Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA

Daniel M. Kashian, Daniel B. Tinker, Monica G. Turner, and Frank L. Scarpace

Abstract: Large disturbances create spatial heterogeneity in vegetation re-establishment, and documenting such variability is critical for understanding and predicting succession. We quantified the spatial heterogeneity of lodgepole pine sapling densities 10 years after the 1988 fires in Yellowstone National Park using color infrared orthophotographs. Densities were classified across the landscape at an accuracy of 70.9%, and landscape metrics were used to characterize their spatial variability. Densities ranged from 0 to > 500 000 saplings/ha, but >60% of the burned area was represented by densities <5000 stems/ha. The burned area consisted of small patches averaging 1.5 ha in area at a mean patch density of 68 patches/100 ha. Densities occurred in nearly equal proportions across the landscape (Shannon's evenness = 0.85) but were well dispersed (contagion index ≈ 20%), suggesting that densities varied in a complex, fine-grained mosaic across the landscape, with high-density patches occurring within a matrix of larger, lower density patches. High-density patches were similar in area to severe surface fires, suggesting that burn severity is an important explanatory variable for spatial variation in sapling density. Large, stand-replacing fires may result in heterogeneous forest landscapes rather than homogenous forests of uniform structure, which may have important consequences for postfire ecological processes.

Résumé : Les perturbations importantes engendrent une hétérogénéité spatiale dans le rétablissement de la végétation et il est crucial de connaître cette variabilité pour comprendre et prédire la succession. Les auteurs ont quantifié l'hétérogénéité spatiale de la densité des gaules de pin lodgepole 10 ans après les feux de 1988 dans le parc national de Yellowstone à l'aide d'orthophotographies infrarouges en couleurs. La densité a été déterminée dans l'ensemble du paysage avec une précision de 70,9 % et des métriques du paysage ont été utilisées pour caractériser leur variabilité spatiale. La densité variait de 0 à plus de 500 000 gaules/ha, mais plus de 60 % des zones brûlées étaient représentées par des densités de moins de 5000 tiges/ha. Les zones brûlées consistaient en de petits îlots d'une superficie moyenne de 1,5 ha avec une densité moyenne de 68 îlots/100 ha. Ces densités étaient dans des proportions presque égales partout dans le paysage (indice d'égalité de Shannon = 0,85), mais elles étaient bien dispersées (indice de contagion ≈ 20 %), indiquant que les densités variaient selon une mosaïque complexe, à grain fin, dans l'ensemble du paysage où des îlots de forte densité étaient répartis dans une matrice plus vaste constituée d'îlots de faible densité. Les îlots de forte densité avaient une superficie semblable à celle des feux de surface sévères, indiquant que la sévérité du brûlage est une importante variable explicative de la variation spatiale de la densité des gaules. Les feux de grande dimension qui entraînent le remplacement des peuplements peuvent être à l'origine de paysages forestiers hétérogènes plutôt que de forêts homogènes avec une structure uniforme, ce qui peut avoir d'importantes conséquences sur les processus écologiques après feu.

[Traduit par la Rédaction]

Introduction

Disturbance has long been recognized as a driver of heterogeneity in landscapes (Watt 1947) and is an important natural process in ecological communities (Wiens 1995; Wu and Loucks 1995). Many studies have addressed the temporal dynamics of ecological communities following disturbance, but increasing attention is being placed on the spatial heterogeneity of ecological structure and function within a disturbed area (Turner et al. 1997*a*). Large disturbances may create substantial variability in vegetation structure and function of the same successional stage across landscapes

Received 18 November 2003. Accepted 28 May 2004. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 25 November 2004.

D.M. Kashian.[1,2] Departments of Zoology and Forest Ecology and Management, University of Wisconsin-Madison, Madison, WI 53706, USA.
D.B. Tinker. Department of Botany, University of Wyoming, Laramie, WY 82071, USA.
M.G. Turner. Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706, USA.
F.L. Scarpace. Environmental Remote Sensing Center, University of Wisconsin-Madison, Madison, WI 53706, USA.

[1] Corresponding author (e-mail: dank@lamar.colostate.edu).
[2] Present address: Department of Forest, Rangeland, and Watershed Stewardship, Colorado State University, Fort Collins, CO 80523, USA.

doi: 10.1139/X04-107

(Turner et al. 1994; Foster et al. 1998; Turner et al. 1998). Understanding the nature of such disturbance-created mosaics is crucial for predicting the dynamics of ecosystems in landscapes prone to disturbance (Turner et al. 2001), yet little research has focused on quantifying this variation.

The 1988 fires in Yellowstone National Park (YNP) burned approximately 250 000 ha of lodgepole pine (*Pinus contorta* var. *latifolia* Englem. ex Wats.) dominated subalpine plateaus, largely due to prolonged, extreme drought, and high winds (Bessie and Johnson 1995). The burned area was markedly heterogeneous, with burned patches varying widely in size and severity, and few burned patches were very isolated from unburned areas (Christensen et al. 1989; Turner et al. 1994). Although potential sources of off-site propagules were readily available to most burned patches, lodgepole pine forests are often recolonized relatively quickly owing to the serotinous trait expressed by many trees that allows viable seeds to be retained within closed cones until fire occurs (Lotan and Critchfield 1990). Sooner than 5 years after the 1988 Yellowstone fires, the density of lodgepole pine regeneration varied substantially within the burned landscape, ranging from <100 seedlings/ha to >100 000 seedlings/ha (Anderson and Romme 1991; Ellis et al. 1994; Turner et al. 2004). At the spatial scale of individual burned patches or smaller, variability in sapling density seemed to be related to both burn severity and prefire cone serotiny, whereas postfire, high-density sapling patches were coincident with areas of high cone serotiny burned by light or severe surface fires (Turner et al. 1997*b*).

Because it initiates succession following fire, initial pine seedling density may control forest structure and function across the landscape for many decades (Turner et al. 1997*b;* Kashian 2002; Kashian et al. 2005*b*). Furthermore, understanding the variation in early succession across disturbed landscapes such as Yellowstone is fundamental to an integrated understanding of variation in ecosystem processes (Turner et al. 2004), landscape-level dynamics, and predicting future changes in landscape pattern (Kashian 2002) following natural or human-induced disturbances. For large disturbances, documenting the nature of early postfire succession, as well as its spatial patterns across the landscape, represents the foundation upon which this future research will be built.

The overall goal of our study was to describe and quantify the landscape patterns of sapling densities across the approximately 250 000 ha burned landscape; in doing so, however, we were also interested in assessing our ability to map this heterogeneity with digital orthophotography created from an existing set of color infrared (CIR) aerial photographs. Prefire sapling regeneration has been mapped using satellite imagery (see Moskal et al. 2001), but few studies have attempted to classify vegetation for an area the extent of Yellowstone's burned landscape or to distinguish areas of differing regeneration density (Franklin et al. 1994; Moskal et al. 2001) rather than a single class of regeneration. Aerial photography has long been a fundamental source of broad-scale data for ecologists and natural resource managers and is commonly used for mapping large land areas. The geometric distortion present in aerial images due to camera tilt, relief displacement, lens distortion, and atmospheric refraction (Alberts 1992; Bolstad 1992; Lillesand et al. 2003) may be removed with orthorectification to create orthophotos, which are free of geometric distortion, are scale accurate, and depict objects in their true planimetric positions (Baltsavias 1996). While once technically complex, laborious, and expensive to produce (Wolf 1983; Lillesand et al. 2003), orthophotos are now relatively easy to create within a digital environment (Scarpace et al. 2000). The resulting digital image contains cell-based data, where each cell is associated with a numeric value that represents the amount of light reflected from that area on the ground. Orthophotos are adjusted for vertical relief (z-coordinate) and are aligned with a conventional horizontal coordinate system (x and y coordinates) and may be output with pixel dimensions appropriate to the task at hand.

We were also interested in using the classified orthophotography to identify and quantify patterns of sapling densities across the Yellowstone landscape as an effort to further investigate the underlying causes of postfire spatial heterogeneity. Based on the spatial patterns of burn severity (Turner et al. 1994) and the variation in early postfire vegetation within burned patches (Turner et al. 1997*b*, 1999), we hypothesized the following postfire spatial patterns in lodgepole pine density: (1) relatively even distributions of density classes across the landscape, represented by high values of evenness of the landscape; (2) relatively small patches (and corresponding high patch density) of high-density lodgepole pine saplings and larger patches (and lower patch density) of low-density lodgepole pine saplings; (3) greater interpatch distances and edge contrast for high-density patches; and (4) a dispersed or noncontagious landscape. Many of our hypotheses were based on the patterns of burn severity across the landscape following the 1988 fires: an even distribution of density classes across the landscape would be similar to that of burn-severity classes, and smaller patches of high-density saplings may reflect smaller patch sizes of light or severe surface fires (3–5 ha) compared with crown fire patches (16–18 ha) (Turner et al. 1994). Finally, because prefire serotiny varied over large areas of Yellowstone (Tinker et al. 1994), we hypothesized that there would be evident geographic variation in the proportion of the landscape occupied by high- and low-density lodgepole pine saplings coincident with high and low values of prefire serotiny, respectively.

Materials and methods

Study area

Yellowstone National Park (YNP) encompasses 9000 km^2 in the northwestern corner of Wyoming and consists primarily of high, forested subalpine plateaus. The plateaus of YNP range in elevation from about 2100 to 2600 m and are surrounded by more mountainous, broken topography to the northeast, northwest, and east that range in elevation from approximately 1900 to 3000 m. Subalpine fir (*Abies lasiocarpa* Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and whitebark pine (*Pinus albicaulis* Engelm.) occur locally on the subalpine plateaus, but 80% of the plateaus are forested by nearly pure stands of lodgepole pine. Our focus in this study was on the 45% of the subalpine plateaus affected by the 1988 fires (Turner et al. 1994). Although infrequent, fires of this extent burn this landscape every 100–300 years, with the last such event occurring in the early 1700s (Romme 1982; Romme and Despain 1989). The interval between these large, infrequent fires is often interrupted by smaller (usually <5000 ha), more frequent fires (Renkin and Despain 1992). As a result of this fire regime, YNP currently contains a mosaic of young stands created both by the 1988 fires and by the small fires that have occurred over the last several centuries, such that stands range in age from 15 to 450 years old.

Field data

Field data used in this study were collected in 1999 as part of a study examining the spatial variability of ecosystem processes across the burned portions of YNP (Turner et al. 2004). Eighty-eight 0.25-ha sample points were selected using an initial visual assessment of the range of pine sapling density across the YNP landscape based on the original CIR photographs (Fig. 1). Sample points were selected according to estimated density, geographic location, and accessibility, were located within the area burned by a stand-replacing fire in 1988, and were located a minimum of 50 m from roads or trails. Because pine sapling density classes were not determined prior to the field season, sample points were selected to represent the observed range of sapling density, and ultimately the classes did not contain equal sample sizes. An additional 61 points sampled similarly during 2000 and 2001 (Fig. 1; Kashian 2002; Litton 2002; Schoennagel 2002) were also used in this study for a total of 149 sample points. At each of the sample points, stand density was measured using the average pine sapling count along three parallel 2 m × 50 m belt transects (100-m^2 sample area along each transect) extended in a random direction. Transects were spaced 25 m apart to obtain a density estimate for a 50 m × 50 m (0.25 ha) area. This spatial scale was most ecologically appropriate for distinguishing among patches of different sapling densities in the field. All sample points were located within an area with pine sapling density observed in the field to be characteristic of that for the surrounding 1-ha area. The Universal Transverse Mercator coordinates were recorded for each sampling point using a global positioning system (GPS) at the center point of the middle transect.

Data sources and orthorectification

Orthophotography was developed from 1 : 30 000 CIR aerial photographs taken during August 1998 from an altitude of approximately 4.6 km. Photography was timed to enhance the visual differences among coniferous saplings, herbaceous vegetation, and bare soil. The burned area in YNP was encompassed by 452 images, but we included an additional 135 images (total images = 587) to create a regular-shaped orthophoto mosaic that encompassed all the burned and unburned subalpine plateaus within the boundaries of the Park (approximately 650 000 ha). Hard-copy photographs were converted to digital form using a flatbed scanner.

The scanned digital images were orthorectified using the software package Orthomapper™ (Scarpace et al. 2000) at the Environmental Remote Sensing Center at the University of Wisconsin-Madison. Within Orthomapper, we used panchromatic digital ortho-quarter-quadrangles (DOQQs) taken in 1994 and a 30-m (1 : 40 000) digital elevation model (DEM) to assist with orthorectification, which requires both interior and exterior orientation of each image. Interior orientation defines the internal geometry of the camera at the time of photographic capture and is used to transform the image pixel coordinate system to the image space coordinate system (Lillesand et al. 2003). Within Orthomapper, we entered the four corner fiducial points of each image rather than information from a camera calibration report for interior orientation. Exterior orientation defines the position and angular orientation associated with an image at the time of image capture and relates a ground coordinate system to the image space coordinate system (Lillesand et al. 2003). For exterior orientation of each image, we used the Visual Orientation™ option provided by Orthomapper, which allows the user to orient an image using control points identifiable on both the digital image and on the DOQQs displayed simultaneously on-screen. As a rule, we used a minimum of six control points per image, with a residual mean square (RMS) error <1 m as an acceptable error in orienting the photo set. The imagery was projected into the Universal Transverse Mercator (UTM) coordinate system with units in metres, using the North American Datum of 1983 and the ellipsoid of Clarke 1866. Based on the resolution of our DEM and field data, orthophotos were output from Orthomapper at a resolution of 50 m to avoid excess "noise" in the classification. Orthophotos were mosaicked within ERDAS Imagine 7.0 (ERDAS 1994) using the appropriate illumination correction algorithms, where applicable.

Classification protocol and accuracy assessment

Upon review of the field data, we classified the densities noted in the field into six density classes based on their hypothesized ecological importance and our expected ability to assess their spectral signatures from the orthophotos (Table 1). We first implemented a supervised classification protocol using a maximum-likelihood algorithm available in ERDAS Imagine to develop a signature file that would distinguish lodgepole pine saplings within burned areas from other features in the images, such as unburned forests, grasslands and wet meadows, water bodies, exposed rock or soil, and thermal features (primarily hot springs and geyser basins). The features on the images, other than regenerating lodgepole pine, were masked from the classification by including a minimum of 20 signature pixels from each unwanted class in the signature file and designating each as a "masked class".

To classify and map the pine sapling classes in the burned areas, we used stepwise discriminant analysis to develop a linear model that best distinguished each density class (Williams 1983). The linear model was built using data from the 149 sample points and was then applied to the set of digital orthophotos as a means of classification within ERDAS Imagine. Within the analysis, density class was used as the dependent variable, and we used independent variables derived from the spectral characteristics of the digital orthophotos. The value of each of the three bands on the CIR image for the pixel representing the sample point on the ground, which is an integer ranging from 0 to 255 representing the amount of reflected light in each band, was included as a variable (Band 1, blue; Band 2, green, Band 3, red).

The spectral signature of a pixel represents an average value that may or may not accurately represent an attribute on the ground, and the immediate spatial variation in the reflectance ("textural indices") of a sample point have proven successful in improving classification accuracy of aerial pho-

Fig. 1. Locations of 149 sample points used for classification and accuracy assessment of pine sapling density in Yellowstone National Park using discriminant analysis. The shaded area represents the area burned in 1988, mapped in this study using digital orthophotos.

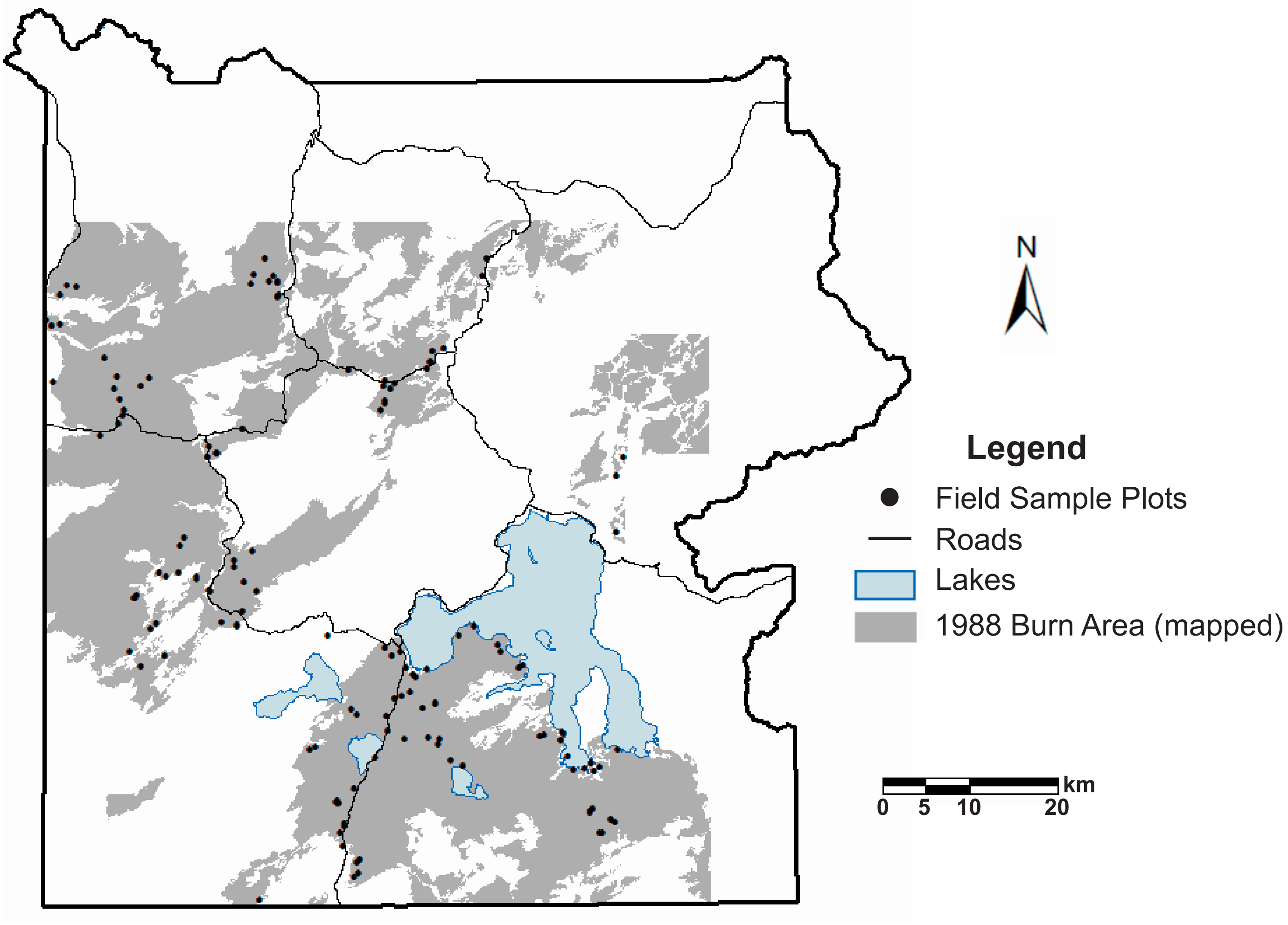

Table 1. Pine sapling density classes used in the classification of color infrared digital orthophotographs in Yellowstone National Park.

Density Class	Density (stems/ha)	No. sample points
1	<1 000	55
2	1 001 – 5 000	38
3	5 001 – 10 000	14
4	10 001 – 15 000	13
5	15 001 – 50 000	14
6	>50 000	15

tography (Duhaime et al. 1997; Musik and Grover 1991). We included a textural index for each of the three bands at each sample point as an independent variable, represented as the standard deviation of the pixel values in each band within a 150 m × 150 m (nine pixel) floating window that included the eight pixels surrounding each sample point. Small textural indices indicate homogeneous pine sapling density around the sampling point, whereas large textural values indicate higher spatial variability in pine sapling density surrounding a given sample point.

One-way analysis of variance (ANOVA) at $\alpha = 0.05$ was used to test for significant differences in the mean values of the six independent variables across all density classes. For these and all statistical procedures, the data structure was examined for normality and equal variances using Lillifor's test for normality and Bartlett's test for equal variances, respectively. Variables found to be significant with ANOVA were entered into forward stepwise discriminant analysis using a stopping rule set to $\alpha = 0.15$ to enter and remove terms. Rather than reduce our set of ground-truth points by creating a validation set, error rates and model bias were tested using the jack-knife method of discriminant analysis (Williams 1983). Because the distributions of the selected variables showed no serious departures from normality or homogeneity, assumptions of discriminant analysis (multivariate normality and equal covariances) were not tested. The overall accuracy and the κ statistic were determined for the classification, and differences in accuracy between all classes were examined using a χ^2 test.

Analysis of landscape pattern

Single pixels were aggregated to define patches of sapling densities across the burned landscape. The software program

Table 2. Descriptive statistics of mean reflectance values (standard deviation in parentheses) for pixel and texture values for 149 validation points across six pine sapling density classes in Yellowstone National Park.

	Classification variable					
Density class (stems/ha)	Band 1	Band 2	Band 3	Text 1	Text 2	Text 3
(1) <1 000	141.4	147.4	171.1	11.3	11.1	10.8
	(35.7)	(32.5)	(38.3)	(5.7)	(6.0)	(5.2)
(2) 1 001–5000	137.3	143.9	162.9	10.3	10.0	9.8
	(32.8)	(32.8)	(36.2)	(4.7)	(5.1)	(4.0)
(3) 5 001 – 10 000	134.0	139.3	168.0	7.8	8.1	7.3
	(30.3)	(31.6)	(16.7)	(3.6)	(4.0)	(3.6)
(4) 10 001 – 15 000	121.3	131.3	159.0	19.0	20.7	20.5
	(47.5)	(45.7)	(35.6)	(13.8)	(15.8)	(14.6)
(5) 15 001 – 50 000	106.8	117.4	144.0	11.5	11.9	8.5
	(50.2)	(47.5)	(50.5)	(8.6)	(7.8)	(8.5)
(6) >50 000	90.2	100.0	134.2	12.0	12.9	12.2
	(33.4)	(28.9)	(43.5)	(3.2)	(3.3)	(3.9)
F statistic	2.61	2.11	1.07	1.55	1.99	2.28
p value	0.02	0.05	0.39	0.19	0.05	0.05

Table 3. Standardized canonical coefficients of the first three canonical variates (CV) using four independent variables.

	CV 1	CV 2	CV 3
Eigenvalue	3.358	1.530	0.460
% variance explained	62.1	26.5	8.0
Band 1	2.120	0.112	0.587
Band 2	0.211	0.245	–1.202
Text 2	–0.638	–2.347	–0.486
Text 3	–0.947	–1.279	0.025

FRAGSTATS (McGarigal and Marks 1995) was used to define patches by including adjacent pixels that shared an edge, and that were of the same density class, as part of the same patch (“four-neighbor rule”). By using the six sapling density classes and by masking the remainder of the landscape, the landscape consisted of six patch types. Once patches were defined across the landscape, spatial patterns of sapling densities on the classified imagery were analyzed using metrics calculated in FRAGSTATS. We used the interpreted imagery to describe the heterogeneity of sapling densities across all density classes, as well as by density class, for the entire landscape burned in 1988. We chose metrics that would address each of our hypotheses regarding landscape pattern (see Introduction) as well as those that would describe aspects of the spatial patterning of pine sapling densities insightful for understanding the effects of large, infrequent fires on postfire succession, ecosystem processes, and future vegetation patterns. To examine the distributions of density classes across the landscape, we calculated the proportion of each class on the landscape and Shannon’s evenness index (which describes the diversity of density classes on the landscape); patch density and mean patch size were used to characterize the landscape and to compare patch characteristics between density classes. Euclidean nearest-neighbor distance index (a measure of the proximity of a patch to the nearest patch of the same class) and total edge contrast index (which describes the contrast, or difference in density, between adjacent patches) were calculated to examine the isolation and contrast of each density class across the landscape. The amount of dispersion of the density classes across the burned landscape was estimated using the contagion index for the entire landscape and the clumpiness index (which ranges from –1 for maximum dispersion to 1 for maximum clumping) for each class.

Results

Classification and mapping of sapling densities

Of the six independent variables, only the red band (Band 3) and the blue texture band (Text 1) were not significantly different across all density classes, although all significant variables except the blue band (Band 1) showed only marginal statistical significance in the ANOVA (Table 2). Band 1 and Text 3 exhibited the lowest mean values of the three band and texture variables, respectively (Table 2). Stepwise discriminant analysis included in the discriminant function each of the four independent variables that were found to be significant using ANOVA (Table 3). The first canonical variate (CV 1) was dominated by the blue band (Band 1) and, to a lesser extent, the red texture band (Text 3). The second canonical variate (CV 2) was dominated by the texture variables, especially the green texture variable (Text 2). The first three canonical variates accounted for 62%, 89%, and 97% of the cumulative variance.

The discriminant function had an overall classification accuracy of 70.9%, and the κ statistic suggests that the classification was improved by 63.1% over a random classification. The jack-knifed classification rate was 68%, indicating that the discriminant classification was largely unbiased. The largest error sources were produced in the moderate to dense classes (particularly Classes 4 and 5), which exhibited the lowest user’s accuracy and the lowest producer’s accuracy (Table 4). Producer’s accuracies were higher than user’s ac-

Table 4. Error matrix derived from discriminant analysis of 149 sampling points of pine sapling density across the Yellowstone landscape (correctly classified observations are shown in bold).

	Predicted density class							
Observed density class (stems/ha)	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Total	User's accuracy
(1) <1 000	**41**	0	3	3	4	4	55	75%
(2) 1 001 – 5 000	2	**26**	2	4	3	1	38	68%
(3) 5 001 – 10 000	1	0	**10**	0	2	1	14	71%
(4) 10 001 – 15 000	2	1	0	**8**	1	1	13	62%
(5) 15 001 – 50 000	1	0	3	0	**8**	2	14	57%
(6) >50 000	1	0	0	0	1	**13**	15	87%
Total	48	27	18	15	18	22	149	
Producer's accuracy	85%	96%	56%	53%	44%	59%		
Overall classification accuracy = 70.9%; κ = 63.1%; χ^2 = 4.67 ($p > 0.05$, df = 5)								

Table 5. Area occupied by each post-1988 sapling density class across Yellowstone National Park, classified using discriminant analysis.

Classification	Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Total
Area (10^3 ha)	58.15	52.49	18.47	14.98	15.16	14.05	173.31
Proportion (%)	33.6	30.3	10.7	8.6	8.7	8.1	

Note: The distribution of areas across the six density classes was not significant (χ^2 = 0.113, $p > 0.05$).

curacies for Classes 1 and 2, indicating that these classes were probably overmapped. The remaining classes, having much higher user's than producer's accuracies, were undermapped (Table 4). Little pattern of misclassification was evident in the error matrix for the discriminant function, and differences in classification accuracy between classes were not statistically significant ($\chi^2_{5,\ 0.05}$ = 4.7, $p > 0.05$).

As a sensitivity analysis, we eliminated selected sets of variables from the discriminant analysis as a means of testing the discriminatory power of each. Except for the blue band (Band 1), classification accuracy decreased only slightly (<2%) when variables were dropped from the model, indicating their relatively small discriminatory power. Notably, when Band 1 was used as the lone independent variable in the model (approximating panchromatic orthophotography), classification accuracy decreased to only 68.9%.

Spatial variability of sapling densities

The density of pine saplings in the 149 sample plots spanned six orders of magnitude, ranging from 0 to 598 500 stems/ha, and the mean and median sapling densities were 22 718 and 2813 stems/ha, respectively. Approximately 173 300 ha of the YNP plateaus included regenerating lodgepole pine saplings (Table 5), but sapling densities were extremely variable across the landscape, creating a very fine-grained mosaic (Fig. 2). Approximately 64% of the landscape was dominated by areas having fewer than 5000 stems/ha (Classes 1 and 2), although these low-density areas were not necessarily concentrated in continuous areas on the landscape. The largest continuous areas of low-density saplings occurred in the north-central area of the landscape, which includes fairly rugged terrain; the east-central area of the landscape; and most of the burned portion of the landscape south of Yellowstone Lake (Fig. 2). Areas of higher density (>5000 stems/ha or Classes 3–6) were less continuous, but very high-density areas (>50 000 stems/ha, Class 6), which occurred on 8% of the landscape, appeared to be concentrated in the northwestern portion of YNP (Fig. 2).

Landscape patterns of sapling densities

When all density classes were considered, the burned YNP landscape consisted of relatively small mean patch sizes (approx. 1.5 ha) that were numerous (68 patches/100 ha), dispersed (average nearest neighbor distance = 151 m), and had low edge contrast (17% of edge exhibits maximum dissimilarity between patch types). The burned landscape was dominated by sapling densities <5000 stems/ha; these lower density classes included patches with larger mean patch size (2–5 ha) that were closer together and had less edge contrast than the high-density classes (Table 6). Shannon's evenness index was relatively high (0.85), suggesting that the landscape is dominated by relatively few density classes, and contagion for the overall landscape was low (19.7%), indicating a relatively fine-grained mosaic of density classes.

Mean patch size of high-density classes was less than 1 ha; the least-dense classes had the highest patch density (12–16 patches/100 ha), and the densest class had the lowest patch density (8 patches/100 ha) (Table 6). Patches of the densest classes also tended to be more isolated from other patches of the same class (nearest neighbor distance > 185 m), whereas the least-dense classes exhibited shorter mean nearest-neighbor distances (122–129 m). Higher density patches also displayed higher edge contrast than less-dense patches, suggesting that denser patches were typically surrounded by patches of lower density. The clumpiness index was positive but low for all density classes, suggesting that spatial distribution of the patches of each class were near-random, regardless of density (Table 6). These results generally supported our initial hypotheses about landscape pattern.

The northwestern region of the landscape (hereafter called "region B") appeared to be very different from the remainder of the burned YNP landscape, having the highest concentra-

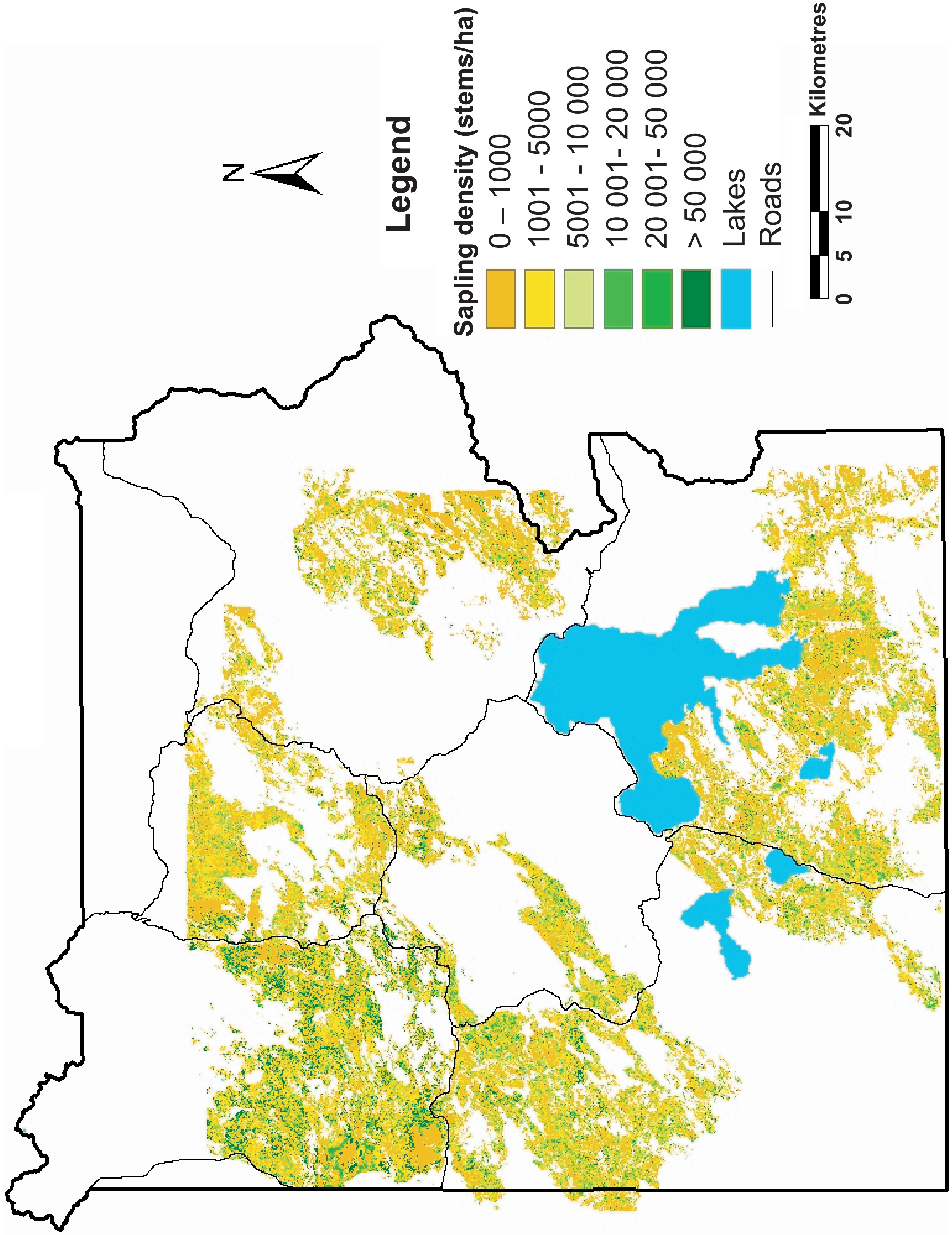

Fig. 2. Pine sapling density across the subalpine plateaus of Yellowstone National Park burned in 1988, as determined by classification using discriminant analysis. Pine sapling density varies in a very complex, fine-grained spatial mosaic.

Table 6. Landscape metrics describing the spatial heterogeneity of lodgepole pine sapling densities across the Yellowstone landscape.

Density class	% of landscape	Clumpiness index (unitless)	Patch density (no./100 ha)	Mean patch size (ha)	Mean nearest-neighbor distance (m)	Total edge contrast index (%)
All classes	na	na	68	1.5	150.9	17.4
1	33.6	0.32	14	5.4	128.5	20.7
2	30.3	0.27	16	1.6	121.9	19.0
3	10.7	0.16	12	0.5	163.4	22.6
4	8.6	0.18	8	0.5	199.9	30.0
5	8.7	0.19	10	0.6	186.4	41.3
6	8.1	0.29	8	0.7	209.7	53.4

Note: na, not applicable.
All metrics were calculated using FRAGSTATS on a raster map of 50 m × 50 m cells.

tion of high-density patches. We compared the landscape heterogeneity of sapling density in this region with that of the region south of Yellowstone Lake (“region A”), which was dominated by patches of lower density classes (Fig. 3). For the two overall landscapes, region A had higher patch densities and thus smaller mean patch sizes; it also had larger mean nearest neighbor distances, lower contagion (18% vs. 24% for region B), and higher Shannon’s evenness index (0.81 vs. 0.63 for region B) than region B (Table 7). These results indicate that density classes are less continuous and more dispersed in region A and that the landscape is finer grained than in region B. Sapling densities <5000 stems/ha were dominant in both landscapes, but the importance of the high-density classes in region B is evident in the larger patch sizes of high-density classes in region B compared with those in region A. In addition, patch densities in region B were higher for the densest class and lower for patches with sapling densities <5000 stems/ha than region A, and mean nearest-neighbor distance was much lower for the highest density classes in region B (131–135 m) compared with that in region A (158–230 m). Patches of all density classes displayed higher edge contrast and clumpiness in region B than in region A (Table 7).

Discussion

Landscape heterogeneity in sapling density

As suggested by previous field-based studies (Anderson and Romme 1991; Ellis et al. 1994; Turner et al. 1997*b*) and analysis of remotely sensed imagery (Moskal et al. 2001), we noted a great deal of spatial heterogeneity in pine sapling density across the YNP landscape (Fig. 2). In contrast with other studies, however, we were able to quantify spatial variation across the entire burned landscape rather than only at a set of sample points. Nearly two-thirds of the landscape burned in 1988 had low (<5000 stems/ha) sapling densities; these low-density patches appeared to be larger in area, particularly in the north-central and east-central regions of the Park, which include more rugged terrain and most of the burned portion of the landscape south of Yellowstone Lake (Fig. 2). Areas of higher density (>5000 stems/ha or Classes 3–6) are less continuous, but very high-density classes (>50 000 stems/ha, Class 6), which occur on 8% of the landscape, appear to be concentrated in the northwestern portion of the mapped landscape (Fig. 2). Overall, however, postfire sapling density appears to vary in a fine-grained spatial mosaic across the YNP landscape. Such fine-grained variability was evident even at the relatively coarse, 0.25-ha scale used in this study; it was not uncommon to find six different density classes within a 2.25-ha (nine-pixel) area at any location across the landscape. Because post-1988 pine sapling density in YNP may vary at scales as fine as 5 m (Plotnick et al. 1996), the degree of variability seen using 50 m × 50 m pixels is quite notable, and actual variability in pine sapling density across the landscape is likely even more heterogeneous than our predicted maps suggest.

The fine-grained heterogeneity across the landscape was confirmed by the landscape metrics we calculated in this study. The least-dense classes not only dominated the landscape, but constituted larger and more numerous patches per unit area that were closer in proximity to each other compared with those found in higher density classes. Dominance of the landscape by one or a few density classes was greater than we hypothesized based on fire severity. Although relatively few classes dominated the landscape, contagion was relatively low and of similar magnitude to that observed for burn severity (Turner et al. 1994). Together with the smaller patch size, lower patch density, greater isolation, and larger edge contrast of the densest classes, these metrics suggest that larger patches of low-density saplings serve as the “matrix” of regeneration across the burned areas of YNP, within which lie smaller patches of higher sapling densities.

Ecologically, the fine-grained variability in pine sapling density is probably related to the spatial heterogeneity in percent serotiny of the prefire forests (Tinker et al. 1994) and the burn severity that occurred during the 1988 fires (Turner et al. 1994, 1998) across the YNP landscape. Using satellite imagery, Turner et al. (1994) noted relatively fine-scale heterogeneity in 1988 fire severity, noting larger patch sizes of crown fire (16–18 ha) compared with smaller patches of light or severe surface fires (3–5 ha). Given the occurrence in YNP of high sapling densities in areas burned by light or severe surface fires (Turner et al. 1997*b*), the smaller high-density patches (<1 ha) and larger low-density patches (2–5 ha) we noted in this study may reflect this spatial patterning of burn severity of the 1988 fires, although sapling density appears to vary at smaller spatial scales than burn severity did in 1988. This scale difference may be due to additional spatial variability in percent serotiny across the YNP landscape. Variability in percent serotiny in YNP has yet to be mapped, but is strongly related to prefire stand density and serotiny in nearby unburned stands (Anderson and Romme 1991; Ellis et al. 1994; Turner et al. 1997*b*) and likely varies at similarly fine scales as sapling density. Both

Fig. 3. Contrasting regions of Yellowstone National Park burned by the 1988 fires that differ in prefire spatial patterns of pine sapling densities.

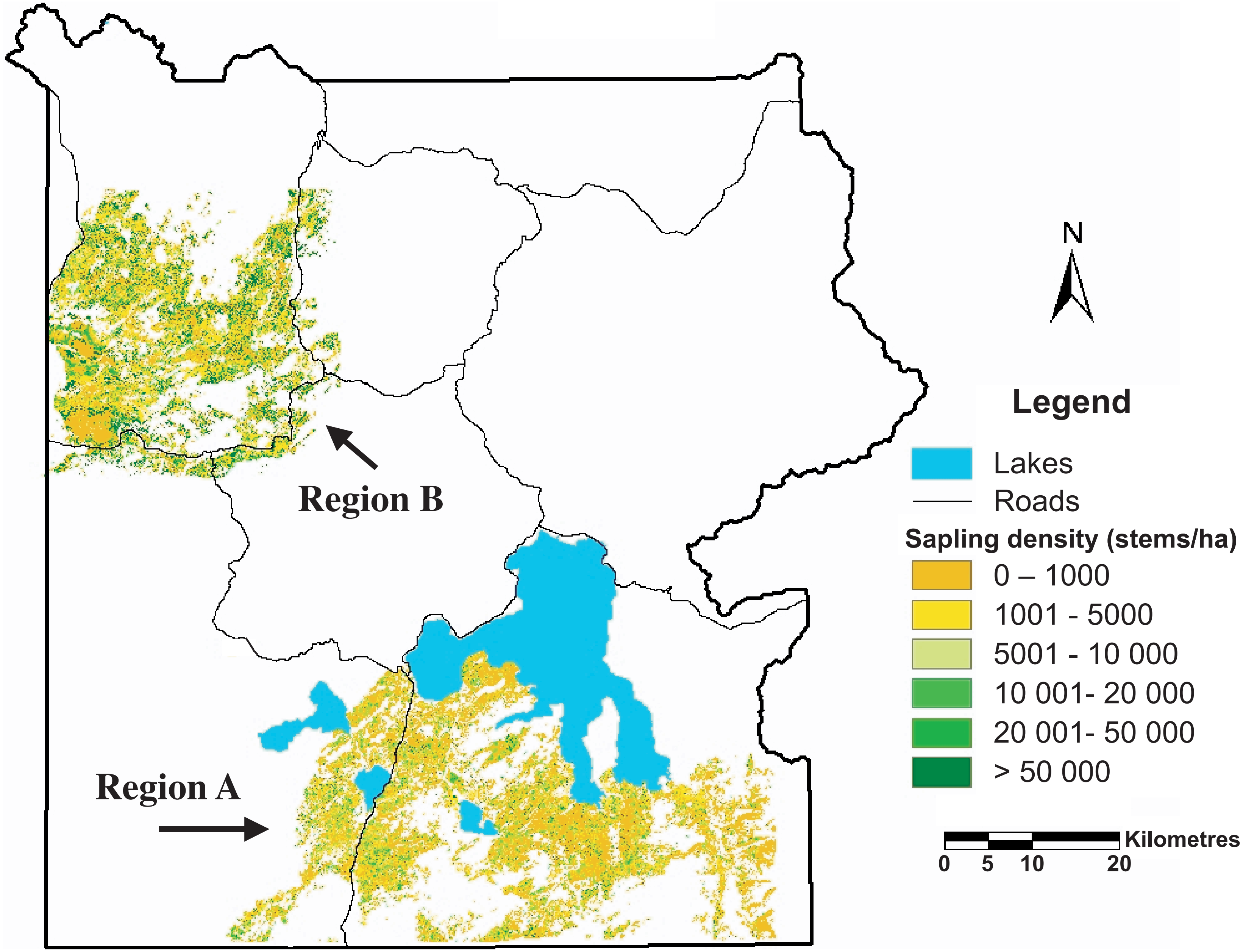

Table 7. Landscape metrics comparing the spatial heterogeneity of lodgepole pine sapling densities in the southern portion of Yellowstone National Park (region A) with those of the northwestern portion of the Park (region B).

Density class	% of landscape	Clumpiness index (unitless)	Patch density (no./100 ha)	Mean patch size (ha)	Mean nearest-neighbor distance (m)	Total edge contrast index (%)
Region A						
All classes	N/A	N/A	122	0.8	152.0	17.4
1	34.7	0.29	22	1.6	138.2	27.0
2	28.6	0.17	28	1.0	131.8	18.7
3	14.5	0.11	25	0.6	144.0	17.7
4	8.7	0.16	17	0.5	169.3	23.3
5	10.2	0.10	21	0.5	158.2	34.4
6	3.3	0.12	8	0.4	229.8	42.8
Region B						
All classes	N/A	N/A	74	1.3	138.5	35.9
1	34.1	0.36	17	2.1	119.1	45.4
2	31.5	0.34	14	2.2	122.1	34.2
3	2.3	0.13	6	0.4	204.6	28.0
4	2.5	0.29	4	0.6	221.0	26.9
5	13.0	0.24	17	0.8	134.9	48.9
6	16.6	0.30	16	1.0	130.5	59.7

Note: All metrics were calculated using FRAGSTATS on a raster map of 50 m × 50 m cells.

burn severity and serotiny are difficult or impossible to measure a decade following the disturbance, and our inability to accurately analyze the spatial heterogeneity of these variables is probably the largest limitation to explaining broad-scale variability in sapling density. Low-density areas in the north-central and east-central regions of YNP may also be related to the steep terrain present there, which may reduce regeneration success regardless of prefire serotiny and burn severity. In any case, the interaction of burn severity and cone serotiny and its influence on postfire regeneration remains an important avenue for future research.

The greater coverage of high-density classes in the northwestern portion of the burned landscape (region B) actually decreased the fine-grained heterogeneity of sapling densities across that landscape as compared with the southern portion of the burned area. Such a pattern may substantiate the role of prefire serotiny and burn severity on the landscape pattern of postfire regeneration. Turner et al. (1994) noted large, contiguous patches of severe surface fires in region B; although they did not quantify the heterogeneity of region A, the region appeared to be patchier and consisted of large patches of crown fire that were not necessarily contiguous. Such a pattern of burn severity is likely related to the timing of burning, where fires burning earlier in the summer (such as those in region B) are more likely to remain on the surface as a result of burning conditions being less conducive to crown fire (Turner et al. 1994). Thus, since postfire seedling regeneration is typically highest in severe surface burns rather than crown fires (Turner et al. 1997*b*), the reduced heterogeneity of region B may in part be related to the timing of the burn. In addition, prefire percent serotiny in this region is higher than anywhere else on the YNP landscape (D.B. Tinker, unpublished data; Turner et al. 1997*b*). Furthermore, field studies have suggested that percent serotiny of forests unburned in 1988, with several exceptions, is relatively low (<10% of trees in a stand) across much of the YNP landscape (D.B. Tinker, unpublished data), a trend that mirrors that of postfire seedling density. If prefire serotiny directly affects postfire seedling densities, then prefire percent serotiny might be expected to be high and to exhibit reduced spatial heterogeneity in region B. Clearly, spatial mapping of percent serotiny is an integral part of understanding the causes of landscape patterns in postfire sapling densities in YNP.

Though useful in describing pattern, landscape metrics are extremely sensitive to the classification and scale of the data used to map the landscape (Turner et al. 2001). Thus, it is important to emphasize that our characterization of landscape pattern may differ if different density classes were chosen or if we had mapped sapling densities at resolutions larger or smaller than 0.25 ha. Although such limitations are inevitable when quantifying pattern, we attempted to select density classes and scales that were most ecologically meaningful and useful for our objectives. The density classes were selected based on their hypothesized ecological importance in the field and our expected ability to differentiate their spectral signatures from the CIR photos. Similarly, we chose to represent sapling densities at 0.25 ha based on previous studies of postfire sapling density in YNP (Anderson and Romme 1991; Ellis et al. 1994; Turner et al. 1997*b*) and our field sampling regime. However, as noted by Turner et al. (2004), comparisons of our results to other locations or future time periods in YNP are only valid if consistency is maintained in both the categories and the scale of the data.

Classification accuracy

Using our six density classes, the overall classification accuracy for the discriminant analysis was approximately 71%, which is within the 60%–85% accuracy range presented in other recent classifications of forest vegetation or regeneration using remotely sensed data (Franklin et al. 1994; Jakubauskas 1996; Duhaime et al. 1997; Carmel and Kadmon 1998). Although our classification with orthophotography was about 71% accurate, similar studies in YNP using satellite data achieved accuracies exceeding 85% (Moskal and Jakubauskas 2001; Moskal et al. 2001). In particular, Moskal et al. (2001) estimated post-1988 pine sapling density in a relatively limited area of YNP (approximately 240 km^2) to 30 m using AVIRIS data with an accuracy of almost 86% and using Landsat data with an accuracy of 75%. Since the bulk of the work in our research was spent during orthorectification of the original CIR images, the higher classification accuracy and higher resolution provided by satellite imagery, rather than orthophotography, is likely more suitable for large study areas such as YNP unless the orthophotographs are output at a similar or higher resolution than available satellite imagery. Since the output resolution of the orthophotos created in the present study was restricted by the spatial scale of our field sampling regime rather than by the nature of the orthophotos themselves, the orthophotos created for this study may be re-output at resolutions more similar to those of satellite imagery, if field data are also available at higher resolutions for the task at hand. Furthermore, we reiterate that we were able to successfully use orthophotography to classify six classes of sapling density across a very large landscape at an accuracy that falls well within the range of acceptability even at a resolution of 50 m.

Eliminating several independent variables from the discriminant model classifier caused very little decrease in the overall accuracy of the classification. In fact, it was possible to eliminate all independent variables but a single band (Band 1) from the model without causing more than a 3% decrease in the overall classification accuracy. This dominance of a single band in the discriminant model may result from our attempt to differentiate classes based on density alone, while the tree species and tree ages were constant across the photography. Since this model approximates the amount of information present in single-band, panchromatic, aerial photography, more expensive CIR photography may be unnecessary to map pine sapling regeneration density in YNP. However, CIR photography contains no information from the blue or middle-infrared portions of the spectrum, which may include ecological information that may improve classification accuracy significantly (Duhaime et al. 1997). Thus, other types of aerial imagery may in fact be useful in mapping pine sapling regeneration in future studies.

As with many landscape studies that use fine-scale field data to extrapolate or predict a given ecological parameter across large spatial scales, an increased number of sample points in all density classes may have significantly improved classification accuracy. For example, the low-density classes were the most accurately classified (Table 5), in part because of the reduced variability of reflectance between patches in this class (since the background reflectance, dominated by herbaceous vegetation in low-density patches, many dominate the signal), but also because of the larger number of sample points collected in these classes (Table 1). Notably, other studies (e.g., Franklin et al. 1994; Duhaime et al. 1997; Carmel and Kadmon 1998; Moskal et al. 2001) have used a similar number of sample points or more as that used in the present study to characterize areas much smaller in extent than the burned areas of YNP. Congalton and Green (1998) have suggested that a minimum of 50 sample points per category or class should be used for classification; for our study, such a rule would have required a minimum of 300 points across the YNP landscape, which would be extremely difficult given time constraints and the remoteness and inaccessibility of many of the burned areas. Thus, a trade-off exists between high overall classification accuracy and a large spatial extent of the study area when attempting to map fine-scale vegetation differences, and computer classification of digital images only partially addresses these concerns (Carmel and Kadmon 1998).

Ecological implications of landscape heterogeneity in sapling density

In YNP and other landscapes characterized by large fires, the ecological importance of spatial variability in sapling density is that it initiates forest succession along a variety of different trajectories of stand development. Using tree rings to reconstruct past densities, Kashian et al. (2005*a*) noted a wide variability in initial stand conditions for stands left unburned on the YNP landscape after 1988, although many of these stands currently look very similar. They used spatial statistics along a chronosequence of mature stands to infer that initially dense stands may develop at variable rates of self- thinning, while initially sparse stands often develop through colonization and infilling. Thus, spatially variable sapling densities not only form interesting patterns across the landscape immediately following fires, but they also shape the rates and trajectories of postfire succession of lodgepole pine forests in this landscape (Kashian et al. 2005*a*).

In examining the patterns of burn severity across the post-1988 landscape, Christensen et al. (1989) and Turner et al. (1994) noted that large fires in subalpine forests such as those in YNP result in a heterogeneous rather than a homogenous landscape. Thus, large fires in this system have a very different effect on landscape structure compared with that of similarly severe and extensive fires in other coniferous forest types, where large, stand-replacing fires may result in extensive, uniform, even-aged forests dominating the landscape (e.g., Graham et al. 2004). Our results reiterate those of Turner et al. (1997, 1999): not only do large fires create heterogeneity in burn severities, but they also create heterogeneity in the subsequent regeneration of lodgepole pine across the landscape. Notably, field observations suggest that relatively little density-dependent mortality is evident even 15 years after the fires, such that the spatial heterogeneity we documented in this study is mainly a result of the interactions of the prefire forest (mainly stand density and percent serotiny) and the fire itself (burn severity), not postfire processes such as self-thinning.

The spatial heterogeneity of sapling densities we have documented have important ramifications for ecological processes across the landscape, and many implications are currently being examined for the areas of YNP burned in 1988. For example, the variability in postfire sapling density has resulted in similar variability in aboveground net primary production (Turner et al. 2004) across the landscape as well as in carbon allocation patterns within stands (Litton et al. 2004), belowground productivity (Litton et al. 2003*a*), and microbial biomass (Litton et al. 2003*b*). In addition, fine and coarse woody debris, which represent important pools of organic matter that will influence future patterns of soil productivity, will inevitably vary spatially with sapling density as the stands mature and undergo various degrees of density-dependent mortality.

In addition to variability, the spatial pattern of density patches within the area burned by the YNP fires may also impact ecological processes across the landscape. Turner et al. (2004) noted a dominant matrix of lower aboveground productivity and leaf area surrounding smaller patches of higher productivity and leaf area within YNP, and Hansen et al. (2000) speculated that such areas of high productivity may provide important habitat for many plants and animals across the Greater Yellowstone Ecosystem. In particular, dense stands of lodgepole pine may provide important cover for some prey species such as elk (*Cervis elaphus*) (Turner et al. 2004) or avian species that may be vulnerable to predation in more open stand conditions. Spatial patterns of high- and low sapling density may also have important implications for the persistence or dispersal of plant populations, since herbaceous and shrub species richness tends to decrease with increasing sapling density across the burned landscape (D.B. Tinker, unpublished data). Thus, landscape patterns of sapling density may directly affect the local or regional distributions of some plant species; in our study, for example, the more clumped, greater coverage of dense sapling patches in region B may greatly reduce the occurrence of some plant species.

Spatial variability in postfire tree recruitment is evident and important for the future landscape structure of other subalpine and boreal forests characterized by large fires, but the drivers of that spatial variability may be very different when species other than lodgepole pine are present. Burn severity and percent serotiny were the two most important factors influencing the spatial pattern of postfire regeneration in YNP (Turner et al. 1997*b*), and landscapes characterized by nonserotinous, shade-tolerant, or site-specific species may exhibit very different patterns or degrees of spatial heterogeneity in regeneration. For example, the spatial pattern of forest landscapes with a large component of spruce or fir may be far less determined by initial postfire spatial variability in sapling densities than by postfire processes such as infilling or colonization of nonserotinous species via off-site propagules. Furthermore, the postfire spatial pattern of regeneration on landscapes having species more sensitive to site conditions and substrate than lodgepole pine may be shaped more by abiotic factors than by the factors we have discussed; several studies of postfire establishment in the boreal forest have stressed the importance of substrate or microsites to regeneration patterns (St. Pierre et al. 1991; Filion and Morin 1996; Simard et al. 1998)

A critical role of large disturbances, in addition to creating complex patterns of disturbance severity, is creating patterns of regeneration across landscapes (Foster et al. 1998). Although many studies have examined spatial heterogeneity in postfire regeneration at fine scales as it relates to substrate (St. Pierre et al. 1991; Duchesne and Sirois 1995; Filion and Morin 1996; Simard et al. 1998) or the timing and mortality of recruitment following the fire (Duchesne and Sirois 1995; Johnstone et al. 2004), it is the broad-scale heterogeneity in postfire regeneration that affects ecological processes across landscapes. In YNP, the 1988 fires created an initial postfire mosaic of sapling densities that will likely affect spatial patterns of forest structure across the landscape for two centuries or more (Kashian 2002) and may affect forest productivity for over a century (Kashian et al. 2005*b*). Given that large, infrequent fires characterize most subalpine and boreal forests in North America (Romme and Despain 1989; Johnson 1992), documenting the broad-scale spatial variability in postfire regeneration is an important and critical process in understanding the nature of forest succession across these landscapes.

Acknowledgements

We thank David M. Bennett and the staff of Horizons, Inc., Rapid City, South Dakota, for obtaining the aerial photos. We thank Jeff Cardille, Jonathan Chipman, and Nick Guries for assistance and advice in data preparation and classification and the Environmental Remote Sensing Center at the University of Wisconsin for technical support and facilities. The hard work of Maria Madsen, Sarah Cross, Jen Folstad, Jay Schotzko, and Jonathan Schroeder in scanning and orthorectifying the photographs was critical to this study. Validation data were provided by Tania Schoennagel and Creighton Litton. Jeff Cardille, Ken Driese, Wayne Walker, and three anonymous reviewers provided helpful comments on earlier drafts of this manuscript. This research was supported by the National Science Foundation Ecology and Ecosystem Studies Programs (Grant No. DEB-9806440) and by the Andrew W. Mellon Foundation.

References

Alberts, D.H. 1992. Distortion: a problem in single aerial photography. GIS World, **5**: 50–51.

Anderson, J.E., and Romme, W.H. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. Int. J. Wildland Fire, **1**: 119–124.

Baltsavias, E.P. 1996. Digital ortho-images — a powerful tool for the extraction of spatial- and geo-information. ISPRS J. Photogramm. Remote Sens. **51**: 63–77.

Bessie, W.C., and Johnson, E.A. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. Ecology, **76**: 747–762.

Bolstad, P.V. 1992. Geometric errors in natural resource GIS data: tilt and terrain effects in aerial photographs. For. Sci. **38**: 367–380.

Carmel, Y., and Kadmon. R. 1998. Computerized classification of Mediterranean vegetation using panchromatic aerial photographs. J. Veg. Sci. **9**: 445–454.

Christensen, N.L., Agee, J.K., Brussard, P.F., Hughes, J., Knight, D.H., Minshall, G.W., Peek, J.M., Pyne, S.J., Swanson, F.J., Thomas, J.W., Wells, S., Williams, S.E., and Wright, H.A. 1989. Interpreting the Yellowstone fires of 1988. Bioscience, **39**: 678–685.

Congalton, R.C., and Green, K. 1998. Assessing the accuracy of remotely sensed data: principles and practice. CRC/Lewis Press, Boca Raton, Fla.

Duchesne, S., and Sirois, L. 1995. Phase initiale de régénération après feu des populations conifériennes subarctiques. Can. J. For. Res. **25**: 307–318.

Duhaime, R.J., August, P.V., and Wright, W.R. 1997. Automated vegetation mapping using digital orthophotography. Photogramm. Eng. Remote Sens. **63**: 1295–1302.

Ellis, M., von Dohlen, C.D., Anderson, J.E., and Romme, W.H. 1994. Some important factors affecting density of lodgepole pine seedlings following the 1988 Yellowstone fires. *In* Plants and their Environments: Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem, Mammoth Hot Springs, 16–17 September 1991. *Edited by* D. Despain. Technical report NPS/NRYE/NRTR-93/XX. US Department of the Interior, National Park Service, Natural Resources Publication Office, Denver, Colo. pp. 139–150.

ERDAS, Inc. 1994. ERDAS field guide [computer manual]. ERDAS, Atlanta, Ga.

Filion, J., and Morin, H. 1996. Spatial distribution of black spruce regeneration eight years after a boreal forest fire, Quebec. Can. J. For. Res. **26**: 601–610.

Foster, D.R., Knight, D.H., and Franklin, J.F. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems, **1**: 497–510.

Franklin, S.E., Titus, B.D., and Gillespie, R.T. 1994. Remote sensing of vegetation cover at forest regeneration sites. Global Ecol. Biogeogr. Lett. **4**: 40–46.

Graham, R.T., McCafferey, S., and Jain, T.B. (*Technical editors*). 2004. Science basis for changing forest structure to modify wildfire behavior and severity. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-120.

Hansen, A.J., Rotella, J.J., Kraska, M.P.V., and Brown, D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecol. **15**: 505–522.

Jakubauskas, M.E. 1996. Thematic mapper characterization of lodgepole pine seral stages in Yellowstone National Park, USA. Remote Sens. Environ. **56**: 118–132.

Johnson, E.A. 1992. Fire and vegetation dynamics. Cambridge University Press, New York.

Johnstone, J.F., Chapin, F.S., III, Foote, J., Kemmett, S., Price, K., and Viereck, L. 2004. Decadal observation of tree regeneration following fire in boreal forests. Can. J. For. Res. **34**: 267–273.

Kashian, D.M. 2002. Landscape variability and convergence in forest structure and function following large fires in Yellowstone National Park. Ph.D. thesis, University of Wisconsin-Madison, Madison, Wis.

Kashian, D.M., Turner, M.G., Romme, W.H., and Lorimer, C.G. 2005*a*. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology. In press.

Kashian, D.M., Turner, M.G., and Romme, W.H. 2005*b*. Variability in leaf area and stemwood increment along a 300-year lodgepole pine chronosequences. Ecosystems. In press.

Lillesand, T.M., Kiefer, R.W., and Chipman, J.W. 2003. Remote sensing and data interpretation. 5th ed. John Wiley and Sons, New York.

Litton, C.M. 2002. Above- and below ground carbon allocation in post-fire lodgepole pine forests: effects of tree density and stand age. Ph.D. thesis, University of Wyoming, Laramie, Wyo.

Litton, C.M., Ryan, M.G., Tinker, D.B., and Knight, D.H. 2003*a*. Belowground and aboveground biomass in young post-fire lodgepole pine forests of contrasting tree density. Can. J. For. Res. **33**: 351–363.

Litton, C.M., Ryan, M.G., Knight, D.H., and Stahl, P.D. 2003*b*. Soil-surface CO_2 efflux and microbial biomass in relation to tree density thirteen years after a stand replacing fire in a lodgepole pine ecosystem. Global Change Biol. **9**: 680–696.

Litton, C.M., Ryan, M.G., and Knight, D.H. 2004. Effects of tree density and stand age on carbon allocation patterns in postfire lodgepole pine. Ecol. Appl. **14**: 460–475.

Moskal, L.M., and Jakubauskas, M.E. 2001. Discriminating forest stand age classes using 2nd order image texture in the Central Plateau of Yellowstone National Park [CD-ROM]. *In* Proceedings of the Third International Conference on Geospatial Information in Agriculture and Forestry, Denver, Colorado, 5–7 November 2001.

Moskal, L.M., Price, J.P., Jakubauskas, M.E., and Martinko, E.A. 2001. Comparison of hyperspectral AVRIS and Landsat TM imagery for estimating burn site pine seedling regeneration densities in the Central Plateau of Yellowstone National Park [CD-ROM]. *In* Proceedings of the Third International Conference on Geospatial Information in Agriculture and Forestry, Denver, Colorado, 5–7 November 2001.

Musik, H.B., and Grover, H.D. 1991. Image textural measures as indices of landscape pattern. *In* Quantitative methods in landscape ecology. *Edited by* M.G. Turner and R.H. Gardner. Springer-Verlag, New York. pp. 77–103.

Plotnick, R.E, Gardner, R.H., Hargrove, W.W., Prestegaard, K., and Perlmutter, M. 1996. Lacunarity analysis: a general technique for the analysis of spatial patterns. Phys. Rev. E, **53**: 5461–5468.

Renkin, R.A., and Despain, D.G. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National Park. Can. J. For. Res. **22**: 37–45.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. **52**: 199–221.

Romme, W.H., and Despain, D.G. 1989. Historical perspective on the Yellowstone fires of 1988. Bioscience, **39**: 695–699.

Scarpace, F.L., Weiler, P.R., and Kruepke, J. 2000. A simplified method of producing orthophotos [CD-ROM]. *In* Proceedings of the American Society of Photogrammetry and Remote Sensing Annual Meeting, Washington, D.C., 22–26 May 2000. American Society for Photogrammetry and Remote Sensing, Bethesda, Md.

Schoennagel, T.L. 2002. The effects of fire interval and climate on successional patterns in Yellowstone National Park. Ph.D. thesis, University of Wisconsin-Madison, Madison, Wis.

Simard, M.J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci. **9**: 575–582.

St. Pierre, H., Gagnon, R., and Bellefleur, P. 1991. Spatial distribution of regeneration following a fire involving the black spruce (*Picea mariana*) and the jack pine (*Pinus banksiana*) in the Ashuapmushuan Animal Reserve (Quebec). Can. J. Bot. **69**: 717–721.

Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., and Litton, C.M. 2004. Postfire stand density and aboveground net primary production in young lodgepole pine stands, Yellowstone National Park (USA). Ecosystems. In press.

Turner, M.G., Hargrove, W.H., Gardner, R.H., and Romme, W.H. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. J. Veg. Sci. **5**: 731–742.

Turner, M.G., Dale, V.H., and Everham, E.H. 1997*a*. Fires, hurricanes, and volcanoes: comparing large disturbances. Bioscience, **47**: 758–768.

Turner, M.G., Romme, W.H., Gardner, R.H., and Hargrove, W.H. 1997*b*. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. **67**: 411–433.

Turner, M.G., Baker, W.L., Peterson, C.J., and Peet, R.K. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems, **1**: 511–523.

Turner, M.G., Romme, W.H., and Gardner, R.H. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildland Fire, **9**: 21–36.

Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. Landscape ecology in theory and practice. Springer-Verlag, New York.

Watt, A.S. 1947. Pattern and process in the plant community. J. Ecol. **35**: 1–12.

Williams, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology, **64**: 1283–1291.

Wolf, P.R. 1983. Elements of photogrammetry. 2nd ed. McGraw-Hill, New York.

Wu, J., and Loucks, O.L. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q. Rev. Biol. **70**: 439–466.