Predicting altered connectivity of patchy forests under group selection silviculture

Seth W. Bigelow · Sean A. Parks

Abstract Group selection silviculture creates canopy openings that can alter connectivity in patchy forests, thereby affecting wildlife movement and fire behavior. We examined effects of group selection silviculture on percolation (presence of continuously forested routes across a landscape) in Sierra Nevada East-side pine forest in northern California, USA. Four $\sim$ 250 ha project areas were analyzed at three map resolutions in three ways: analyzing forest cover maps for percolation before and after group-selection treatment, placing simulated group openings in forest cover maps until fragmentation occurred, and comparing project areas to neutral maps that varied in forest cover and self-adjacency. Two project areas were fragmented (i.e., did not percolate) prior to treatment, one resisted fragmentation, and the other became fragmented by treatment when analyzed at 30 m cell resolution. Median simulated openings required to create fragmentation agreed well with the actual number. There was a well-defined transition between percolating and non-percolating neutral maps;

increased aggregation of forest lowered the critical value at which forests percolated. A logistic model based on these maps predicted percolation behavior of the project areas effectively, but alternative generating algorithms gave slightly different predictions. A graph of this model provides a straightforward way to visualize how close a landscape is to fragmentation based on its forest cover and aggregation. In East-side Sierran landscape, fragmentation from group-selection openings may make the landscape less hospitable to the American marten but more resistant to crown fire.

Keywords Fragmentation · Percolation · Spatial pattern analysis · Sierra Nevada East-side pine · Group selection · Silviculture · Connectivity · Neutral map

Introduction

Group selection silviculture is sometimes proposed as a low-impact, ecologically benign alternative to large clearcuts (McKelvey and Weatherspoon 1992; Franklin et al. 1997). In group-selection silviculture, small groups of trees are harvested, typically leaving openings of up to 0.5 ha in the forest canopy (e.g., Leak and Filip 1977; McDonald et al. 2009). Normally, such small openings dispersed throughout a forest landscape would not raise concerns about forest fragmentation, but given a sufficient density of openings, or a patchy forest, any forest landscape may become fragmented

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(Franklin and Forman 1987; Li et al. 1993; With 2002). Such forest fragmentation can have adverse effects on ecological processes such as mesocarnivore movement, or beneficial effects on prevention of catastrophic fire. The discipline of landscape ecology offers many tools for analyzing fragmentation (or its inverse, connectivity), but there is still a need for simple tools for analyzing structural connectivity under forested landscape harvesting scenarios (Calabrese and Fagan 2004).

Percolation, a central theoretical construct of landscape ecology (Stauffer and Aharony 1985; Li 2001; Turner et al. 2001), posits a critical or threshold value of cover (p_c) of one element (i.e., forest) at which a landscape element transitions from connected to disconnected (Peterson 2002). In binary neutral (or random) landscapes, $p_c = 0.59275$ when a focal cell has four neighbors. This suggests a rule of thumb for predicting conditions under which forest operations such as group selection may diminish structural connectivity, but the presence of spatial structure (either clumping or regular spacing of forest elements) invalidates the assumption of randomness that underlies the $p_c = 0.59275$ critical value (With 2002). Actual landscapes have spatial structure and thus have different percolation thresholds than neutral simulated landscapes (Turner et al. 2001).

Landscapes with clumped elements usually percolate at cover proportions below thresholds for random landscapes, and landscapes with regularly dispersed elements may percolate at cover proportions above the threshold for random elements (Gustafson and Parker 1992; Wallin et al. 1994; Hargis et al. 1998). Nevertheless, no predictive expression exists for the general case of spatially structured yet non-hierarchically organized landscapes. Such an expression would be valuable for planning group selection silviculture projects, as well as any other forest treatment that disturbs the overstory canopy. Indeed, given the importance of percolation theory in the discipline of landscape ecology (Turner et al. 2001), such an expression might prove to have a much wider application.

We carried out a study on group selection in patchy, semi-arid forest of the Eastern Sierra Nevada, USA. In these forests, forest patch connectivity has significance for mesocarnivore movement and for fire propagation. The American marten (*Martes americana*) is an old-forest specialist (Spencer et al. 1983)

that occurred throughout the Sierra Nevada range in the early twentieth century (Grinnell et al. 1937). Fragmentation of old-growth habitat has been implicated as a factor leading to decline in marten populations (Zielinski et al. 2005), and the marten is missing in parts of its historical range in the Eastern Sierra. In contrast, diminished connectivity may play a beneficial role in slowing the propagation of crown fire. Tree crown continuity enhances the spread of high-intensity canopy fire (Turner and Romme 1994; Miller and Urban 2000; Finney 2001), which has become common in these landscapes. Fuel discontinuity is an important principle of fire planning; indeed, percolation theory has been used to test fuel break function (Nahmias et al. 2000; Hargrove et al. 2000; Bevers et al. 2004; Spyratos et al. 2007).

Our study had four goals: two were narrowly focused on the specific landscape we were working in, and two were of broader scope. The first was to apply percolation analysis to landscapes recently treated with group selection silviculture to determine whether forest treatments adversely affected connectivity. The second was to use simulated placement of group selections to estimate the number of groups that could be placed in a specific landscape before causing a percolation transition (i.e., a change from percolating to non-percolating). The third was to determine the effect of map resolution on percolation behavior. The fourth was to derive a general expression for percolation probability with respect to forest cover and clumping of forest elements, for use in prediction of threshold behavior.

Methods

Study site and treatment

An analysis of landscape connectivity was carried out at the site of a forest management project in patchy Sierra Nevada East-side pine forest (Eyre 1980) in the upper reaches of the Middle Fork of the Feather River watershed (Fig. 1), in the Northern Sierra/Cascades transition zone (40.0°N, 120.5°E). Common canopy tree species are Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*). The Plumas National Forest (Beckwourth Ranger District) initiated the Red Clover project in 1999 as part of a

Fig. 1 Aerial photograph showing location of the four group selection project areas (mean size 254 ha) in Plumas National Forest, California, USA
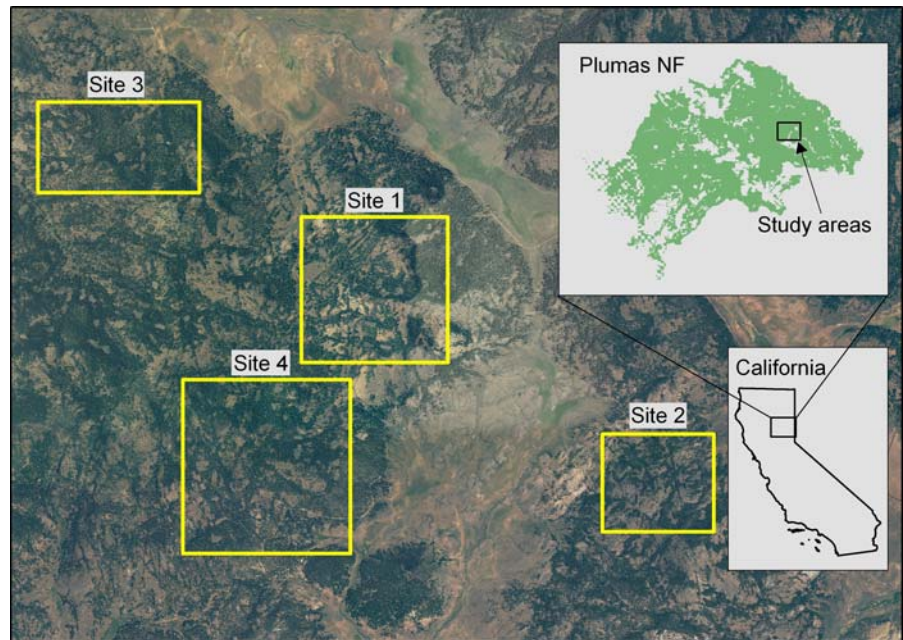
legislatively mandated program of work (HFQLG 1998). One element of the project called for placement of group selection openings, each ∼0.8 ha in size, within a larger landscape selected as being appropriate for group selection silviculture. Forest managers randomly selected center-points of groups in a GIS, and retained stands if mean quadratic breast-height diameter of trees was ≥30.5 cm. Field crews marked approximately circular openings, and logging operations occurred in 2002 (Patti Millet *personal communication*).

Creating the binary landscape from photographs and testing for percolation

We delineated four rectangular study sites within the Red Clover group selection project area using DOQQs taken in 1998 (digital orthorectified quarter-quadrangles are aerial photographs corrected for displacement and distortion). Study sites were selected to encompass as many group selection openings as possible while avoiding roads, streams, and meadows; mean site area was 254 ha (Figs. 1, 2a; Table 1). We ran an unsupervised classification on the DOQQs using the Feature Analyst (Visual Learning Systems, 2001) extension of ArcMap (ESRI Inc. 2002), using Manhattan pattern with a 3 × 3 window. We placed the 20 resulting classes in either

forest (F) or open ground (O) categories, and used these rules to produce binary maps of the study sites. We aggregated the 1 m^2 pixels of the binary image into square cells of 9, 100, or 900 pixels (i.e., cells with 3, 10, or 30 m sides) to investigate the influence of map resolution on percolation. We classified a cell as forested if ≥50% of its pixels were classified as forest. Fifty percent canopy cover is thought to be the approximate value at which habitat suitability changes from low to moderate or high for three important wildlife species in the study area (California spotted owl, American marten, and fisher; California Interagency Wildlife Task Group, 2005).

We delineated the boundaries of the group selection openings using 2005 (i.e., post-treatment) National Agricultural Imagery Program images. We created post-treatment maps by overlaying group selection boundaries on the binary images created earlier and converting forested cells within the boundaries to open ground (Fig. 2b). Binary maps were analyzed for percolation before and after group selection in ArcView GIS (Fig. 2c).

Simulated placement of group selection openings

In addition to assessing the effects of actual group selections on percolation, we iteratively placed simulated group selection openings at each percolating

Fig. 2 Aerial photographs illustrating percolation analysis at site 2. **a** Site prior to treatment with outlines of planned group selection openings. **b** Site prior to treatment, with outline of percolating forest cluster (classified at 30 × 30 m cell resolution). **c** Site after treatment showing absence of percolation due to truncation of cluster


site until there was a percolation transition (i.e., until the site ceased to percolate). We created an Avenue script in ArcView GIS to apply openings and test for percolation. Simulated opening shapes were circular, and sizes were randomly chosen from a list of the actual group selection openings. An opening of average size (0.58 ha; Table 1) was represented by ~6 of the large 30 × 30 m cells, or 644 of the small 3 × 3 m cells. Minimum forest cover value was selected from the real pre-treatment forest cover value to prevent openings from being placed in areas of sparse cover. Group selection openings were placed until the site failed to percolate. This procedure was run 100 times at each (percolating) site and map resolution.

Assessing vulnerability to percolation transition by analysis of neutral landscape models

We predicted probability of landscape percolation by stochastically generating binary maps with a range of forest cover and self-aggregation, testing the maps for percolation, and applying logistic regression. We used two alternative methods for generating maps with auto-correlated (i.e., aggregated) spatial structure (see review in Keitt 2000); one was a simplification of the hierarchical system of O'Neill et al. (1992) in which the probability of a focal cell becoming forest ($p(fc = F)$) is expressed as the sum of two joint probabilities. The first is the product of the conditional probability that the focal cell is forest given that a neighboring cell is forested ($p(F|F)$) and the probability that the neighboring cell is forested ($p(F)$). The second is the product of the conditional probability that a focal cell is forest if a neighboring cell is open ($p(F|O)$) and the probability that the neighboring cell is open ($1-p(F)$). The expression,

$$p(fc = F) = p(F|F)p(F) + p(F|O)(1 - p(F)),$$

was rearranged by substituting $p(F)$ for $p(fc = F)$, then solving for $p(F|O)$:
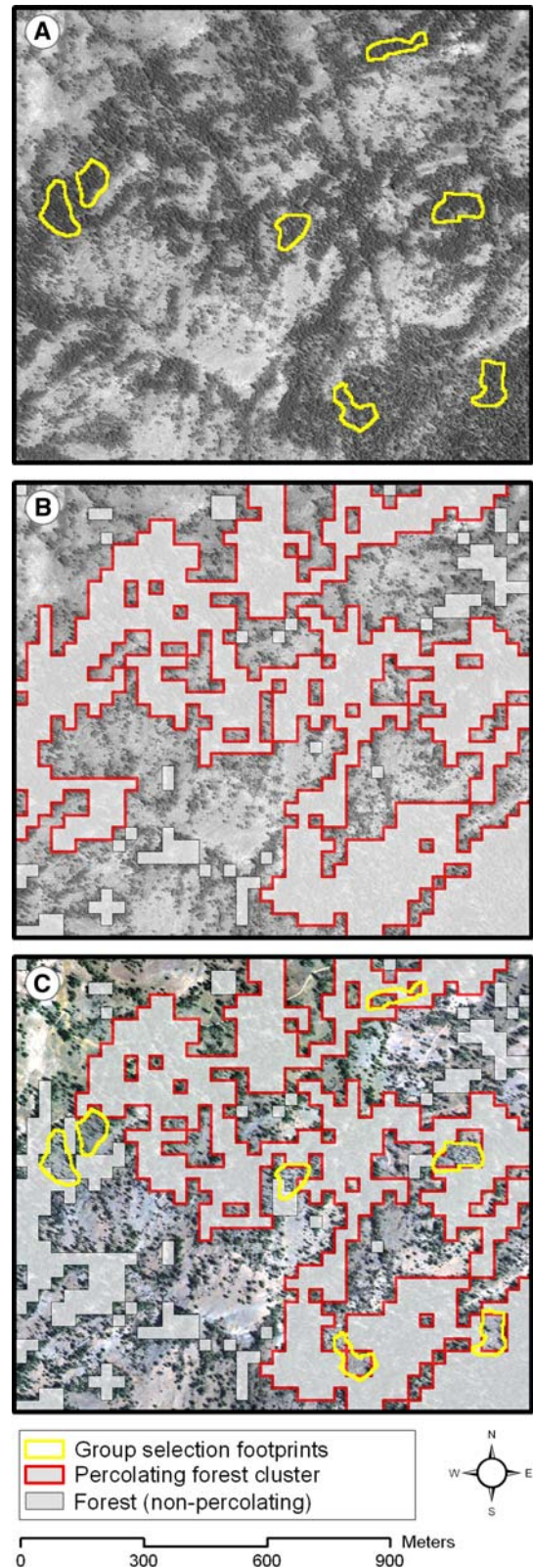
Table 1 Size of East-side study sites and group selection (GS) openings, and proportion of forest cover ($pr(F)$) and forest self-adjacency ($pr(F|F)$) in binary maps of the sites before and after treatment at three map resolutions

| Site | Site area (ha) | GS area (ha) | GS (#) | 3 × 3 m cells | | | | 10 × 10 m cells | | | | 30 × 30 m cells | | | |
| | | | | $pr(F)$ | | $pr(F\|F)$ | | $pr(F)$ | | $pr(F\|F)$ | | $pr(F)$ | | $pr(F\|F)$ | |
				Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post	Pre	Post
1	284	7.4	13	0.42	0.40	0.79	0.78	0.43	0.41	0.76	0.74	0.42	0.39	0.71	0.70
2	146	3.9	7	0.47	0.45	0.84	0.84	0.48	0.45	0.81	0.80	0.48	0.45	0.72	0.68
3	196	9.9	17	0.60	0.56	0.83	0.82	0.63	0.58	0.82	0.79	0.66	0.61	0.81	0.78
4	390	8.0	13	0.40	0.39	0.73	0.72	0.41	0.39	0.71	0.70	0.39	0.37	0.67	0.65

$$p(F|O) = (p(F)(1 - p(F|F))/(1 - p(F)).$$

Maps were generated by specifying $p(F)$ and $p(F|F)$, then randomly selecting a focal cell and a neighboring cell. If the neighboring cell had an identity of F, the variable p was assigned the probability $p(F|F)$; otherwise p became $p(F|O)$. A random number (Z) between zero and one was selected from the uniform distribution; if $Z \leq p$ then the focal cell became forest, and if $Z > p$ then the focal cell became open. This process was repeated until each cell on a map had changed 10 times on average.

The other, cluster-growth approach for generating spatially structured maps (Anderson and Family 1988; Fahrig 1997) also required two parameters, one for forest cover and the other for fragmentation (FRAG). It begins with an open map, and randomly selects a cell location and a uniform number (Z) from 0–1. If any neighboring cell is forest or if $Z <$ FRAG then the selected cell becomes forest. The process continues until cover reaches the specified value. Simulations were done in square grids of 50, 150, or 500 cells per side for both map-generation approaches. The dimensions reflected the extent and resolution at which the study site images were classified, e.g., a square 225 ha study area divided into 30 m cells has 50 cells per side. Calculation of $pr(F)$ and $pr(F|F)$ and determination of percolation were done after each map was created; percolation was assessed with a cellular automaton that advanced from left to right across the map following a set of rules to search for a continuous route (Fig. 3). [We use the notation $p()$ to indicate theoretical probabilities or model parameters, and $pr()$ to indicate measured quantities such as proportion of map cells that are forest ($pr(F)$), or proportion of forest cells that are adjacent to other forest cells ($pr(F|F)$)].
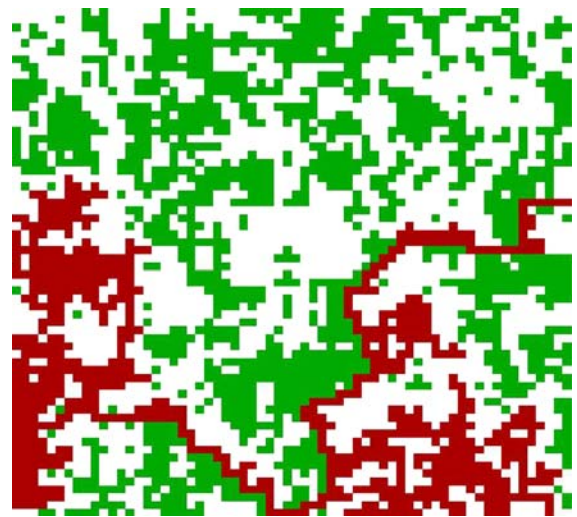
Fig. 3 Simulated landscape of forested (*green*) and open areas (*white*) showing continuous path taken by the cellular automaton (*red*). Even though the proportion of forest cover $pr(F) = 0.51$ is well below the theoretical percolation threshold for unstructured landscape $pc = 0.59275$, the landscape percolates because the proportion of forest self-adjacency $pr(F|F) = 0.68 > 0.59275$

Simulations were done at $p(F) = 0.4$–0.8 in increments of 0.01, and at $p(F|F) = 0.20$–0.99 in increments of 0.01. The resulting data sets each had $\sim 3{,}000$ observations.

Data sets generated from multiple simulation runs were analyzed with logistic regression to determine the combined effect of forest cover and self-aggregation on probability of percolation (p_p). Probability of percolation was estimated by fitting a logistic equation,

$$p_p = e^J/(1 + e^J) + \varepsilon,$$

in which the exponent J was modified to express alternative models of percolation probability, and ε is

Table 2 Logistic equation models for estimating percolation probability (p_p) as a function of forest cover ($p(F) = x$) and self-adjacency ($p(F|F) = y$)

M^a	K^b	Logistic equation [$p_p = e^J/(1 + e^J)$] exponent	Description
1	2	$J = a + bx$	Univariate
2	3	$J = a + bx + cy$	Bivariate
3	4	$J = a + bx + cy + dxy$	Bivariate with interaction
4	6	$J = a + bx + cy + dxy + ex^2 + fy^2$	Bivariate with 2nd-order terms
5	7	$J = a + bx + cy + dxy + ex^2 + fy^2 + g(xy)^2$	Bivariate with 2nd-order interaction

[a] Model identifier

[b] Number of parameters in model

the binomial error model (Table 2). Maximum likelihood principles were used to select the most-likely equation and parameters given the data (Hilborn and Mangel 1997; Burnham and Anderson 2002). Analyses were done in *R* version 2.7.2 (R Development Core Team 2008). Equations were fitted to data with the Metropolis simulated annealing algorithm (Szymura and Barton 1986), in an implementation in *R* by Lora Murphy and Charles Canham (Cary Institute of Ecosystem Studies).

Assessment of percolation predictions

In any neutral, binary, non-spatially structured map, the probability of randomly selecting a cell with an *F* identity is independent of the identity of neighboring cells (i.e., $p(F) = p(F|F)$); by extension, any map in which $p(F) = p(F|F)$ is unstructured. In unstructured maps with four-neighbor geometry, $p_p = 0.50$ when $p(F) = 0.59275$ (Stauffer and Aharony 1985). In theory, then, maps characterized by $p(F) = p(F|F) = 0.59275$ are unstructured and have $p_p = 0.50$ probability of percolating. This relationship provides a benchmark for assessment of generating equations and regression analyses, so we superimposed a symbol denoting this known percolation probability on scatter-plots of the percolation outcomes and contour plots of the logistic equations.

The effectiveness of this system in predicting percolation thresholds was also determined by comparing study site percolation behavior with predicted probability of percolation (p_p) from the most-likely equations and parameters. We created contour graphs from the most-likely equations, in which $pr(F)$ and $pr(F|F)$ are respectively the horizontal and vertical axes and p_p is indicated by contour lines and colors

(Lattice graphics; Sarkar 2008). Percolation status of the four study sites was plotted on the contour plots with respect to $pr(F)$ and $pr(F|F)$.

Results

Percolation in East-side landscapes

Three of the four sites had pre-treatment forest cover below the $p_c = 0.59275$ percolation threshold; $pr(F)$ of the four sites ranged from 0.39 to 0.66 (Table 1). Sites 2 and 3, which had higher $pr(F)$ than the other sites, percolated (i.e., had a continuous route across the landscape via pixels connected by common edges) at all map resolutions (i.e., 3, 10, and 30 m cell sizes). Sites 1 and 4, which had $pr(F) \leq 0.43$, did not percolate. Self-adjacency ($pr(F|F)$) exceeded $pr(F)$ at all sites, indicating that forested landscape cover was clumped. Forest cover and $pr(F|F)$ decreased by 0.02–0.03 after group selection treatment at most sites. Group selection openings occupied from 2–6% of the total area of each site, and they caused a percolation transition only at Site 2 at 30 m map resolution.

Simulated placement of group selection openings for the two sites that percolated pre-treatment showed a median of 8–51 groups required for a percolation transition (Fig. 4). Results are displayed as a density graph (Sarkar 2008). There was a tendency toward a bimodal distribution. The trend in change in median number of groups required for percolation transition varied with site and with resolution. At Site 2, increasing map resolution increased the number of simulated groups required to effect a percolation transition. At Site 3, though, the maximum number of

Fig. 4 Density plots of number of simulated group selection openings required to cause fragmentation in sites 2 and 3, analyzed at 3 map resolutions. Each panel shows results of 100 simulation runs
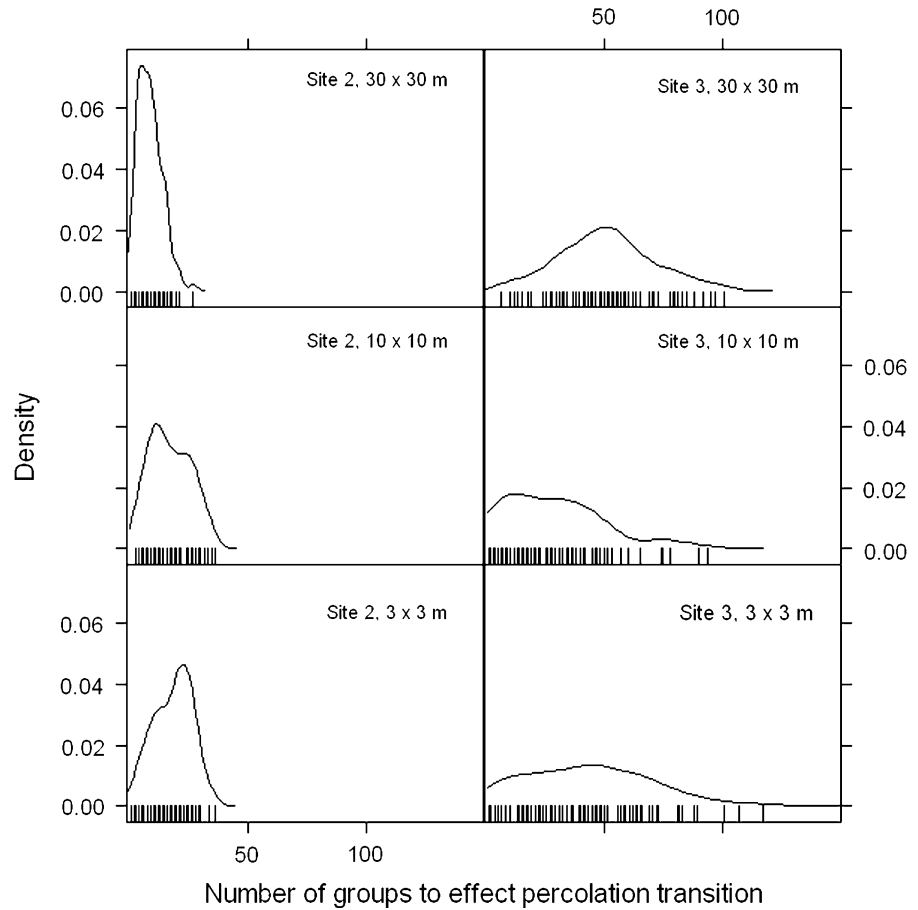

groups required to effect a percolation transition occurred at the 10 × 10 m map resolution. It was only possible to compare simulated and actual number of groups required to effect percolation transition at Site 2 at 30 m resolution, but there was good agreement: a median of 8 simulated groups versus 7 actual groups.

Predicting vulnerability to percolation transition from neutral landscape maps

Maps generated with the simplified hierarchical algorithm described in this paper showed a consistent pattern of percolation in response to forest cover $pr(F)$ and self-aggregation ($pr(F|F)$). There was a well-defined transition zone between percolating and non-percolating maps (Fig. 5a), revealing that increased $pr(F|F)$ decreased the $pr(F)$ at which maps would percolate. Increasing $pr(F|F)$ allowed maps to percolate down to $pr(F) \approx 0.53$, and there was distinct curvature in the relationship. The best logistic

regression model of probability of percolation (p_p) contained second-order terms of $pr(F)$ and $pr(F|F)$ and a first-order interaction (Model 4; Tables 3, 4). This model was the best (i.e., had lowest AIC_c) regardless of map resolution; the main difference among map resolutions was that there was a better-defined percolation transition zone at high resolution. This difference among transition zones was reflected in R^2 values, which increased from 0.80 to 0.95 as map resolution increased.

Maps generated with the cluster-growth algorithm confirmed the general relationship between $pr(F)$, $pr(F|F)$, and percolation observed with the other algorithm (Fig. 5c), though with some differences. Increased $pr(F|F)$ still allowed percolation at relatively low $pr(F)$ but there was less curvature in the transition zone. As a result, at low map resolution the best model incorporated both $p(F)$ and $p(F|F)$ but did not include a statistical interaction term between them (Model 2; Table 3). An interaction between
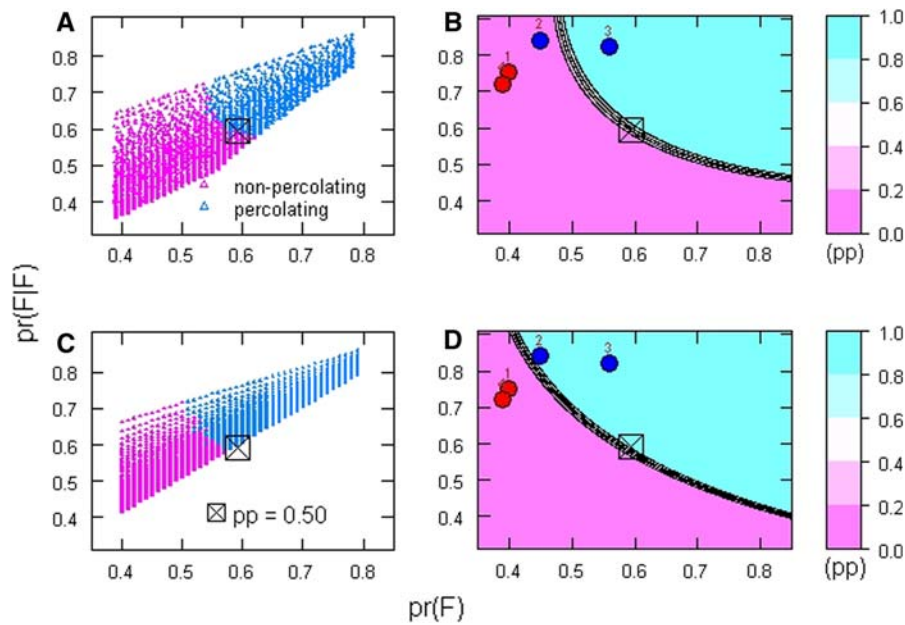
Fig. 5 Percolation in simulated and actual landscapes with respect to forest cover ($pr(F)$) and self-adjacency ($pr(F|F)$). Sites were analyzed at 500×500 cell, 3×3 m-per cell resolution. *Crossed-box benchmarks* show theoretical 0.50 percolation probability. **a** Percolation of neutral maps generated with hierarchical algorithm. **b** Percolation probability (pp) surface generated by logistic model of data in (**a**), superimposed with percolation status of East-Side Sierra forestry sites (*circles*). **c** Percolation of maps generated with cluster-growth algorithm. **d** Percolation probability surface generated from analysis of (**c**), superimposed with percolation status of East-side Sierra forestry sites

Table 3 Likelihood analyses of percolating maps generated from the algorithm described in this paper (A, upper table) and the algorithm of Anderson and Family (1988; B, lower table)

M^{a}	500×500 cells				150×150 cells				50×50 cells			
	$\ln(L)$	AIC	$\Delta_i{}^{b}$	R^2	$\ln(L)$	AIC	Δ_i	R^2	$\ln(L)$	AIC	Δ_i	R^2
A												
1	−326.4	656.8	450	0.82	−355.2	714.4	354	0.81	−509.0	1,022	249.6	0.73
2	−112.9	231.8	25	0.94	−184.6	375.2	14.8	0.9	−385.7	777.4	5	0.77
3	−111.5	231.0	24.2	0.94	−184.5	377.0	16.6	0.9	−387.0	782.0	9.6	0.80
4	**−97.4**	**206.8**	**0**	**0.95**	**−174.2**	**360.4**	**0**	**0.91**	**−380.2**	**772.4**	**0**	**0.80**
5	−97.2	208.4	1.6	0.95	−175.4	364.8	4.4	0.91	−381.4	776.8	4.4	0.80
B												
1	−309.6	623.2	408.6	0.88	−385.2	774.4	321.4	0.85	−552.5	1,109	176.2	0.78
2	−116.2	238.4	23.8	0.96	**−223.7**	**453.4**	**0.4**	**0.91**	**−463.4**	**932.8**	**0**	**0.81**
3	−105.7	219.4	4.8	0.96	−223.6	455.2	2.2	0.91	−464.1	936.2	3.4	0.81
4	**−101.3**	**214.7**	**0**	**0.96**	−220.6	453.2	0.2	0.91	−461.4	934.8	2	0.81
5	102.0	218.0	3.4	0.96	−219.5	453.0	0	0.91	−463.1	940.2	7.4	0.81

Models $M = 1$ through 5 express percolation probability as a function of forest cover ($pr(F)$) and forest self-adjacency ($pr(F|F)$). Bold font denotes best model for each grid scale and map-generation algorithm

[a] See Table 1 for model descriptions

[b] An AIC difference (Δ_i) of < 2 indicates substantial support for a model, an Δ_i of 4–7 indicates much less support, and $\Delta i > 10$ indicates essentially no support

Table 4 Parameters for most-likely equations of probability of percolation (Model 4, second order bivariate logistic equation, 500×500 cell maps) with respect to forest cover ($pr(F)$) and probability of self-adjacency of forest cover ($pr(F|F)$)

Generating algorithm	a	b	c	d	e	f
Modified hierarchical[a]	−84.79	43.6	41.51	241.9	−69.39	−76.34
Cluster-growth[b]	−85.77	−23.09	44.60	241.6	16.12	−45.73

[a] Bigelow and Parks (this paper) modification of O'Neill et al. (1992)

[b] Anderson and Family (1988) as described by Fahrig (1997)

$pr(F)$ and $pr(F|F)$ was only detected at the highest map resolution.

Maps produced with the modified hierarchical algorithm reproduced the location of the theoretical benchmark (i.e., $p_p = 0.50$ when $pr(F) = pr(F|F) = 0.59275$) better than the cluster-growth algorithm. The benchmark fell precisely in the percolating/non-percolating transition zone of maps generated by the former algorithm (Fig. 5a), but was slightly displaced from the transition zone of maps generated by the latter (Fig. 5c).

Comparison of binary maps of real landscapes with predictions from neutral maps

All of the East-side landscapes showed high forest self-aggregation (i.e., had high $pr(F|F)$; Fig. 5b, d). Neither algorithm could produce maps with the same combination of high $pr(F|F)$ and low $p(F)$ seen in the real landscapes (note blank upper left corner, Fig. 5b, d); prediction probabilities therefore are an extrapolation from the simulated runs. Sites 1 and 4, which had post-treatment $pr(F) \leq 0.40$ (Table 1), were predicted to have low probability of percolation and indeed did not percolate. Site 3 had post-treatment $pr(F)$ of 0.56 and thus would not be expected to percolate under the usual, $p_c = 0.59725$ paradigm. Nevertheless, it was predicted to have high probability of percolation under the model in this paper and did indeed continue to percolate. The models produced by the two generating algorithms differed in their predictions for site 2; the modified hierarchical model predicted a low probability of percolation for this site, and the model derived from the cluster-growth algorithm predicted a high probability of percolation. Despite a rather low post-treatment canopy cover of 0.45, the site persisted in percolating, therefore the model derived from the cluster-growth algorithm made a more accurate prediction.

Discussion

Forest connectivity in the East-side landscape

Group selection has been proposed as an appropriate silviculture for dry forests in general (Kimmins 1992) and East-side pine in particular (Helms 1980), partly because the dry soils may resist compaction that results from the required network of roads and skid trails. Yet many of the semi-arid, East-side pine forests of northern California have a patchy, sparse canopy due to harvest history (Laudenslayer et al. 1989), substrate geology (DeLucia et al. 1988; Leiberg 1902), and competition for scarce moisture (Callaway et al. 1994). East-side pine is part of a transition from west-side mixed-conifer to the west and sagebrush scrub to the east; such ecotones are particularly vulnerable to disruptions of canopy connectivity (Milne et al. 1996; Peterson 2002).

Did the group selection openings implemented by loggers indeed fragment the East-side forest landscapes we examined, "insidiously whittling away the percolating cluster" (With 1997)? Visually, the group selection openings represented a significant disturbance to the structure of the forests, and would seem to have the potential to diminish connectivity at least until trees reestablish and grow back. Of the four sites examined, two did not percolate even prior to any silviculture treatment. Of the other two, one resisted fragmentation from group selection (and could have tolerated many additional group selection openings), but the other (site 2) was near a percolation threshold and did change from percolating to non-percolating with treatment when analyzed at a coarse resolution. There is some possibility, therefore, that group selection will increase fragmentation of East-side landscapes.

Might there have been some opportunity to mitigate the effects of group selection openings on fragmentation? Groups were approximately circular, which is the

shape least likely to lead to interruption of percolation. A conscious effort by marking crews to retain at least a border of trees around each group, i.e., to make each group interior and not to connect any group with a larger opening, might provide insurance against fragmentation particularly if groups are analyzed at a fine (e.g., 3 m) resolution. Planners perhaps should plan to include buffers, or at least retain a thin border of trees around group selection openings.

The issue of the correct or best resolution for analysis is challenging. The neutral landscape generated maps at the highest resolution (500 cells per edge) showed a distinct boundary between conditions of forest cover and aggregation that would and would not allow percolation. The boundary was much less clear for maps at lower resolution. A higher proportion of variation in the data (as measured by the adjusted correlation coefficient, R^2) was explained by increasing map resolution from 50 to 150 cells per edge (i.e., from $R^2 = 0.80$ to 0.91) than by increasing from 150 to 500 cells per edge ($R^2 = 0.91$–0.95). This observation supports the recommendation of Turner et al. (2001) that neutral landscape maps should have at least 100 rows and columns to avoid artifacts from truncation of patches. By extension, percolation analyses on real landscapes should probably use maps of with resolution of at least 100 cells per edge; our use of 30×30 m cells to classify ~225 ha landscapes (i.e., 50 cells per edge) was excessively coarse by this reckoning.

The structured neutral maps showed that not just the proportional coverage of forest but the spatial pattern has a large effect on probability of percolation. Others have commented on this relationship (Gustafson and Parker 1992; Wallin et al. 1994; Hargis et al. 1998), but heretofore no mathematical relationship between forest cover, a spatial metric, and percolation probability has been articulated as far as we are aware (but see Chayes et al. 1988 regarding the special case of hierarchical landscapes). We were able to identify this relationship by focusing on connectedness of only one landscape element (i.e., forest canopy), rather than using a composite metric such as contagion which reflects connectedness of all landscape elements (e.g., forest and open ground) simultaneously.

Our analysis showed that increased self-adjacency of forest cover allows percolation to occur at cover proportions lower than normal (i.e., at $pr(F) <$

0.59275). The effects of forest self-adjacency are particularly strong when forest cover is near the critical value and forest elements are randomly distributed (i.e., near $pr(F) = pr(F|F) = 0.59275$). Here, small increases in forest self-adjacency lead to large increases in percolation probability, or, similarly, allow percolation to occur at much lower cover proportions (Fig. 5b). At lower levels of forest cover, much higher increases in forest self-adjacency are required for percolation. The main uncertainty about this relationship comes under conditions of very high self-adjacency and low cover (e.g., $pr(F|F) > 0.7$ and $pr(F) < 0.5$). Under these conditions, percolation may only occur if shapes of forest have some linearity or directionality, in contrast to the amorphous clusters generated by the two algorithms we used to generate the structured random maps. The East-side landscapes we studied contained distinct linear features (Fig. 2), and possibly for this reason they fell into the vacant region of parameter space (Fig. 5a, upper left corner) that was unfilled by the random-map generation algorithms we used. This coincidence suggests a need for an extension of our work using map-generating algorithms that produce patch shapes with linear elements, and for classification of other patchily forested landscapes to determine how common such linear features are. Nevertheless, the consistency of the predictions from the alternative generating algorithms indicates that the logistic function provides a far more useful measure of landscape vulnerability to fragmentation than the $p_c = 0.59275$ threshold.

Implications for group selection in East-side Sierran landscapes

If this landscape is increasingly fragmented by group selection, what might be the implication? Connectivity, or the linkage of habitats, communities and ecological processes at multiple spatial and temporal scales, is an overarching principle of forest management for biodiversity (Noss 1991; Metzger and Decamps 1997; Lindenmayer et al. 2006), and there is increasing demand for connectivity analyses in forest management plans (e.g., Blackwell and Troyer 2004).

Percolation theory has proven useful in studies of conservation biology (Boswell et al. 1998; He and Hubbell 2003), but use of connectivity metrics as surrogates for biodiversity measurements (Metzger

and Decamps 1997; Lindenmayer et al. 2006) has been criticized on several accounts. One is that the interaction between organism behavior and landscape pattern determines connectivity, so connectivity can only be determined in relation to organism movement (Wiens et al. 1997; With 2002; Goodwin 2003). It may, however, be legitimate to use a generalized connectivity metric if it is clear that structural rather than functional connectivity is being measured (Calabrese and Fagan 2004). The use of general connectivity thresholds for classes of animals (e.g., large mobile animals) has also been criticized (Mönkkönen and Reunanen 1999), but development of a generalized, spatially explicit framework is deemed essential to conservation biology because of the impracticality of developing individual models for every species of management concern (With 1997).

The range of the American marten, continuous throughout the southern Cascades and northern Sierra in the twentieth century, now has large gaps. The marten was present in East-side forest in Plumas County early in the twentieth century, but there have been no detections in recent years despite populations to the north and south (Kucera et al. 1995; Kirk and Zielinski 2009). This absence is thought due to fragmentation and diminution of its preferred old-forest habitat (Zielinski et al. 2005). Martens avoid young forest and recently clear-cut or pre-commercially thinned forest (e.g., Godbaut and Ouellet 2008); in one study, martens were more likely to use patches of high quality forest that were within 45 m of contiguous forest than more distant patches (Chapin et al. 1998). The potential for group selection openings to further fragment the landscape in our study area, then, could aversely impact the ability of marten to recolonize the landscape.

In contrast, increased forest fragmentation due to group selection may help forests to resist crown fire. Wildfire is a major concern in national forest management in the western USA, and recent fires just in eastern Plumas County include the Antelope complex (2007; 9,200 ha), the Moonlight fire (2007; 26,300 ha) and the Boulder complex (2006; 1,400 ha). Percolation concepts are used to model fire spread (Hargrove et al. 2000; Bevers et al. 2004; Spyratos et al. 2007), although the wind and firebrand dynamics that characterize large fires may expand local interactions beyond nearest neighbors (Nahmias

et al. 2000). The coarser map resolutions (i.e., 30 m cells) at which we modeled landscapes may provide a more appropriate model for risk of fire spread than the smaller cells. Group selection openings are not intended as fuels treatments, but their apparent ability to function as part of a network of fuel breaks should be considered a potential benefit.

Summary

Group selection silviculture can increase fragmentation of East-side Sierran forest in areas that already have patchy canopy. We know of no adverse impacts on currently resident organisms, but such fragmentation would make the landscape less hospitable for one animal, the American marten, that was historically present and that has some possibility of naturally recolonizing. In contrast, there are potential benefits of fragmenting these forests for fire hazard reduction. We present a method for determining probability of percolation (and hence, fragmentation) from two parameters, proportion of forest cover and aggregation of forest elements, that can be derived from binary maps of forest project areas. The ability of our quantitative expression of percolation probability to reproduce percolation behavior observed in real landscapes suggests it may have applications beyond forest management.

References

Anderson SR, Family F (1988) Percolation in an interactive cluster-growth model. Phys Rev A 38(8):6

Bevers M, Omi PN, Hof J (2004) Random location of fuel treatments in wildland community interfaces: a percolation approach. Can J Forest Res 34:164–173

Blackwell J, Troyer JD (2004) Record of decision: Sierra Nevada forest plan amendment final supplemental environmental impact statement. USDA forest service management bulletin R5-MB-046, Pacific Southwest Region, Vallejo, California

Boswell GP, Britton NF, Franks NR (1998) Habitat fragmentation, percolation theory and the conservation of a keystone species. Proc R Soc Lond B 265:1921–1925

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Front Ecol Environ 2(10):529–536

California Interagency Wildlife Task Group (2005) Users manual for version 8.1 of the California Wildlife Habitat Relationships System and Bioview. California Department of Fish and Game, Sacramento

Callaway RM, DeLucia EH, Moore D et al (1994) Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology 77(7):2131–2140

Chapin TG, Harrison DJ, Katnik DD (1998) Influence of landscape pattern on habitat use by American marten in an industrial forest. Conserv Biol 12:196–227

Chayes JT, Chayes L, Durret R (1988) Connectivity properties of Mandelbrot's percolation process. Probab Theory Rel 77:307–324

DeLucia EH, Schlesinger WH, Billings WD (1988) Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. Ecology 69:303–311

Eyre FH (ed) (1980) Forest cover types of the United States and Canada. Society of American Foresters, Washington, DC

Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. J Wildlife Manage 61:603–610

Finney MA (2001) Design of regular landscape fuel treatment patterns for modifying fire growth and behavior. Forest Sci 47(2):219–228

Franklin JF, Forman RT (1987) Creating landscape patterns by cutting: ecological consequences and principles. Landscape Ecol 1:5–18

Franklin JF, Graber D, Johnson KN et al (1997) Alternative approaches to conservation of late-successional forest in the Sierra Nevada and their evaluation. In: Sierra Nevada Ecosystem Project: status of the Sierra Nevada: final report to congress: Addendum, Wildland Resource Center Report No. 40. University of California, Davis, pp 53–70

Godbaut G, Ouellet J-P (2008) Habitat selection of American marten in a logged landscape at the southern fringe of the boreal forest. Ecoscience 15(3):332–342

Goodwin BJ (2003) Is landscape connectivity a dependent or independent variable? Landscape Ecol 18(7):687–699

Grinnell J, Dixon J, Linsdale JM (1937) Fur-bearing mammals of California. University of California Press, Berkeley

Gustafson EJ, Parker GR (1992) Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecol 7(2):101–110

Hargis CD, Bissonette JA, David JL (1998) The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecol 13:167–186

Hargrove WW, Gardner RH, Turner MG et al (2000) Simulating fire patterns in heterogeneous landscapes. Ecol Model 135:243–263

He FL, Hubbell SP (2003) Percolation theory for the distribution and abundance of species. Phys Rev Lett 91:4

Helms JA (1980) The California region. In: Barrett JW (ed) Regional silviculture of the United States. Wiley, New York, pp 391–446

HFQLG (1998) The Herger-Feinstein Quincy Library Group Forest Recovery Act. P.L. 103–354, Section 401(j), Oct 1998

Hilborn R, Mangel M (1997) The ecological detective: confronting models with data. Princeton University Press, Princeton

Keitt TH (2000) Spectral representation of neutral landscapes. Landscape Ecol 15:479–493

Kimmins H (1992) Balancing act: environmental issues in forestry. UBC Press, Vancouver

Kirk TA, Zielinski WJ (2009) Developing and testing a landscape habitat suitability model for the American marten (Martes americana) in the Cascades mountains of California. Landscape Ecol 24:759–773

Kucera TE, Zielinski WJ, Barrett RH (1995) Current distribution of the American marten, *Martes americana*, in California. California Fish and Game 81(3):96–103

Laudenslayer WF, Darr HH, Smith S (1989) Historical effects of forest management practices on eastside pine communities in northeastern California. Multiresource Management of Ponderosa pine forest. RMRS-GTR-185, Rocky Mountain Forest and Range Experiment Station

Leak WB, Filip SM (1977) Thirty-eight years of group selection in New England northern hardwoods. J Forest 75:641–643

Leiberg JB (1902) Forest conditions in the northern Sierra Nevada, California. Forestry. Professional Paper No. 8, Series H, Forestry, 5, US Government Printing Office, Washington DC

Li BL (2001) Applications of fractal geometry and percolation theory to landscape analysis and assessments. In: Jensen ME, Bourgeron PS (eds) A guidebook for integrated ecological assessments. Springer, New York, pp 200–210

Li H, Franklin JF, Swanson FJ et al (1993) Developing alternative forest cutting patterns: a simulation approach. Landscape Ecol 8(1):63–75

Lindenmayer DB, Franklin JF, Fischer J (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. Biol Conserv 131(3):433–445

McDonald PM, Fiddler GO et al (2009) Naturally seeded versus planted ponderosa pine seedlings in group-selection openings. West J Appl For 24(1):48–54

McKelvey KS, Weatherspoon CP (1992) Projected trends in owl habitat. In: Verner J, McKelvey KS, Noon BR, et al (eds) The California spotted owl: a technical assessment of its current status. USDA Forest Service General Technical Report PSW-GTR-133, Pacific Southwest Research Station, Albany, California, pp 261–273

Metzger JP, Decamps H (1997) The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. Acta Oecol 18(1):1–12

Miller C, Urban DL (2000) Connectivity of forest fuels and surface fire regimes. Landscape Ecol 15:145–154

Milne BT, Johnson AR, Keitt TH et al (1996) Detection of critical densities associated with piñon-juniper woodland ecotones. Ecology 77(3):805–821

Mönkkönen M, Reunanen P (1999) On critical thresholds in landscape connectivity: a management perspective. Oikos 84(2):302–305

Nahmias J, Tephany H, Duarte J et al (2000) Fire spreading experiments on heterogeneous fuel beds. Applications of percolation theory. Can J Forest Res 30:1318–1328

Noss RF (1991) Landscape connectivity: different functions at different scales. In: Hudson WE (ed) Landscape linkages and biodiversity. Island Press, Covelo, pp 27–39

O'Neill RV, Gardner RH, Turner MG (1992) A hierarchical neutral model for landscape analysis. Landscape Ecol 7(1):55–61

Peterson GD (2002) Estimating resilience across landscapes. Conservation Ecology 6(1):17. [online] URL: http://www.consecol.org/vol6/iss1/art17/

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Sarkar D (2008) Lattice: multivariate data visualization with R. Springer, New York

Spencer WD, Barrett RH, Zielinski WJ (1983) Marten habitat preferences in the northern Sierra Nevada. J Wildlife Manage 47(4):1181–1186

Spyratos V, Bourgeron PS, Ghil M (2007) Development at the wildland-urban interface and the mitigation of forest-fire risk. Proc Natl Acad Sci 104:14272–14276

Stauffer D, Aharony A (1985) Introduction to percolation theory. Taylor and Francis, London

Szymura JM, Barton NH (1986) Genetic analysis of a hybrid zone between the firebellied toads near Cracow in southern Poland. Evolution 40(6):1141–1159

Turner MG, Romme WH (1994) Landscape dynamics in crown fire ecosystems. Landscape Ecol 9(1):59–77

Turner MG, Gardner RH, O'Neill RV (2001) Landscape ecology in theory and practice: pattern and process. Springer, New York

Wallin DO, Swanson FJ, Marks B (1994) Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecol Appl 4(3):569–580

Wiens JA, Schooley RL, Weeks RD (1997) Patch landscapes and animal movements: do beetles percolate? Oikos 78(2):257–264

With KA (1997) The application of neutral landscape models in conservation biology. Conserv Biol 11(5):1069–1080

With KA (2002) Using percolation theory to assess landscape connectivity and effects of habitat fragmentation. In: Gutzwiller K (ed) Applying landscape ecology in biological conservation. Springer, New York, pp 105–130

Zielinski WJ, Truex RL, Schlexer FV et al (2005) Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. J Biogeogr 32(8):1385–1407