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Spatial Patterns of Pinyon–Juniper Woodland Expansion in Central Nevada

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Abstract

The expansion of the pinyon–juniper (*Pinus monophylla* Torr. & Frém.–*Juniperus osteosperma* Torr.) woodland type in the Great Basin has been widely documented, but little is known concerning how topographic heterogeneity influences the temporal development of such vegetation changes. The goals of this study were to quantify the overall rates of pinyon–juniper expansion over the past 3 decades, and determine the landscape factors influencing patterns of expansion in central Nevada. Aerial panchromatic photos (1966–1995) were used to quantify changing distribution of pinyon–juniper woodland, over multiple spatial scales (0.002-, 0.02-, and 0.4-ha median patch sizes), and for discrete categories of elevation, slope aspect, slope steepness, hillslope position, and prior canopy cover class. An object-oriented multiscale segmentation and classification scheme, based on attributes of brightness, shape, homogeneity, and texture, was applied to classify vegetation. Over the 30-year period, the area of woodland has increased by 11% over coarse, ecotonal scales (0.4-ha scale) but by 33% over single-tree scales (20-m^2 scale). Woodland expansion has been dominated by infilling processes where small tree patches have established in openings between larger, denser patches. Infilling rates have been greatest at lower elevations, whereas migration of the woodland belt over coarser scales has proceeded in both upslope and downslope directions. Increases in woodland area were several times greater where terrain variables indicated more mesic conditions. Management treatments involving removal of trees should be viewed in a long-term context, because tree invasion is likely to proceed rapidly on productive sites.

Resumen

La expansión del bosque de tipo "Pinyon–Juniper" (*Pinus monophylla* Torr. & Frém.–*Juniperus osteosperma* Torr.) en la Gran Cuenca ha sido ampliamente documentada, pero poco se sabe respecto a como la heterogeneidad topográfica influye en el desarrollo temporal de tales cambios de vegetación. Las metas de este estudio fueron cuantificar las tasas generales de expansión del boque de "Pinyon–Juniper" en las tres últimas décadas y determinar los factores del paisaje que influyen en los patrones de expansión en la parte central de Nevada. Se usaron fotografías aéreas pancromáticas (1966–1995) para cuantificar la distribución cambiante del bosque de "Pinyon–Juniper" en múltiples escalas espaciales (parches tamaño medio de 0.002, 0.02, y 0.4 ha) y para categorías discretas de elevación, aspecto de la pendiente, inclinación de la pendiente, posición en la pendiente, y clase de cobertura de copa anterior. Una segmentación multiescala objeto-orientada y un esquema de clasificación, basado en atributos de brillantez, forma, homogeneidad, y textura, se aplicaron para clasificar la vegetación. En el periodo de 30 años el área de bosque se incrementó en 11% en las escalas ecotonales (escala de 0.4 ha), pero aumentó en 33% en la escala de árbol (escala de 20 m^2). La expansión del bosque ha estado dominada por procesos de colonización donde pequeños parches de árboles se han establecido en claros entre parches más grandes y densos. Las tasas de colonización han sido mayores en las elevaciones bajas, mientras que la migración de la franja de bosque en escalas menos finas se ha dado tanto hacia arriba como hacia abajo de la pendiente. Los incrementos del área de bosque fueron varias veces más grandes en los sitios más mésicos. Los tratamientos de manejo que involucran la remoción de los árboles deben ser contemplados en un contexto de largo plazo ya que la invasión de los árboles probablemente ocurrirá rápidamente en los sitios mésicos después del tratamiento de remoción.

Key Words: aerial photography, landscape dynamics, spatial analysis, topography, tree invasion

INTRODUCTION

Shrublands, savannas, and woodlands have experienced dramatic increases in density and cover of many woody species at a global scale, across diverse ecosystems (Hobbs and Mooney 1986; Archer et al. 1995; Van Auken 2000; Ueckert et al. 2001). One example of rapid woodland expansion in the western United States has been the encroachment of *Pinus* and *Juniperus* species into sagebrush and other vegetation types of the Great Basin (e.g., Cottam and Stewart 1940; Blackburn and Tueller 1970; Miller and Wigand 1994). According to one estimate, there has been a 10-fold increase (from 3 million ha to 30 million ha) in pinyon–juniper (P–J) woodland area within the western United States, since Euro-American settlement in the mid-1800s (Miller and Tausch 2001). Expansion of woodlands has been associated with numerous ecological and economic effects.

Current controversy over restoration and management of P–J woodlands (Belsky 1996; West 1999; Baker and Shinneman 2004) stems from a lack of quantitative ecological understanding

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of historical driving factors, and differing public perceptions regarding the value of wooded areas. The increase in distribution and density of P–J woodlands has been attributed to livestock grazing, a climatic shift toward warmer and wetter conditions, reduced fire frequency resulting in part from overgrazing, and increases in atmospheric CO_2 (Miller and Wigand 1994). Grazing, disturbance, climate, topography, and vegetation succession have all interacted over the past century to produce complex landscape dynamics.

Woodland expansion has likely been spatially variable over landscape scales, yet most studies of P–J expansion have been conducted at the level of individual field sites over small study areas (e.g., Young and Evans 1981; Soulé and Knapp 1999; Tausch and Nowak 1999; Ffolliott and Gottfried 2002). Although several investigations have quantified spatial patterns of woodland expansion at landscape or regional scales (Blackburn and Tueller 1970; Milne et al. 1996; Huebner et al. 1999; Harris et al. 2003; Johnson 2005), few of these have analyzed spatial variation in expansion rate due to topoclimatic or edaphic factors. For this reason, little is known about how rates and patterns of expansion have been influenced by different site conditions or landscape features.

The goals of this study were to quantify overall rates of woodland expansion over a 30-year period (1966–1995) and determine how landscape features have influenced expansion patterns for a 25-km^2 area in the Simpson Park Range of central Nevada. We define woodland expansion rate as net change in woodland area across the 30-year period. To better comprehend the scale dependence of the expansion process and the spatial patterns of recent change, we estimated expansion rates at single-tree (0.002-ha), small-patch (0.02-ha), and ecotonal-shift (0.4-ha) scales of investigation. These scales refer to median tree patch areas resulting from an object-oriented classification, and not to map resolution or pixel size, which is 1 m^2 for all 3 cases. We evaluated the following hypotheses:

1) *Expansion rate is scale-dependent, with apparently more rapid expansion when a finer spatial resolution is considered.* This implies that the current period of expansion is one of in-filling more than a migration of the woodland belt into adjacent vegetation types. Through gradual processes of succession, the woodland becomes denser.
2) *Expansion has been most rapid on more productive (moister) sites.* This would be expected if the main cause for expansion has been a reduced frequency of wildfire, which would formerly have occurred with greater regularity on sites with more abundant fuels. Woodland expansion due primarily to a warmer climate might also have occurred more rapidly on moister sites, but would be less closely associated with topographically influenced spatial patterns of historical fire regime. For the Simpson Park study area, site productivity is generally greater on north- and east-facing slope aspects, and on more gradual slopes and valley bottoms where soils are deepest.
3) *Expansion has been most rapid into lower elevations, and less rapid into higher elevations.* The P–J belt has occupied middle elevations over the past several millennia (Miller and Wigand 1994). We expect recent expansion to be more pronounced in a downslope direction, because the upper elevations of the Simpson Park range are characterized by thin, rocky soils and harsh winter conditions. However, expansion due solely to climate change (and not to altered fire regime or other factors) would be expected to lead to an upward movement of the P–J belt, as has occurred elsewhere in the Great Basin during warming episodes of the more distant past (Miller and Wigand 1994).
4) *Expansion rate becomes more rapid once a critical minimal cover of woodland has been reached.* This would be due to amelioration of harsh microsites ("nurse tree" effect) and abundance of propagules.

METHODS

Study Area

The 25-km^2 study area comprises the southern portion of the Simpson Park Mountains (lat 39°22′–39°34′N, long 116°44′–116°53′W), which is near the geographic center of the Great Basin in the western United States, and is broadly representative of many Great Basin mountain ranges of similar elevation. Elevation ranges from 1 980 m in the valleys at the edge of the study area to 2 675 m at the summit of Bates Mountain. Lithology is predominantly Tertiary andesite, interlaced with silicaceous ash-flow tuff formations (Raines et al. 1996). Many ridge tops are covered by a rimrock of steep, andesite cliffs. Soils range from deep, poorly drained Torriorthents on valley floors, to moderately deep, well-drained Xerollic Haplargids on alluvial fans, to well-drained and shallow Lithic Haploxerolls at the higher elevations (NRCS 2004).

This portion of the Great Basin can be considered a "cold desert," with most precipitation accumulating as winter snowfall. Mean annual precipitation values range from 200–350 mm, depending on elevation, and varying considerably among years. The study area consists of 3 major vegetation units or ecoregions (Omernik 1995; Bryce et al. 2003): a shrub-dominated community at the lower elevations and adjacent valley flats (Central Nevada High Valleys), a mid-elevation band of P–J woodland (Central Nevada Mid-Slope Woodland and Brushland), and a shrub-dominated community again at the highest elevations (Central Nevada Bald Mountains ecoregion). The high valleys adjacent to the mountain range are dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & A. Young), planted crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.) and associated native bunchgrasses, along with a substantial component of the invasive cheatgrass (*Bromus tectorum* L.). The mid-elevation woodland is a complex mosaic of tree-dominated and shrub-dominated patches, with occasional small wetlands surrounding seeps and springs. The tree-dominated component contains primarily singleleaf pinyon (*Pinus monophylla* Torr. & Frém.), with Utah juniper (*Juniperus osteosperma* [Torr.] Little) co-occurring on xeric sites and rocky ridge tops. The upper elevations of the study area support few trees except for scattered curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.) and alderleaf mountain-mahogany (*Cercocarpus montanus* Raf.). Shrub cover is dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle), snowberry (*Symphoricarpos* spp. Duham.), and low sagebrush

(*Artemisia arbuscula* Nutt.). Current land use includes cattle grazing and limited mining activities along the eastern ridge.

Image Processing

We used repeat aerial photography to quantify changes in canopy area of P–J woodland between 1966 and 1995. For 1995, panchromatic United States Geological Survey (USGS) digital orthophoto quadrangles (DOQs) were available at 1-m resolution. For the earlier time period, we merged two sets of large-scale (1:15 840) black-and-white aerial photographs for the years 1965 and 1966. We scanned the photos at 600 dots per inch (dpi) to achieve a grain size (0.65 m) of less than 1 m, such that all photos would be consistent with 1-m resolution following orthorectification.

An image-to-image registration process was used to orthorectify the 1965–1996 photographs to the 1995 DOQs, using ENVI software. A nearest neighbor resampling method was used for image warping, based upon a minimum of 50 ground control points (GCPs) per photo. Images were orthorectified to within 5-m root mean squared (RMS) error. We were prevented from achieving greater spatial precision because clearly defined GCPs, including road intersections, sharp topographic features, and cultural features such as buildings, are scarce in this remote study area. Our RMS values are comparable to those of similar studies documenting changes in woody plant cover using repeat aerial photography (Mast et al. 1997; Hudak and Wessman 1998; Peinetti et al. 2002). All images were projected to Universal Transverse Mercator (UTM) coordinates (Zone 11, NAD83 datum), prior to mosaicking using image overlay with histogram stretching in the software TNTmips (MicroImages, Inc., Lincoln, NE). The photomosaics for the two years were then clipped to the same 25-km^2 study area boundary.

Traditional image classification schemes based solely upon pixel brightness can provide unsatisfactory results when applied to large-scale panchromatic aerial photographs, where there can be great variation in local brightness values even within the same vegetation type (Anderson and Cobb 2004). Such images provide great detail in texture, form, topology, and context, all of which would be utilized in an ideal classification. We used an object-oriented classification, implemented in eCognition software (Benz et al. 2004), to distinguish pinyon–juniper patches ("tree") from other vegetation types ("non-tree"). Object-oriented classification, as implemented in eCognition, first segments an image into homogeneous patches ("object primitives"), given particular combinations of spectral and spatial parameters. In a subsequent step, object primitives are classified according to user-defined functions which can account for form, texture, context, and spectral information. By delineating and classifying "natural" patches, the object-oriented approach avoids the "salt and pepper" effect of pixel-based classification, and can do so over multiple spatial scales (Koch et al. 2003).

By varying the scale parameter used for the multiresolution segmentation process, we developed our classification over two distinct spatial scales: a "tree" scale (scale parameter = 10; post-classification median patch size ≈ 20 m^2) and a "patch" scale (scale parameter = 50; median patch size ≈ 200 m^2). Trees were then differentiated from non-trees on the basis of member functions using mean, minimum, and standard deviation of within-patch brightness (scaled to the global mean brightness value of the image); relative border length shared with neighboring patches of the same type (i.e., an iterative classification protocol was used); and difference in brightness relative to neighboring patches (for further details, see Pillai et al. 2006). The resulting eCognition protocol provides an automated process for classification of woodland distribution and cover using any set of black-and-white aerial photographs of similar scale, with only minor tuning required for adjusting parameters according to image-specific variation in brightness and contrast. The output of the classification procedure is a binary map distinguishing tree-dominated patches ("woodland") from openings.

We were not successful in using the eCognition segmentation algorithms to scale up to an "ecotonal" level, demarcating only the largest patches within zones of woodland and open areas. Our efforts to do so resulted in overly generalized boundaries that incorporated large open areas into tree-dominated patches, and vice versa. We therefore developed our ecotonal characterization within the ArcGIS environment using a two-step process. First, a neighborhood function was used to calculate the percentage of woodland area within each 21-m^2 square "moving window" iteratively applied to each focal 1-m pixel within the study area. The number of pixels classified as woodland from the single-tree level, binary classification of woodland and openings was divided by the number of pixels within the moving window to obtain percentage of woodland area. The entire neighborhood was then reclassified as woodland if 90% of the area was of the woodland type; otherwise, it was classified as opening. Note that we conducted the analysis for thresholds (60%, 75%) other than 90% and obtained similar results. The second step employed a low-pass filter to remove all patches of woodland or open areas less than 63-m^2 (i.e., 3 pixels from the previous step) in area, and to reclassify each pixel as the dominant (majority) class within that neighborhood. The result is a highly aggregated map of woodland and open areas which maintains the location of important boundaries, but allows for inclusions of larger patches (Figs. 1e, 1f). The functional resolution of the ecotonal-scale classifications is 3 969 m^2, or approximately 0.4 ha. The image processing steps described above resulted in binary maps at 3 spatial scales (tree, patch, and ecotonal), separating tree-dominated areas from areas dominated by shrub or herbaceous species.

To analyze how changes in P–J woodland area might be influenced by prior woodland cover (Hypothesis 4), we then aggregated the tree-scale maps for 1966 and 1995 to GIS grids showing P–J cover class for pixels of 1-ha resolution. This required tallying all 1-m pixels classified as woodland within 1-ha grid cells, dividing by grid cell area (10 000 m^2), and reclassifying the resulting 1-ha resolution grid according to six discrete cover classes, using 10% increments through 50% and then lumping all pixels with cover greater than 50%. Although we only report results for the 1-ha resolution, we also conducted analyses at 2-ha and 4-ha resolutions and found that results did not vary substantially with aggregation scale.

We assessed the accuracy of the tree-scale (20-m^2) object-oriented classification in two ways. First, we evaluated how well the automated eCognition classification would match a photo-interpreted classification, using 592 randomly selected,

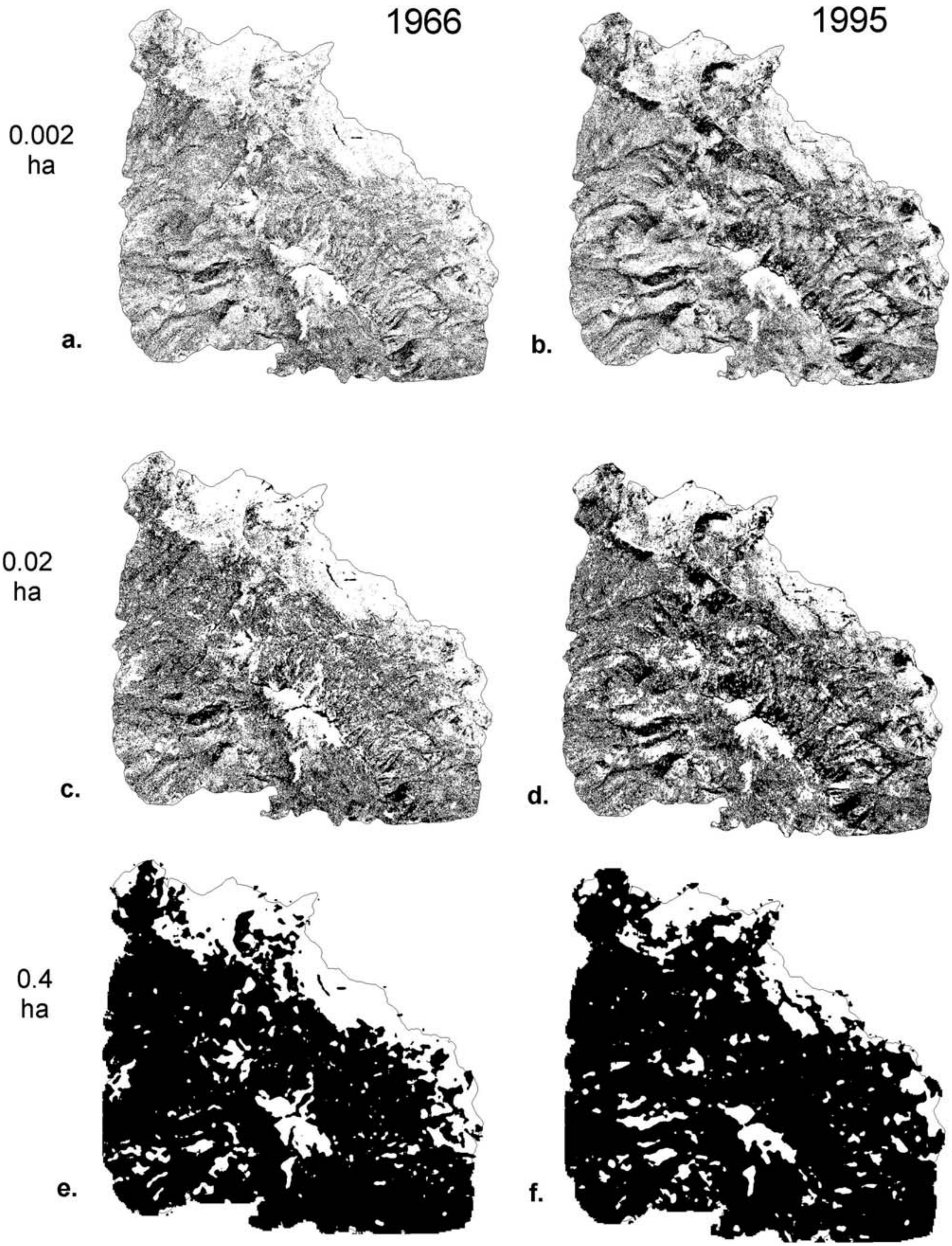

Figure 1. Woodland area classified from 1-m resolution, panchromatic aerial photography across 3 spatial scales of classification (rows), for 1966 and 1995 (columns). Dark patches represent pinyon–juniper woodland; clear areas represent other land cover types. **A, B,** ''Tree'' scale (0.002 ha). **C, D,** ''Patch'' scale (0.02 ha). **E, F,** ''Ecotone'' scale (0.4 ha).

Table 1. Error matrix for the classification of the 1966 data, comparing values from the automated, object-oriented classification for 592 randomly selected pixels with their corresponding photo-interpreted values. Classification data are shown as rows, and photo-interpreted reference data are shown as columns. Overall classification accuracy and the kappa statistic are shown at bottom right.

	Photo-interpreted reference data			
Class	Tree	Non-tree	Row total	User's accuracy
Classified data				
Tree	160	27	187	86%
Non-tree	13	392	405	97%
Column total	173	419	592	Overall: 93%
Producer's accuracy	92%	94%		Kappa: 0.84

Table 2. Error matrix for the classification of the 1995 data, comparing values from the automated, object-oriented classification for 592 randomly selected pixels with their corresponding photo-interpreted values. Classification data are shown as rows, and photo-interpreted reference data are shown as columns. Overall classification accuracy and the kappa statistic are shown at bottom right.

	Photo-interpreted reference data			
Class	Tree	Non-tree	Row total	User's accuracy
Classified data				
Tree	187	47	234	80%
Non-tree	15	343	358	96%
Column total	202	390	592	Overall: 90%
Producer's accuracy	93%	88%		Kappa: 0.78

photo-interpreted points for each photo year. Second, we assessed the accuracy of the classification for 1995 by comparing the "tree vs. non-tree" classification with 307 randomly selected field observations, sampled in 2004 and located to submeter precision using a Trimble GeoXT global positioning system (GPS) unit. Classification error matrices were constructed, and standard measures of accuracy calculated (i.e., user's and producer's accuracies, and kappa statistic; Congalton and Green 1999).

Environmental Variables

We used USGS Digital Elevation Models (DEMs) with an inherent spatial resolution of 30 m to indicate the elevation (m) of each map pixel, and to generate several topographic variables of interest: slope aspect (degrees), slope steepness (degrees), and hillslope position. Slope aspect was not calculated for level sites with steepness < 5 degrees. The hillslope position data layer classifies each pixel as valley bottom, toe slope, side slope, or ridgetop, and was calculated from the DEM using a multiscale approach for determining topographic exposure of a focal grid cell (Zimmermann 2004). This approach uses the difference between the local elevation of each focal cell and the mean elevation of a circular neighborhood to determine topographic exposure, doing so for successively decreasing neighborhood sizes, at each step comparing standardized elevational differences and retaining the maximum absolute value. In a subsequent step, highly negative values are reclassified as valley bottoms, values near zero are reclassified as side or toe slopes, and highly positive values are reclassified as ridge tops. We note that the spatial resolution of P–J woodland delineation from the digital orthophotos (1 m) is finer than the resolution of the environmental layers used to predict P–J woodland change. This scale mismatch should be especially significant for those layers that can vary significantly over short distances (i.e., slope aspect, steepness).

Analysis Methods

Changes in distribution of P–J woodland between 1966 and 1995 were quantified as differences in woodland area for the entire study area; for discrete altitudinal bands within the study area; and for categories of slope aspect, slope steepness, and hillslope position. Each comparison was quantified separately for the 3 spatial scales of woodland delineation (i.e., tree, patch, and ecotonal scales). For the entire study area, changes in woodland area were reported relative to the 1966 landscape as:

$$\left[\frac{(W_{i,95} - W_{i,66})}{W_{i,66}}\right] \cdot 100, \qquad [1]$$

where $W_{i,95}$ and $W_{i,66}$ refer to woodland area (ha) in 1995 and 1966, respectively, at spatial scale i. For comparisons across topographic categories, differences in woodland area among the time periods were relativized according to the area available in each category (A_j), as:

$$\left[\frac{(W_{ij,95} - W_{ij,66})}{A_j}\right] \cdot 100, \qquad [2]$$

where $W_{ij,95}$ and $W_{ij,66}$ refer to woodland area (ha) in 1995 and 1966, respectively, for topographic category j given spatial scale i.

Pixel-by-pixel comparisons were not conducted because of small errors in spatial registration which would have confounded change detection analyses on a per-pixel (1 m^2) basis. The one exception was the analysis of vegetation change according to prior level of woodland cover, where a transition matrix was constructed to show changes on a per-pixel basis for 1-ha pixels. At this aggregated resolution, the effects of spatial mis-registration of pixels among photo-years should be minimized. Statistical models or hypothesis tests were not utilized because comparisons were conducted at the level of the entire population (of pixels). Experimental units (pixels) were not sufficiently spatially consistent among photo-years to have permitted a sampling approach, due to errors inherent in the orthorectification process.

RESULTS

Accuracy and Interpretation of the Classification

The automated eCognition classification accurately represented what would be produced by a manual photointerpretation (Tables 1 and 2). The classification accuracy and kappa coefficient were high for both years. The earlier (1966) classification was based upon higher quality photographs than those used to produce the 1995 DOQs, and was only

Table 3. Error matrix for the classification of the 1995 data, comparing values from the automated, object-oriented classification for 307 pixels with their corresponding values from independent field data. Classification data are shown as rows, and photo-interpreted reference data are shown as columns. Overall classification accuracy and the kappa statistic are shown at bottom right.

	Field-checked reference data			
Class	Tree	Non-tree	Row total	User's accuracy
Classified data				
Tree	64	8	72	89%
Non-tree	35	200	235	85%
Column total	99	208	307	Overall: 86%
Producer's accuracy	65%	85%		Kappa: 0.65

slightly more accurate (3% improvement). For both years, user's accuracy for the "tree" class was slightly higher than the producer's accuracy. This indicates that most of the misclassifications were errors of omission, resulting in an underestimate of the proportion of woodland area. However, the magnitude of this error was similar among years, suggesting that the change detection analysis was not significantly biased.

As would be expected, accuracy was lower when the classification was compared to an independent data set obtained from field observations which postdated image acquisition by 9 years (Table 3). The great majority (96%) of validation sites classified as openings really were openings. However, approximately 35% of sites classified as trees were, in fact, openings. Of the 35 observations misclassified as tree patches, 2 were willow thickets, 2 were covered by riparian herbaceous patches, 1 was upland grassland, and 30 were sagebrush-dominated. Thus, field validation results suggest that the classification over-predicted woodland area. However the values of the overall accuracy (86%) and kappa statistic (0.65) were sufficiently high to indicate a robust classification, where kappa values between 0.40 and 0.80 indicate moderately good agreement (Congalton and Green 1999).

Changes in Woodland Area and Distribution

There has been substantial expansion of P–J woodland in this mountain range, although the rate of expansion over the 30-year period decreased with increasing spatial resolution of woodland patch discrimination (Table 4, Fig. 1). The area of woodland patches increased by 11% over coarse, ecotonal scales (0.4 ha resolution), but by 33% over fine, single-tree scales (20-m^2 patches).

Expansion rate varied considerably with topographic setting (Fig. 2). Increase in woodland area was most rapid on gradual slopes, although there was also considerable net increase into locations of steeper slope (Fig. 2a). At the single-tree scale, there was a U-shaped relationship between relative expansion rate and slope steepness class, with reduced expansion in areas of moderate slope. This effect was less pronounced at the patch scale, where expansion at the ecotonal scale declined with increasing slope steepness. On the very steepest slopes, there was a net decrease in woodland area at the ecotonal scale. However, the net 7.1% decrease in P–J area on slopes exceeding 30 degrees represented a loss of only 6.8 ha of P–J, or 0.3% of the entire study area.

Table 4. Changes in woodland area between 1966 and 1995, at 3 different spatial scales. Values given are the areas classified as pinyon–juniper woodland at the different scales, with values in parentheses in the Year columns indicating the percentage of the study area (2 499 ha) that these values represent. The percentage increase of woodland area (parenthetical numbers in the last column) reflects the net increase relative to the 1966 landscape.

	Year		P–J Area
Scale	1966	1995	Increase
20 m^2 (0.002 ha)	630.1 ha (26.4%)	837.3 ha (35.1%)	207.2 ha (32.9%)
200 m^2 (0.02 ha)	891.0 ha (37.4%)	1 127.8 ha (47.3%)	236.8 ha (26.6%)
4 000 m^2 (0.4 ha)	1 847.1 ha (73.9%)	2 044.2 ha (81.8%)	197.1 ha (10.7%)

At tree and patch scales, P–J expansion was most rapid on mesic slope aspects (Fig. 2b). This effect was dramatic, with expansion rates approximately four times greater on north-facing slopes than south-facing slopes at the single-tree scale. Results are more ambiguous at the ecotonal scale, although the lowest rates of expansion were still observed for the driest southwest and west slope aspects. Across all scales, expansion rates were most rapid on level sites.

Expansion rates across all scales were greatest for valley bottoms, moderate for side and toe slopes, and least for ridgetops (Fig. 2c). Also, expansion rate for tree and patch scales decreased with increasing elevation (Fig. 2d). At the ecotonal scale, a U-shaped relationship is apparent, with least rapid expansion into intermediate altitudinal bands. This reflects movement of the P–J zone in both upslope and downslope directions, from an earlier, narrower band at moderate elevations of 2 100–2 300 m. Within this band, however, increases in woodland area occurred more rapidly at lower elevations (Fig. 2d).

Effects of Prior Woodland Cover on Subsequent Woodland Expansion

The probability for a particular 1-ha pixel to increase or decrease in woodland cover varied weakly but consistently with prior (1966) cover class (Table 5). The probability of increasing in cover class was greatest (0.69) for sites previously in the 10%–20% class, declined very slightly (to 0.67) for sites previously in the 20%–30% class, then declined still further to 0.57 and 0.53 for sites in the 30%–40% and 40%–50% classes, respectively. Sites with less than 10% cover in 1966 had the lowest probability of increasing in cover (0.47).

Across all prior woodland cover classes, 55% of the area increased in woodland cover class, 30% of the area remained the same, and 15% of the area declined (Table 5, taking the sums of upper-right, diagonal, and lower-left portions of the matrix, respectively). Although a small portion of the apparent losses in woodland cover might have arisen from inconsistencies in spatial registration and classification among the two time periods, much was the result of natural disturbances such as bark beetles and root rots, and a small amount due to anthropogenic clearing of woodland for rangeland restoration, fuel wood, and fence-posts. The greatest decline in woodland cover was for the $>$ 50% cover class in 1966, which had a 0.38 probability of cover loss over the 30-year period. These

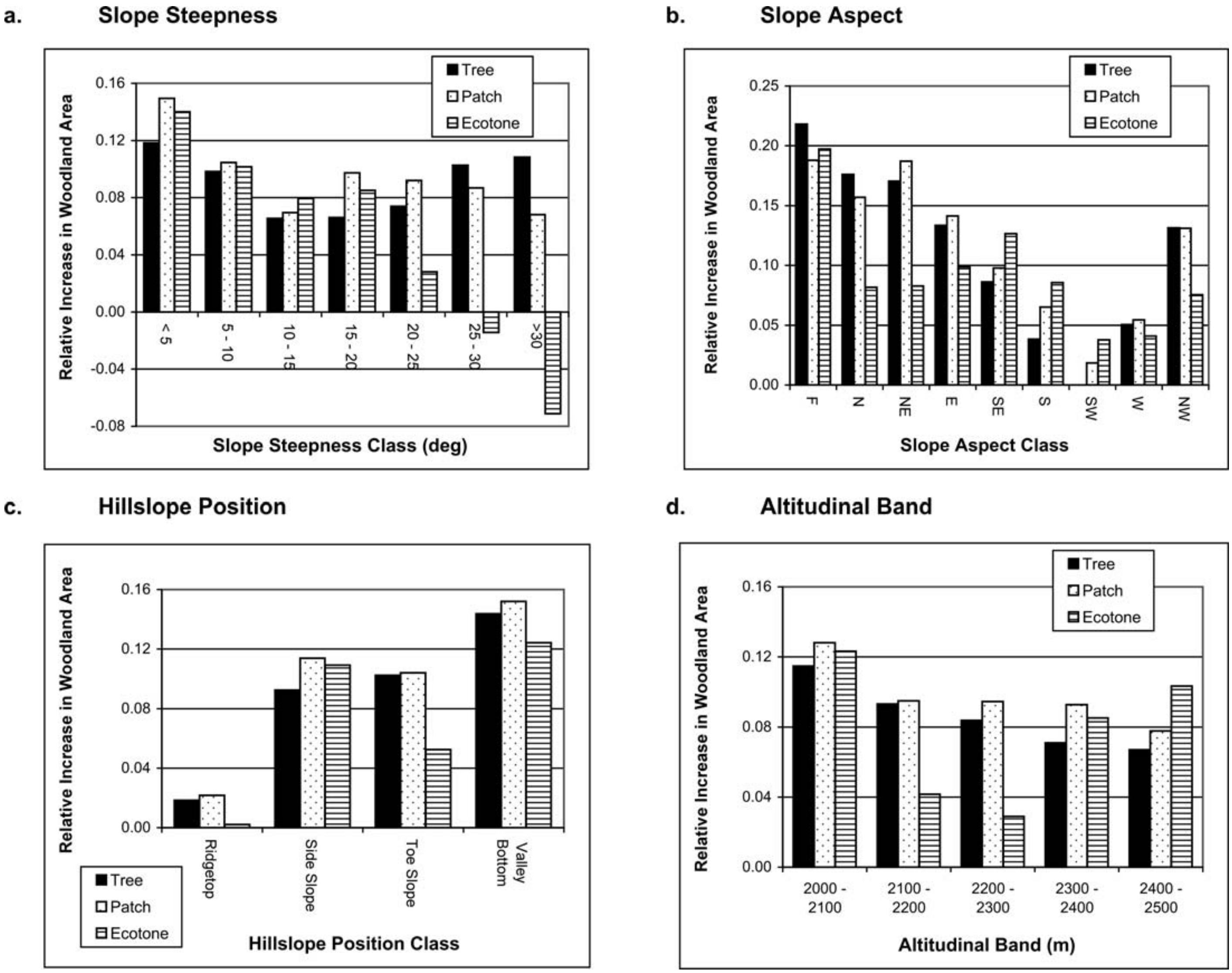

Figure 2. The effects of topographic variables on the net rate of change for pinyon–juniper woodland area. For all plots, the y-axis shows the relative (i.e., proportional) increase in woodland area with respect to the area available for each topographic category (i.e., slope steepness, slope aspect, altitudinal, hillslope position). Each plot shows relationships with topography across 3 spatial scales of woodland mapping, "Tree" (0.002 ha), "Patch" (0.02 ha), and "Ecotone" (0.4 ha). The four plots are: **A,** Slope steepness class (degrees). **B,** Slope aspect class, where "F" indicates "Flat" (i.e., slope steepness < 5 degrees). **C,** Hillslope position. **D,** Altitudinal band (m).

"downward" transitions occurred mainly into the 40%–50% and 30%–40% cover classes, with probabilities of 15% and 17%, respectively.

DISCUSSION

Scale Dependence of Expansion Process

In our 25-km^2 study area, the area of woodlands has increased by as much as 33% over a recent 30-year period (Table 4). Although this increase is substantial, it is less than the doubling in woodland area reconstructed by Soulé et al. (2003) over a similar time period for several western juniper dominated sites in central Oregon. However, our results show that any quantification of P–J woodland expansion is likely to be scale-dependent (Table 4). For studies of vegetation change in these systems to be comparable, they need to consider similar spatial scales. The study by Soulé et al. (2003) evaluated change at a single spatial resolution of 0.25 m^2, which would be expected to result in a greater apparent magnitude of change than our finest scale (i.e., median patch size) of 20 m^2, if our results of greater expansion rates at finer scales are broadly generalizable.

Results support our first hypothesis, that expansion of woodland area has been dominated during this recent time period by trees filling in small openings between extant woodland patches, with more limited expansion of the overall woodland boundary into adjacent vegetation types (Table 4). It is an interesting question whether the pattern of woodland expansion has developed in this manner over a long time period, with rapid, continual infilling of openings accompanied by less frequent, long-range colonization of microsites more or less distant from the prevailing woodland boundary. Because the rate of site closure (i.e., progression from a shrub-dominated site to a completely tree-dominated site) varies

Table 5. Transition matrix showing changes in cover class for 1-ha pixels, where cover class indicates the proportion of area within each 1-ha pixel that is covered by P–J woodland at the single-tree scale. In each cell, the top number shows the actual area (ha), and the bottom number (in parentheses) indicates the proportion of the study area relative to the total area in that cover class in 1966. The diagonal portion of the matrix (in bold) highlights the number of cells that have maintained the same P–J cover. The upper right portion of the matrix indicates increases from lower (1966) to higher (1995) P–J cover, whereas the lower left portion indicates transitions from higher to lower P–J cover.

	1995						
	< 10%	10%–20%	20%–30%	30%–40%	40%–50%	> 50%	*1966 Area (ha)*
1966							
< 10%	**190** **(0.53)**	94 (0.26)	51 (0.14)	8 (0.02)	8 (0.02)	7 (0.02)	*358*
10%–20%	19 (0.05)	**102** **(0.26)**	132 (0.34)	79 (0.21)	36 (0.09)	17 (0.04)	*385*
20%–30%	10 (0.02)	60 (0.11)	**118** **(0.21)**	152 (0.27)	129 (0.23)	95 (0.17)	*564*
30%–40%	1 (0.01)	28 (0.06)	67 (0.14)	**110** **(0.23)**	114 (0.24)	158 (0.33)	*478*
40%–50%	0	7 (0.02)	26 (0.09)	52 (0.18)	**52** **(0.18)**	152 (0.53)	*289*
> 50%	0	0	9 (0.06)	27 (0.17)	24 (0.15)	**98** **(0.62)**	*158*
1995 Area (ha)	*220*	*291*	*394*	*401*	*339*	*429*	

greatly with site productivity (Johnson and Miller 2006), one would expect the infilling process to dominate less productive sites for longer time periods. On more productive sites, infilling should occur within a matter of few decades and represent only a transient process of landscape change.

Landscape Factors Influencing Expansion

Site Productivity Gradients. Results support our second hypothesis, in that we found more rapid rates of woodland expansion on more mesic sites, as have other studies of recent P–J establishment (Tausch et al. 1981; Johnson and Miller 2006). Mesic sites in the study area are characterized by more northerly slope aspects, and by lower hillslope positions and more gradual slopes where soil water-holding capacity is greater due to deeper, finer-textured soils. Such sites develop more abundant and continuous fuels, and thus are more susceptible to vegetation changes resulting from direct fire suppression, or indirect fire suppression arising from consumption of fine fuels by livestock (Young and Evans 1981). Mesic sites are also more likely to have been heavily grazed, due to a greater abundance of high-quality forage. More rapid tree expansion into mesic areas might also be explained by differential tree seedling mortality and competitive relationships with shrub and herbaceous species. In the Simpson Park range, tree seedlings on sites with a less favorable water balance would be unlikely to survive periods of extended drought. Mesic sites are also more likely to host a greater cover of sagebrush and other shrub species, which serve important roles as "nurse shrubs" facilitating pinyon establishment (Chambers 2001). Tree invasion into grasslands and shrublands elsewhere in the western United States has been shown to be facilitated by more mesic site conditions, including pine invasion into Rocky Mountain grasslands (Mast et al. 1997; Andersen and Baker 2005), and invasion of multiple species into subalpine meadows of the western Cascades (Rochefort and Peterson 1996; Miller and Halpern 1998) and Colorado Rocky Mountains (Weisberg and Baker 1995).

Elevational Gradients. In support of our third hypothesis, the rate of P–J expansion at single-tree and patch scales was greatest in a downslope direction (Fig. 2d). This would be expected if the climate trend over the past 150 years had been toward wetter conditions, given that tree establishment at lower elevations in these semiarid rangelands is limited by available moisture (Chambers 2001; Soulé et al. 2004). However, although the climate in the Great Basin has clearly warmed over the past 150 years, this trend has been accompanied by more xeric conditions (Tausch et al. 2004). Warming conditions should result in an expansion of P–J vegetation toward upper elevations, as has been observed for western juniper (*Juniperus occidentalis* Hook.) during previous periods of milder winters (Miller and Wigand 1994), and for the current study particularly when coarse, ecotonal scales are considered.

Tausch et al. (1981) observed similar trends where P–J expansion was more prevalent in a downslope direction. Potential causes for more rapid downslope expansion include shorter growing seasons and harsher winter conditions at upper elevations, greater competitive ability of upper-elevation shrub communities, and a history of anthropogenic disturbance at lower elevations (Tausch et al. 1981). Any of these explanations could apply for the Simpson Park range, which is surrounded by areas of historically intensive mining. Severe deforestation of P–J woodland in the vicinity of these areas has been documented (Hattori and Thompson 1987), although direct evidence of historical logging activity in the study area is local in its distribution.

In contrast to our results, Johnson (2005) found recent western juniper establishment to be greatest at higher elevations. However, higher elevations in his regional-scale, Oregon and Idaho study area represent more productive sites. In our landscape-scale study of Simpson Park woodlands, the upper elevations are rockier, have thinner soils, and are more xeric than sites closer to the valley bottoms.

Density Dependence and the Process of Pinyon–Juniper Expansion

Results weakly support our fourth hypothesis, that expansion rate increases after a certain threshold level of woodland cover has been reached (perhaps 10%; Table 5). However, the rate of infilling subsequently levels off as sites increase in cover, suggesting an upper threshold of cover or density for tree establishment. Similar thresholds have been suggested for western juniper (Young and Evans 1981; Soulé and Knapp 2000; Soulé et al. 2004). As suitable microsites for establishment become limited and interspecific competition increases, tree establishment might come into balance with mortality. This might be especially true for pinyon, which relies heavily upon "nurse shrubs" for establishment (Chambers 2001), because denser stands of P–J woodland tend to lose the woody understory component (Young and Evans 1981; Tausch and Tueller 1990).

The greatest declines in woodland cover, indicating mortality over the 30-year period, occurred for patches with the highest cover in 1966 (Table 5). Although this result is weak and confounded with spatial errors in patch locations among years, it suggests the hypothesis that pinyon and juniper mortality are density-dependent. Further research is needed to test this hypothesis against field data and to determine the spatial scales (i.e. patch sizes) over which such density-dependent mortality could be operative.

Our results, showing that woodland expansion over most of the Simpson Park study area is dominated by in-filling processes, are consistent with the general observations of Slatyer and Noble (1992) for upper treeline dynamics, and those of Lyford et al. (2003) for long-term Utah juniper colonization patterns in Montana and Wyoming. The regeneration niche of ecotonal tree species can be quite narrow, yet such species can be very persistent once established, capable of survival under environmental conditions that would not have been suitable for range expansion. Hence, the advance of tree species from ecotonal areas can be slow, punctuated by episodic, long-distance dispersal events that become more likely during periods of favorable climate. Regeneration behind the advancing front proceeds rapidly because the trees themselves modify their environment through altered microclimate and, in the case of P–J woodland, elimination of understory plant species that compete effectively with tree seedlings. Pinyon and especially juniper are well-adapted to environmental stressors and have low mortality rates, such that ground gained by the encroaching trees is not readily lost. Exceptions occur due to large-scale disturbances such as fire and beetle kill (e.g., *Ips confusus*), which could in turn be associated with episodic drought.

MANAGEMENT IMPLICATIONS

The patterns and rate of P–J woodland expansion are not spatially random, but vary according to landscape gradients of topography and productivity. This conclusion has relevance for natural resource managers who seek to counteract expansion of P–J woodlands through prescribed fire or mechanical clearing of trees. The great majority of recent P–J woodland expansion in our study area has occurred on mesic slope aspects and canyon bottoms. Tree removal on such sites should be viewed in a long-term context, because tree invasion is likely to proceed rapidly following the intervention, barring significant changes in climate or fire regime. High-resolution remote sensing applications coupled with GIS analysis can provide historical, landscape-level context for management decisions, and allow for long-term monitoring of the efficacy of current rangeland restoration efforts. Setting of scientifically defensible management objectives requires further study of causes and patterns of recent woodland expansion, as well as effects of woodland expansion on habitat mosaics and fuel continuity.

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