's forests. Part 2: National forest fragmentation and pattern. *Canadian Journal of Remote Sensing*, Vol. 34, No. 6, pp. 563–584.
- Wulder, M.A., White, J.C., Cranny, M., Hall, R.J., Luther, J.E., Beaudoin, A., Goodenough, D.G., and Dechka, J.A. 2008b. Monitoring Canada's forests. Part 1: Completion of the EOSD land cover project. *Canadian Journal of Remote Sensing*, Vol. 34, No. 6, pp. 549–562.
- Zharikov, Y., Lank, D.B., and Cooke, F. 2007. Influence of landscape pattern on breeding distribution and success in a threatened Alcide, the marbled murrelet: model transferability and management implications. *Journal of Applied Ecology*, Vol. 44, pp. 748–759.