

Greater variability in local forest structure increases resistance to wildfire

MICHAEL J KOONTZ¹, MALCOLM P NORTH^{1, 2}, CONSTANCE I MILLAR³, STEPHEN E FICK⁴, CHHAYA M WERNER⁵,
and ANDREW M LATIMER¹

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. We test this phenomenon at a broad spatial extent in California's Sierra Nevada region using remotely-sensed data corroborated with on the ground measurements. We find that greater heterogeneity in local forest structure reduces the severity of wildfires. Heterogeneous forest structure thus makes mixed conifer forest in the Sierra Nevada more resistant to this inevitable disturbance, and may increase the probability of its long-term persistence. Management activities that seek to increase forest heterogeneity, such as prescribed fire, should be continued.

Key words: resilience; wildfire severity; RdNBR; remote sensing

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,

36 Millar and Stephenson 2015). Thus, it is critical to understand the mechanisms underlying the effect of
37 spatial heterogeneity in forest structure on forest resilience.

38 Forest structure is defined by the size and distribution of trees on the landscape. Differences in tree crown
39 heights characterize vertical structure, while differences in the rooting locations of trees characterizes horizontal
40 structure (North et al. 2009). Structural patterns can be further parsed by the constituent species present.
41 In the Sierra Nevada range of California, forests are dominated by a mixture of conifer species including
42 ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense-cedar (*Calocedrus decurrens*),
43 Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), and red fir (*Abies magnifica*) (Stephens and
44 Collins 2004, Collins et al. 2015). Tree density in the early 20th century was relatively low, with about
45 25-79 trees/ha and about 8-30 m²/ha of live basal area (Collins et al. 2015). Previous work described the
46 historical distribution of trees in the Sierra Nevada as an “ICO pattern,” which refers to its three distinct
47 features: individual trees (I), clumps of trees with interlocking crowns (C), and openings with no tree cover
48 at all (O) (Larson and Churchill 2012). The ICO pattern manifests at small spatial extents between 0.2
49 and 1.2 ha and is maintained by feedbacks with spatially explicit ecological processes (Larson and Churchill
50 2012, Lydersen et al. 2013, Fry et al. 2014). Competition for light, water, and other resources can yield
51 aggregations of trees within favorable microsites or more widely spaced trees to ameliorate detrimental
52 interactions (Clyatt et al. 2016). Demographic processes of dispersal, recruitment, and mortality affect forest
53 structure by adding or subtracting whole trees. Reciprocally, the forest structure can also influence these
54 pattern-forming processes such as when vegetation overstory alters microclimate or changes tree demographic
55 rates (Larson and Churchill 2012, De Frenne et al. 2013, Ford et al. 2013). The stabilizing effects of these
56 reciprocal processes in forests are hallmarks of a resilient system (Folke et al. 2004). In the Sierra Nevada
57 range of California, the strongest feedbacks between forest structure and pattern-generating ecological process
58 relate to the widespread disturbances caused by wildfire and bark beetle outbreaks (Raffa et al. 2008, Larson
59 and Churchill 2012, Millar and Stephenson 2015). Wildfire and bark beetle outbreaks both kill live trees,
60 affect hundreds of thousands to millions of hectares of forested area per year, and interact dynamically with
61 the forest structures they encounter (Westerling et al. 2006, Raffa et al. 2008, Park Williams et al. 2012,
62 Larson and Churchill 2012).

63 In an ecological framework, wildfire is typically classified into different fire regimes that describe how frequently
64 and how intensely they burn (Mandle et al. 2011, Keeley et al. 2011, Steel et al. 2015). For instance,
65 mixed conifer forests in the Sierra Nevada burned every 11 years on average for several centuries prior to
66 Euro-American settlement (Steel et al. 2015). These relatively frequent burns prevented the accumulation
67 of fuel on the ground, and limited the intensity of the next fire. This average fire return interval is short

compared to the regeneration time of the dominant species, so the fire regime of Sierra Nevada mixed conifer forests in this period is usually classified as a “high frequency/low-mid severity” (Steel et al. 2015). However, wildfire behavior is inherently complex and is influenced by local weather, topography, and heterogeneous fuel conditions created by departures from the average fire return interval at any particular place (Sugihara and Barbour 2006, Collins and Stephens 2010). Wildfire can affect the future forest structure by changing demographic rates of individual trees (e.g. increasing growth or germination via increasing light or nitrogen availability), but its most lasting impact to forest structure is in the pattern of killed trees left in its wake (Larson and Churchill 2012). Reciprocally, forest structure can influence fire behavior: for instance, high tree density and presence of “ladder fuels” in the understory increase the probability of crown fire that kills a high proportion of trees (Stephens et al. 2008, North et al. 2009).

Resilience has gained new attention in light of anthropogenic global change because of the potential for novel disturbance regimes to exceed a system’s capacity to recover (Millar et al. 2007, Turner et al. 2013). Beyond these thresholds, catastrophic shifts in ecosystems are likely, with myriad consequences for ecosystems and the services they provide (Scheffer et al. 2001, Turner et al. 2013). Changes in wildfire disturbance regimes and bark beetle outbreak dynamics are particularly suited to catalyze catastrophic shifts in ecosystems because of their feedback with spatial forest heterogeneity at multiple scales (Raffa et al. 2008). Anthropogenic global change and a century of fire suppression policy in the United States have resulted in forest conditions far outside their range of historic variability, with potentially dire consequences for society (North et al. 2015). In California, increasing temperature couples with increasing drought frequency to exacerbate water stress and drive tree mortality during “hotter droughts” (Park Williams et al. 2012, Millar and Stephenson 2015). Further, a century of fire suppression policy has led to drastic changes in forest structure (North et al. 2015). Canopy cover has increased by 25-49%, overall tree density has increased by >75%, and white fir (*Abies concolor*) makes up a greater percentage of basal area compared to forests in the early 20th century (Stephens et al. 2015). The change in tree density is underlain by a shift in size distribution: modern mixed conifer forests have 2.5 times as many trees between 30.4 and 61.0cm diameter at breast height (dbh) per hectare (103.9 versus 41.0 trees/ha) and half as many trees greater than 91.4cm dbh per hectare (8.7 versus 16.7 trees/ha) compared to forests in 1911 (Stephens et al. 2015). Thus, western North American forests are experiencing novel, “unhealthy” conditions (*sensu* Raffa et al. (2009)) that are liable to upset the feedbacks 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. 2016). Here, I ask two questions: 1) What is the effect of heterogeneity of forest structure on wildfire severity, and 2) Has there been an increase in forest precariousness over the last 30 years, as measured by changes in patch size distribution?

Methods

We used on-the-ground measurements of wildfire severity, the Composite Burn Index

Wildfire severity is defined by the percentage of fire-killed vegetation in an area, and it can be reliably measured by comparing pre- and post-fire satellite imagery. I used imagery from the Landsat 5 satellite, which provided publically available imagery of the whole earth at 30m spatial resolution every 16 days from 1984 to 2013. The relativized difference in normalized burn ratio (RdNBR) is a measurement of wildfire severity that is calculated using the near infrared (band 4) and short wave infrared band (band 7) of the Landsat 5 satellite according to Miller and Thode (2007):

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

$$dNBR = NBR_{postfire} - NBR_{prefire}$$

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

This measure positively correlates with burn severity in mixed conifer forests in California (Miller et al. 2009a). All analyses were performed within the bounds of known fire perimeters >4 hectares in the Sierra Nevada region since 1984 as defined by the Fire and Resource Assessment Program (FRAP, http://frap.fire.ca.gov/projects/fire_data/fire_perimeters_index), which is the most comprehensive digital record of fire occurrence in California. Prefire NBR was calculated as the median NBR value per pixel for the 3 months prior to the fire date after masking clouds and non-forest pixels (median of approximately 6 images). The post-fire NBR was calculated as the median NBR value per pixel from images between 9 and 12 months after the fire (i.e. exactly one year after the set of pre-fire NBR images). RdNBR was calculated for all fires within the Sierra Nevada between 1985 and 2012.

What is the effect of spatial heterogeneity on wildfire resistance?

Publically available digital elevation maps (DEM) were used to assess slope and aspect of the forested area within fire perimeters at a 30m spatial resolution. I added 135 degrees to all aspect values and cosine transformed them so that values of -1 represented northeast aspects, and values of 1 represented southwest aspects to best capture heat loading in the northern hemisphere (McCune and Keon 2002). The normalized difference in vegetation index (NDVI) can be used to assess canopy density, and it was calculated for all pixels using bands 3 and 4 from the Landsat 5 imagery:

$$NDVI = \frac{NIR(Band_4) - RED(Band_3)}{NIR(Band_4) + RED(Band_3)}$$

A measure of heterogeneity was derived which used focal operations to calculate the standard deviation of NDVI 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 NDVI 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.”

Results

1. On-the-ground CBI measurements correlate well with our derived severity measurements.
2. (?) Heterogeneity of local NDVI is a meaningful measure of heterogeneity
3. The best model used heterogeneity at the smallest spatial scale.
4. Greater heterogeneity reduces wildfire severity.
5. The relative importance of heterogeneity is stronger than all other variables.

Discussion

The heterogeneity measure (standard deviation of NDVI 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:

Possible holes

1. We bump into the lower limit of neighborhood window when using Landsat
2. Best way to demonstrate heterogeneity of NDVI is meaningful
3. To include or not include the value of NDVI of the focal pixel
- 4.

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:

208 Quantitative characterization using recent fires in a long-established natural fire area. *Landscape Ecology*
209 25:927–939.

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

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

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

216 Crowther, T. W., H. B. Glick, K. R. Covey, C. Bettigole, D. S. Maynard, S. M. Thomas, J. R. Smith, G.
217 Hintler, M. C. Duguid, G. Amatulli, M.-N. Tuanmu, W. Jetz, C. Salas, C. Stam, D. Piotto, R. Tavani, S.
218 Green, G. Bruce, S. J. Williams, S. K. Wiser, M. O. Huber, G. M. Hengeveld, G.-J. Nabuurs, E. Tikhonova, P.
219 Borchardt, C. F. Li, L. W. Powrie, M. Fischer, A. Hemp, J. Homeier, P. Cho, A. C. Vibrans, P. M. Umunay,
220 S. L. Piao, C. W. Rowe, M. S. Ashton, P. R. Crane, and M. A. Bradford. 2015. Mapping tree density at a
221 global scale. *Nature* 525:201–205.

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

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

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

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

237 Fry, D. L., S. L. Stephens, B. M. Collins, M. P. North, E. Franco-Vizcaíno, and S. J. Gill. 2014. Contrasting

238 spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests.
239 PLoS ONE 9:e88985.

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

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

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

247 Hansen, M. C., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, and A. Tyukavina. 2013.
248 High-resolution global maps of 21st-century forest cover change. *Science* 342:850–853.

249 Holling, C. S. 1973. Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*
250 4:1–23.

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

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

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

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

260 Lenoir, J., B. J. Graae, P. A. Aarrestad, I. G. Alsos, W. S. Armbruster, G. Austrheim, C. Bergendorff, H. J.
261 B. Birks, K. A. Bråthen, J. Brunet, H. H. Bruun, C. J. Dahlberg, G. Decocq, M. Diekmann, M. Dynesius,
262 R. Ejrnæs, J. A. Grytnes, K. Hylander, K. Klanderud, M. Luoto, A. Milbau, M. Moora, B. Nygaard, A.
263 Odland, V. T. Ravolainen, S. Reinhardt, S. M. Sandvik, F. H. Schei, J. D. M. Speed, L. U. Tveraabak,
264 V. Vandvik, L. G. Velle, R. Virtanen, M. Zobel, and J. C. Svenning. 2013. Local temperatures inferred
265 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. *Science* 349:823–826.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications* 17:2145–2151.

Miller, J. D., and A. E. Thode. 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment* 109:66–80.

Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009a. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment* 113:645–656.

Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009b. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.

Moritz, M. A., M. E. Morais, L. A. Summerell, J. M. Carlson, and J. Doyle. 2005. Wildfires, complexity, and highly optimized tolerance. *Proceedings of the National Academy of Sciences* 102:17912–7.

North, M. P., S. L. Stephens, B. M. Collins, J. K. Agee, G. Aplet, J. F. Franklin, and P. Z. Fulé. 2015. Reform forest fire management. *Science* 349:1280–1281.

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

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

295 Park Williams, A., C. D. Allen, A. K. Macalady, D. Griffin, C. A. Woodhouse, D. M. Meko, T. W. Swetnam,
 296 S. A. Rauscher, R. Seager, H. D. Grissino-Mayer, J. S. Dean, E. R. Cook, C. Gangodagamage, M. Cai, and
 297 N. G. McDowell. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality.
 298 *Nature Climate Change* 3:292–297.

299 Questad, E. J., and B. L. Foster. 2008. Coexistence through spatio-temporal heterogeneity and species
 300 sorting in grassland plant communities. *Ecology Letters* 11:717–726.

301 Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008.
 302 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle
 303 eruptions. *BioScience* 58:501.

304 Raffa, K. F., B. Aukema, B. J. Bentz, A. Carroll, N. Erbilgin, D. A. Herms, J. A. Hicke, R. W. Hofstetter,
 305 S. Katovich, B. S. Lindgren, J. Logan, W. Mattson, A. S. Munson, D. J. Robison, D. L. Six, P. C. Tobin,
 306 P. A. Townsend, and K. F. Wallin. 2009. A literal use of 'forest health' safeguards against misuse and
 307 misapplication. *Journal of Forestry*:276–277.

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

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

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

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

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

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

321 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.