Greater variability in local forest structure increases resistance to wildfire

Michael J Koontz[1], Malcolm P North[1,2], Constance I Millar[3], Stephen E Fick[4], Chhaya M Werner[5], and Andrew M Latimer[1]

[1] *Graduate Group in Ecology, University of California, Davis, CA 95616 USA*
[2] *USDA Forest Service, Pacific Southwest Research Station, Davis, CA 95618 USA*
[3] *USDA Forest Service, Sierra Nevada Research Center, Pacific Southwest Research Station, Albany, CA 94710 USA*
[4] *Stockholm Environment Institute, Stockholm 115 23, Sweden*
[5] *Center for Population Biology, University of California, Davis, CA 95616 USA*

Abstract

Variation in the size and distribution of trees can enable a forest to withstand ongoing disturbances and retain its essential identity and function. In the few centuries prior to Euro-American settlement, Sierra Nevadan mixed conifer forests in California exhibited such structural variation, and persisted with a disturbance regime of frequent, low- to moderate-severity wildfire and bark beetle activity. Climate change-induced hotter droughts and a century of fire suppression have disrupted this variability in forest structure, with unknown consequences for forest persistence. I use three approaches to assess how variability in forest structure affects resilience of mixed conifer forests: 1) correlate remote-sensed measures of forest structure variability with wildfire severity, 2) simulate an agent-based model of western pine beetle (WPB) outbreak spread through different forest structures, and 3) rear WPB from different forest structures in a common garden to assess variation in its pheromone-mediated dispersal.

Introduction

Biological systems comprising heterogeneous elements can retain their fundamental properties in the face of regular disturbance. This ability of a heterogeneous system to absorb disturbances, reorganize, and to persist within a domain of stability with respect to its identity, structure, function, and feedbacks is termed resilience (Holling 1973, Gunderson 2000, Folke et al. 2004, Walker et al. 2004). Resilience (*sensu* Walker et al. (2004)) is characterized by four critical features: 1) latitude, which describes the degree to which a system can deviate from an attracting state and still recover to that state, 2) resistance, which describes the intensity or duration of a disturbance required to change the system state, 3) precariousness, which describes the proximity of a system to a threshold of a different domain of stability, and 4) panarchy, which describes how resilience features interact across multiple scales of organization. Resilience has been demonstrated in complex biological systems characterized by a variety of different types of "heterogeneity" including genetic diversity ((Reusch et al. 2005, Baskett et al. 2009, Agashe 2009), species diversity ((Tilman 1994, Chesson 2000, Cadotte et al. 2013), functional diversity (Gazol and Camarero 2016), topoclimatic complexity (Ackerly et al. 2010, Lenoir et al. (2013)), and temporal environmental variation (Questad and Foster 2008). An emerging paradigm in forest ecology is that spatial heterogeneity in the structure of vegetation on the landscape can

confer resilience to disturbances such as wildfire, drought, and insect outbreaks (Stephens et al. 2008, North et al. 2009, Virah-Sawmy et al. 2009). Forests are globally important ecosystems threatened in a number of ways, and protection of forests is of high management priority (Hansen et al. 2013, Crowther et al. 2015, Millar and Stephenson 2015). Thus, it is critical to understand the mechanisms underlying the effect of spatial heterogeneity in forest structure on forest resilience.

Forest structure is defined by the size and distribution of trees on the landscape. Differences in tree crown heights characterize vertical structure, while differences in the rooting locations of trees characterizes horizontal structure (North et al. 2009). Structural patterns can be further parsed by the constituent species present. In the Sierra Nevada range of California, forests are dominated by a mixture of conifer species including ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and red fir (*Abies magnifica*) (Stephens and Collins 2004, Collins et al. 2015). Tree density in the early 20th century was relatively low, with about 25-79 trees/ha and about 8-30 m2/ha of live basal area (Collins et al. 2015). Previous work described the historical distribution of trees in the Sierra Nevada as an "ICO pattern," which refers to its three distinct features: individual trees (I), clumps of trees with interlocking crowns (C), and openings with no tree cover at all (O) (Larson and Churchill 2012). The ICO pattern manifests at small spatial extents between 0.2 and 1.2 ha and is maintained by feedbacks with spatially explicit ecological processes (Larson and Churchill 2012, Lydersen et al. 2013, Fry et al. 2014). Competition for light, water, and other resources can yield aggregations of trees within favorable microsites or more widely spaced trees to ameliorate detrimental interactions (Clyatt et al. 2016). Demographic processes of dispersal, recruitment, and mortality affect forest structure by adding or subtracting whole trees. Reciprocally, the forest structure can also influence these pattern-forming processes such as when vegetation overstory alters microclimate or changes tree demographic rates (Larson and Churchill 2012, De Frenne et al. 2013, Ford et al. 2013). The stabilizing effects of these reciprocal processes in forests are hallmarks of a resilient system (Folke et al. 2004). In the Sierra Nevada range of California, the strongest feedbacks between forest structure and pattern-generating ecological process relate to the widespread disturbances caused by wildfire and bark beetle outbreaks (Raffa et al. 2008, Larson and Churchill 2012, Millar and Stephenson 2015). Wildfire and bark beetle outbreaks both kill live trees, affect hundreds of thousands to millions of hectares of forested area per year, and interact dynamically with the forest structures they encounter (Westerling et al. 2006, Raffa et al. 2008, Park Williams et al. 2012, Larson and Churchill 2012).

In an ecological framework, wildfire is typically classified into different fire regimes that describe how frequently and how intensely they burn (Mandle et al. 2011, Keeley et al. 2011, Steel et al. 2015). For instance,

2

⁶⁸ mixed conifer forests in the Sierra Nevada burned every 11 years on average for several centuries prior to

⁶⁹ Euro-American settlement (Steel et al. 2015). These relatively frequent burns prevented the accumulation

⁷⁰ of fuel on the ground, and limited the intensity of the next fire. This average fire return interval is short

⁷¹ compared to the regeneration time of the dominant species, so the fire regime of Sierra Nevada mixed conifer

⁷² forests in this period is usually classified as a "high frequency/low-mid severity" (Steel et al. 2015). However,

⁷³ wildfire behavior is inherently complex and is influenced by local weather, topography, and heterogeneous

⁷⁴ fuel conditions created by departures from the average fire return interval at any particular place (Sugihara

⁷⁵ and Barbour 2006, Collins and Stephens 2010). Wildfire can affect the future forest structure by changing

⁷⁶ demographic rates of individual trees (e.g. increasing growth or germination via increasing light or nitrogen

⁷⁷ availability), but it's most lasting impact to forest structure is in the pattern of killed trees left in its wake

⁷⁸ (Larson and Churchill 2012). Reciprocally, forest structure can influence fire behavior: for instance, high tree

⁷⁹ density and presence of "ladder fuels" in the understory increase the probability of crown fire that kills a

⁸⁰ high proportion of trees (Stephens et al. 2008, North et al. 2009).

⁸¹ Resilience has gained new attention in light of anthropogenic global change because of the potential for novel

⁸² disturbance regimes to exceed a system's capacity to recover (Millar et al. 2007, Turner et al. 2013). Beyond

⁸³ these thresholds, catastrophic shifts in ecosystems are likely, with myriad consequences for ecosystems and the

⁸⁴ services they provide (Scheffer et al. 2001, Turner et al. 2013). Changes in wildfire disturbance regimes and

⁸⁵ bark beetle outbreak dynamics are particularly suited to catalyze catastrophic shifts in ecosystems because of

⁸⁶ their feedback with spatial forest heterogeneity at multiple scales (Raffa et al. 2008). Anthropogenic global

⁸⁷ change and a century of fire suppression policy in the United States have resulted in forest conditions far

⁸⁸ outside their range of historic variability, with potentially dire consequences for society (North et al. 2015).

⁸⁹ In California, increasing temperature couples with increasing drought frequency to exacerbate water stress

⁹⁰ and drive tree mortality during "hotter droughts" (Park Williams et al. 2012, Millar and Stephenson 2015).

⁹¹ Further, a century of fire suppression policy has led to drastic changes in forest structure (North et al. 2015).

⁹² Canopy cover has increased by 25-49%, overall tree density has increased by >75%, and white fir (*Abies*

⁹³ *concolor*) makes up a greater percentage of basal area compared to forests in the early 20th century (Stephens

⁹⁴ et al. 2015). The change in tree density is underlaid by a shift in size distribution: modern mixed conifer

⁹⁵ forests have 2.5 times as many trees between 30.4 and 61.0cm diameter at breast height (dbh) per hectare

⁹⁶ (103.9 versus 41.0 trees/ha) and half as many trees greater than 91.4cm dbh per hectare (8.7 versus 16.7

⁹⁷ trees/ha) compared to forests in 1911 (Stephens et al. 2015). Thus, western North American forests are

⁹⁸ experiencing novel, "unhealthy" conditions (*sensu* Raffa et al. (2009)) that are liable to upset the feedbacks

⁹⁹ between forest structure and pattern-forming ecological disturbances that historically stabilized the system

and made it resilient (Raffa et al. 2008, Millar and Stephenson 2015).

What are the mechanisms by which spatial variability in forest structure confers resilience to California mixed conifer forests?

Background

Previous work has suggested that forests with heterogeneous structures are more resistant to wildfire, and are less precariously positioned with respect to alternative system states (Graham et al. 2004, Moritz et al. 2005, Stephens et al. 2008). However, it is unclear whether this is true at broad spatial extents, nor is it resolved at what scale heterogeneity in forest structure is meaningful for resilience (Kotliar and Wiens 1990). Low resistance or high precariousness could imply a more likely catastrophic shift to an alternate stable state as anthropogenic change alters the feedback between forest structure and pattern-forming disturbance regimes in the Sierra Nevada. A forest that is resistant to wildfire will be less impacted following a disturbance of that type. In forests with relatively intact fire regimes and heterogeneous stand conditions such as in the Jeffrey pine forests of the Sierra San Pedro Martir in Baja, California, there tends to be reduced vegetation mortality after wildfires compared to fire-suppressed forests (Stephens et al. 2008). A heterogeneous forest can largely avoid overstory tree mortality because a reduced amount of accumulated ladder fuel decreases its ability to get into the crown (where mortality is more likely to result), because widely-spaced tree clumps interrupt fire spread across the landscape, and because tree clumps with fewer trees don't facilitate self-propagating fire behavior (Graham et al. 2004, Scholl and Taylor 2010). Thus, forests with heterogeneous structure are predicted to persist in that state due to resistance to inevitable wildfire disturbance. The distribution of patch sizes of fire may represent a key pattern signaling resilience in a forest (Kefi et al. 2011, Svejcar et al. 2015). There is some evidence that this distribution is stable under typical wildfire disturbance regimes, but is fundamentally altered when disturbance regimes lie outside the range of their historical variation (Collins et al. 2009, Miller et al. 2009b). For instance, in fire-suppressed forests, there has been an increase in the average and maximum patches of high severity fire compared to historic conditions (Miller et al. 2009b). The patch size distribution of fires can be described with a power law distribution (Malamud et al. 2005, Moritz et al. 2005), and departures can be early warning signals of regime shifts (Kefi et al. 2011). Changes from historic distributions would indicate a shift in the underlying parameters that historically constrained the systems' movement within the stability landscape. It is unclear whether observed increases in mean and maximum patch sizes through time are also accompanied by fundamental shifts in the distribution of patch sizes, a potential signal of forest precariousness to a threshold of an alternate stable state (Coppoletta et al.

4

130 2016). Here, I ask two questions: 1) What is the effect of heterogeneity of forest structure on wildfire severity,

131 and 2) Has there been an increase in forest precariousness over the last 30 years, as measured by changes in

132 patch size distribution?

133 Approach

134 Wildfire severity is defined by the percentage of fire-killed vegetation in an area, and it can be reliably

135 measured by comparing pre- and post-fire satellite imagery. I used imagery from the Landsat 5 satellite,

136 which provided publically available imagery of the whole earth at 30m spatial resolution every 16 days from

137 1984 to 2013. The relativized difference in normalized burn ratio (RdNBR) is a measurement of wildfire

138 severity that is calculated using the near infrared (band 4) and short wave infrared band (band 7) of the

139 Landsat 5 satellite according to Miller and Thode (2007):

$$NBR = \frac{NIR(Band4) - SWIR(Band7)}{NIR(Band4) + SWIR(Band7)}$$

$$dNBR = NBR_{postfire} \smile NBR_{prefire}$$

$$RdNBR = \frac{dNBR}{\sqrt{\left|\frac{NBR_{prefire}}{1000}\right|}}$$

140 This measure positively correlates with burn severity in mixed conifer forests in California (Miller et

141 al. 2009a). All analyses were performed within the bounds of known fire perimeters >4 hectares in

142 the Sierra Nevada region since 1984 as defined by the Fire and Resource Assessment Program (FRAP,

143 http://frap.fire.ca.gov/projects/fire_data/fire_perimeters_index), which is the most comprehensive digital

144 record of fire occurrence in California. Prefire NBR was calculated as the median NBR value per pixel for

145 the 3 months prior to the fire date after masking clouds and non-forest pixels (median of approximately 6

146 images). The post-fire NBR was calculated as the median NBR value per pixel from images between 9 and

147 12 months after the fire (i.e. exactly one year after the set of pre-fire NBR images). RdNBR was calculated

148 for all fires within the Sierra Nevada between 1985 and 2012.

149 What is the effect of spatial heterogeneity on wildfire resistance?

150 Publically available digital elevation maps (DEM) were used to assess slope and aspect of the forested area

151 within fire perimeters at a 30m spatial resolution. I added 135 degrees to all aspect values and cosine

152 transformed them so that values of -1 represented northeast aspects, and values of 1 represented southwest

153 aspects to best capture heat loading in the northern hemisphere (McCune and Keon 2002). The normalized

154 difference in water index (NDWI) can be used to assess canopy density, and it was calculated for all pixels

according to Jackson et al. (2004) using bands 4 and 5 from the Landsat 5 imagery:

$$NDWI = \frac{NIR(Band4) - SWIR(Band5)}{NIR(Band4) + SWIR(Band5)}$$

A measure of heterogeneity was derived which used focal operations to calculate the standard deviation of NDWI within a certain sized neighborhood around each pixel (Tuanmu and Jetz 2015). Five neighborhood sizes were used (radii of 30m, 45m, 56m, 79m, 113m) corresponding to a moving neighborhood window of 0.28 ha, 0.64 ha, 0.99 ha, 2.0 ha, and 4.0 ha. Imagery was downsampled by a factor of 100 to reduce spatial autocorrelation. I scaled all predictor variables, and treated each individual fire as having a random intercept effect using the following mixed effects model:

Each neighborhood size was substituted in turn for the heterogeneity of NDWI covariate, to generate a candidate set of 5 models which were compared using AIC. The model with the best out-of-sample prediction was further analyzed by comparing the B coefficients to assess the relative effect of each predictor on wildfire severity. Has there been an increase in forest precariousness over the past 30 years? We correlated the RdNBR values calculated above to field-measured severity (composite burn index, or CBI) collated from two separate Joint Fire Sciences Program projects (Zhu et al. 2006, Sikkink et al. 2013). We determined the threshold RdNBR value that corresponded to "high severity" classification in the CBI data (CBI > 2.25). For the entire dataset, all pixels greater than this threshold were considered "high severity burns." I vectorized all neighboring pixels classified as high severity to generate polygons that represented distinct patches of high severity. The centroid of each patch, and the patch area were calculated. We separated the patches by whether they occurred in areas that experienced a large influence of fire suppression or not relative to pre-Euro-American settlement expectations (Safford and Van de Water 2014). If the centroid of the patch was located in an area with >33% Mean Fire Return Interval Depature (mFRID), it was considered to have burned under a heavy influence of fire suppression. The distributions of fire-suppressed versus fire-restored high severity patch sizes were evaluated using a Power Law. Power law distributions are described by the following model:

Preliminary Results

Figure 1. Downsampled RdNBR data from the Hamm Fire of 1987 (part of the Stanislaus Complex Fire) The model that used a standard deviation of NDWI within a 56m radius (approximately a 1ha window) had the best out-of-sample prediction. In this model, the heterogeneity had a strong negative effect on RdNBR

that was greater in magnitude than slope (by a factor of 3) or aspect (by a factor of 4). Slope appeared to have a negative correlation with severity, which was counter to expectations. Further exploration of these results may explain this seeming discrepancy.

Figure 2. Example of mapped high severity patch sizes within the Hamm Fire. Circles are centered at the centroid of each patch and circle area is proportional to patch area.

Figure 3. High severity patch size distribution and departures from pure power law in fire suppressed (mean Fire Return Interval Departure [mFRID] greater than 33%) and fire restored areas (mFRID less than 33%) in the Sierra Nevada. Between 1985 and 2012, 107,182 high severity patches were identified ranging in size from 0.09ha to 9,074ha. As a first step to a fully hierarchical solution, I fit the patch sizes from fire-suppressed and fire-restored areas to different power law distributions by regressing the log of the patch sizes on the log of the proportion of patch sizes greater than each size. I compared the slopes of each fit, and estimated the patch size at which each distribution departed from a true power law. High severity patch sizes in fire-suppressed forests tend to be larger (shallower slope indicates that, for a given patch size, there is a greater probability of another patch being larger). Also, the patch size at which the distribution departs from a pure power law distribution is much smaller relative to the total range of patch sizes in the fire-suppressed compared to fire-restored areas. Departures from power law distributions of the high severity patch size in fire-suppressed forests could be an early warning signal of a catastrophic shift in the patch generating process, but further work is needed to assess how this framework may apply to systems in which the "patches" represent the disturbance rather than the system state itself (Kefi et al. 2011, Kéfi et al. 2014).

Future Directions

The heterogeneity measure (standard deviation of NDWI in a 2ha moving window) can be fine-tuned and put into context by cross walking it with imagery at a finer spatial resolution (but with a cost in temporal resolution and time series depth; e.g. NAIP imagery at 1m resolution but with only 3 total images starting in 2008) (Dickinson et al. 2016). Additional metrics of heterogeneity such as vegetation patch size distributions or non-vegetated gap size distributions, may also be more tractable using the finer spatial resolution of NAIP imagery, though the specific fires used in these analyses will be limited to those taking place after 2008. If heterogeneous forests are more resilient to fire, then we expect heterogeneity to be relatively maintained after fire. I plan to test this hypothesis using the finer spatial resolution imagery provided by NAIP. The spatial autocorrelation inherent in analyses of spatial processes is an important consideration for model inference, because it challenges the assumptions of standard statistical techniques. Future directions for this work will

include more explicit tests of spatial autocorrelation in the residuals of the model, and modeling techniques that account for some of the autocorrelated residual error with neighborhood effects. Rather than a simple linear model, the model would be:

Ackerly, D. D., S. R. Loarie, W. K. Cornwell, S. B. Weiss, H. Hamilton, R. Branciforte, and N. J. B. Kraft. 2010. The geography of climate change: Implications for conservation biogeography. Diversity and Distributions 16:476–487.

Agashe, D. 2009. The stabilizing effect of intraspecific genetic variation on population dynamics in novel and ancestral habitats. The American Naturalist 174:255–67.

Baskett, M. L., S. D. Gaines, and R. M. Nisbet. 2009. Symbiont diversity may help coral reefs survive moderate climate change. Ecological Applications 19:3–17.

Cadotte, M., C. H. Albert, and S. C. Walker. 2013. The ecology of differences: Assessing community assembly with trait and evolutionary distances. Ecology Letters 16:1234–1244.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clyatt, K. A., J. S. Crotteau, M. S. Schaedel, H. L. Wiggins, H. Kelley, D. J. Churchill, and A. J. Larson. 2016. Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. Forest Ecology and Management 361:23–37.

Collins, B. M., and S. L. Stephens. 2010. Stand-replacing patches within a 'mixed severity' fire regime: Quantitative characterization using recent fires in a long-established natural fire area. Landscape Ecology 25:927–939.

Collins, B. M., J. M. Lydersen, R. G. Everett, D. L. Fry, and S. L. Stephens. 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecological Applications 25:1167–1174.

Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. Van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. Ecosystems 12:114–128.

Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecological Applications 26:686–699.

Crowther, T. W., H. B. Glick, K. R. Covey, C. Bettigole, D. S. Maynard, S. M. Thomas, J. R. Smith, G. Hintler, M. C. Duguid, G. Amatulli, M.-N. Tuanmu, W. Jetz, C. Salas, C. Stam, D. Piotto, R. Tavani, S. Green, G. Bruce, S. J. Williams, S. K. Wiser, M. O. Huber, G. M. Hengeveld, G.-J. Nabuurs, E. Tikhonova, P.

Borchardt, C. F. Li, L. W. Powrie, M. Fischer, A. Hemp, J. Homeier, P. Cho, A. C. Vibrans, P. M. Umunay, S. L. Piao, C. W. Rowe, M. S. Ashton, P. R. Crane, and M. A. Bradford. 2015. Mapping tree density at a global scale. Nature 525:201–205.

De Frenne, P., F. Rodríguez-Sánchez, D. A. Coomes, L. Baeten, G. Verstraeten, M. Vellend, M. Bernhardt-Römermann, C. D. Brown, J. Brunet, J. Cornelis, G. M. Decocq, H. Dierschke, O. Eriksson, F. S. Gilliam, R. Hédl, T. Heinken, M. Hermy, P. Hommel, M. A. Jenkins, D. L. Kelly, K. J. Kirby, F. J. G. Mitchell, T. Naaf, M. Newman, G. Peterken, P. Petrík, J. Schultz, G. Sonnier, H. Van Calster, D. M. Waller, G.-R. Walther, P. S. White, K. D. Woods, M. Wulf, B. J. Graae, and K. Verheyen. 2013. Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences of the United States of America 110:18561–5.

Dickinson, Y., K. Pelz, E. Giles, and J. Howie. 2016. Have we been successful? Monitoring horizontal forest complexity for forest restoration projects. Restoration Ecology 24:8–17.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557–581.

Ford, K. R., A. K. Ettinger, J. D. Lundquist, M. S. Raleigh, and J. Hille Ris Lambers. 2013. Spatial heterogeneity in ecologically important climate variables at coarse and fine scales in a high-snow mountain landscape. PLoS ONE 8:e65008.

Fry, D. L., S. L. Stephens, B. M. Collins, M. P. North, E. Franco-Vizcaíno, and S. J. Gill. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. PLoS ONE 9:e88985.

Gazol, A., and J. J. Camarero. 2016. Functional diversity enhances silver fir growth resilience to an extreme drought. Journal of Ecology.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. Page 43. US Department of Agriculture, Forest Service, Rokcy Mountain Research Station, Fort Collins, CO.

Gunderson, L. H. 2000. Ecological resilience– in theory and application. Annual Review of Ecology and Systematics 31:425–439.

Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, and A. Tyukavina. 2013.

High-resolution global maps of 21st-century forest cover change. Science 342:850–853.

Holling, C. S. 1973. Resilience and Stability of Ecological Systems. Annual Review of Ecology and Systematics 4:1–23.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16:406–11.

Kefi, S., M. Rietkerk, M. Roy, A. Franc, P. C. De Ruiter, and M. Pascual. 2011. Robust scaling in ecosystems and the meltdown of patch size distributions before extinction. Ecology Letters 14:29–35.

Kotliar, N. B., and J. a Wiens. 1990. Multiple Scales of Patchiness and Patch Structure: A Hierarchical Framework for the Study of Heterogeneity. Oikos 59:253–260.

Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.

Lenoir, J., B. J. Graae, P. A. Aarrestad, I. G. Alsos, W. S. Armbruster, G. Austrheim, C. Bergendorff, H. J. B. Birks, K. A. Bråthen, J. Brunet, H. H. Bruun, C. J. Dahlberg, G. Decocq, M. Diekmann, M. Dynesius, R. Ejrnæs, J. A. Grytnes, K. Hylander, K. Klanderud, M. Luoto, A. Milbau, M. Moora, B. Nygaard, A. Odland, V. T. Ravolainen, S. Reinhardt, S. M. Sandvik, F. H. Schei, J. D. M. Speed, L. U. Tveraabak, V. Vandvik, L. G. Velle, R. Virtanen, M. Zobel, and J. C. Svenning. 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. Global Change Biology 19:1470–1481.

Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: Reference conditions and long-term changes following fire suppression and logging. Forest Ecology and Management 304:370–382.

Malamud, B. D., J. D. A. Millington, and G. L. W. Perry. 2005. Characterizing wildfire regimes in the United States. Proceedings of the National Academy of Sciences of the United States of America 102:4694–4699.

Mandle, L., J. L. Bufford, I. B. Schmidt, and C. C. Daehler. 2011. Woody exotic plant invasions and fire: Reciprocal impacts and consequences for native ecosystems. Biological Invasions 13:1815–1827.

McCune, B., and D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13:603–606.

Millar, C. I., and N. L. Stephenson. 2015. Temperate forest health in an era of emerging megadisturbance.

299 Science 349:823–826.

300 Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: Managing

301 in the face of uncertainty. Ecological Applications 17:2145–2151.

302 Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative

303 version of the delta Normalized Burn Ratio (dNBR). Remote Sensing of Environment 109:66–80.

304 Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009a.

305 Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of

306 fire severity in the Sierra Nevada and Klamath Mountains, California, USA. Remote Sensing of Environment

307 113:645–656.

308 Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009b. Quantitative evidence for increasing

309 forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA.

310 Ecosystems 12:16–32.

311 Moritz, M. A., M. E. Morais, L. A. Summerell, J. M. Carlson, and J. Doyle. 2005. Wildfires, complexity, and

312 highly optimized tolerance. Proceedings of the National Academy of Sciences 102:17912–7.

313 North, M. P., S. L. Stephens, B. M. Collins, J. K. Agee, G. Aplet, J. F. Franklin, and P. Z. Fulé. 2015.

314 Reform forest fire managment. Science 349:1280–1281.

315 North, M., P. Stine, K. O. Hara, W. Zielinski, and S. Stephens. 2009. An Ecosystem Management Strategy

316 for Sierran Mixed- Conifer Forests. General Technical Report PSW-GTR-220:1–49.

317 Park Williams, A., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam,

318 S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and

319 N. G. McDowell. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality.

320 Nature Climate Change 3:292–297.

321 Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species

322 sorting in grassland plant communities. Ecology Letters 11:717–726.

323 Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008.

324 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle

325 eruptions. BioScience 58:501.

326 Raffa, K. F., B. Aukema, B. J. Bentz, A. Carroll, N. Erbilgin, D. A. Herms, J. A. Hicke, R. W. Hofstetter,

327 S. Katovich, B. S. Lindgren, J. Logan, W. Mattson, A. S. Munson, D. J. Robison, D. L. Six, P. C. Tobin,

P. A. Townsend, and K. F. Wallin. 2009. A literal use of 'forest health' safeguards against misuse and misapplication. Journal of Forestry:276–277.

Reusch, T. B. H., A. Ehlers, A. Hämmerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proceedings of the National Academy of Sciences 102:2826–2831.

Safford, H. D., and K. M. Van de Water. 2014. Using fire return interval departure (FRID) analysis to map spatial and temporal changes in fire frequency on National Forest lands in California. Page 59. US Department of Agriculture Forest Service, Albany, CA, USA.

Scheffer, M., S. Carpenter, J. a Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. Ecological Applications 20:362–380.

Sikkink, P. G., G. K. Dillon, R. E. Keane, P. Morgan, E. C. Karau, Z. A. Holden, and R. P. Silverstein. 2013. Composite Burn Index (CBI) data and field photos collected for the FIRESEV project, western United States. Forest Service Research Data Archive, Fort Collins, CO.

Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6:1–23.

Stephens, S. L., and B. M. Collins. 2004. Fire regimes of mixed conifer forests in the North-Central Sierra Nevada at multiple scales. Northwest Science 78:12–23.

Stephens, S. L., D. L. Fry, and E. Franco-Vizcaíno. 2008. Wildfire and spatial patterns in forests in northwestern Mexico: The United States wishes it had similar fire problems. Ecology and Society.

Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6:1–63.

Sugihara, N. G., and M. G. Barbour. 2006. Fire and California vegetation. Pages 1–9 *in* N. G. Sugihara, J. W. Van Wagtendonk, K. E. Shaffer, J. Fites-Kaufman, and A. E. Thode, editors. Fire in california's ecosystems. 1st editions. University of California Press, Berkeley; Los Angeles, CA, USA.

Svejcar, L. N., B. T. Bestelmeyer, M. C. Duniway, and D. K. James. 2015. Scale-dependent feedbacks

between patch size and plant reproduciton in desert grassland. Ecosystems 18:146–153.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tuanmu, M.-N., and W. Jetz. 2015. A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. Global Ecology and Biogeography:n/a–n/a.

Turner, M. G., D. C. Donato, and W. H. Romme. 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: Priorities for future research. Landscape Ecology 28:1081–1097.

Virah-Sawmy, M., K. J. Willis, and L. Gillson. 2009. Threshold response of Madagascar's littoral forest to sea-level rise. Global Ecology and Biogeography 18:98–110.

Walker, B., C. S. Holling, S. R. Carpenter, and A. Kinzig. 2004. Resilience, adaptability, and transformability in social-ecological systems. Ecology and Society 9:5.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

Zhu, Z., C. Key, D. Ohlen, and N. Benson. 2006. Evaluate Sensitivities of Burn-Severity Mapping Algorithms for Different Ecosystems and Fire Histories in the United States. Final Report to the Joint Fire Science Program, Project JFSP 01-1-4-12:1–35.