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Characterizing and managing drivers of change in Mediterranean forest and grassland communities

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By

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Committee in charge:

Professor John Battles, Chair
Professor Wayne Sousa
Professor Katharine Suding
Professor Robert York

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ABSTRACT

Characterizing and managing drivers of change in Mediterranean forest and grassland communities

by Joan Celeste Dudney

Doctor of Philosophy in Environmental Science, Policy, and Management

University of California, Berkeley

Professor John J. Battles, Chair

Over the three chapters of my dissertation, I combined manipulative experiments and long-term monitoring data from grasslands, mixed conifer, and high elevation forests to explain emerging community shifts in California. I also applied these results to management strategies focused on global change. In the first chapter of my dissertation, I focused on the effects of shifting weather patterns on California's annual grassland communities. The results highlighted the importance of lagged rainfall effects and two important mechanisms (dry litter and propagule production) driving grass and forb responses to lagged rainfall. For the second chapter of my dissertation, I focused on the causes and consequences white pine blister rust and bark beetles in the Sierra Nevada. Resampling long-term monitoring plots, I characterized how the invasion of white pine blister rust (*Cronartium ribicola*) shifted over twenty years and how recent bark beetle populations were affecting white pine health in the southern Sierra. My third chapter concludes this dissertation by critiquing resilience applications in natural resource management. By combining resilience theory with concepts from the novel ecosystem literature, management of global change can be improved.

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INTRODUCTION

Across the globe ecosystems are experiencing unprecedented changes. Record-breaking beetle outbreaks in Western North America and widespread coral bleaching events have dramatically transformed systems (Ratajczak et al. 2018), and many predict we will continue to see major alterations in environmental conditions in the future (Millar and Stephenson 2015, Ratajczak et al. 2018). In less than 100 years, many ecosystems will need to adapt rapidly to anomalous temperatures, predicted to rise between a 0.5°- 8.6° (IPCC 2013). If current land-conversion trends continue today, Barnosky et al. (2012) predicted that by 2045, the world may reach a tipping point. Innovation in both science and management will be needed to develop effective strategies that support natural systems in an unpredictable future (Seastedt et al. 2008).

In California, global change events have already altered many regions. Invasive species have transformed the majority of California's grasslands to non-native dominated (Seabloom et al. 2003) and the combination of the recent drought and bark beetles killed an estimated 129 million trees over the past nine years (Fettig et al. 2019). Understanding and managing the invasive species and rising temperatures that will continue to threaten California's wildlands is a critical challenge moving forward. Throughout the three chapters of my dissertation, I characterized two drivers of global change in California's terrestrial ecosystems, shifting weather patterns and invasive species. I then applied this knowledge and synthesized current trends in natural resource management to improve resilience-based strategies. Using a combination of manipulative experiments and long-term monitoring data, I focused on the following: 1) climate change impacts in grassland communities, 2) invasive pathogen spread through Sierra Nevada white pine forests, and 3) a synthesis of two influential ecological ideas, novel ecosystems and resilience theory, to improve contemporary management of global change.

Chapter 1: Rainfall is a key determinant of production and composition in arid and semiarid systems. Long-term studies relating composition and water availability in annual grasslands primarily focus on current-year precipitation patterns. Pairing a long-term study with two manipulative experiments, we identified important, overlooked patterns and mechanisms of lagged precipitation effects in annual grasslands. The results underscored the importance of previous-year precipitation in structuring annual community composition and identified two important biotic pathways, seed rain and RDM, that regulated lagged community responses to rainfall. Incorporating lagged effects into models of grassland diversity and productivity can improve predictions of climate change impacts in annual grasslands.

Chapter 2: The combination of the invasive pathogen, white pine blister rust (*Cronartium ribicola*), mountain pine beetle (*Dendroctonus ponderosae*), drought, and changing fire regimes has caused precipitous declines in populations of white pines (*Pinus* subgenus *Strobus)* in North America. Here we characterized long-term spread patterns of bister rust through the southern Sierra. Over the past 20 years, incidence dropped by an estimated 76% in *P. lambertiana* populations, but increased by an estimated 360% in *P monticola*. For the first time, blister rust was recorded in *P. albicaulis* plots but no blister rust was confirmed in *P. balfouriana*. While mortality rates were lowest in whitebark and foxtail pines, high mortality rates were calculated for sugar pines, warranting further investigation into the population's status in the Sierra Nevada. These findings also suggest that blister rust and beetles are becoming an increasing threat to high-elevation white pines and efforts to restore and protect these species will likely be necessary in the future.

Chapter 3: Resilience theory is increasingly applied to the management of global change impacts. There is growing concern, however, that misapplications of resilience-based management (RBM) can sometimes lead to undesirable outcomes. We address an inescapable conundrum in the application of resilience theory: systems will need to track environmental change, but management that aims to support adaptive capacity can introduce undesirable levels of change. We developed a framework that links concepts from novel ecosystems and resilience theory to inform management of ecosystem change, and highlights that resilience-based applications need to address risks associated with novel human impacts to improve management outcomes.

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It is truly humbling to consider all the incredible people who have made this dissertation possible. Working under John Battles' guidance and brilliance has been a life-changing experience. With a plethora of insightful feedback, John challenged me to become a critical thinking, rigorous scientist, to ask cutting-edge questions, and to seek scientific adventures that far surpassed my expectations. John encouraged me to pursue a diversity of intellectual pursuits and helped me write many successful grant proposals and papers. He even allowed me to work independently for two years, and I am so grateful for his flexibility. Most importantly, John provided the intellectual

support and freedom to become the scientist I am today. Because of his unparalleled mentorship, I have achieved far more than I ever thought possible for myself, and I can only hope to pay my experience forward.

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CHAPTER 1

Lagging behind: have we overlooked previous year rainfall effects in annual grasslands

Lauren M. Hallett, Loralee Larios, Emily C. Farrer, Erica N. Spotswood, and Katharine N. Suding

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ABSTRACT

Rainfall is a key determinant of production and composition in arid and semiarid systems. Long-term studies relating composition and water availability primarily focus on current-year precipitation patterns, though mounting evidence highlights the importance of previous-year rainfall particularly in grasslands dominated by perennial species. The extent to which lagged precipitation effects occur in annual grasslands, however, remains largely unexplored. Here we pair a long-term study with two manipulative experiments to identify patterns and mechanisms of lagged precipitation effects in annual grasslands. The long-term study captured variation in functional group (exotic annual forbs and grasses) abundance and precipitation across eight years at three northern California grassland sites. We then tested whether lagged rainfall effects were created through seed production and litter (residual dry matter) by manipulating rainfall and grazing, respectively. Rainfall from the previous-year growing season (both seasonal and total rainfall) influenced functional group abundance. High lagged rainfall was associated with increased grass and decreased forb abundance the following year. Current-year seasonal rainfall also had impacts, with winter rain increasing forb and decreasing grass abundance. Lagged precipitation effects were generally stronger for forbs than for grasses. Our experimental studies provided evidence for two mechanisms that contributed to lagged effects in annual grasslands. Higher rainfall increased seed production for grasses, which translated to more germinable seed the following year. Higher rainfall also increased biomass production and litter (residual dry matter), which benefited grasses and reduced forb abundance. Our results highlight the importance of previous-year precipitation in structuring annual community composition and suggest two important biotic pathways, seed rain and RDM, that regulate lagged community responses to rainfall. Incorporating lagged effects into models of grassland diversity and productivity could improve predictions of climate change impacts in annual grasslands.

INTRODUCTION

Describing how resource availability modifies ecosystem structure is a longstanding ecological challenge and increasingly more important given the uncertainties surrounding climate change. Water availability is a strong driver of plant community structure in a number of systems (Noy-

Meir 1973, Westoby et al. 1989) and can lead to shifts in species diversity and composition over time (Cleland et al. 2013). Rainfall-driven fluctuations in composition are particularly pronounced in annual grasslands. For example, wet years often promote recruitment of all species, while only a subset of species survive in dry years (Cleland *et al.* 2013). In addition, different life history strategies may generate trade-offs between species in response to rainfall patterns ((Pitt and Heady 1978, Huenneke et al. 2002, Robertson et al. 2010), yielding rainfall-induced species shifts across years.

Mounting evidence indicates that previous-year rainfall (i.e., a lagged effect) also drives community composition (Gibbens and Beck 1988, Dunnett et al. 1998, Adler and Levine 2007, Sherry et al. 2012). Lagged effects have been investigated almost exclusively in mixed perennial grasslands, though Hobbs and Mooney (1995) demonstrated a significant previous-year rainfall effect on the native forb, *Lasthenia californica (Lindl.)* in serpentine soils. Lagged effects can explain a significant portion of the unexplained variance in models with current-year precipitation and production (Sherry et al. 2008, Reichmann et al. 2012a). Lagged rainfall shifts dominance hierarchies among species (Sherry *et al.* 2012) and modifies competitive advantages with consecutive dry or wet conditions (Dunnett et al. 1998). A variety of mechanisms, including precipitation-driven changes in plant reproduction and litter dynamics (Herben et al. 1995, Sherry et al. 2008), help explain these lagged effects. Here, we extend this research to consider broader patterns and mechanisms of lagged effects in annual-dominated communities.

Previous-year rainfall could impact annual community composition the following year by altering seed production (Hobbs and Mooney 1995). Because many grass species rely on transient seedbanks (i.e., seed from the previous year) (Bartolome 1979, Seabloom et al. 2003), their growth is highly dependent on the conditions that influenced seed production (Chippendale and Milton n.d., Major and Pyott 1966). Other species with persistent seedbanks (Peco et al. 1998, Scott and Morgan 2012) may exhibit minimal lagged effects, as their seeds can accumulate across multiple years. Longer seed viability enables these species (e.g., various forbs) to wait until growing conditions are more favorable (Levine et al. 2004) and reduces their dependence on previous-year seed rain. Thus, different seed banking strategies, combined with previous-year seed production, could create lagged effects on species composition in annual-dominated systems.

Lagged effects may also occur if biomass production from the previous year produces litter that modifies microsite availability in the current-year. In annual grasslands, precipitation has a strong control on community productivity and the litter remaining at the end of the season (Bartolome et al. 2002). Litter can modify the germination environment the following year by shading microsites and increasing nutrient deposition (Bartolome et al. 1980, Foster and Gross 1998). In fact, accumulation of litter in annual grasslands decreases forb richness and perpetuates dominance of high biomass-producing species (Hobbs and Mooney 1995, Huenneke et al. 2002, Suttle et al. 2007a, Bartolome et al. 2007b). Thus, the interplay among rainfall, biomass production, microsite conditions, and species recruitment produce complex effects on species composition that warrant further study.

Here we evaluate whether previous-year annual and seasonal precipitation is a significant determinant of community composition in annual-dominated grasslands. Using three long-term species composition records from California, we observe how historical rainfall relates to functional group abundance. California's annual-dominated grasslands are an ideal system, as they are characterized by high precipitation variability (Potts et al. 2012) and strong rainfall effects (Pitt and Heady 1978, Hobbs and Mooney 1991, Jackson and Bartolome 2002, Zavaleta et al. 2003). We then experimentally isolate two potential mechanisms of lagged precipitation effects. We hypothesize: 1) differences in seed production between functional groups is directly related to precipitation and 2) litter (residual dry matter) shifts species composition the following year (Figure 1 a-c).

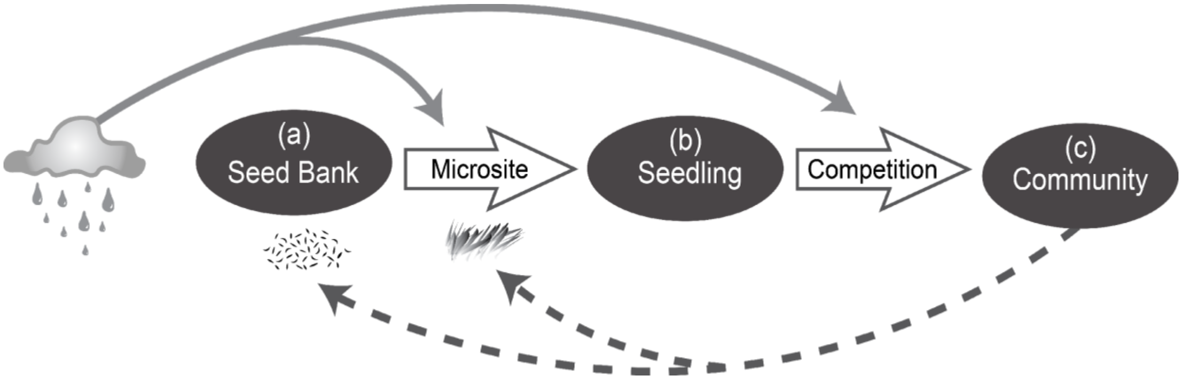

Figure 1: Conceptual diagram of lagged effects in annual-dominated grasslands (i.e., the carry-over effects of vegetation from the previous year on current year's species composition). (a) Species germination is mediated by the magnitude of rainfall, seed bank dynamics, and microsite availability. (b) Species that germinate grow and compete; their growth and competitive interactions are constrained by the magnitude of rainfall throughout the growing season (fall, winter, and spring). (c) Seed production and peak biomass from the resulting community become the biotic feedbacks that modify the seed bank and microsite availability the following year.

METHODS

System

We conducted the observational study and associated manipulative experiments in northern California valley grasslands within the California Ecological Province (Bartolome et al. 2007a). We collected abundance data at three sites in the East Bay Regional Park District, USA (37° N, 121° W): Vasco Caves Regional Preserve, Pleasanton Ridge Regional Park, and Sunol Regional Wilderness. Manipulative experiments were difficult to conduct in the East Bay Parks due to open space regulations and high human and other animal traffic. Thus, conducted the experiments in a valley grassland at the University of California Sierra Foothill Research Extension Center (SFREC), located in Browns Valley, California, USA (39º 15' N, 121º 17' W). Valley grasslands at SFREC and East Bay

Parks are dominated by non-native annual species with patches of remnant natives. The most abundant species included *Avena fatua* Link*, Avena barbata* L.*, Festuca perennis* L.*, Bromus hordeaceus* L., *Erodium botrys (Cav.) Bertol.*, and *Erodium cicutarium (L.) Aiton* (nomenclature follows (Baldwin and Goldman 2012); (see Appendix 1). Based on species composition and average annual rainfall, both sites fall within the annual grassland/hardwood range (Bartolome et al. 2002). Grasslands at both locales are characterized by having silty and clay loamy soils (Dahlgren et al. 2003, Gea-Izquierdo et al. 2007). Because of the similarities in vegetation type, soils and climate, we expect parallel responses to precipitation between both research areas.

Detecting a pattern of lagged precipitation effects

Sampling design

Between 2005 and 2012, we sampled 18 permanent plots (six plots in each of the three East Bay Parks). Permanent plots were established in 2003 using a stratified random sampling design, which ensured plot placement at least 300 meters from non-grassland vegetation (e.g. oak woodland, chaparral) (Spiegal et al. 2014). Returning researchers trained the new field assistants in species identification techniques to maintain consistency throughout years. Species composition was measured at peak biomass between April and May, depending on rainfall conditions. Four, 17-meter transects were arrayed in the cardinal directions from the center of each ~ 900 m^2 circular plot (Heady et al. 1959). Using a small-diameter, metal pole placed perpendicular to the transect line, either first-hit species, litter or bare ground was recorded 70 times along each of the four transects, for a total of 280 individual records per plot (Spiegal and Wenk 2009). Species abundance was determined by counting the number of individuals identified in each plot. We did not relativize species abundances to avoid artificially inducing covariance among species (Hallett et al. 2013a). All plots within the East Bay Parks were lightly cattle or sheep grazed throughout the study period.

Functional group classification

We classified the 80 different species sampled in our plots into six functional groups: exotic annual grasses, exotic annual forbs, exotic perennial forbs, native annual forbs, native perennial forbs and native perennial grasses. These functional groups were similar to previous classifications in California grasslands (Sandel et al. 2010, Fernandez-Going et al. 2012) and based on the Jepson Manual, the standard flora for California (Baldwin & Goldman 2012).

Precipitation data

Precipitation data were downloaded from three different weather stations within the California Irrigation Management Information System (wwwcimis.water.ca.gov/). All stations were located within 20 miles of each sampling site. We used Station 47 records with abundance data collected at Vasco Caves, Station 191 for Pleasanton Ridge, and Station 171 for Sunol Regional Wilderness. Rainfall variables were calculated based on the local growing season, starting October 1 and ending May 31. We omitted the summer season (June-September) from our analysis, as previous research indicated these months do not significantly impact the vast majority of exotic annual species in our dataset (Pitt & Heady 1978 p. 19). All but one of the exotic annual grasses (*Elymus* *caput-medusae*) and all but two of the exotic annual forbs (*Centaurea melitensis* and *Centaurea solstitialis)* in our dataset were either at peak biomass or senescing during the time we sampled. *Centaurea* spp. and *Elymus caput-medusae,* however, are invasive species that produce the bulk of their biomass during late/early summer (Thomsen 1996). Consequently, their dynamics are affected by summer precipitation (Chiariello 1989) and our results are more relevant for grasslands that are not heavily invaded by these species.

For our seasonal analyses, we summed precipitation across the following months: fall (October-November), winter (December-February) and spring (March-May). Because Station 191 did not have daily precipitation records before 2005, we regressed Station 191 with Station 171 weather variables and used the intercepts and estimates (p-value < 0.001) to calculate estimated precipitation for 2004. For all our precipitation data, lagged rainfall was simply the precipitation that fell the previous year. Lagged precipitation variables spanned the years 2004-2011 and current precipitation variables spanned the years 2005-2012. We scaled rainfall variables across years and within season (fall, winter and spring) at each site to ensure that fall and spring variability was not masked when compared against higher winter rainfall.

Over the study period, mean current-year, growing season rainfall was 378 mm (CV 0.36), while mean, previous-year rainfall was 391 mm (CV 0.33). On average, the majority of precipitation fell during the winter months, December-February (54%), about a third fell during the spring months, March-May (30%), and only 16% fell in fall, October-November. The magnitude of seasonal precipitation also fluctuated across growing seasons. For example, a wet winter was followed by a dry spring in 2008 (Figure 2).

Statistical analysis

Using a general linear mixed model analysis with R software (R Core Team, 2015), we tested how current and previous-year precipitation altered functional group abundances over eight years. Since our count data were overdispersed (variance was greater than the mean), it was likely that using a Poisson model would inaccurately estimate the significance of the relationships between precipitation and abundance (Hilbe 2011). To account for the overdispersion, we used the negative binomial maximum likelihood (ML) method, which considers the mean as a random variable and assumes the extra variance is a quadratic function of the mean (Lindén and Mäntyniemi 2011). By using the negative binomial model, we could accept the significance of the independent variables with greater confidence (Zuur et al. 2009, Hilbe 2011).

To test for possible correlations among weather variables, we used Kendall's tau correlation matrix (Kendall 1948). None of the seasonal precipitation variables were significantly correlated above absolute value 0.3 (Robertson et al. 2009); however annual precipitation was highly correlated with seasonal precipitation (see Appendix 3). To avoid confounding regression results, we created two sets of models for annual and seasonal precipitation parameters.

We fit six models using the function glmer.nb() from R package lme4 (Bates et al. 2014) for each of the functional groups to determine current and previous rainfall effects: 1) functional group abundance with current-year annual precipitation, 2) functional group abundance with previous-year annual precipitation, 3) functional group abundance with both current and lagged annual precipitation, 4) functional group abundance with current-year seasonal (fall, winter, and spring) precipitation, 5) functional group abundance with previous-year seasonal precipitation, 6) functional group abundance with current and lagged seasonal precipitation. We conducted our analyses at the plot-level and accounted for the site-level variation among the three East Bay Parks and among all plots by including a nested random effects term in all our models (plot nested within site). To determine which model best explained abundance patterns, we used Akaike information criterion (AIC) to compare across all six models. Due to the exceptionally low abundances and high temporal variability (see Appendix 4) of the three native functional groups (native annual forbs, native annual grasses and native perennial forbs), we focused only on exotic annual forbs and grasses (Onwuegbuzie and Daniel 1999, Case and Ambrosius 2007).

Testing possible mechanisms of lagged effects in annual systems

We tested two likely mechanisms of lagged precipitation effects: 1) an effect of residual dry matter (RDM) on current-year species composition and 2) a differential effect of rainfall on species seed production, which should influence composition the following year. We implemented our experiments in two pastures at SFREC that were previously grazed by cattle but were fenced prior to our study to allow controlled manipulations.

Mechanism 1: Residual dry matter and species composition

Residual dry matter (RDM) is the result of biomass production (associated with rainfall) and biomass removal (e.g., via grazing) (Bartolome et al. 2007). Biomass removal was the most feasible way to manipulate RDM in the field. Therefore, we tested the effect of RDM on species composition using a mowing/trampling experiment. We used a combination of trampling by livestock and mechanical mowing treatments to establish a gradient of six RDM levels. Our lowest RDM level corresponded closely with the stocking rate regulations at the East Bay Parks, which stipulate that RDM must not fall below 112g/m2 (www.ebparks.org/about/stewardship/grazing). Our highest RDM level (no biomass removal), corresponded roughly with the maximum potential RDM at the Parks, which have similar species composition but lower average rainfall than SFREC. Thus, the RDM manipulations at SFREC were likely within the range of RDM variation at the East Bay Parks, as well as other studies that manipulated RDM (Bartolome et al. 2007b, Amatangelo et al. 2008).

The RDM treatments were replicated four times in two pastures for a total of eight 10 m × 3 m replicate blocks per level (described by (Stein et al. 2014). The gradient was created as follows: 1) not trampled or mowed; 2) trampled once per year, in late March when plants started flowering; 3) trampled twice per year, in late March and in June/July after most plants were senescent; 4) an additional mowing right before the late March trampling treatment; 5) mowing prior to each trampling treatment; and 6) an additional mowing in late February during early plant growth. We repeated this experiment over four growing seasons (2008-2011).

We harvested RDM in early October each year by clipping a 0.25 m × 0.25 m subplot within each replicate, drying the biomass (60°C for 72 h) and weighing it. To avoid re-harvesting the same area, we shifted the subplot position each year. We verified that our mowing/trampling treatments resulted in an RDM gradient using a linear mixed effect model with RDM level and year as fixed factors, and plot nested in block nested in pasture as random effects. Analyses were conducted using the lme function in the nlme package in R (Pinheiro et al. 2015).

We visually estimated species cover (cover classes included: 1, 2, 5, 10, 20, 30 . . . up to 100 percent cover per species) in a 1 m × 1 m subplot within every replicate in mid-April of each year. Total species cover could be greater than 100, owing to canopy overlap, or less than 100, owing to bare ground. We aggregated the cover of annual grass and annual forb species separately and analyzed their response to the RDM gradient using a linear mixed effect model with cover as the response variable. Fixed factors included functional group (grass, forb), RDM level, year, and functional group × RDM level. Random effects comprised plot nested in block nested in pasture. An effect in which grass cover increased with RDM while forb cover decreased would support RDM accumulation as a mechanism of lagged precipitation effects on functional group abundance.

Mechanism 2: Seed production and rainfall variation

To test whether rainfall shifted seed production, we manipulated rainfall using rainout shelters and irrigation to create dry and wet conditions over the course of the 2012 growing season. Each dry/wet pair was replicated eight times for a total of 16 plots. We situated this experiment next to one of the pastures used in the RDM experiment. The rainout shelters were constructed with removable, solid, clear polyethylene roofs that fit over a 1.3 m × 2.6 m area. After the first germinating rains of the season, we erected the roofs shortly before subsequent rainfall events and removed them afterward; the roofs were only erect for 10% of the growing season to minimize effects of solar radiation. Shelter runoff was collected and used to irrigate the wet plots.

We maintained rainfall treatments over the course of two growing seasons (October 2012-May 2014). Both years experienced below-average rainfall (510 mm in the 2013 growing season and 398 mm in 2014 compared to average annual rainfall of 730 mm). Due to extreme drought in the 2014 growing season, we irrigated the wet plots using (non-chlorinated) well water. We monitored the effect on soil moisture using two 15 cm deep time-domain reflectometer (TDR) probes in each plot and 5 cm deep continuous data-loggers in half of the plots (EC-5 soil moisture probes, Decagon Devices, Pullman, WA). To confirm that rainfall manipulations generated a dry and wet condition, we used a linear mixed effects model with soil moisture as the response variable, treatment and year as fixed factors, plot nested in block as a random effect using R package nlme (Pinheiro *et al.* 2015) function lme().

Annual rainfall at SFREC ranged between 230 mm and 1310 mm over the past 50 years (sfrec.ucanr.edu/Data/Weather/) and annual rainfall within the East Bay Parks region ranged between 163 mm and 1041 mm over the last 40 years (http://www.wrcc.dri.edu/). Because we applied rainfall from the dry plots to the wet plots, we estimated that the wet treatments received approximately 1000 mm of rain in 2013 and 800 mm in 2014, reflecting the higher ranges of rainfall at SFREC and East Bay Parks. In addition, the rainfall treatments resulted in significant differences in soil moisture throughout the growing season ($F1,108 = 1119$, $P < 0.001$), with on average 28.9 ±0.48% soil moisture in the wet plots compared to 22.5 ±1.2% in the dry treatments (Figure 3).

Within each plot, we measured seed production of *A. barbata*, the most abundant-grass, and *E. botrys*, the most-abundant forb, within a 0.25 m × 0.25 m subplot that was situated to avoid any edge effects. We focused on these two species because they were common in all plots prior to the implementation of the rainfall treatments. Further, they represent a high percentage of the grass and forb cover in the East Bay Parks dataset (*Erodium* comprised, on average, 52% of the forb cover and *Avena,* 25% of the exotic annual grass cover). We also expected similar seed production responses to precipitation among the other species within both annual functional groups (Bartolome 1979a). While there is likely species-level variation in fecundity patterns, exotic annuals within this system characteristically germinate under a wide range of conditions to maximize their reproduction (Wainwright and Cleland 2013).

Because *Erodium* and *Avena* differ in their phenology, we censused seed production twice: once in late March, when *Erodium* was at peak biomass, and again in late April/early May slightly after *Avena* was at peak. *Erodium* seed pods burst when ripe and contain five fertile filaments. Because *Erodium* seed production was staggered throughout the early spring, we counted the bases of burst seed pods, ripening seed pods and healthy flowers. To assess *Avena* seed production, we counted spikelets, each contain two florets that can be identified by papery coverings left behind after seeds drop (Marshall and Jain 1969). Counts were made at the stand level.

We analyzed seed production using a linear mixed effects model with peak seeds produced as the response variable, species, rainfall treatment and a species × rainfall interaction as explanatory variables, and plot nested in block as random effects (function lme in the nlme R package; (Pinheiro *et al.* 2015). An interaction effect in which *Avena* seed production was relatively greater in wet plots, whereas *Erodium* seed production was relatively greater in dry plots, would support a seed-rain effect as a potential mechanism of lagged precipitation effects on functional group abundance.

In addition to seed production, we measured peak biomass in each replicate by clipping a 0.25 m x 0.25 m subplot in late April/early May, drying the biomass (60°C for 72 h) and weighing it. To avoid re-harvesting the same area, we sifted the subplot position each year. This allowed us to relate rainfall-driven shifts in biomass with the range in RDM we created in our experiment.

RESULTS

Detecting a pattern of lagged precipitation effects

Functional group abundance patterns

Among the three sites, exotic annual grasses (*n* =17 species) were the dominant functional group, making up 66% of the community across years (CV 0.33). Exotic annual forbs were the subdominant group (*n* = 39 species, 18% of total abundance) with high inter-annual fluctuations

(CV 0.801). Combined, exotic annual forbs and grasses comprised 84% of the grassland community, while native species only 16%. Exotic annual forb and grass abundance negatively covaried across years (Z = -3.34, P< 0.001; df =7) (Figure 4).

Functional group responses to precipitation

Both grass and forb abundances were more strongly correlated with previous-year, growing season precipitation than current year rainfall (Table 1). For example, our annual precipitation model predicted that a one standard deviation (SD) increase in previous-year precipitation would lead to a 30% decrease in forb abundance. In contrast, simulating a one SD increase in current-year precipitation decreased forb abundance by only 4%. Although grasses were less responsive to precipitation overall, a similar difference in current versus lagged responsiveness occurred. A one SD shift in lagged precipitation predicted a 7% increase in grass abundance, compared to a 1.5% increase with current-year precipitation.

The best-fit seasonal model for grasses and forbs included current and lagged rainfall (Table 1). Grasses responded to current and lagged seasonal precipitation nearly equally, whereas forbs responded more strongly to lagged rainfall (Table 1). Exotic annual forbs and grasses showed opposite directional responses to seasonal precipitation. Previous dry fall (T = -3.16, P < 0.001) and spring seasons (T = -4.77, P < 0.001) were associated with higher forb abundances, while previous wet falls (T = 2.23, P = 0.03) and springs (T = 3.13, P = 0.002) were associated with higher grass abundances (Figure 5). The trend flipped with current-year winter precipitation, resulting in lower grass (T = -2.55, P = 0.01) and higher forb (T = 3.30, P< 0.001) abundances (Figure 5). (See Appendix 2 for figures displaying direct relationships between functional groups and precipitation.)

Characterizing mechanisms of lagged precipitation effects in annual systems

Residual dry matter affects species composition

Species relative cover shifted along the RDM gradient: *Avena* cover declined with lower RDM, while *Erodium* cover increased (RDM x species interaction $F_{5,328}$=2.5, P=0.031, Figure 6a). The RDM treatment successfully created a gradient in RDM ($F_{5,39}$=9.47, P<0.001), with lower RDM levels at the higher mowing/trampling levels (Figure 6b). RDM also varied among years ($F_{1,95}$=91.02, P<0.001). The highest average RDM levels in the un-mowed/un-trampled plots occurred in 2010 (517.0 +/- 112.6 g/m^2), whereas the lowest levels occurred in 2011 (283.4 +/- 50.3 g/m^2).

Rainfall affects biomass and seed production

Mean biomass in the wet treatment was 480.6 +/-26.4 g/m^2, which was similar to the RDM produced in the un-mowed/un-trampled (M1) treatment (Figure 6b). Mean biomass in the dry treatment was 216.8 +/- 19.0 g/m^2, corresponding with the RDM levels produced in the moderate mowing/trampling treatments (M3 and M4) (Fig 6b). Given that all the East Bay Parks are grazed with reasonably consistent stocking rates, it is likely that the range in RDM associated with rainfall would be similar to our manipulative experiment at SFREC.

Seed composition and production was strongly influenced by precipitation. While total seed production was reduced under dry conditions ($F_{1,52}$ = 11.5, P = 0.0014), there was a strong differential response by species (species × wet-dry treatment interaction, $F_{1,52} = 4.61$, $P = 0.036$). *Avena* seed production was much lower under dry than wet conditions, whereas *Erodium* seed production did not significantly differ across rainfall treatments (Figure 7).

DISCUSSION

Understanding precipitation controls on vegetation structure is essential for predicting how climate change will alter communities in the future. Our findings indicated that lagged rainfall effects may help explain a significant proportion of compositional variation in annual plant communities. Although there is a well-documented link between current-year rainfall and annual species composition (Hobbs and Mooney 1991, Epstein et al. 1999, Zavaleta et al. 2003), other studies have found that current-year rainfall alone was not a good predictor of composition (Duncan and Woodmansee 1975, Hobbs and Mooney 1995, Dukes and Shaw 2007, Hobbs et al. 2007). By including lagged precipitation in our models, we demonstrated that predictions of abundance improved for annual grasslands. Our experimental work provided support for two pathways creating these lagged effects: rainfall can affect litter production which then modifies recruitment the following growing season, and rainfall can shift seed production, which changes the quantity of germinable seed the next year.

Lagged rainfall shifts community composition

The results from our long-term observational study supported our hypothesis that community composition shifted with lagged precipitation. Both exotic grasses and forbs responded more to total previous-year than total current-year rainfall. Strong lagged effects have also been found in England's perennial-dominated grasslands (Dunnett et al. 1998). More common in semi-arid grasslands, however, is an important current-year precipitation effect that is bolstered by including lagged effects (Oesterheld et al. 2001, Wiegand et al. 2004). Though the strength of lagged effects in our system is perhaps surprising, the mechanisms discussed below begin to elucidate why lagged precipitation may be critically important for annual grasslands.

Previous-year seasonal rainfall also differentially affected functional group abundance. For example, lagged spring rain, and to a lesser degree lagged fall rain, were the strongest predictors of forb and grass abundances. These lagged seasonal associations are consistent with results from earlier studies that describe current-year rainfall effects in our system (Murphy 1970a, Duncan and Woodmansee 1975, Pitt and Heady 1978). Because both current and lagged precipitation effects were in the same direction, sequential wet or dry conditions may compound to cause stronger, potentially non-linear changes in community structure (Suttle et al. 2007b, Sala et al. 2012, Collins et al. 2012, Hsu and Adler 2014). It is important to note that although two sequential dry years increased forb abundance in our system, forbs decline after four consecutive dry years (Harrison et al. 2015). Seasonal rainfall legacies also suggest that biotic carry-over effects are influenced by the timing of rainfall during the previous year, which helps explain why season-specific management can be useful for increasing production and diversity, particularly for exotic species (Stahlheber and D'Antonio 2013).

Overall, lagged rainfall affected forbs more than grasses, indicating that grasses may be less constrained by dry litter and seed production. Thus, directional shifts in rainfall could impact grasses less, which has important implications for management in the face of climate change. Lagged precipitation, however, explained more variation in forb abundance, suggesting that community effects, such as competition with grasses (Seabloom et al. 2003) and higher levels of RDM (Suttle et al. 2007b), strongly suppress forb growth in wet conditions. Below, we discuss further how precipitation influences biotic legacies that shape annual grasslands.

Mechanisms of lagged effects

By isolating the biotic mechanisms creating lagged effects, we can begin to understand how previous-year precipitation differentially impacts species composition in annual grasslands. Vegetative reproduction is commonly cited as an important mechanism for lagged effects in perennial grasslands. Meristem production, including buds, tillers, and branches (Dalgleish and Hartnett 2006, Reichmann et al. 2012b) can create protracted responses to rainfall. Annual plants, however, reproduce primarily through seed and senesce after one growing season, suggesting that the mechanisms of lagged effects for annuals operate through the seed bank and biomass production (Hobbs and Mooney 1995).

By manipulating rainfall, we demonstrated that seed production, particularly for annual exotic grasses such as *Avena,* declined in years with lower rainfall. *Avena* has a transient seed banking strategy (Seabloom et al. 2003), and a decline in the number of seeds may limit *Avena* the next year because of the tight connection between seeds produced in one year and the amount of germinable seed available the next. Since the majority of *Avena* seeds in the topsoil sprout during the following growing season (Miller and Nalewaja 1990, Russi et al. 1992), *Avena* has decreased capacity to buffer its abundance than species with more persistent seed banking strategies. Thus, a dry year may reduce *Avena* the following year, while a previous wet year could lead to a corresponding increase.

In contrast, dry conditions did not have a significant impact on the number of *Erodium* seeds, which is consistent with an experimental study in Australia showing that drought stress did not significantly impact *Erodium* fruit production (Cox and Conran 1996). Lower variability in seed production, as well as reduced competition with annual grass seeds*,* may help explain why a previous dry year increased forb abundance in our long-term study. Persistent seed banking strategies also enable some forbs to capitalize on colonizing windows without relying on the preceding year's seed quantities (Bartolome 1979). Thus, forb seed production and seed banking strategies are consistent with their positive responses to a previous dry year in our long-term study. There may also be additional species-level effects that depend on seed bank longevity and seed production sensitivity to rainfall that our manipulative experiment was unable to capture.

Our RDM experiment provided support for another pathway leading to lagged effects in annual grasslands, where litter from one season influenced recruitment in the following year. In our system, rainfall partially moderates RDM from year-to-year (Bartolome et al. 1980, Jackson and Bartolome 2007) and these shifts are often associated with different groups of species (Levine et al. 2004, Bartolome et al. 2007b, Stahlheber and D'Antonio 2013). The negative lagged precipitation effect on forbs in our long-term study is consistent with our experimental results showing that higher RDM levels suppress forb germination and growth. In contrast, the positive lagged effect on *Avena* highlighted in our long-term study can be linked to higher RDM levels that enhance growth the following year. It is likely that RDM has species-specific effects, and previous research indicates that shifts in RDM may not always positively affect all annual grass species (Amatangelo et al. 2008). Additional research teasing apart RDM effects could explain the complexity of lagged effects within functional groups. RDM may also have spatially-explicit impacts that are not necessarily related to rainfall. For instance, biomass production that leads to RDM has long been linked to rainfall patterns (Murphy 1970b, Duncan and Woodmansee 1975, Bartolome et al. 1980), but factors such as soil fertility, slope, and aspect may be equally if not more important(Gelbard and Harrison 2003, Bartolome et al. 2007b). Thus, across California's environmental gradients, there may be varying impacts of RDM on species composition (Olff and Ritchie 1998, Osem et al. 2002, Stahlheber and D'Antonio 2013).

Caveats and Future directions

Because our study focused on grasslands with a predominance of exotic annuals, we were unable to describe lagged effects associated with native and perennial species. However, we expect that our results and the mechanisms we identified apply to systems with native annuals. Hobbs and Mooney (1995), for example, found previous-year rainfall linked to a native annual forb, *Lasthenia californica (L.),* in serpentine grasslands. Research on perennial plants also provides insight into the likely mechanisms (e.g., meristem production) (Reichmann et al. 2012a, Reichmann and Sala 2014) that could be associated with lagged effects on perennials species in our system. In addition, while we expect that litter and seed production are important mechanisms for annual grasslands, studies that assess disturbance regimes (Hobbs and Mooney 1991), herbivory (Peters et al. 2006), soil moisture and microbial interactions (Wardle et al. 2004) also provide additional evidence for lagged effects on species composition.

Our RDM experiment effectively created a dry litter gradient and represents the effects of RDM on species composition (Stein et al. 2016). The design did not include important grazing components such as selective grazing, timing of grazing, or fecal deposition. Further experimentation that teases apart these effects, including trampling, would provide more detail into how grazing could be manipulated to shift species composition the following year. Considering the interactions between precipitation legacies and grazing impacts may also be an interesting extension. For example, how does nutrient deposition and selective grazing shift species composition and do they modify or parallel legacy effects? Finally, air (Pitt and Heady 1978, Chiariello 1989, Zavaleta et al. 2003) and soil temperatures (Henry et al. 2006) are important controls in our system. Investigating into temperature lags may provide further insight into legacy effects in annual communities.

Broader implications

Climate models for semi-arid systems forecast shifts in precipitation regimes, including increased inter- and intra- annual variability and extreme rainfall events (Weltzin et al. 2003, Min et al. 2011, Durack et al. 2012). Recent studies indicate that rainfall may increase in our system and extend the growing season (Pan et al. 2011, Kendon et al. 2014), which could favor annual grasses. There is growing consensus in annual (this study and Hobbs & Mooney 1995), mixed perennial (Sala et al. 2012, Sherry et al. 2012) and woodland (Weiss et al. 2004) systems that including lagged rainfall effects can greatly improve predictions of community responses to shifts in weather patterns. This is particularly true for our annual system, where previous-year total rainfall better predicted annual plant abundance than current-year rainfall. Grass abundance is especially important for rangeland managers and much effort has been made to develop predictive models (Heady 1956, Bartolome et al. 1980, 2002). By including lagged precipitation, managers can better predict forage production, regardless of current-year rainfall.

Our results also contribute to an ongoing ecological debate about the relative role of abiotic factors (e.g., precipitation) and biotic factors (e.g., grazing) that influence plant composition (Sullivan and Rohde 2002, Jackson and Bartolome 2002, Vetter 2005). Strong lagged effects in annual systems suggest that grazing and precipitation may affect species composition through shared mechanisms. Specifically, both precipitation and grazing can modify the levels of residual dry matter (Bartolome et al. 1980, Huntsinger et al. 2007, Jackson and Bartolome 2007), which in turn influences species composition (Hayes and Holl 2003) (though grazing may affect species composition through additional mechanisms, including fecal deposition and selective consumption). Thus managers may use grazing or mowing to offset the impacts of weather patterns on vegetation. For example, during high rainfall periods grazing may encourage forb cover and greater diversity by reducing grass dominance (Collins et al. 1998, Stahlheber and D’Antonio 2013, Skaer et al. 2013). Alternatively, rangeland managers may be concerned with decreased grass production in dry years (Huntsinger et al. 2007), which could be mitigated by reducing stocking rates. These recommendations parallel traditional range dogma regarding grazing intensity (Murphy 1970b, Duncan and Woodmansee 1975, Bartolome et al. 2002), and highlight the importance of flexible grazing practices to maintain grassland plant diversity and production across rainfall conditions (Hayes & Holl 2003; Stahlheber & D’Antonio 2013).

CONCLUSION

Many studies investigate the high temporal variability of community composition in semiarid systems, but few have considered how lagged effects contribute to these fluctuations in annual-dominated grasslands. Our results demonstrated that lagged effects were important drivers of species composition and can operate through biotic mechanisms, such as seed and litter production, that are carried over from the previous year. The effect of previous-year precipitation was greater for forbs than grasses, indicating that rainfall-induced biotic effects strongly constrain forb growth and weakly impact grasses. We suggest that understanding the complexity of lagged precipitation effects will be necessary for robust predictions of climate change impacts on annual grasslands and appropriate management responses in the future.

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FIGURES AND TABLES

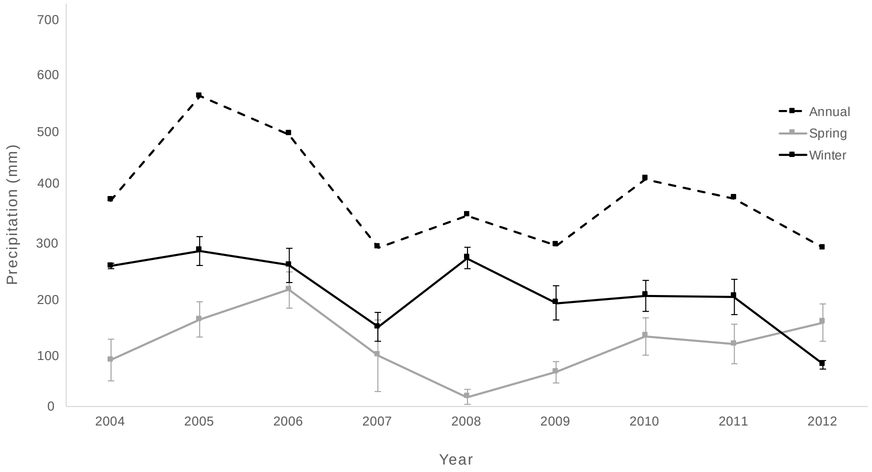

Figure 2: Average growing season (October-May), spring (March-May) and winter (December-February) precipitation across nine years. Averaged across the three weather stations. All points displaying standard deviation.

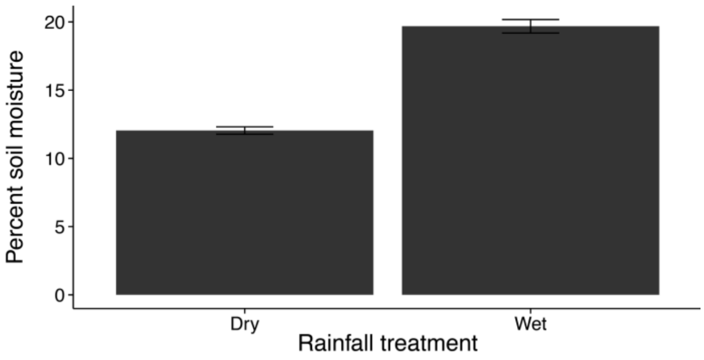

Figure 3: Rainfall treatment significantly modified soil moisture levels, creating a rainfall effect on species (showing standard error bars).

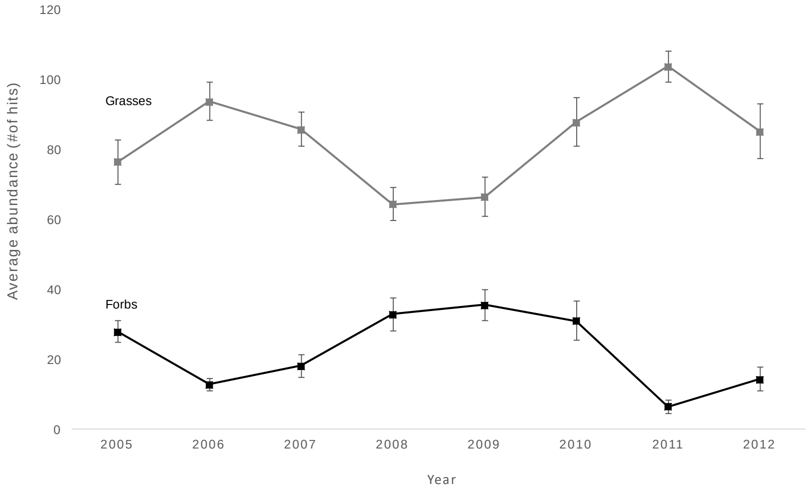

Figure 4: Average functional group abundance across eight years (averaged across plots; displaying standard error bars).

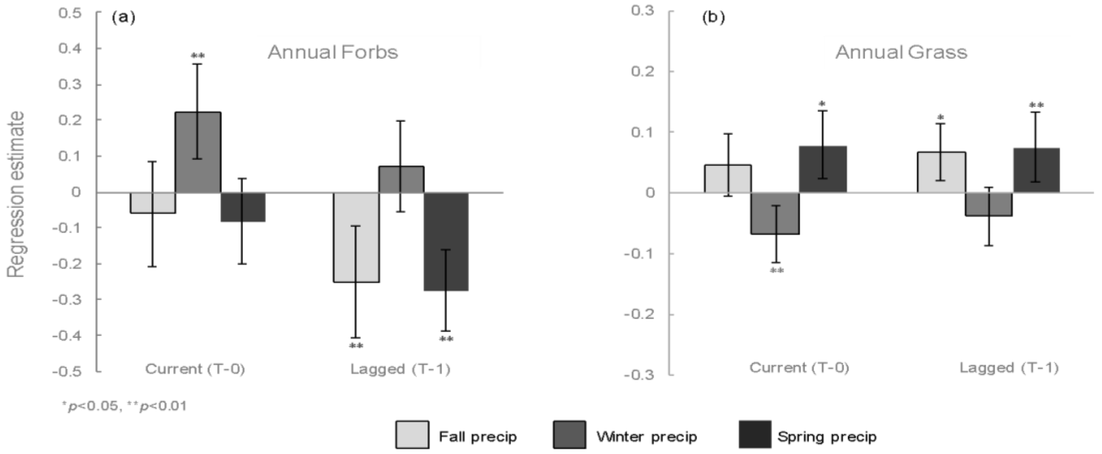

Figure 5: Regression estimates (with corresponding standard error bars) from models of exotic annual grass and forb abundances. Figure illustrates that lagged seasonal precipitation (T-1) is a strong driver of functional group abundance in annual grasslands.

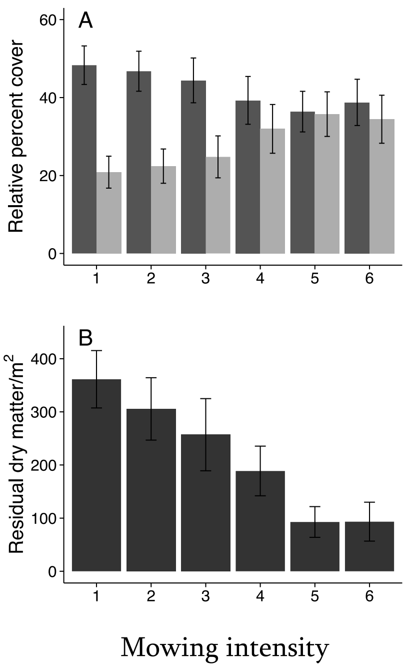

Figure 6: RDM manipulations shift species composition of forbs and grasses. a) Mowing/trampling intensity decreased relative percent cover of grasses and increased forb relative cover. b) High mowing/trampling intensity reduced RDM. Both graphs show standard error bars.

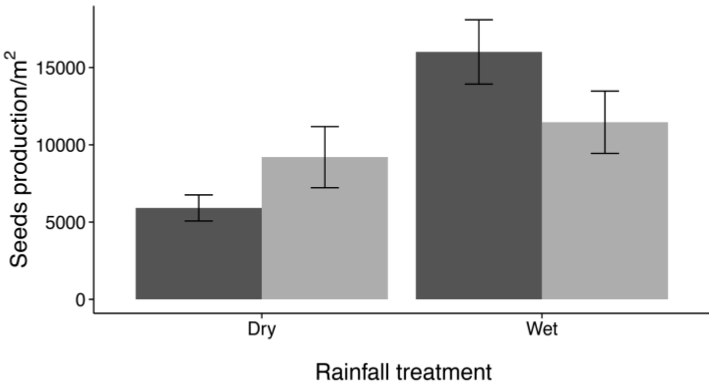

Figure 7: Seed production of *Avena* and *Erodium* shifted with wet and dry treatments*;* Rainfall treatments significantly affected *Avena* but not *Erodium* seed production (showing standard error bars)

	Exotic annual forbs			Exotic annual grass		
Seasonal Models	Current precip.	Lagged precip.	Current& lagged	Current precip	Lagged precip	Current & lagged
AIC	1132.7	1113.9	**1108.7**	1337.7	1339.8	**1328.6**
Precipitation variables						
Current fall	0.019	--	-0.061	0.017	--	0.046
Current winter	**0.173***	--	**0.224****	**-0.06***	--	**-0.068***
Current spring	**-0.177****	--	-0.081	**0.099****	--	**0.079****
Previous fall	--	**-0.194****	**-0.251****	--	**0.059***	**0.066***
Previous winter	--	0.028	0.072	--	-0.03	-0.039
Previous spring	--	**-0.302****	**-0.275****	--	**0.085****	**0.075****
Annual Models	Current precip.	Lagged precip.	Current & lagged	Current precip.	Lagged precip.	Current & lagged
AIC	1143.7	1122.9	**1122.3**	1353	1346.3	**1345.9**
Precipitation variables						
Annual	0.003	--	0.049	0.024	--	0.016
Previous annual	--	**-0.314****	**-0.32****	--	**0.071****	**0.069****

*p<0.05, **p<0.01

Table 1: Generalized linear mixed model (GLMM) regression estimates for exotic annual forb and grass functional groups. Seasonal and annual precipitation models with lowest AIC values always comprised current and previous-year precipitation. Bolding indicates significant results or most parsimonious model (lowest AIC).

CHAPTER 2

Long-term patterns and impacts of white pine blister rust spread in the southern Sierra

Jonathan Nesmith, Adrian Das, Nathan Stephenson, John Battles

ABSTRACT

Biotic agents of mortality are increasingly recognized as major drivers of disturbance in forest ecosystems. Although often overlooked as predominant factors, pathogens can incite major changes in forest composition, severely degrading ecosystem structure and function. While pathogens play an important role in forest mortality, few studies investigate long-term trends and the subsequent impacts, greatly limiting our ability to characterize and predict forest health outcomes. The combination of the invasive pathogen, white pine blister rust (*Cronartium ribicola* Fisch.), bark beetles, drought, and changing fire regimes has caused precipitous declines in populations of white pines (*Pinus* subgenus *Strobus*) in North America. The southern Sierra Nevada, however, have historically lower levels of mountain pine beetle and blister rust, which has important implications for white pine conservation. Here we characterized long-term spread patterns of bister rust through the southern Sierra. We found that over the past approximately 20 years, incidence dropped by almost 76 percent in *P. lambertiana* populations, but increased by 360 per cent in *P monticola*. For the first time, blister rust was recorded in *P. albicaulis* plots but no blister rust was confirmed in *P. balfouriana*. In addition, we recorded dramatically high mortality rates in sugar pines, warranting further investigation into the population's health status in the Sierra Nevada. Our findings suggest that blister rust and beetles are becoming an increasing threat to high-elevation white pines and efforts to restore and protect these species may be necessary under climate change scenarios.

INTRODUCTION

Biotic agents of mortality are widely recognized as major drivers of disturbance in forest ecosystems (Campbell and Antos 2000, Das et al. 2016). For example, pathogens can incite major changes in forest composition (Lewis and Lindgren 2000), which can alter ecosystem structure and function (O'Halloran et al. 2012). While pathogens play an important role in forest dynamics, few long-term studies investigate possible changing trends and the subsequent impacts, greatly limiting our ability to characterize and predict forest health outcomes (Telford et al. 2014).

The invasive pathogen, white pine blister rust (*Cronartium ribicola* Fisch), is an insidious agent of mortality in white pines (Genus *Pinus,* Subgenus *Strobus*). Since its arrival in 1906 (Maloy 1997, Geils et al. 2010), white pine blister rust has infected many white pine populations throughout the

US and Canada (Maloy 1997, Tomback and Achuff 2010). The impacts on white pine forests have been so severe that blister rust ranked as one of the worst disease epidemics in history (Campbell and Antos 2000). Early efforts to control blister rust, including *Ribes* eradication and topical fungicides were met with little success (Maloy 1997, Geils et al. 2010), and management today is focused on developing genetic resistance and silviculture techniques that constrain spread (see Zeglen et al. 2010).

The successful spread of blister rust depends on a number of factors, including the presence of susceptible hosts and suitable climatic conditions. Blister rust has a complex life cycle that alternates between white pine aecial hosts and telial host species from the genera *Ribes, Castellja* and *Pedicularis* (McDonald et al. 2006, 2006, Geils et al. 2010). Because blister rust is a non-native pathogen, frequencies of genetic resistance and associated mechanisms are relatively low across North American hosts (Van Arsdel 1972, King et al. 2010). Consequently, all white pine species except for the Great Basin bristlecone (*P. longaeva* DK Baley) Mexican white pine (*P. ayacahuite* Ehrenb.) have been documented with infections (Kinloch 2003, Blodgett and Sullivan 2004). Blister rust also requires mild temperature and higher moisture conditions for successful reproduction (Van Arsdel et al. 1956, Wong and Daniels 2017). When these conditions align, spores can disperse on wind currents for hundreds of kilometers, infecting numerous hosts during “wave years” (Kinloch 2003).

In addition, blister rust infections can interact with other important drivers of mortality. Bark beetles (e.g. *Dendroctonus* spp.) for instance, will preferentially select trees weakened by blister rust infections, often resulting in more immediate mortality than caused by blister rust alone (Larson 2011, Bockino and Tinker 2012). Bark beetle induced mortality can in turn shift fire behavior by modifying the quantity of flammable fuels, particularly immediately following severe outbreaks (Hicke et al. 2012). Though many studies have documented interactions between bark beetles and blister rust (Schwandt et al. 2004, Larson 2011, Bockino and Tinker 2012), and bark beetles and fire (Parker et al. 2006, Jenkins et al. 2013), the impacts of fire on blister rust remain largely unexplored (Tomback et al. 1995).

While white pine species have dramatically declined throughout the Western United States, the southern Sierra Nevada have had lower levels of infections and outbreaks (Dunlap 2012, Maloney et al. 2012). To determine the current extent of blister rust and bark beetles in southern Sierra white pines, we sampled long-term monitoring plots in Sequoia and Kings Canyon National Parks (SEKI). We characterized changes in blister rust spread over the past approximately twenty years, as well as current bark beetle attacks, across four white pine species. To quantify the long-term impacts of blister rust spread on white pines, we estimated demographic trends, including mortality, recruitment and population stability.

Specifically, because all white pine species are susceptible to blister rust (McDonald and Hoff 2001), we hypothesized that incidence and severity would increase across the four white pine species. We predicted that environmental variables associated with blister rust and beetles in other North American systems would also explain patterns in the southern Sierra, including the presence of alternate hosts, tree density, pine host size, and elevation. We also expected that bark beetles and blister rust would be strongly associated. Because fire has been hypothesized to increase selection for resistance (Tomback et al. 1995), we expected that burned plots would lower blister rust infection rates. Finally, we hypothesized that tree size class, blister rust infections, and elevation would partially explain patterns of mortality across white pines.

METHODS

Study site

The jointly administered Sequoia and Kings Canyon National Parks (SEKI) encompass 350,500 ha in the southern Sierra Nevada of California. The climatic is Mediterranean, characterized by hot, dry summers and wet, cold winters (van Mantgem et al. 2011). Elevations range from 300-4200 m, supporting a large diversity of forested communities. At higher elevations, thunderstorms are periodic during the summer, and snowpack accumulates during the winter starting around 1500 meters (Margulis et al. 2016).

Forests in the southern Sierra Nevada host five white pine species (*Pinus,* subgenus *Strobus*), all potentially threatened by white pine blister rust and bark beetles. Throughout SEKI, the white pines have distinct ranges with moderate overlap (Figure 8A). Sugar pine (*P. lambertiana* Dougl.) is a co-dominant species in mixed conifer forests, growing between 1000-2300 meters and often associated with ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), black oak (*Quercus kelloggii* Newberry), scrub oak (*Quercus berberidifolia* Liebm.), giant sequoia (*Sequoiadendron giganteum* [Lindl.] J. Buchholz) and cedar (*Calocedrus decurrens* [Torr.] Florin). Western white pine (*P. monticola* Dougl.) occurs between 2100-3200 and often grows on well-drained exposed sites with thin soils (Graham 1990). Associated species include foxtail pine, whitebark pine, red fir (*Abies magnifica* A. Murray) and lodgepole pine (*Pinus contorta* Douglas) (Graham 1990, Miller and Urban 2000). Foxtail pine (P. *balfourniana* Grev. and Balf.) is endemic to California and dominates more arid regions of the eastern Sierra typically above 2800 meters (Mastrogiuseppe and Mastrogiuseppe 1980). Whitebark pine (*P. albicaulis* Engelm.) often grows in denser stands on the western slopes of the Sierra and overlaps with foxtail and western white between 2800-3000m throughout SEKI (Nesmith et al. 2019). Whitebark is also associated with mountain hemlock (*Tsuga mertensiana* [Bong.] Carr) and lodgepole pine (Nesmith et al. 2019).

Sampling design

Plots were originally established in 1995-1997 using a stratified random sampling design based on the range of white pine species within the parks (Duriscoe and Duriscoe 2002). The original sampling method subdivided all major watersheds based on physiographic features for a total of 50 subunits. Plots were randomly generated within each subunit to fall within the predicted range of a white pine species. A total of 154 plots were established between 1995-1999 (Figure 1B), and plot size averaged 30m by 50m, though was adjusted to capture a minimum of 30 white pine stems.

Plot establishment and first survey, 1995-1999

Crews navigated to the randomly selected points and established a plot if more than 30 white pines stems greater than or equal to one meter tall were within 500m of the random point (Duriscoe and Duriscoe 2002). The plot starting points were marked with brass tags. The location (NAD27), slope (%), aspect (degrees) and elevation (m) at the plot tag were recorded. Using the plot tag as the origin, a center line was located along the contour to define the long axis of the rectangular plot. The location of each live white pine tree within 15m of the center line was mapped (x = distance from plot tag, y = distance from center line). For each mapped tree, Duriscoe and Duriscoe (2002) measured species, diameter at breast height (1.37m, DBH), height (m), and presence of blister rust.

Re-measure, 2013-2017

The location of each white pine stem originally surveyed was identified from mapped locations. New ingrowth (trees greater than or equal to one meter tall) that were not present in the original survey were mapped and assessed. For each plot tree, crews measured DBH, height, occurrence of fire scars, presence of blister rust signs, and symptoms of bark beetles. Two of the original plots were re-located but not re-measured due to poor tree location data from the original survey.

Blister rust and bark beetle identification

Crews scanned each tree from all sides searching for signs of blister rust, using binoculars on tall trees (Smith et al. 2008), and counted branch and bole cankers. Branch cankers were included only if all of the following symptoms were present: pitching, swelling or sunken bark, and discoloration of the bark on a specific section of the branch (see Appendix 5). Rodent chewing and aeciospores were included in the diagnosis when present (Hoff 1992). Bole cankers were verified by the following symptoms: heavy pitching from a specific area, swelling or sunken bark and an "entry point" (i.e., a branch canker that clearly led to bole canker).

In addition, crews searched each plot tree for signs and symptoms of two bark beetles: mountain pine beetle (MPB*, Dendroctonus ponderosae* Hopkins) and a commonly associated secondary bark beetle, red turpentine beetle (RTB, *Dendroctonus valens* LeConte). Attacks of MPB were identified based on the pitch tubes, streaming pitch, frass, or exit holes (Stephenson, 2019). When present, RTB attacks were identified within the first two meters from the base of the bole by larger, red-tinged pitch tubes and frass (Fettig et al. 2008).

Fire data

Fire history vector data were obtained from Sequoia and Kings Canyon National Parks (data also linked to the Wildland Fire Management Information database). Using ArcGIS Desktop 10.5.1, we extracted fire histories that occurred over the past 20 years for every sugar pine plot. We validated these data with plot and tree-level observations of fire, which included field observations of recent burns or fire scars. Three plots were recently burned (characterized by the presence of charred standing dead trees, scattered biochar, and multiple pitching white pine tree scars) but were just outside the boundary polygon, so they were included as burned plots. We categorized a plot as burned if one or more fires occurred in the plot between surveys. Fire sizes averaged around 8,700 acres and ranged between 0.22 to 151,000 acres. Seventy percent of the fires were human caused, including controlled burns.

Calibrating surveys

To calibrate crews and maintain accurate field measurements throughout the season, field technicians were trained by the same forest pathologist and entomologist at the beginning of each summer in the identification of blister rust and bark beetles. In addition, a crew member from the first survey in the late 1990s trained all new crews during the second survey. Because the resurvey occurred over multiple years with different crews, approximately 15% of the plots were surveyed a third time to determine among-crew variation. On average, there was an approximate 0.5 canker count difference between the crew reads, which was not significantly different, suggesting that the crews were sufficiently calibrated throughout the survey period (see Appendix 6).

Managing challenges encountered during the second survey

Three major challenges occurred during the second surveys: 1) high white pine mortality dramatically reduced the live stem sample sizes even with plot extensions, 2) whitebark pine growth patterns made DBH difficult to remeasure, and 3) a severe drought occurred throughout the second survey period. First, to address the major difference in sample sizes between surveys, crews extended plot transects until at least a minimum of 30 live stems were measured or a maximum transect length of 200 meters was reached (200 m by 30 m). Plot extensions primarily occurred in sugar pine plots, though a few were conducted in other white pine plots when sample sizes dropped below the 30 live stem minimum. Second, because whitebark often grows in clumps with multiple stems, it was not always possible to remeasure the same stem. When the crews were uncertain, the largest live stem in the clump was selected and new stem-level data recorded; these trees were removed from mortality analyses. Third, it is important to highlight that the second survey occurred during an extreme drought that began in 2012 and ended in 2016 (Stephenson et al. 2017). The drought impacts were likely more significant for the beetle populations (Stephenson 2019), though may have affected white pine blister rust as well (Van Arsdel 1972, Sturrock et al. 2011).

DATA ANALYSES

Blister rust extent, incidence, spread rate, and severity

We calculated plot-level and tree-level estimates of incidence, severity, and spread rate for each white pine species. We defined extent (E) simply, where P_{it} was the number of plots at time (t) with at least one infected individual and P_t was the total number of plots surveyed at time (t) (Table 2). Incidence was calculated for each species, where N_{it} was the number of trees infected at time (t), and N_t was the total number of trees surveyed at time (t) for that species. Our primary plot-level estimate for spread rate (*SR*) was calculated where I_1 is the incidence of blister rust at time 1 (2013-2016), I_o is the incidence at time 0 (1995-1999), and Δt is the average sampling interval in years between sample times t_1 and t_0 (Table 2). Severity of infection was calculated for each survey from the count of cankers and size of infected pines (modified from Duriscoe and Duriscoe 2002)

(Table 2). Even though both surveys spanned four years, the first survey results were labeled "1996" and the second survey results "2016" to maintain consistency.

Because the tree sample sizes differed between surveys, we estimated species-level incidence by subsampling the original survey data using the same sample sizes. Specifically, using the smallest sample size for each plot, we randomly selecting trees from the larger population 100 times. If more trees were added during the second survey due to recruitment or plot extensions, we used the original number of plot trees to estimate the incidence during the second survey. We averaged the incidence across all iterations and calculated the 95% confidence interval of the estimated mean.

Modeling blister rust incidence

Using logistic regression from R package (Lme4), we modeled live stem presence/absence of blister rust across all white pines, and we only included infections observed in the second survey. The independent variables included DBH, tree density, slope, aspect, elevation, presence/absence of MPB and/or RTB, and presence/absence of alternate hosts. We used plot nested within species as random effects. To test whether the model was overdispersed (variance > mean), we used R package (blmeco) (Korner-Nievergelt et al. 2015) and found that our model was not overdispersed. With R package (GGally), we estimated the correlations among independent variables. All variables except *Ribes* and elevation were loosely correlated (<0.2). To determine whether the collinearity between *Ribes* and elevation would result in unreliable coefficients, we estimated the variance inflation factor using R package (Car) (Fox et al. 2012), which was <0.2. Thus, we included both variables in the model (Quinn and Keough 2002).

To test whether fire interacted with blister rust spread in sugar pines, we compared differences in incidence between burned and unburned plots. To isolate the effect of fire, we only used new infections (trees that were infected after the first survey) in our analyses. Due to the decrease in sugar pine sample sizes between surveys, we compared groups using the percent of live trees with infections for each plot. We also tested whether fire affected the magnitude of the change in incidence ($I_{t1} - I_{t0}$) between burned and unburned plots using infected trees from both surveys. Due to unequal sample sizes and distributions that were not normally distributed, we used Wilcoxon non-parametric tests (Dalgaard 2008).

Modeling bark beetle attacks

RTB is a secondary bark beetle that often attacks white pines that are weakened by MPB (Fettig et al. 2007). Thus, we lumped these two species for our analyses and corresponding figures. Using logistic regression from R package (Lme4), we modeled the presence/absence of live trees with beetle attacks across all white pines. The explanatory variables and regression diagnostics were the same as blister rust model (see above), except we excluded *Ribes* and added presence/absence of blister rust. We also used plot nested within species as our random effects. In addition, to test whether fire impacted bark beetle in sugar pine, we compared the differences between burned and unburned plots using the percent number of live trees with bark beetle attacks. Due to unequal sample sizes, we compared groups using the Wilcoxon non-parametric test.

White pine demography

We calculated annual tree mortality following the methods outlined by Eitzel et al. (2015) and Sheil et al. (1995) (Table 2). We did not include new recruits in the analyses. We estimated 95% confidence intervals using a profile likelihood (Eitzel et al. 2015). Recruitment (*R*) and population stability (*St*) were calculated using equations described by Sheil et al. (1995) and Gomes et al. (2003) (Table 2). Corresponding 95% confidence intervals were calculated following Quinn and Keough (2002).

In addition, we used logistic regression from R package (Lme4) to explain mortality (1=dead, 0=alive) in sugar pine and western white pines. Independent variables were not significantly correlated (Quinn and Keough 2002) and included DBH, plot-level white pine basal area, tree-level blister rust presence from the first survey, slope, aspect, and elevation. We used plot as a random effect, and we verified that both models were not significantly overdispersed (Korner-Nievergelt et al. 2015). Because so few trees died in foxtail and whitebark pine plots, we did not develop models for these species.

RESULTS

Changes in blister rust incidence and severity

Between 1995 and 2017, the extent of blister rust increased by 41 percent across all plots (Table 3). Change in blister rust incidence varied greatly by species. Incidence increased in western white pines by 360% and decreased by over 76% in sugar pine populations. In contrast, only 1% of whitebark pines were infected and no confirmed infections were found on foxtail pines. (However, foxtail pines outside monitoring plots did express confirmed infections (Appendix 7)). The highest spread rate occurred in western white populations with approximately five new infections per plot per year. Some trees also changed in infection status. Specifically, 15% (*n*=70 sugar pines and *n*=4 western white pines) of infected trees during the first survey were still alive but either showed no signs of blister rust infections or only a subset of symptoms. In addition, blister rust severity followed similar patterns of incidence with greater severity in higher elevation white pines (Figure 9B). On average, severity was highest in whitebark pine populations, as a larger proportion of infections were bole cankers (Figure 9B).

Factors associated with blister rust incidence

Blister rust incidence was strongly, positively associated with the presence of *Ribes* (T = 2.15, P = 0.03), larger diameter trees (T = 2.65, P = 0.008) and bark beetles (T = 2.58, P = 0.01), and negatively correlated with elevation (T = -3.47, P = 0.001) (Figure 10A). In contrast, slope, aspect, and basal area of white pine hosts were not significantly correlated with blister rust. Fire also impacted blister rust spread in sugar pine plots. Between the survey period, 46% of sugar pine plots experienced a fire, and burned plots had significantly fewer infected trees than unburned plots (P = 0.003) (Figure 11).

Bark beetle attacks across white pines

Mountain pine beetle attacks declined in the higher elevation white pines. On average, less than 3% of sugar pines and less than 1% of western white, foxtail, and whitebark pines showed signs and symptoms of mountain pine beetle attacks (Figure 12). In addition, 14% of white pine stems (including sugar pine, western white and whitebark pine) with blister rust also showed signs of beetle attacks. Bark beetles were more abundant than blister rust in sugar pines and foxtail pines, while blister rust infections were more abundant in western white and whitebark pines.

Factors associated with bark beetle attacks

Bark beetle attacks were significantly correlated with larger diameter trees ($T = 13.29$, $P < 0.001$) and blister rust infections ($T = 2.25$, $P = 0.03$) (Figure 10). Bark beetle attacks also significantly declined with elevation ($T = -6.86$, $P < 0.001$). Slope, aspect, and white pine basal area, however, were not significantly associated with beetle attacks. While fire affected blister rust spread, fire did not shift the number of beetle attacks in sugar pines plots (Figure 11).

White pine demography

Highest rates of mortality occurred in sugar pine populations (4.3%/year), while lowest rates of mortality occurred in the high elevation whitebark (0.18%/year) and foxtail (0.16%/year) pines (Figure 13). Both foxtail and whitebark population’s recruitment rates (0.18%/year and 0.19%/year, respectively) were slightly greater than their death rates, while sugar pine and western white pine death rates were much greater than recruitment rates (0.63%/year and 0.14%/year, respectively). The disproportionately high mortality rate in sugar pine corresponded with extremely low stability (73%), followed by moderately low stability in western white (13.9%), foxtail (8.15%) and whitebark pines (7.99%) (Figure 13). Stability is at a maximum when $St=0$. Thus, all white pine populations experienced low stability between the survey period.

Factors explaining white pine mortality

The majority of white pines infected with blister rust (74.3%) died over the survey period, and the vast majority comprised sugar pines ($N = 298$), compared to western white pines ($N = 60$). Probability of mortality was highest for small diameter sugar pines with blister rust, and in general, infected white pines had higher probabilities of mortality than uninfected white pines (Figure 14). These results were corroborated by logistic regression estimates of the effects of DBH and blister rust on both sugar pine and western white pine mortality (Figure 15). Specifically, smaller diameter trees died more frequently across the sugar pine population ($T = -8.63$, $P < 0.001$), though this relationship was only marginally significant in western white pines ($T = 1.68$, $P = 0.09$). In western white pines, mortality declined with increasing elevation ($T = -5.97$, $P < 0.001$), a trend that was not significant in sugar pine populations (Figure 15).

DISCUSSION

Biotic drivers of mortality have caused widespread declines in North American white pines (Kinloch 2003, Bernard 2013). Historically, the southern Sierra had minimal blister rust and bark beetle outbreaks compared to other regions (Smith and Hoffman 2000). Our results highlighted that these trends are changing and caused major impacts in white pine populations. For example, in the 1990's, blister rust incidence was highest in sugar pines. While blister rust decreased dramatically since then, mortality rates were extremely high in sugar pines. In addition, blister rust spread relatively rapidly into western white pines, and they are currently the most heavily infected species in the southern Sierra. Though blister rust incidence slowed at high elevation, trends from this study, as well as other recent studies (Millar et al. 2012, Stephenson et al. 2019), suggest that these biotic agents of mortality will continue to increase with rising temperatures in high elevation white pines.

Blister rust spread into higher elevations threatens western white and whitebark pines

Changes in blister rust spread patterns are particularly concerning for western white pine populations. While incidence rates in the southern Sierra were still lower than other regions of the Intermountain West (Kim et al. 2003, Tomback and Achuff 2010), blister rust was the most abundant, major biotic driver of mortality (compared to bark beetles) in southern Sierra western white pines. Given western white's low resistance to blister rust (Kinloch 2003) and the predicted increases in California's minimum temperatures (Mann and Gleick 2015) that control blister rust spread (Cayan et al. 2008, Larson 2011, Smith et al. 2012), western white pine populations could follow similar demographic trends found in sugar pine today.

The spread of blister rust into higher elevations also threatened whitebark pine but not foxtail pine in our plots. Blister rust has caused major declines in whitebark pine throughout the Rocky Mountains and Canadian Rockies (Zeglen 2002, Smith et al. 2012) and foxtails in the northern Sierra and Klamath Mountains are more heavily impacted by blister rust (Dunlap 2011, Maloney 2011). Thus, the southern Sierra populations still remain some of the least negatively impacted by blister rust. Because both foxtail and whitebark pine are highly susceptible to blister rust (Kinloch 2003, Schoettle 2004), the spread of blister rust was likely constrained by the cooler temperatures and the arid conditions characteristic of the high southern Sierra Nevada (Costa-Cabral et al. 2012). These climate conditions may change in the future (Pierce and Cayan 2012), however, and even small increases in blister rust could have disproportionately large, negative impacts on these slow-growing, long-lived pines (Mastrogiuseppe and Mastrogiuseppe 1980, Krakowski et al. 2003).

Decline in sugar pine incidence linked to multiple factors

Historically, sugar pines were the most heavily impacted white pines in the southern Sierra (Duriscoe and Duriscoe 2002). Over the past twenty years, however, the majority of infected sugar pines died and relatively few new infections occurred in our plots, resulting in major declines in incidence and severity. While decreases in sugar pine incidence have also been documented at Happy Camp in the northern Sierra (Sniezko et al. 2004), the current incidence across the North American range remains largely unknown. In addition, our results likely underestimated the full impact of blister rust. Infections that occurred in small diameter trees or high canopy branches after the first survey could have been missed during the second survey because infected trees died or branch cankers were suppressed (Das et al. 2016).

The decline in sugar pine incidence and severity can be linked to a combination of factors including fire, fewer "wave years", higher resistance, and reduced host density. Specifically, burned sugar pine plots had significantly lower incidence than unburned plots, highlighting that fire played an important role in suppressing new infections. Fires can control blister rust through two mechanisms: 1) facilitating selection for rust resistance in recruiting individuals (Tomback et al. 1995) and 2) reducing spore propagules by burning both the white pine and alternate hosts. Spore reduction is likely an ephemeral effect, however, as nearby infected regions can disperse blister rust spores into burned areas. Many *Ribes* spp. can also resprout following fire and sugar pine recruitment is often stimulated by fire (Quick 1962, van Mantgem et al. 2004, Zambino 2010), suggesting that these impacts are highly site and species specific.

In addition, higher maximum temperatures may have suppressed blister rust reproduction in sugar pine stands. Blister rust is considered a mild weather pathogen (Van Arsdel et al. 1956, 1956, Kinloch 2003) and has a highly weather-contingent reproductive cycle (Bega 1960). Over the past twenty years, average temperatures in California have increased (Mann and Gleick 2015, Stephenson et al. 2017) and the recent drought culminated near the end of the second survey. The drought may have obscured visible symptoms of blister rust (e.g., aeciospores on white pines, pitching heavily at infection sites), resulting in fewer confirmed infections. Hotter maximum temperatures may have also reduced the number of "wave" years, or suitable climatic windows for blister rust reproduction (Sturrock et al. 2011). Gene-by-environment interactions have been widely documented in the literature to control spread (Van Arsdel 1972, Woo et al. 2004, McDonald et al. 2005, Zambino 2010), and further investigation into these dynamics may highlight their important role in constraining blister rust in sugar pine.

Selection for resistance in progeny and alternate hosts may also partially explain the decrease in sugar pine incidence, though it was unlikely the major contributing factor. For instance, the current frequency of *R* resistance genes are relatively low in southern Sierra sugar pines (Kinloch et al. 2003, Sniezko et al. 2004) and alternate host understory species (Geils et al. 2010), suggesting that selection pressures were relatively weak during the past twenty years. In addition, both the length of the sugar pine life cycle and age-related resistance, or ontogenetic resistance (Kinloch Jr and Scheuner 1990, King et al. 2010) can slow selection for resistance. Sugar pine trees, for instance, often live for over 400 years (Kinloch Jr and Scheuner 1990) and 18 percent of sugar pines in our plots "recovered" from infection. Consequently, larger trees with less severe infections, as well as trees expressing ontogenetic resistance still produced susceptible offspring (Kinloch Jr and Scheuner 1990), thereby reducing selection pressures.

Mortality events particularly concerning for sugar pines, followed by western white pines

Previous research suggested that sugar pine has been declining slowly over the past few decades in the southern Sierra Nevada due to combined effects from blister rust and fire suppression (van Mantgem et al. 2004, Das et al. 2016). Our research highlights that the rates of decline are much higher than previously documented. Sugar pine mortality was best explained by size class and blister rust, which is consistent with previous studies (van Mantgem et al. 2004, Nesmith et al. 2011). In addition, while we were surveying sugar pine plots during the drought, the majority of trees died in 2015, just after we finished half of the sugar pine plot surveys. Surveys in 2017 from outside of our plots suggested that mortality rates were as high as 80% in some areas (unpublished data), suggesting that our results likely underestimated the interacting effects of drought and beetles. In addition, recruitment rates in western white pines were lower than death rates, leading to low stability calculations. While western white pine mortality rates were much lower relative to sugar pine, mortality will likely increase in the future as a result of blister rust.

Bark beetle most active in low elevation white pines

Bark beetle activity was greatest in sugar pine populations and declined in higher elevation white pine species, particularly whitebark and foxtail pines. These findings are consistent with previous studies that show elevation and cooler climatic conditions at higher elevations can limit beetle reproduction and spread of *Dendroctonus* spp. (Chapman et al. 2012, Mitton and Ferrenberg 2012). While mountain pine beetle has caused widespread mortality events in whitebark pine in the northern Sierra Nevada (Millar et al. 2012) and other regions of the Western US (Logan and Powell 2001, Kurz et al. 2008), the cooler climate associated with the high elevations of southern Sierra likely constrained beetle reproduction. New studies, however, report that beetle activity was recently elevated in whitebark pine (Meyer et al. 2016, Slayton et al, 2019), suggesting that rising temperatures will continue to shift patterns of beetle populations in the future. The impacts of bark beetles in western white pine were also likely underestimated, as the majority of western white pine plots were surveyed in 2013, just before the bark beetle's exponential growth during the drought (Stephenson et al. 2019).

Blister rust and bark beetles are associated with each other and similar drivers

Incidence across white pines increased with tree size, and was positively associated beetles, a pattern commonly noted in other white pine populations (Tomback et al. 1995, Wong and Daniels 2017). Larger trees, for instance, are more likely to be infected with blister rust because they have been exposed for longer (Tomback et al. 1995). In addition, beetles and blister rust were significantly correlated in both sugar pine and western white pines, a common pattern found in other regions (Campbell and Antos 2000, Schwandt et al. 2004, Bockino and Tinker 2012). Blister rust infections can predispose white pines to beetle attack by weakening their defense mechanisms (Bockino and Tinker 2012), though this trend was found to decline in larger diameter trees (Bockino and Tinker 2012). Finally, temperature controls on the blister rust and bark beetle reproductive cycles (Van Arsdel et al. 1956, Smith-Mckenna et al. 2013) likely curtailed impacts in the subalpine, which is a common pattern in montane systems (Dahir and Carlson 2001, Smith et al. 2013). The predicted rise in minimum temperatures in the Sierra Nevada over the next century, however, may facilitate faster rates of blister rust expansion and beetles attacks into high elevation white pines in the future.

Future directions

Climatic conditions (e.g. temperature) can limit reproduction and spread of blister and beetles. Identifying the specific climate drivers specific to the southern Sierra will be important for predicting climate change impacts on white pines. In addition, the dramatic decline of sugar pine and the elevated mortality rates in western white pine (mortality > recruitment as well as very low stability) warrants further investigation across the species' range to assess their current health status. While it is difficult to disentangle the biotic and abiotic drivers of mortality acting on this system, increasing annual surveys and expanding monitoring efforts will enable more detailed analyses and better identification of the most important threats (e.g., blister rust, mountain pine beetle, fire severity, fire suppression, vs. drought). In addition, further research into whether gene-by-environment effects confer greater resistance in foxtail pines will be important to disentangle complexity of blister rust pathosystem in the Sierra Nevada. While recent trials from the USFS demonstrated that foxtail pine is one of the most susceptible species (Sniezko forthcoming), our *in situ* results suggested that foxtails are the least susceptible.

Relevance to management

The major decline of sugar pine is particularly important for mixed conifer forest management. Sugar pines are critical subdominant species that are the second largest trees (second largest to the largest trees in the world, giant sequoia) and provide important ecosystem services, including food, forage and habitat for wildlife. Their loss could have major ramifications for the health of mixed conifer forests in California. Our results also highlight for the first time that fire can have an important impact on curtailing the spread of blister rust in sugar pine. Planting rust resistant trees following fire may help assist recovery. In addition, efforts to document the changes of beetles and blister rust over the coming decades will be critically important for whitebark management efforts, as it is currently being considered for listing under the Endangered Species Act (Slayton et al. 2019).

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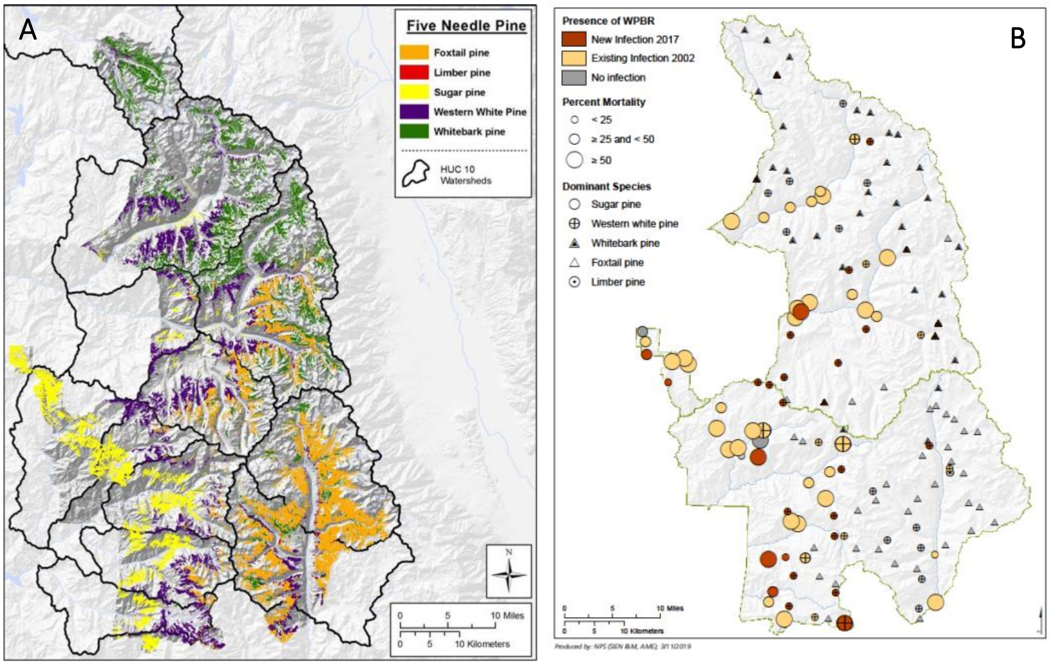
FIGURES AND TABLES



Produced by: NPS (SIEN I&M, AME); 3/11/2019

Figure 8: Maps of species distributions and plot locations in SEKI. A) Displaying the distributions of white pine species within both parks (colored regions). B) Displaying all plots sampled, plot-level tree mortality, and the number of trees infected with blister rust in each plot (denoted by colored circles).

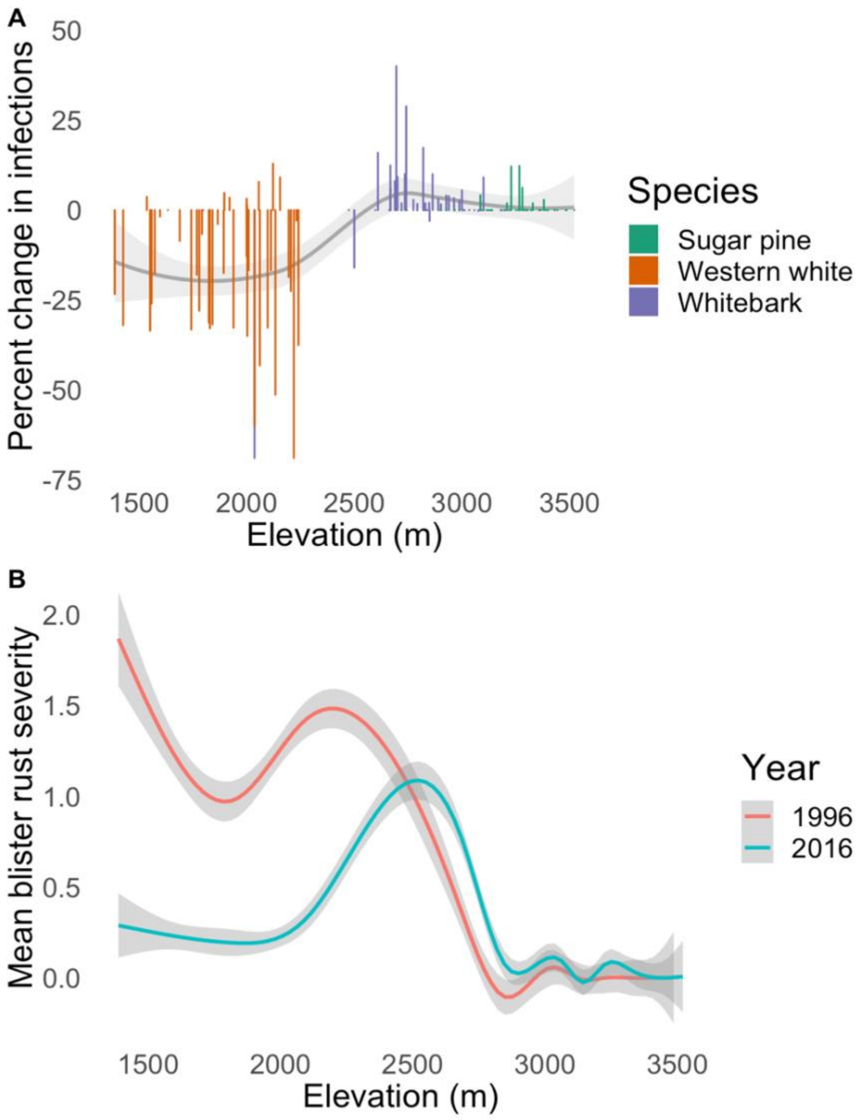


Figure 9: Change in the number of blister rust infections and mean blister rust severity between surveys. A) Percent change in the number of trees infected per plot across elevation and species. Includes all plots with sugar pine, western white and whitebark pine; foxtail was excluded because there was no change in blister rust infection between surveys. B) Smoothed lines of average tree-level severity from both surveys across elevation. Shaded regions show 0.95% confidence intervals.

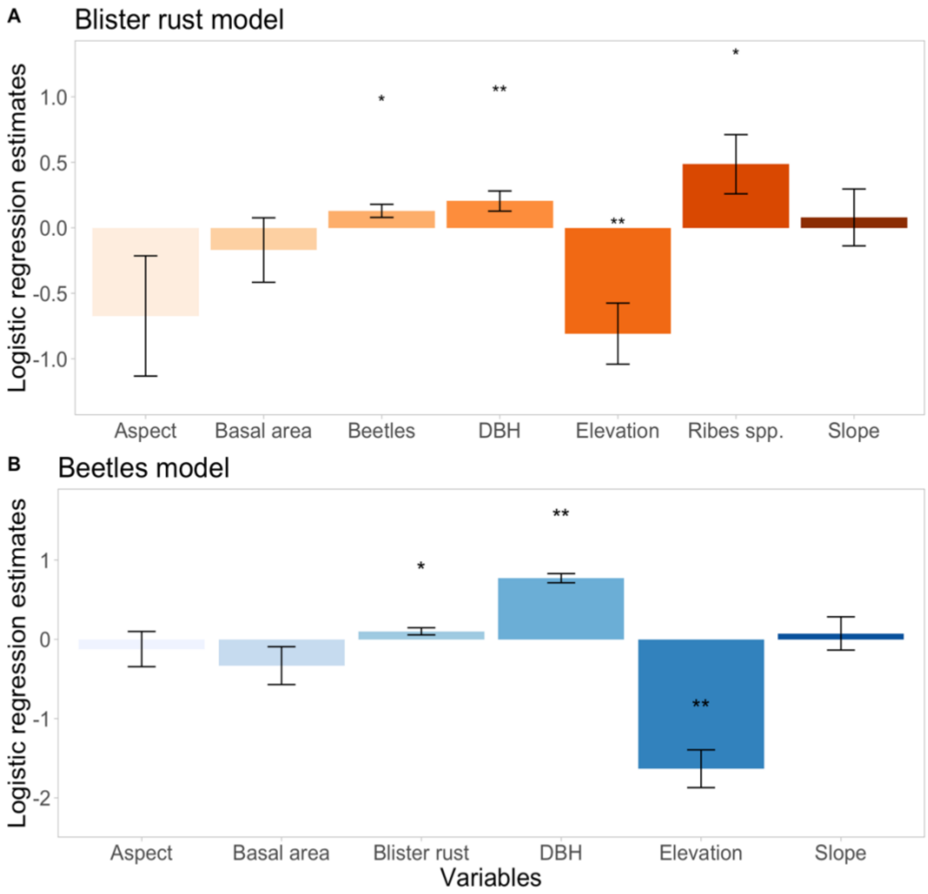


Figure 10: Factors explaining blister rust infections and beetle attacks from the 2013-2017 survey. Bars represent logistic regression estimates of tree-level blister rust infections (A) and tree-level beetle attacks (B). White pine BA is white Displaying standard error bars with significance levels: *P* <0.01**, *P*<0.05*.

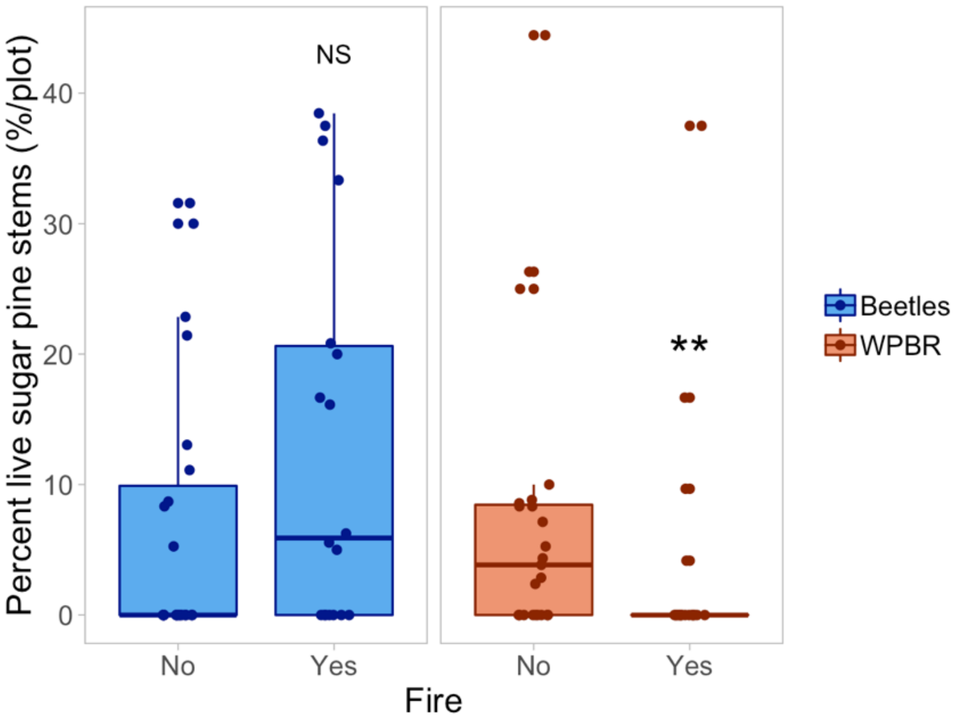


Figure 11: Impact of fire on blister rust incidence beetle attacks. Showing average percent number of live trees with infections (orange) and beetle attacks (blue) between burned (yes fire) and unburned (no fire) plots. Boxplot is jittered and significance is labeled as: *P* <0.01** and NS = not significant.

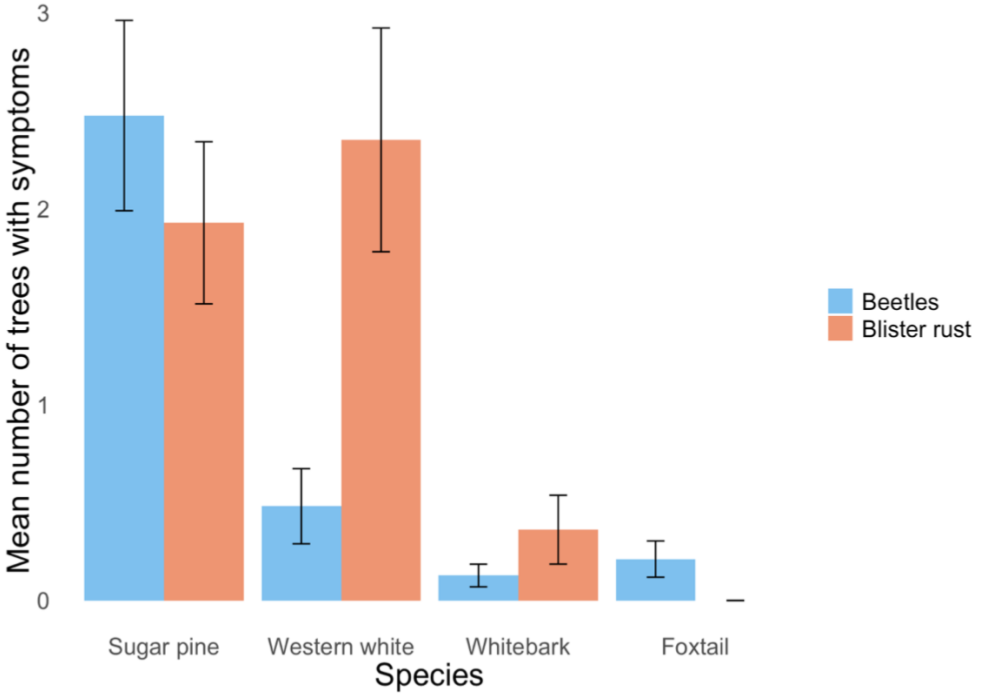


Figure 12: Variation in the number of blister rust infections and beetle attacks across species. Displaying the mean number of trees with blister rust and bark beetles attacks per plot across all live white pine stems. Showing standard error bars.

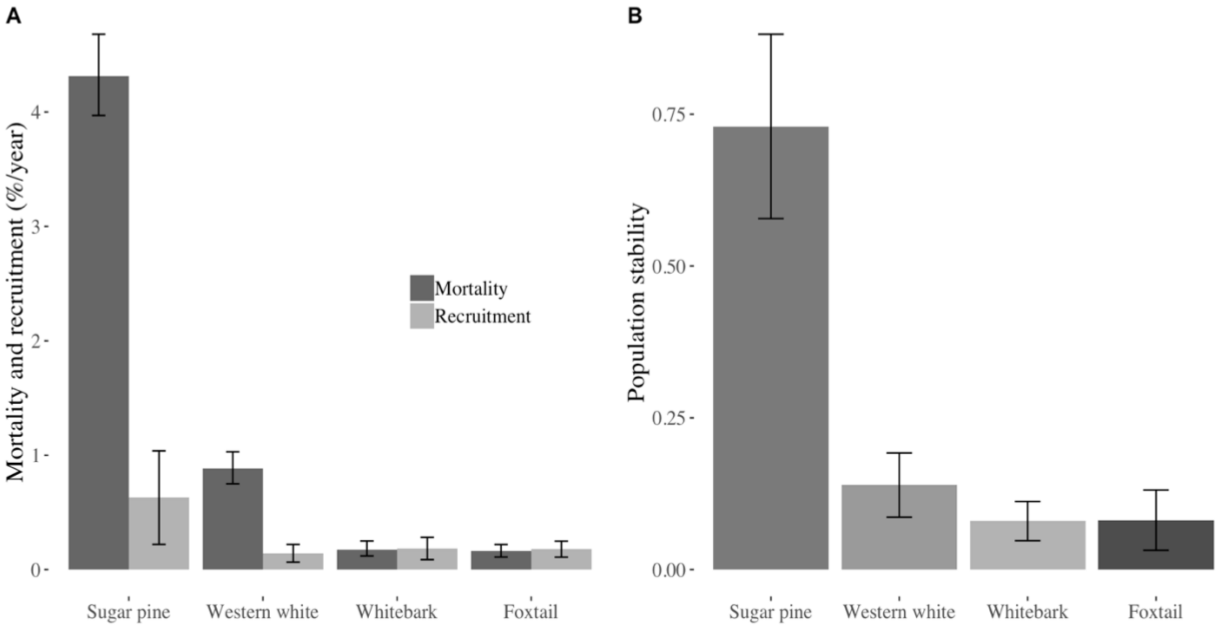


Figure 13: A) Average mortality rates and recruitment rates across species; showing 95% confidence intervals. B) Showing population stability. Stability is at maximum when St = 0.

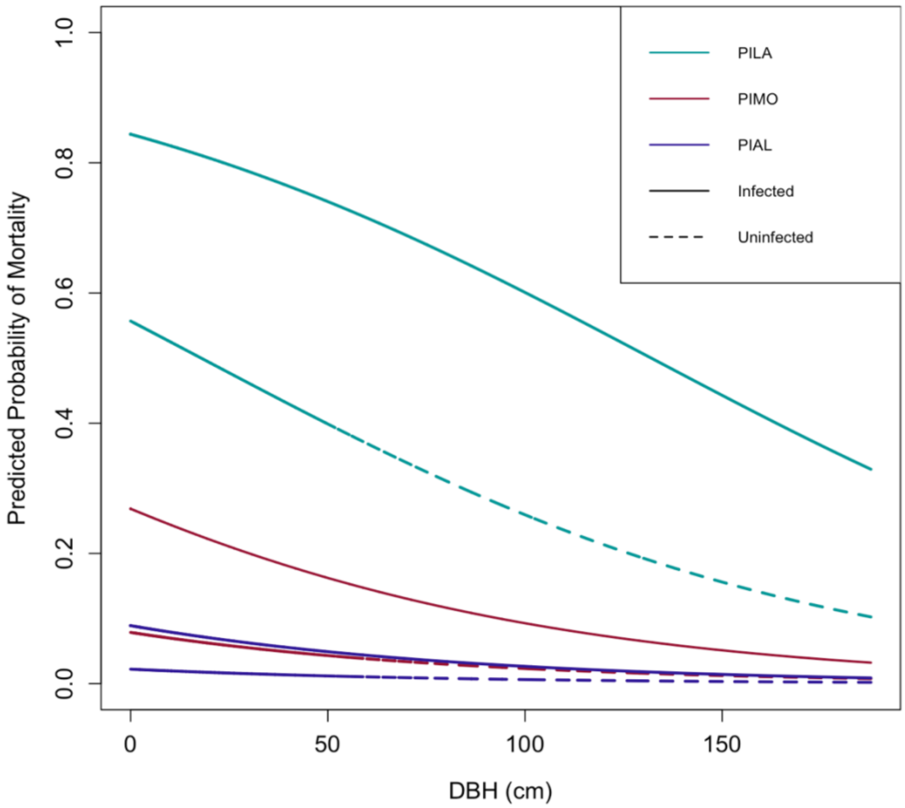


Figure 14: Predicted probability of mortality with and without blister rust infections for three white pine species with confirmed blister rust infections. Probability of mortality is higher with blister rust infections for all species (filled lines).

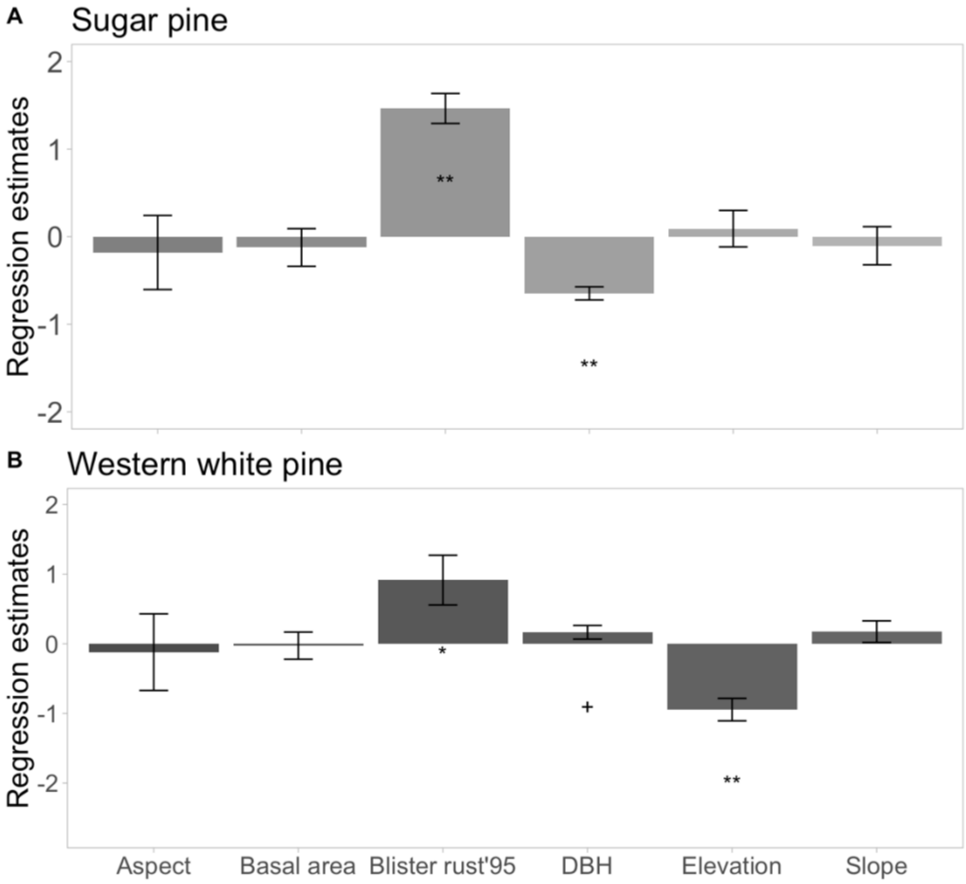


Figure 15: Significance of independent variables used to estimate mortality in sugar pine (A) and western white pine (B). Displaying standard error bars from logistic regression outputs; significance codes: **p<.01, *p<.05, +<0.1

TABLES

Variable	Equation	Description
Extent		P_{it} = # plots at time t with >1 infection; P_t = total number of plots surveyed at t.
Incidence		N_{jt} = # of infected trees N_t = total # trees surveyed
Severity		*cs* = canker severity class (0 = 1 branch canker, 1 = 1-3 branch cankers, 2 = 4-9 branch cankers, 3 = 10-25 branch cankers, 4 >25 branch cankers, 5 = bole canker).*
Spread Rate		I_1 = incidence *1* (2013-2017), I_o = incidence at time 0 (1995-1999), and Δt = average time interval between t_1 and t_0.
Mortality		N_1 = #live stems at time 1; N_0 = # live stems at time 0; Δt = time interval between t_1 and t_0.
Recruitment		*r* = # individuals recruited, N_0 = # live stems at time 0, Δt = time interval between t_1 and t_0
Stability		*r* = # individuals recruited, *m* = # individuals that died, N_0 = # live stems at time 0

Table 2: Equations used in calculating mortality (*M*), recruitment (*R*), stability (*St*) and blister rust spread (*SR*), severity (*S*) and incidence (*I*). * DBH is the tree diameter at breast height (in inches); if tree diameter is greater than 25 inches, then DBH = 25, unless the *cs* component is zero, in which case *S* = 0.

Species	Incidence 1996 (%)	Incidence 2016 (%)	%Change	Spread rate
Whitebark	0	1.01 (0.005, 0.016)	NA	0.9
Foxtail	0	0	NA	0
Sugar pine	19.4 (0.17, 0.22)	4.7 (0.03, 0.06)	-75.58	-2.22
Western white	2.4 (0.172, 0.32)	6.6 (0.054, 0.076)	360	5.47
Extent	27	38	41	0.85

Table 3: Summary statistics of blister rust extent, incidence, spread rate for SEKI. Showing

CHAPTER 3

Navigating novelty and risk in resilience management

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ABSTRACT

Resilience has long been championed as a framework to manage climate change impacts. There is growing concern, however, that certain resilience-based management (RBM) strategies are in conflict with traditional restoration and conservation goals. More recently, the theory of novel ecosystems has gained momentum to help conceptualize management of unprecedented global change. Here, we directly link novel ecosystems concepts with resilience theory to provide a framework illustrating how RBM can facilitate or even accelerate the emergence of novel ecosystems. These novel ecosystems may be beneficial by sustaining critical ecosystems services or destructive, leading to ecosystem degradation. We then provide a framework that links concepts from novel ecosystems and resilience theory to inform management of ecosystem change. We highlight that resilience-based applications need to address risks associated with novel human impacts to improve management outcomes.

INTRODUCTION

Across the globe ecosystems are experiencing unprecedented changes in environmental conditions. Record-breaking beetle outbreaks in Western North America and widespread coral bleaching have dramatically transformed ecosystems (Ratajczak et al. 2018). Such events are often considered harbingers of global change, and many predict we will continue to see major alterations in environmental conditions (Millar and Stephenson 2015, Ratajczak et al. 2018). Developing management approaches that support natural systems in an unpredictable future is therefore becoming an increasingly important challenge.

Resilience theory is gaining international attention in natural resource management as a conceptual foundation to help mitigate or guide ecosystem shifts (Folke et al. 2010) (see Online Supplementary Material Figure S1). Resilience thinking -- in both the conceptualization and operationalization of ecosystem management -- continues to diversify, comprising various informal and formal frameworks, including adaptive management (Williams 2011), ecosystem stewardship (Chapin et al. 2010), resilience-based governance (Garmestani and Benson 2013) and adaptive resilience-based management (Anthony et al. 2015). We use the term resilience-based management (RBM) to encompass the diversity of resilience applications in ecosystem management.

Although RBM plans are highly diverse (Table 4), a unifying theme is a shift away from steady-state approaches to view management in the context of changing environmental and social conditions (Chapin et al. 2010). One frequently stated goal is to enhance the system's ability to bounce back from disturbance to a previously defined state (Table 4). Manipulating herbivorous fish populations, for example, can facilitate coral reef recovery following bleaching events (Scheffer et al. 2015). RBM approaches can also encourage a system to track environmental change, which can include enabling a transformation into a more resilient state (Chapin et al. 2010, Millar and Stephenson 2015). Global change is leading to higher frequencies of megadisturbances in forests, which threatens many ecosystem services (Millar and Stephenson 2015, Bradford et al. 2018). Some RBM approaches advocate facilitating forest transitions to more disturbance-tolerant and climate-adapted forests (Millar and Stephenson 2015).

As RBM is increasingly applied, there is growing concern that the uncertainties of future global change impacts (Aplet and McKinley 2017), as well as the ambiguities of resilience theory, can lead to misapplications. To help improve RBM outcomes, we address an important conundrum in the operationalization of resilience theory: systems will need to track environmental change, but management that aims to support this ability to change can also inadvertently lead to undesirable outcomes (Newton 2016, Sinclair 2016, Aplet and McKinley 2017). Below we describe the relationship between resilience, ecosystem change and novelty. We then present a framework that highlights how resilience-based applications differently embrace change and novelty.

Resilience, ecosystem change, and novelty

Ecosystem resilience describes the ability to resist and reorganize in response to a disturbance while retaining similar structure, function, and feedbacks, *sensu* Walker and colleagues (Walker et al. 2004). Though resilience and adaptive capacity are closely related terms (some suggest they mean the same thing (Gallopín 2006)), adaptive capacity tends to emphasize a system's flexibility (Carpenter and Brock 2008), or the ability to adjust to environmental conditions (Smit and Wandel 2006). Thus, strategies that enhance adaptive capacity ultimately lead to long-term resilience. Depending on the interpretation of these terms, resilience and adaptive capacity are differentially applied in natural resource management. For instance, some organizations are focused primarily on building resilience in response to global change (National Parks Service, Table 4), others are more interested in adaptation strategies (Canadian Council of Forest Ministers, Table 4), while still others emphasize both (US Forest Service, Table 4).

Theory advocates that a certain amount of ecosystem change is critical for tracking environmental shifts, as it ultimately enhances a species' or ecosystem's resilience (Folke et al. 2010, Allen and Holling 2010). The key to achieving success is to ensure the elements needed for change are available, such as diversity in nearby patches, redundant hierarchies that support function, dormant elements such as seedbanks, or rare genes in a population (Allen and Holling 2010, Oliver et al. 2015, Chaffin et al. 2016a). If these elements (e.g., genes, species or functions) were not historically present within the system, they are considered novel (Witt 2009). Some argue that the ability to generate and use novelty is central to the resilience of species and ecosystems (Allen and Holling 2010, Chaffin et al. 2016a). For instance, in water fleas (*Daphnia*), an increase in genetically-derived thermal tolerance, a novel genetic adaptation, enables them adjust to higher temperatures (Geerts et al. 2015). Novel species can also assist ecosystem recovery following unprecedented disturbances. For instance, the non-native gorse shrub (*Ulex* spp.) in New Zealand facilitates succession of native species in deforested pastureland by providing more shade and nutrients compared to the denuded landscape (Barker 2008).

Although ecosystem change and novelty can enhance resilience, they can also be counterproductive by facilitating shifts towards undesirable states (Allen and Holling 2010, Chaffin et al. 2016a, Aplet and McKinley 2017). Invasive species in particular are widely recognized for enabling transformations (Guy-Haim et al. n.d., Chaffin et al. 2016b). Non-native grasses, for instance, can establish dominance over native species through positive feedbacks that shift nutrient cycling and light availability (Richardson and Gaertner 2013). Once past a threshold, stabilizing feedbacks can create novel ecosystems (see Glossary), a class of alternate states comprising non-historical abiotic and biotic conditions that did not previously exist (Hobbs et al. 2013, Richardson and Gaertner 2013) (see Appendix 8 for greater detail on the connection between resilience and novelty). Depending on the type of transformation, novelty and change can compromise management goals by reducing function or biodiversity (Hobbs et al. 2009). We present a conceptual model of a resilience-based management (Figure 17) and suggest there are two fundamental ways to improve the effectiveness of RBM: 1) clearly articulate management goals; and 2) identify how different management approaches embrace novelty and change. Ultimately, conversations about when and how RBM strategies should build resilience and introduce novelty are critical for mitigating an undesirable state emergence.

1. Clearly articulate management goals

Goals define desired outcomes and give direction to management (Wallace 2012). Goals also reflect human values such as aesthetics, spiritual contentment, protection from other organisms, and adequate provisioning of resources (Wallace 2012). Although effective natural resource management depends upon the clear articulation of goals and values (Wallace 2012), some RBM plans sidestep this stage by embracing generic calls to “build resilience” or “support adaptive capacity.” For instance, the Paris Agreement Article 7 described the global goal on adaptation as “enhancing adaptive capacity and resilience”. Ecosystem resilience and adaptive capacity, however, are characteristics that best accompany other management goals. Certain types of resilience help sustain ecosystem services and biodiversity, while in other circumstances resilience can impede management (Standish et al. 2014). Many historically intact, biodiverse reefs, for instance, are very susceptible to global change impacts (Oppen et al. 2015). In contrast, degraded, weed dominated reefs can be very resilient due to their adaptations to multiple stressors (Côté and Darling 2010). By focusing on generic resilience as the ultimate goal, managers can favor a system that might be in conflict with other values and goals, such as biodiversity conservation (Newton 2016).

Clearly identifying which system attributes should be resilient can also help managers address a common concern that resilience is too ambiguous for effective policy application (McEvoy et al.

2013, Olsson et al. 2015, 2015, Newton 2016). As the concept of resilience has evolved, the definition has become increasingly vague and flexible, leading to greater risks to biodiversity (Newton 2016). Resilience has been invoked in Europe, for example, to advocate for assisted migration, genetic modifications, and introductions of non-native species, actions which can threaten old growth forests and reduce the evolutionary fitness of locally adapted species (Koskela et al. 2014). Placing greater emphasis on which characteristics of a system should be resilient to different stressors (Standish et al. 2014, Olsson et al. 2015) can help guide the selection of strategies. Certain elements in a system, for instance, might need to change (e.g., species turnover as climate shifts) for target processes to be resilient (e.g. ecosystem productivity). Given the current limitations around identifying which factors contribute to resilience (Quinlan et al. n.d.), this is a tremendous challenge. Specific goals that identify aspects of the system that enhance resilience and whether ecosystem recovery or transitions are desired can help guide management actions.

It is also important to consider all aspects of a system that contribute to resilience (Oliver et al. 2015) and move away from single causation approaches. For instance, identifying the possible trade-offs that can emerge in the operationalization of resilience can help mitigate unintended outcomes (Bestelmeyer and Briske 2012). Particularly when facing unprecedented mortality events, catastrophic fires, or flooding threats, factors that do not directly build resilience to such events might be overlooked or deprioritized, at times facilitating greater levels of undesirable novelty. For example, agencies are applying resilience strategies to manage the increasing threats of droughts and megafires in California. A recent report highlighted “the need for decisive action to restore California’s forests to resiliency” (“Fire on the Mountain: Rethinking Forest Management in the Sierra Nevada | Little Hoover Commission” n.d.). The treatments recommended included forest thinning and prescribed burning, which are known to reduce resistance to invasion of non-native species, including the grass, *Bromus tectorum* (Keeley et al. 2005). *B. tectorum* can shift the fire regime, reducing fire severity but increasing fire frequency (Brooks et al. 2004). In chaparral environments, this positive feedback between fire and invasive grasses has enabled a complete type conversion to grass dominated systems (Keeley 2006). Thus, long-term ecosystem resilience can be compromised if RBM goals and strategies do not consider the complex causal networks within an ecosystem.

Finally, global change is driving systems away from historical conditions, forcing some level of change in most ecosystems (Radeloff et al. 2015, Aplet and McKinley 2017). RBM is often motivated by the hope of preventing an undesirable state shift, while at the same time encouraging ecosystem adaptations that can cope with global change. RBM must therefore balance 1) the risk that global change could precipitate undesired transformations within the system, with 2) the risk that management interventions themselves reorganize the system towards an undesired state (Aplet and McKinley 2017). Conversations around ideal states, as well as acceptable vs inevitable levels of ecosystem change, can help reduce the possibility that management interventions are misapplied. RBM management plans for systems in peril of a state change might be more willing to frame approaches using language of adaptation, and implement strategies that add greater novelty (Table 4 – Canadian Forest Council). In these circumstances, identifying how these interventions can fail and developing strategies to mitigate such failures can minimize associated dangers.

2. Identify how different management approaches embrace novelty and change

Managers can select from a variety of approaches when applying RBM (Figure 17). At one end, managers might decide that current or predicted ecosystem changes are acceptable and no intervention is necessary. Even when facing unprecedented shifts in temperatures and disturbance regimes, some systems might be relatively well equipped to cope (Hobbs et al. 2018). Chihuahuan Desert grasslands, for instance, are surprisingly resilient to pulse perturbations (Bestelmeyer et al. 2013), as are one of the largest nesting rookeries of loggerhead sea turtles (*Caretta caretta*) in West Africa (Abella Perez et al. 2016). Thus, in more resilient systems, letting nature respond to drivers of change can result in desired outcomes (Corlett 2016). Managers can also decide to accept the emerging shifts in ecosystems. Treeline advance in the arctic, for instance, can alter species diversity and ecosystem function in the tundra, but it might also increase the rate of carbon sequestration in certain areas depending on the level of warming (Zhang et al. 2013). Acceptance might also be a default given limited resources and uncertainty surrounding the likely success of interventions.

When managers choose to intervene, RBM often provides three approaches to enhance resilience: 1) manage drivers of change; 2) increase adaptive capacity; or 3) enable transformation (Figure 17) (Folke et al. 2010, Chapin et al. 2010). On-the-ground strategies associated with these approaches are highly diverse and not necessarily exclusive to RBM, as many were developed under different paradigms, including conservation, restoration, and even steady-state approaches (Aplet and McKinley 2017). In addition, the focus on ecosystem change in many RBM approaches demands not only that new strategies be developed (Seastedt et al. 2008, Hobbs et al. 2018), but also that they balance the need for adaptation with the possible emergence of undesirable outcomes. Introducing climate adapted, novel ecosystem engineers into a system can be more risky than adding novel, subordinate species, as engineers are more likely to facilitate ecosystem transformations (Chaffin et al. 2016a) (Box 1). Below we highlight how three commonly used RBM approaches represent dramatically different relationships towards risk tolerance and the need for bold measures in the face of unprecedented change. Few agencies using RBM are explicitly drawing links between their strategies, expected outcomes, and associated risks. By drawing these connections, surprise outcomes can be reduced.

Box 1: Enabling change and planning for failure

The National Fish, Wildlife and Plants Climate Adaptation Strategy (USFWS) featured an adaptation strategy in Alaska where local agencies are replanting beetle killed areas with white spruce and non-native lodgepole pines (*Pinus contorta*) (Nfwpcap 2012). Here the RBM intervention ideally restores the forest and encourages adaptive capacity. However, by adding novel species into the system, they could be introducing elements that have known risks of being transformative. Lodgepole pines used in replanting are considered an aggressive invasive species in New Zealand (

Figure 16) that alters native landscapes, negatively impacting farming and tourism industries and reducing water availability. Though lodgepole pines are native to other areas in North America, without transparent discussions of risk tolerance, it remains unclear whether migrating lodgepole pine as an adaptation strategy will result in desired outcomes.

Figure 16: Red trees in the foreground are invasive lodgepole pines (*P. contorta*) killed by herbicide in an attempt to control spread around Lake Pukaki, New Zealand (Photo taken January 2018).

Manage drivers of change

In some cases, multiple drivers of change reduce the resilience of a system. Focusing on the drivers that are manageable, typically those occurring at local or regional scales, can increase resilience to drivers of change at broader scales (Figure 18B). For example, interactions between land use, fire, and climate change raise the possibility of a state change in large regions of the Amazon, shifting the forested state to a savannah-like grassland (Nepstad et al. 2008). The imminent state shift is supported by theory (Nes et al. 2014), model experiments (Boers et al. 2017) and field-based evidence (Brando et al. 2014). To reduce the likelihood of a state shift, managers can mitigate local anthropogenic impacts, in this case deforestation and fire frequency, to increase the resilience of the Amazon system to climate change (Nepstad et al. 2008, Nobre et al. 2016, Boers et al. 2017). Managing local threats can therefore help constrain ecosystem shifts by sustaining the system's natural adaptive capacity to global pressures. Relying upon the system's ability to naturally adapt to global threats also avoids active manipulation of the system and reduces the likelihood of undesirable novelty emerging in response to management interventions.

Increase adaptive capacity

Common strategies to increase adaptive capacity include: 1) encouraging characteristics that organically give rise to adaptation or 2) actively introducing adaptive elements into the system (Figure 18C). The U.S. Government's Priority Agenda for Enhancing Climate Resilience of America's Natural Resources, for example, suggests protecting system properties that foster resilience by increasing species diversity, pathways for movement and migration, and topographic and climate gradients. Because these strategies facilitate processes that increase natural adaptive capacity (e.g., species turnover, dispersal, local adaptation), success can be achieved without directly introducing novelty into the system.

In contrast, when the natural processes that enable adaptive capacity cannot keep pace with shifting environmental conditions, interventions can encourage a system's ability to track change. RBM strategies can directly introduce novel elements into a system that both increase the adaptive capacity and modify the historic state's identity and function. For example, forest pests and pathogens can be more adapted to warming temperatures than their hosts and cause extensive tree mortality (Keenan and Nitschke 2016, Lindenmayer et al. 2016). The introduction of appropriate biocontrols (Pawson et al. 2013) to constrain pest population growth or planting climate-adapted genotypes (Millar et al. 2007) are possible management strategies that could help prevent undesirable forest shifts. These interventions can modify trophic interactions and the genetic composition of elements in the forest, but also help sustain much of the historic state's structure and function. Although risks of undesirable states shifts associated with the intervention itself is lower using such strategies, the adaptive capacity approach is dependent on clear definitions of the type of resilience being managed for, as well what type of change that is acceptable (e.g., only native species).

Enable transformation

In certain cases, environmental conditions could change to such an extent that the system can no longer support the historic identity and function. Managers can decide if interventions to preserve desired system characteristics, such as specific ecosystem services or native species, are worth the risks (Millar and Stephenson 2015, Lindenmayer et al. 2016) (see Table 4). For example, recent studies suggest that some plants will not be able to keep pace with changing climatic conditions (Corlett and Westcott 2013, Allen et al. 2015, Schelhaas et al. 2015). To prevent an undesirable state shift or species extirpation, management can translocate a dispersal-limited species (Buma and Wessman 2013, Barnosky et al. 2017) or enable a shift to a novel forest that sustains desirable characteristics and functions (Millar and Stephenson 2015, Stanturf 2015). Similarly, introducing stress tolerant corals (Figure 18D), breeding heat tolerant dinoflagellate communities, or hybridizing corals (Oppen et al. 2015, Levin et al. 2017) to increase the resilience of vulnerable reefs might lead to the emergence of desirable novel ecosystems. Such strategies typically embrace greater levels of novelty in ecosystems (Aplet and McKinley 2017), and are associated with risks of unintended outcomes due to the management intervention itself (Aplet and McKinley 2017). Risk-benefit analyses and plans for failure, including reduced diversity or increased vulnerability to disease (Hoegh-Guldberg et al. 2008, Rout et al. 2013), are therefore necessary to improve management outcomes (see Appendix 9 for more examples of the various ways beneficial novelty can be encouraged in ecosystems).

CONCLUSION

Resilience theory is a helpful tool to guide management of dynamic and often unpredictable systems. However, given the ambiguities of resilience, the uncertainties of predicting global change impacts, and the capricious human behavior that drives global change, a tremendous amount of humility is required in RBM applications (see Outstanding questions). RBM also needs specificity in the identification of goals that can help define the desirability of different ecosystem states. In addition, RBM strategies need to balance the risks that undesirable ecosystem states can emerge without intervention with the risks that management itself can lead to undesirable outcomes. Different strategies seek to curtail the emergence of novel ecosystems altogether, while others encourage transformations towards desired novel ecosystems. Clearly delineating the relationship between RBM and novelty and change can improve resilience-based applications in the future.

Resilience theory is a helpful tool to guide management of dynamic and often unpredictable systems. However, given the ambiguities of resilience, the uncertainties of future global change impacts, and the capricious human behavior that drives global change, a tremendous amount of humility is required in RBM applications. Because RBM approaches have dramatically different relationships with change and novelty, greater specificity is needed in goal-setting that clearly aligns with underlying values. RBM should also foresee risks that the management itself can lead to undesirable outcomes. By drawing direct links between RBM interventions and novelty, management strategies can be improved.

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Glossary

Historic ecosystems: ecosystem states often considered to have occurred at some pre-determined point in the past (e.g., pre-Anthropocene, AD 1800 (Radeloff et al. 2015)) that currently retain similar structure, function and composition within range of environmental conditions.
Hysteresis: two or more contrasting stable states that can exist for a specific environmental condition. Once a transition to a contrasting state occurs, a reversal back to the starting state is difficult and will require different environmental conditions (Suding and Hobbs 2009).
Novel ecosystem: a system of abiotic, biotic, and social components that differ from those that prevailed historically and have a tendency to self-organize and manifest non-historic qualities without intensive human management (Hobbs et al. 2013).
Non-historical: an ecosystem or elements within an ecosystem that are new to the system; they do not resemble the system's historic structure, function, and/or identity.
Undesirable state: a state of an ecosystem that does not provide the target ecosystem services, biodiversity, or fails in other ways to meet management goals.
Vulnerability: the risk of shifting to a different state. Also can be referred to as precariousness, the probability of the system tipping to an alternate state (Hodgson et al. 2015).

FIGURES AND TABLES

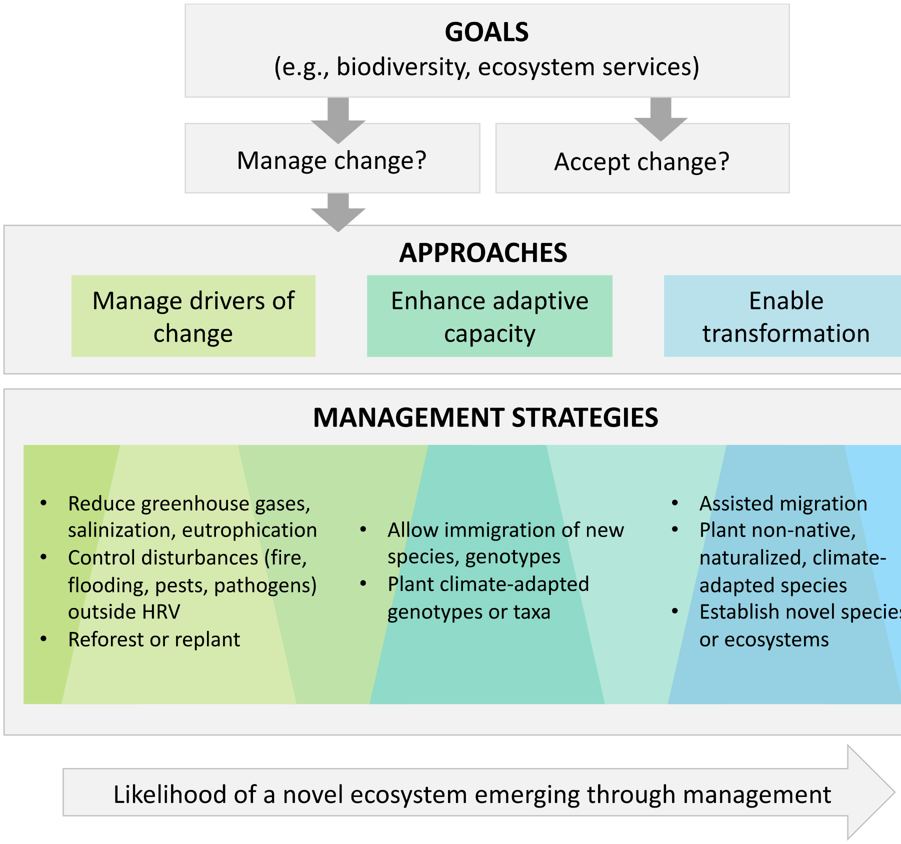

Figure 17: A conceptual model of resilience-based management. Depending on the goals, managers can choose to accept or manage change. If management actions are required, different approaches can be applied, including managing drivers of change, enhancing adaptive capacity and/or enabling transformation. The strategies associated with these approaches are overlapping and can be used to achieve multiple outcomes. Strategies focused on actively introducing change and novelty, particularly strategies that enable transformations, embrace higher levels of novelty and more actively shift systems towards novel ecosystems. (Examples strategies derived from Table 4 and [3,6,9].)

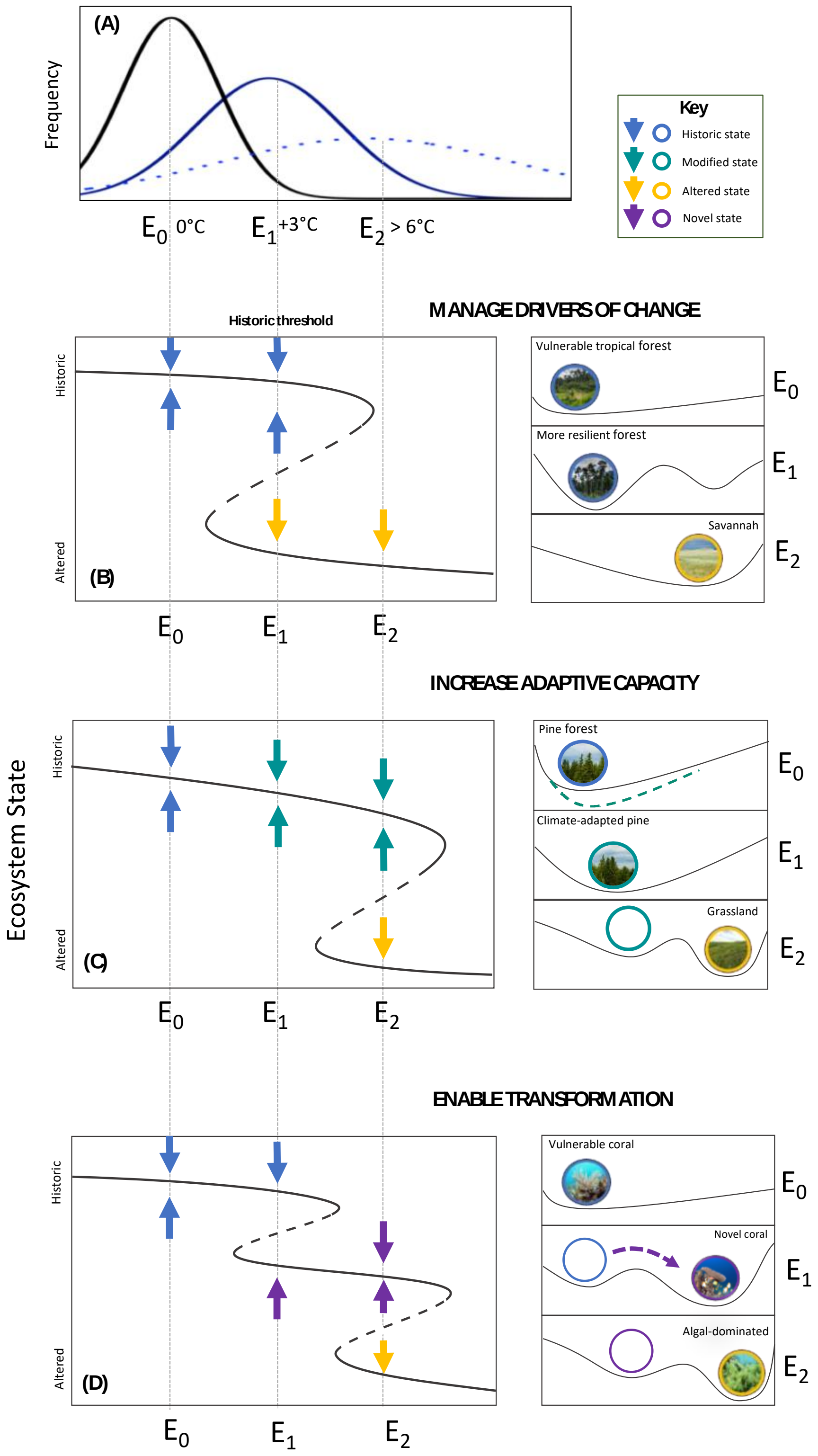
(A)
Frequency
E$_0$ 0°C
E$_1$ +3°C
E$_2$ > 6°C
Key
Historic state
Modified state
Altered state
Novel state
MANAGE DRIVERS OF CHANGE
Historic threshold
Historic
Altered
(B)
E$_0$
E$_1$
E$_2$
Vulnerable tropical forest
More resilient forest
Savannah
INCREASE ADAPTIVE CAPACITY
Ecosystem State
(C)
Pine forest
Climate-adapted pine
Grassland
ENABLE TRANSFORMATION
(D)
Vulnerable coral
Novel coral
Algal-dominated

Figure 18: Options and outcomes of resilience based management. Against the backdrop of directional change in an environmental condition, such as temperature (panel A: E_0, E_1, E_2), we present three scenarios with different management aims: (B) manage drivers of change, (C) increase adaptive capacity, and (D) enable transformation. To the right of the main panels B-D, ball and cup diagrams illustrate the ecosystem states corresponding to the bisection of the hysteresis diagram associated with environmental conditions E_0-E_2. Dotted lines show direction of RBM management. For clarity, we use hysteresis diagrams to illustrate the possible management interventions under a RBM framework, although we acknowledge that there are other types of ecosystem dynamics.

If drivers of change can be mitigated, then the system can persist beyond the historic threshold (B:E_1). In contrast, if the rate of environmental change overwhelms existing resilience, then increases in adaptive capacity are necessary to sustain the historic state (C). Particularly if novelty is added or naturally generated within the system, the historic identity and functions are altered. The novelty widens the basin of attraction and shifts the system towards a modified state (C:E_1) that does not, however, constitute a state change (C:E_2). In more extreme cases (D) where a shift is inevitable (D:E_2), management might need to consider actions to guide a beneficial shift to a novel ecosystem (D:E_1) that is able to maintain more functions or services than the highly altered state.

Document	Date	Agency	Resilience-related goals	Example strategies that mitigate drivers of change	Example strategies that enhance adaptive capacity	Example strategies that can transform systems
Managing Mangroves for Resilience to Climate Change	2006	International Union for Conservation of Nature (IUCN)	'goals of maintaining biodiversity, promoting ecosystem values, and enhancing resilience.'	Manage human stresses on mangroves Protect climate adapted areas	Adaptive strategies that compensate for species range changes Establish greenbelts to allow for migrations	
England Biodiversity Strategy Climate Change Adaptation Principles	2008	United Kingdom Department for Environment, Food and Rural Affairs	'Increasing the resilience of ecosystems to the impacts of climate change, will help . . . biodiversity to survive and adapt'	Maintain existing ecological networks Control spread of invasive species	Aid gene flow	Consider the role of species translocation and ex-situ conservation

Vulnerability of Canada’s Tree Species to Climate Change and Management Options for Adaptation	2009	Canadian Council of Forest Ministers	‘by modifying forest management policies and practices [adaptation] has the potential to reduce vulnerability’			Genetic outposts to hasten forest adaptation Establish forests less vulnerable to climate change
National Park Service Climate Change Response Strategy	2010	U.S. National Parks Service	Implement adaptation strategies that promote ecosystem resilience and enhance restoration, conservation, and preservation’	Protect refugia	Increase redundancy Increase connectivity	
Australia’s Biodiversity Conservation Strategy 2010 – 2030	2010	Department of Environment and Energy (Australia)	‘Australia’s biodiversity is healthy and resilient to threats, and valued . . . for its essential contribution’	Address threats to biodiversity	Restore habitat connectivity	Ex situ conservation strategies for species that may not be able to survive

Responding to Climate Change in National Forests: A Guidebook for Developing Adaptation Options	2011	United States Forest Service	‘sustainable resource management . . . encompasses four management strategies—resistance, resilience, response, and realignment’	Minimize habitat fragmentation Remove roads	Enhance riparian habitats and dispersal corridors	Assisted migration Plant novel species mixes Transition towards more adapted genotypes
Taking Steps toward Marine and Coastal Ecosystem-Based Management - An Introductory Guide	2011	United Nations Environment Programme (UNEP)	‘Resilience is the ability to return toward a previous state following a disturbance . . . healthy and productive [ecosystems] . . . maintain their resilience.’	Ensure that forest systems remain healthy Shield against storm surges		
Adaptation to climate change in grassland management	2012	Saskatchewan Research Council	‘Create resistance to change . . . ; Promote resilience to change . . . ; Enable ecosystems to respond to change (long-term adaptation).’	Reduce stocking rates Increase protected areas Mitigate threats such as exotic invasion	Increase landscape connectivity	Assist northward migration of selected species

European Union Forest Strategy	2013	European Commission	‘Maintain, enhance and restore forest ecosystems' resilience and multi-functionality . . . providing key environmental services’	Fire prevention Climate change mitigation	Enhance genetic diversity	
Adapting to climate change in the Pacific: the PACC programme	2013	The Secretariat of the Pacific Regional Environment Programme and UNDP	‘A resilient community [can] quickly respond to and recover . . . resulting in a similar or improved state . . . strong linkages between resilience and adaptive capacity.’	Strengthen early warning systems	Develop crop germplasm banks Risk insurance schemes for risk transfer and risk sharing	
Priority Agenda: Enhancing the Climate Resilience of America's Natural Resources	2014	U.S. Council on Climate Preparedness and Resilience	‘foster climate-resilient lands and waters . . . enable species and ecosystems to rebound in the face of great stresses without transforming’	Assess climate impacts on landscapes and habitats Build landscape-scale resilience	Protect habitat areas with redundant linkages Minimize barriers that restrict adaptive movement	

Adapting to a changing climate: A proposed framework for the conservation … in New Zealand	2014	New Zealand Department of Conservation	‘manage and restore ecosystem function . . . maintain and enhance ecosystem resilience’	Increase protected areas Reduce pressures on species from sources other than climate change	Improve replication within protected areas Protect movement corridors, stepping stones and refugia	Translocate species at risk Establish captive populations that would otherwise go extinct
South Australian Murray-Darling Basin Natural Resources Management Plan	2015	Government of South Australia, South Australian Murray-Darling Basin Management Board	‘Improved condition and resilience of natural systems.’	Manage nutrient and salinity levels Minimize impacts of pollutants	Barriers to migration overcome River system connectivity significantly improved	

Table 4: A diversity of resilience-based management plans from around the world and the differing strategies associated with them.

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APPENDICES

Appendix 1: All annul exotic species present in sampling plots over eight years.

Exotic annual forbs*

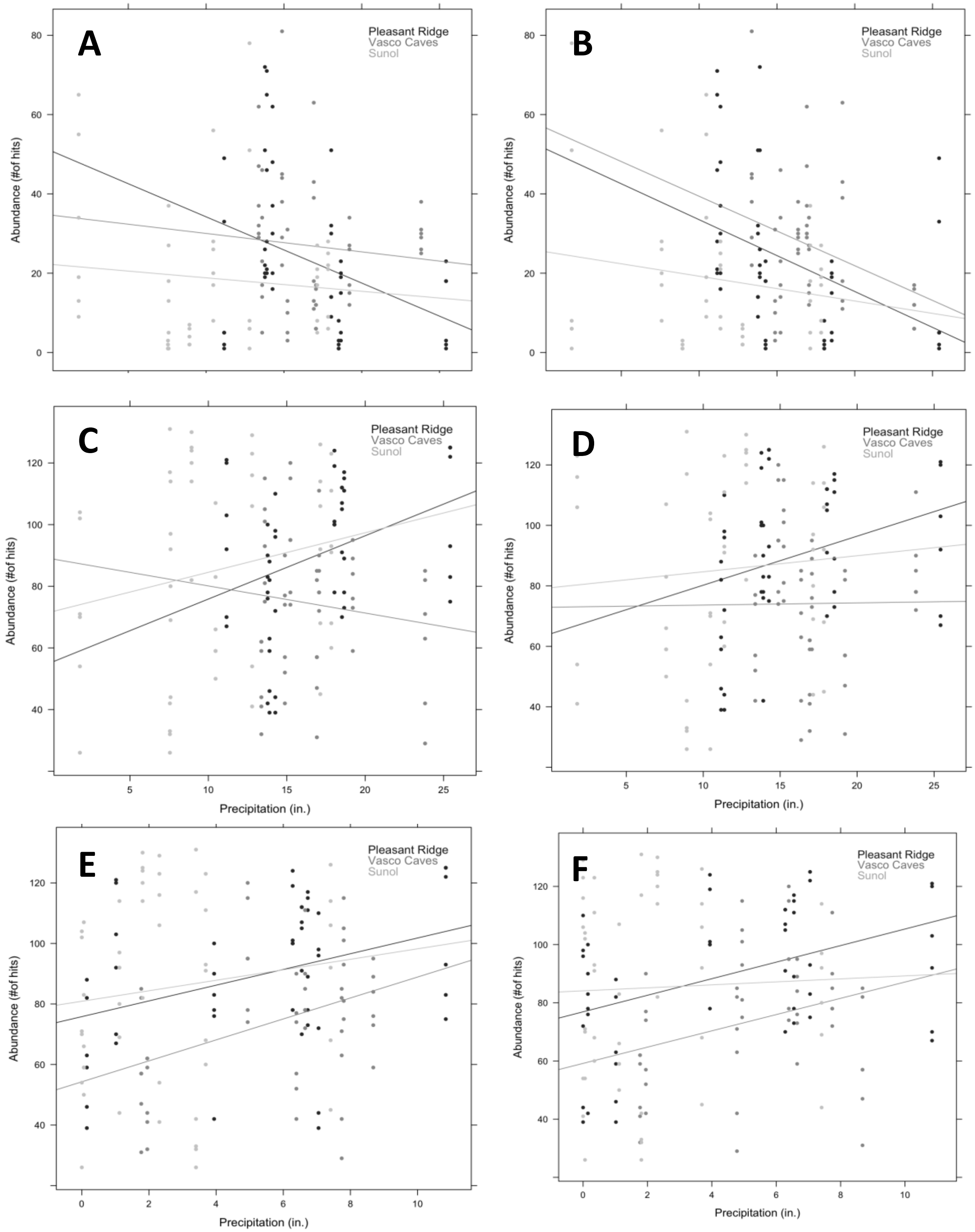
1. Bellardia trixago
2. Lysimachia arvensis
3. Carduus tenuiflorus
4. Brassica nigra
5. Carduus pycnocephalus
   Cerastium glomeratum
7. Centaurea melitensis
8. Erodium botrys
9. Centaurea solstitialis
10. Erodium cicutarium
11. Erodium moschatum
12. Logfia gallica
13. Galium parisiense
14. Geranium dissectum
15. Geranium molle
16. Hypochaeris glabra
17. Galium murale
18. Lactuca serriola
19. Medicago polymorpha
20. Melilotus indicus
21. Oxalis sp.
22. Phalaris paradoxa
23. Ranunculus muricatus
24. Sherardia arvensis
25. Silene gallica
26. Silybum marianum
27. Sonchus asper subsp. asper
28. Sonchus oleraceus
29. Stellaria media
30. Torilis arvensis
31. Torilis nodosa
32. Trifolium angustifolium
33. Trifolium campestre
34. Trifolium dubium
35. Trifolium glomeratum
36. Trifolium hirtum
37. Trifolium subterraneum
38. Vicia sativa
39. Vicia villosa

Exotic annual grass

1. Aira caryophyllea
2. Avena fatua
3. Brachypodium distachyon
4. Briza minor
5. Bromus diandrus
6. Bromus hordeaceus
7. Bromus madritensis
8. Bromus sp.
9. Bromus sterilis
10. Cynosurus echinatus
11. Hordeum marinum ssp.
12. Hordeum murinum
13. Festuca perennis
14. Polypogon monspeliensis
15. Elymus caput-medusae
16. Festuca bromoides
17. Festuca myuros

* Baldwin, B.G. & Goldman, D.H. (2012) The Jepson Manual: Vascular Plants of California.University of California Press

Appendix 2: Direct relationships of functional groups with precipitation. A) Exotic annual forbs and total current-year rainfall. B) Exotic annual forbs and total lagged rainfall. C) Exotic annual grass and total current-year rainfall. D) Exotic annual grass and total lagged rainfall. E) Exotic annual grass and current-year spring rainfall. F) Exotic annual grass and lagged spring rainfall.



Appendix 3: Correlation coefficients for current and lagged precipitation variables (seasonal and annual).

Current rainfall

	Current spring	*Current winter*	*Current fall*
Current spring	1	0.109	0.138
Current winter	0.109	1	0.160
Current fall	0.138	0.160	1
Previous spring	0.210	-0.029	-0.029
Previous winter	0.094	0.014	-0.145
Previous fall	0.171	0.105	-0.272
Current annual	0.435	0.630	0.297
Previous annual	0.181	0.060	-0.058

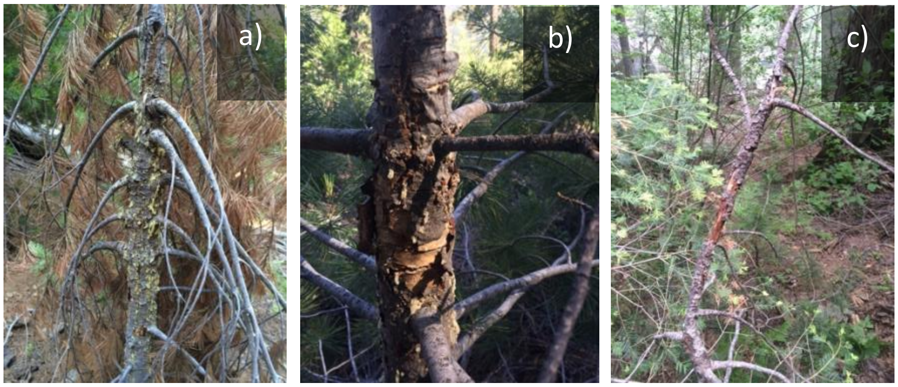
Lagged rainfall

	Previous spring	*Previous winter*	*Previous fall*	*Current annual*	*Previous annual*
Current spring	0.210	0.094	0.1706	0.435	0.181
Current winter	-0.029	0.014	0.105	0.630	0.058
Current fall	-0.029	-0.145	-0.272	0.297	-0.058
Previous spring	1	0.159	0.178	0.080	0.594
Previous winter	0.159	1	0.192	0.051	0.507
Previous fall	0.178	0.192	1	0.069	0.352
Current annual	0.0798	0.0508	0.069	1	0.080
Previous annual	0.594	0.507	0.352	0.080	1

Appendix 4. The coefficient of variation for each functional group across eight years.

	Exotic annual grass	*Exotic annual forb*	*Native annual forb*	*Native perennial forb*	*Native perennial grass*
Mean abundance	83 ± 27.37	22.91 ± 18.47	6.3 ± 6.17	7.46 ± 7.61	5.96 ± 6.91
CV	0.33	0.801	0.98	1.02	1.14

Appendix 5: Examples of cankers from the field: a) bole canker on a dead sugar pine; b) bole canker on live sugar pine with *Dioryctria sp*. moth (family Pyralidae), often observed in sugar pine cankers during the survey, c) suspected branch canker too old to verify in the field. Some examples of suspected cankers include but are not limited to: 1) a canker area showing a little swelling but not pitching, 2) the canker was too high in the canopy to discern all symptoms of blister rust, 3) the canker was too old to confidently discern all symptoms of blister rust, and 4) woodpecker holes or other animal damage obscured blister rust symptoms.

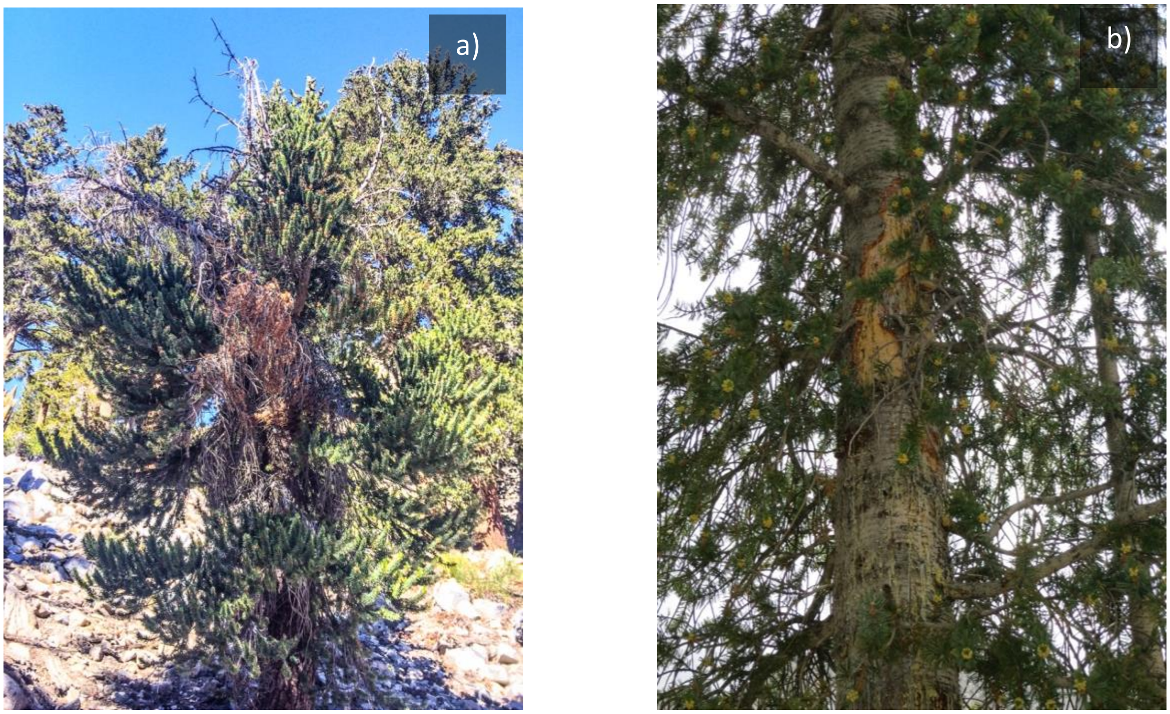


Appendix 6. Results from the calibration surveys to measure differences in blister rust identification among crews. Overall, twelve plots were calibrated (Table 6A). Although there were differences between surveys, the total number of infected trees in each plot was not significantly different between crews (calculated using the Student's t-test).

PLOT NUMBER	FIRST READ	SECOND READ
1	0	0
11	2	0
14	18	14
40	3	0
42	0	0
47	3	0
54	30	14
78	0	7
121	2	3
128	10	4
132	7	20
149	2	9
TOTAL	77	71
MEAN	6.42	5.92

Table 6A. Calibration results for 12 plots. First and second read columns show the total number of infected trees per plot.

Appendix 7: Examples of foxtail pine with bole cankers confirmed by US Forest Service pathologists. A) Multiple branch cankers and a bole canker on foxtail pine at high elevation (above 10,000). B) Single bole canker on foxtail pine on medium sized foxtail pine around 10,000 ft.



Appendix 8: Greater detail on the connections between novelty and resilience-based management.

The necessity of novelty in resilience-based management

Broadly, novelty can be defined as "something that was unknown before a particular point in time and was discovered or created at that point in time" (Witt 2009). For ecosystems, novelty can emerge through various processes and properties inherent to complex systems (Allen and Holling 2010). For example, novelty can be generated through gene mutation, natural selection, shifts in community composition, changes in key ecosystem processes, and self-organizing interactions.

Because global change is rapidly modifying the organization and dynamics of ecosystems (Ellis 2011), novelty and management innovation will be necessary to maintain resilience and encourage adaptation to changing environmental conditions (Seastedt et al. 2008, Standish et al. 2014). Therefore, some amount of novelty is fundamental to resilient ecosystems and long-term sustainability (Allen and Holling 2010). We refer to RBM that facilitates the generation of novelty as "process-based approaches", while strategies that add novel elements to a system are referred to as "structural approaches" (see section "Encouraging beneficial novelty through RBM").

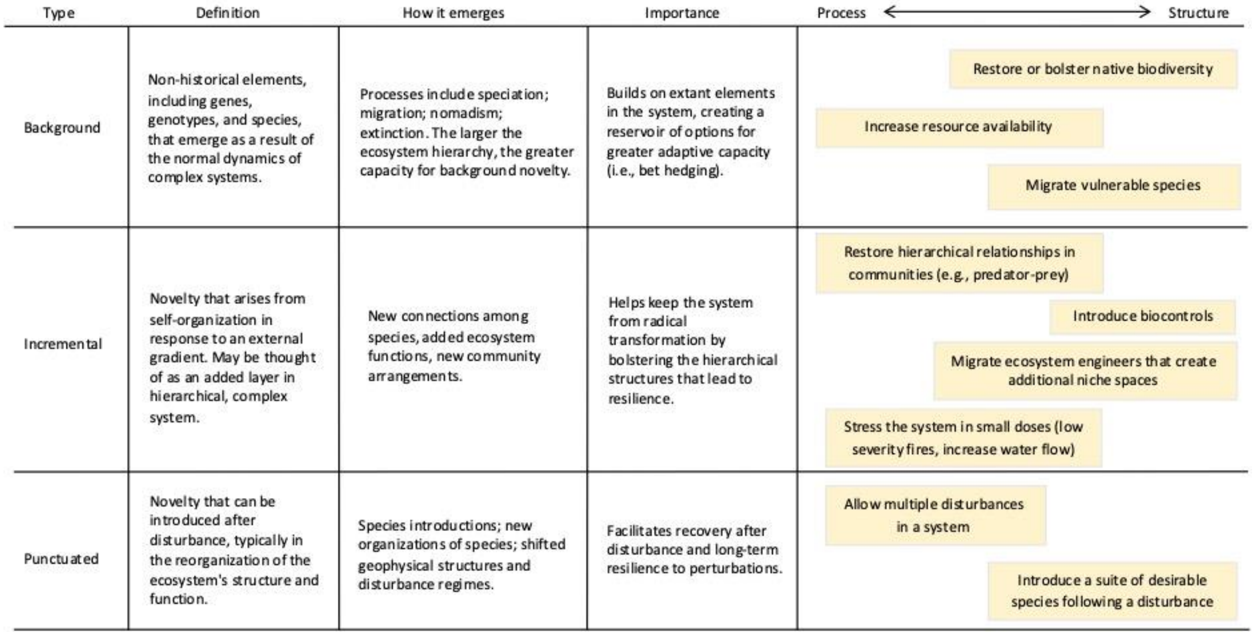
Novelty itself is not always helpful, however. Novel ecosystem components, such as invasive species, can alter basic processes and structures in ecosystems, causing shifts to undesirable ecosystems (Allen and Holling 2010). Because novelty, innovation and failure are closely linked processes (Allen and Holling 2010, D'Este et al. 2016), developing frameworks to minimize the negative impacts of novelty may be critical to enhance management success. To this end, it is important to identify when novelty is helpful, destructive, or unnecessary.

Linking novel ecosystems to resilience theory

In the Anthropocene, novelty is largely generated by human activities, including global and land-use change (Radeloff et al. 2015). Anthropogenic novelty that causes a state transformation is often described in the novel ecosystems literature (Hobbs et al. 2009). The combination of land-use and climate change has precipitated a rapid increase of novel ecosystems characterized by non-historical biotic and abiotic elements that are self-organizing (Hobbs et al. 2013). The use of the Hobbs et al. definition of novel ecosystems is intentional, as it helps link the concept of novel ecosystems to resilience theory and RBM. We recognize that, in practice, the boundaries defining novel ecosystems are vague (Marris et al. 2013) and dissimilarity may be a more practical measure of ecosystem novelty (Radeloff et al. 2015). Critical to many novel ecosystems are non-linear dynamics (e.g., feedbacks and thresholds) that can increase the state's stability through self-organization (Suding and Hobbs 2009).

Self-organization can be transformative and stabilizing. For example, non-native species can create positive feedbacks that ultimately lead to more exotic species invasion, at times causing a shift to a novel ecosystem (Richardson and Gaertner 2013). Once established, self-organizing processes and negative feedbacks (Leemput et al. 2016) can help stabilize the community (e.g., non-native species establishing dominance in grasslands) (Perry 1995, Richardson and Gaertner 2013). Self-organizing processes also make it difficult for managers to shift novel ecosystems back to historic states (Hallett et al. 2013b) and can create hysteresis effects. Thus novel ecosystems may be considered a class of alternate stable states, as described in resilience theory (Richardson and Gaertner 2013), though they are non-historical alternate states.

Appendix 9. How to cultivate three types of novelty important for ecosystem resilience and adaptation. The examples are illustrative and not exhaustive. The emergence of novelty in ecosystems has been organized into three terms: 1) background, 2) incremental, and 3) punctuated (Allen & Holling, 2010). All three types of novelty are important for building long-term resilience.



Type	Definition	How it emerges	Importance	Process ⟷ Structure
Background	Non-historical elements, including genes, genotypes, and species, that emerge as a result of the normal dynamics of complex systems.	Processes include speciation; migration; nomadism; extinction. The larger the ecosystem hierarchy, the greater capacity for background novelty.	Builds on extant elements in the system, creating a reservoir of options for greater adaptive capacity (i.e., bet hedging).	Restore or bolster native biodiversity Increase resource availability Migrate vulnerable species
Incremental	Novelty that arises from self-organization in response to an external gradient. May be thought of as an added layer in hierarchical, complex system.	New connections among species, added ecosystem functions, new community arrangements.	Helps keep the system from radical transformation by bolstering the hierarchical structures that lead to resilience.	Restore hierarchical relationships in communities (e.g., predator-prey) Introduce biocontrols Migrate ecosystem engineers that create additional niche spaces Stress the system in small doses (low severity fires, increase water flow)
Punctuated	Novelty that can be introduced after disturbance, typically in the reorganization of the ecosystem's structure and function.	Species introductions; new organizations of species; shifted geophysical structures and disturbance regimes.	Facilitates recovery after disturbance and long-term resilience to perturbations.	Allow multiple disturbances in a system Introduce a suite of desirable species following a disturbance

Table 9A. Different strategies that can be used to cultivate beneficial novelty in natural resource management. The examples are illustrative and not exhaustive. The emergence of novelty in ecosystems has been organized into three terms: 1) background, 2) incremental, and 3) punctuated (Allen & Holling, 2010). All three types of novelty are important for building long-term resilience.