

ANNOTATED BIBLIOGRAPHY FOR WHITEBARK PINE ECOLOGY

Additions April 2014 - April 2016
Prepared by Nancy Bockino & Kelly McCloskey
Grand Teton National Park

Notes:

- a. Making management decisions based on the most recent and accurate science is imperative to successful conservation of whitebark pine. This bibliography has become my bi-annual contribution to the success of this portion of a complex management challenge. Enjoy!
 - b. As always, if I missed any key work or if you have additional interpretations from any given paper, please let me know.
 - c. Because these annotations are a summary, not a review, of each paper direct quotations are extracted from the literature cited below.
 - d. Please contact me for any full publications you would like to read: Nancy_Bockino@nps.gov
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1. **Iglesias V, Krause TR, Whitlock C. 2015. Complex Response of White Pines to Past Environmental Variability Increases Understanding of Future Vulnerability. PLoS ONE 10(4): e0124439. doi:10.1371/journal.pone.0124439**

Background & Objectives

This paper addresses a broader perspective regarding climate change and the projected reduction in habitat suitable for whitebark, by examining the climate conditions, disturbance regimes and biotic associations from paleoecological data from the past 15,000 years. Temperature-based projections indicate a significant loss of suitable climate for whitebark pine in the next 50 years as a result of increased summer temperatures and decreased moisture. Paleoenvironmental data provide information on vegetation responses to a broader array of environmental conditions than can be observed at present.

Main Findings

- Site-specific species histories are limiting and historic regional-scale responses to climate better inform projections.
- Pollen data indicate that the long-term susceptibility of the region's conifers to past climate variations, fire conditions, and biotic interactions differs from our understanding based on associations between modern climate and tree abundance.
- Pollen data suggest that white pine populations in the Greater Yellowstone region had sufficient phenotypic plasticity/genetic variability to survive large-magnitude variations in postglacial climate.
- Pinus pollen was most abundant during the period of highest solar insolation.
- Such differences highlight the shortcomings of extrapolating bioclimatic data beyond observed correlations and suggest that;
 - o (i) relationships between present-day species distributions and modern climate only define a fraction of their niche and may underestimate species capacity to respond to climate variability;
 - o (ii) modern relationships based on mature individuals may not capture the conditions required for seedling establishment and growth across the species range;
 - o (iii) the importance of biotic interactions (e.g., competition, predation) is underestimated in many ecological niche studies because of co-linearity between climate and other species abundance.

Implications

- Elevated summer temperatures and drought are not a primary constraint on the distribution of white pines, rather warmer and drier winters.
- There are significant shortcomings associated with extrapolating current bioclimatic data.

2. Schaming TD (2015) Population-Wide Failure to Breed in the Clark's Nutcracker (*Nucifraga columbiana*). PLoS ONE 10(5): e0123917.

Background & Objectives

This paper summarizes 5 years of work monitoring the Clark's Nutcracker in the Greater Yellowstone Ecosystem.

Main Findings

- 2009 and 2011 no breeding or breeding attempts were observed.
- 2010, 2012, 2013 breeding occurred/fledglings present in study area.
- Douglas-fir seeds are an alternate food source; however an individual nutcracker requires 9,939 whitebark pine seeds or 197,117 Douglas seeds to survive each winter.
- Nonbreeding years coincided with low whitebark pine cone crops & above average snowpack.
- The author could not separate the effects of cone crop and snowpack.
- Low whitebark pine cone crop, high snowpack, or an interaction between the two, may have influenced the population-wide nonbreeding.

Implications

- An increase in the number of Clark's nutcracker nonbreeding years could also have serious ecosystem-wide consequences.
- Skipping breeding can be an effective adaptive strategy for survival-reproduction trade-off.
- If conditions (lack of whitebark seeds) that may lead to skipping breeding occur more often than in the past, nutcracker populations could decline.

3. Diana F. Tomback, Lynn M. Resler, Robert E. Keane, Elizabeth R. Pansing, Andrew J. Andrade and Aaron C. Wagner. 2016. Community Structure, Biodiversity, and Ecosystem Services in Treeline Whitebark Pine Communities: Potential Impacts from a Non-Native Pathogen. Forests: 7, 21. doi:10.3390/f7010021

Background & Objectives

This study synthesized data from 10 studies to document geographic variation in structure, conifer species, and understory plants in whitebark pine alpine treeline ecotone communities, and examine the potential role of these communities in snow retention and regulating downstream flows.

Main Findings

- Whitebark pines are found on the windward side of all alpine tree islands in the study.
- The presence of tree stands and tree islands influences local hydrologic processes, including snowpack deposition distribution, depth and snowmelt runoff.
- Reduced seed production in subalpine communities from tree mortality reduces seed dispersal by Clark's nutcrackers.
- Blister rust infection at treeline damages and kills trees.

Implications

- Mortality from blister rust will impact whitebark as a tree island initiator and therefore treeline response to climate change.
 - Reducing whitebark pine as a frequent component of tree islands could also lead to altered community composition and reduction in tree island density.
 - Understory plant composition may change as well, since patterns of snow retention and nutrient deposition may be impacted.
4. **Carl E. Fiedler & Shawn McKinney. 2014. Forest Structure, Health, and Mortality in Two Rocky Mountain Whitebark Pine Ecosystems: Implications for Restoration. *Natural Areas Journal* 34:290–299.**

Background & Objectives

This study surveyed two major whitebark pine ecosystems: the Northern Divide Ecosystem (NDE), including Glacier National Park, and the Greater Yellowstone Ecosystem (GYE) to quantify stand density, structure, species composition, blister rust infection, and mortality. Field data were collected from June to September, 2004–2006 at 18 elevationally and geographically variable sites.

Main Findings

- 74% of all whitebark pine in the NDE were dead; 22% in the GYE.
- 92% of the live whitebark in the NDE were infected with blister rust; 62% in the GYE.
- In the GYE, there were proportionally more small trees than large trees.
- Live whitebark per hectare: 79 in NDE; 274 in the GYE.
- Dead whitebark per hectare: 230 in the NDE; 77 in the GYE.

Implications

- This paper provides baseline data to monitor change over time.
 - Restoration strategies must address characteristics and conditions unique to each ecosystem and appropriate for the current condition of whitebark pine.
5. **Barbara J. Bentz, Celia Boone and Kenneth F. Raffa. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. *Agricultural and Forest Entomology*. DOI: 10.1111/afe.12124.**

Background & Objectives

This study investigated MPB host use and reproductive capacity and host tree secondary compounds of whitebark and lodgepole pine growing in mixed stands at relatively high elevations. This study occurred from 2007-2009 at two sites - Fish Creek (Bridger-Teton National Forest) and Union Pass (Shoshone National Forest).

Main Findings

- Whitebark pines had higher proportions of α -pinene and myrcene, which MPB exploits to facilitate mass attacks, and lodgepole pines had higher proportions of β -phellandrene, which MPB exploits for host recognition.
- Over the 3 years of the study, lodgepole pines were more frequently attacked than whitebark pines
- The frequency of lethal attacks, which are the product of entry and success, did not vary between the two hosts.
- A lower percentage of attacks on lodgepole pine resulted in lethal attacks than on whitebark pine.
- Among all trees, 24.3% of lodgepole pines and 8.4% of whitebark pines showed nonlethal attacks.

Implications

- Understanding the chemotype of *Pinus* species will help us understand the expansion of MPB, host tree defensive response, and host tree mortality.

6. Barbara Bentz, Jacob Duncan and James Powell. 2016. Elevational shifts in thermal suitability for mountain pine beetle population growth in a changing climate. *Forestry*: 0, 1–13.

Background & Objectives

This study used a mechanistic, phenology-based demographic model based on daily temperature data, called the mountain pine beetle demography model (MPB-R). The authors use this model to describe recent and future spatial and temporal thermal suitability for mountain pine beetle population growth in a topographically complex region. In this study high elevation is ≥ 2400 m, middle elevations are 1200–2400 m and low elevation is ≤ 1200 m. Observed mountain pine beetle-caused tree mortality was estimated from the USFS Forest Health Protection Aerial Detection Survey data between 1994 and 2005.

Main Findings

- Across all climate models, there was an approximate 3–4 degree C increase in mean temperatures based on the RCP 4.5 scenario and a 6–7 degree C increase using the RCP 8.5 scenario depending on elevation.
- MPB-R predictions suggest that mountain pine beetle population response to the increasing temperatures will differ across elevations within the study area.
- MPB-R predictions suggest a transition to bivoltinism at 50% of low elevations sites in the next 25 years.
- At the highest elevations, bivoltine lifecycles were only predicted after 2070 using the warmest RCP8.5 scenario.
- MPB-R was significant in predicting the increasing trend in beetle-caused tree mortality observed during a recent outbreak between 1999 and 2013.
- Climate change can result in both beneficial and maladaptive phenological shifts in insects.

Implications

- Evolved developmental thresholds and rates that promote univoltine generations and synchronized adult emergence in MPB are predicted to become no longer viable in middle elevation thermal regimes.
- An area of great uncertainty is the lack of understanding of potential adaptations in mountain pine beetle temperature-dependent traits.
- Host tree migration may occur from elevations where bivoltinism is predicted to be the greatest into an elevational zone of relatively low predicted mountain pine beetle population growth.
- Conversely upward migration of lodgepole and limber pine would retain suitable hosts at the highest elevations where thermal suitability for mountain pine beetle univoltine population growth is predicted to be most optimal

7. Michael Case & Joshua Lawler. 2015. Relative vulnerability to climate change of trees in western North America Climatic Change DOI 10.1007/s10584-016-1608-2

Background & Objectives

This paper assessed the relative vulnerability to climate change of 11 tree species in western North America using a multivariate approach to quantify elements of sensitivity to climate change, exposure to climate change, and the capacity to adapt to climate change. This assessment was performed through a series of workshops throughout the region to synthesize knowledge and insight on species' sensitivities and adaptive capacities from experts and groups of experts. This information was combined with climate-change projections and a literature review.

Main Findings

- Whitebark pine was determined to be highly sensitive to climate change.
- Whitebark pine had the highest sensitivity to interacting non-climatic stressors including dispersal limitations.

Implications

- Management objectives should be adaptive and seek to increase the resistance and resilience of species.
- Both climate change and species vulnerability are uncertain.
- Whitebark pine may exhibit the ability to tolerate climatic conditions different than those found in its current distribution.

8. **K. Jane Van Gunst, Peter J. Weisberg, Jian Yang, Yuanchao Fan. 2016. Do denser forests have greater risk of tree mortality: A remote sensing analysis of density-dependent forest mortality. *Forest Ecology and Management* 359: 19–32.**

Background & Objectives

This study used archival Landsat imagery to assess the widespread but largely untested generalization that increased stand density causes increased levels of forest mortality.

Main Findings

- Probability of mortality increased with density in low elevation, dry forests.
- Increased density resulted in decreased probability of mortality, in mid- to upper-elevation forests, especially during wet periods.
- Risk of tree mortality was higher on north-facing slopes across all forests and all climate periods, even when stand density was controlled for.
- Forest mortality is complex and hard to predict and results from a unique combination of interacting factors including drought duration and intensity, bark beetle population dynamics, climate extremes and forest structure.

Implications

- The effect of forest structure on forest mortality is linked to climate variability.
- The authors suggest that no single density-reduction forest management strategy will increase forest resilience under all climate periods and in all forest types.

9. **Edith M. Dooley, Diana L. Six, and James A. Powell. 2015. A Comparison of Mountain Pine Beetle (Coleoptera: Curculionidae, Scolytinae) Productivity and Survival in Lodgepole and Whitebark Pine after a Region-Wide Cold Weather Event. *For. Sci.* 61(2):235–246.**

Background & Objectives

This study assessed emergence rates of the mountain pine beetle in both lodgepole pine and whitebark pine in mixed stands. Weather conditions during this study in 2009/2010 provided a unique opportunity to assess how cold weather events interact with the tree host to affect beetle emergence rates and survival. The cold event occurred in October 2009, with temperatures dropping to -15°C.

Main Findings

- During the study most beetles died, likely due to the cold weather event in October 2009 which occurred before beetles had cold-hardened for the upcoming winter.
- Both tree diameter and whitebark pine host were significantly positively correlated with entrance hole density.
- MPB emergence rate increased 5.6% per 1 cm increase in dbh.
- Emergence rates declined exponentially as the entrance hole density increased for all diameters and for both host species.
- Beetle productivity did not differ between host species.
- Greater MPB emergence occurred with small (<30cm diameter) whitebark pine compared to larger diameter lodgepole and whitebark pine.
- Small diameter whitebark pine phloem is thicker than small diameter lodgepole pine phloem.

Implications

- This study helps to explain why MPB outbreaks are extensive and severe in whitebark pine.
- This model can help to predict the timing of beetle phenology and subsequent mortality.
- Regardless of warming climate trends, early season cold weather events can still have strong negative impacts on mountain pine beetle populations.

10. Edith M. Dooley and Diana L. Six. 2015. Severe White Pine Blister Rust Infection in Whitebark Pine Alters Mountain Pine Beetle (Coleoptera: Curculionidae) Attack Density, Emergence Rate, and Body Size. *Environmental Entomology*. 44 (5):1384-1394

Background & Objectives

This study assessed attack and emergence rates, and size and sex ratio of mountain pine beetle in whitebark pines exhibiting varying white pine blister rust infection severities.

Main Findings

- MPB attack density was lowest on the most severely infected trees.
- Emergence rates and beetle size were greater from these severely infected trees than from uninfected and less severely infected trees.
- Beetles initially responding positively to increasing infection severity, but at some point when severity becomes high, there is evidence of switching to a negative response to severity.
- Low rates of attack were related to greater emergence rates and overall beetle size.

Implications

- Low attack rates on severely infected whitebark pine may indicate these trees have lower defenses and that fewer beetle attacks are needed to kill them.
- Higher beetle emergence rates from severely infected trees may be due to low intraspecific competition resulting from low attack rates or may be due to differences in nutrient quality in severely infected trees.
- These factors may increase individual beetle fitness and fecundity.

11. Evan D. Esch, David W. Langor, and John R. Spence. 2016. Gallery success, brood production, and condition of mountain pine beetles (Coleoptera: Curculionidae) reared in whitebark and lodgepole pine from Alberta, Canada. Can. J. For. Res. 46: 557–563

Background & Objectives

This laboratory-based study compared gallery density and length, reproductive success, brood production, and adult condition in breeding pairs of MPB in bolts, or portions of the main bole of a tree used as samples, from both whitebark and lodgepole.

Main Findings

- Larval gallery density was significantly higher in whitebark pine than in lodgepole pine.
- Egg galleries were shorter in whitebark pine.
- Brood production, female body size, mass, and fat content of brood adults and survival from larva to adult did not differ between beetles reared in the two hosts.
- Egg gallery initiation was less successful on whitebark than lodgepole pine bolts.

Implications

- Brood production is similar in numbers and condition in both whitebark and lodgepole pines.
- An understanding of the interactions of this reproduction data with stand density, tree size, whitepine blister rust infection severity and climate is needed to predict growth and spread of MPB.

12. Dana L. Perkins, Carl L. Jorgensen, and Matthew J. Rinella. 2015. Verbenone Decreases Whitebark Pine Mortality Throughout a Mountain Pine Beetle Outbreak. For. Sci. 61(4):747–752.

Background & Objectives

This study was conducted for 7 years through an entire mountain pine beetle outbreak in the Sawtooth Mountains in Central Idaho.

Main Findings

- Survival - 68% of trees treated with verbenone once per year survived through the end of the outbreak while only 34% of control trees survived.
- Evidence from a separate study site using verbenone applications indicate that applying verbenone twice a year increases host tree survival over applying verbenone only once per year.
- Increased survival did not vary with tree diameter.

Implications

- The increased survival documented in this long-term study indicates that verbenone is successful at reducing loss of whitebark pine.
- Use of verbenone plays an important role in conserving whitebark and also can be used to increase survivorship of individual whitebark pine with specific and identified genetic traits for blister rust resistance.

- 13. Signe B. Leirfallom, Robert E. Keane, Diana F. Tomback, and Solomon Z. 2015. The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire. Dobrowski. *Can. J. For. Res.* 45: 1597–1606.**

Background & Objectives

This study sampled regeneration and seed source health in 15 burns ranging from 5 to 23 years old and located within six national forests and three Wilderness Areas in Montana.

Main Findings

- There is a significant and positive relationship between seed source health and seedling density in adjacent burns.
- Natural regeneration was lower when the proportion of damaged or dead whitebark pine in the seed source exceeded 50%.
- Seedlings were present throughout most burns.
- Sites closer to seed sources had higher probabilities of seedling occurrence.
- Whitebark pine regeneration presence was also influenced by vegetation cover and potential solar radiation.
- Whitebark pine regeneration occurs for many years following fire.

Implications

- This study can help to guide managers as they prioritize restoration plantings of whitebark pine seedlings after wildfire based on the health status of the nearest seed sources.

- 14. Greater Yellowstone Whitebark Pine Monitoring Working Group. 2016. Monitoring whitebark pine in the Greater Yellowstone Ecosystem: 2015 annual report. Natural Resource Report NPS/GRYN/NRR—2016/1146. National Park Service, Fort Collins, Colorado.**

Background & Objectives

This annual report is a summary of the current data for an interagency whitebark pine long-term monitoring program initiated in 2004. The objectives of the whitebark pine monitoring program are to detect and monitor changes in the health and status of whitebark pine populations across the GYE due to infection by white pine blister rust, attack by mountain pine beetle, and damage by other environmental and anthropogenic agents.

Main Findings

- Based on monitoring data collected from 2008 to 2011, the estimated rate of blister rust infection among whitebark pine ranged from 20% to 30%.
- Overall mortality attributable to mountain pine beetle attack is decreasing in the GYE, although some new MPB activity was observed.
- A summary report of the first step-trend analysis (Shanahan et al. 2014) is available from GRYN or the Integrated Resource Management Applications website - <https://irma.nps.gov/DataStore/DownloadFile/504276>

Implications

- This long-term monitoring program will continue into the future and provides critical information that will help determine the likelihood of whitebark pine persisting as a functional and vital part of the ecosystem.
- Data from this program are currently being used to inform managers, to guide management strategies and restoration planning and conservation efforts throughout the GYE and to support whitebark pine research.

15. Mary F. Mahalovich, Mark J. Kimsey, Jennifer K. Fortin-Noreus, Charles T. Robbins. 2016. Isotopic heterogeneity in whitebark pine (*Pinus albicaulis* Engelm.) nuts across geographic, edaphic and climatic gradients in the Northern Rockies (USA). *Forest Ecology and Management* 359 (2016) 174–189

Background & Objectives

This study investigates the abundance and spatial and temporal variation in whitebark pine nut tissue encompassing six seed zones using stable isotopes for carbon, nitrogen and sulfur. Stable isotopes in plants are used to discern atmospheric and decomposition processes, characterize plant interactions, describe trophic food webs, and to determine water-use efficiency. This study also developed a predictive model to characterize isotopic signatures.

Main Findings

- ^{13}C may be a viable proxy for drought tolerance in whitebark pine.
- Whitebark growing at the highest elevations (in the GYGT) had the most ^{13}C enrichment.
- ^{15}N enrichment increased from NW to SE following a gradient of moist to arid ecosystems.
- Nitrogen enrichment was also related to soil parent material.
- Sulfur enrichment and soil parent material are directly related.
- Whitebark pine exhibits a wide-range of edaphic variation.

Implications

- Spatially explicit isotope maps (isoscapes) have practical applications in monitoring and managing changing landscapes.
- These data provide a quantitative measure of adaptive capacity and can help further refine predicted species distributions and limitations.
- Information regarding nitrogen isoscapes could inform anticipated post-disturbance tree response and also help decipher anthropogenic nitrogen deposition.
- Knowledge of these regional patterns in whitebark pine will be important for understanding spatial heterogeneity over larger geographic areas and for prioritizing areas for conservation.
- The edaphic variation exhibited by whitebark pine will influence the species distribution and help managers to understand genotype-environment interactions and help them to achieve successful seedling deployment.
- The authors are very hopeful that ^{13}C will serve as a cost-effective measure to evaluate the correlated response of water use efficiency (WUE), blister rust resistance and late winter cold hardiness to refine seed selections, seedling deployment and conservation strategies for whitebark pine.

- 16. Robert E. Keane, Rachel Loehman, Jason Clark, Erica A.H. Smithwick and Carol Miller. 2015. Exploring Interactions Among Multiple Disturbance Agents in Forest Landscapes: Simulating Effects of Fire, Beetles, and Disease Under Climate Change. In A.H. Perera et al.(eds) Simulation Modeling of Forest Landscape Disturbances, Springer International Publishing Switzerland.**

Background & Objectives

This chapter explores ecological interactions among the disturbances that are common across many US Rocky Mountain landscapes: wildland fire, mountain pine beetle, and white pine blister rust. This chapter includes a literature review and a landscape simulation model to evaluate how interacting disturbances respond to changes in climate and influence landscapes.

Main Findings

- Mountain pine beetle activity influences wildland fire by altering the quantity, type, vertical and horizontal arrangement, and chemical and moisture properties of dead and live vegetative biomass available to burn, and the abundance of individual species on the landscape.
- MPB outbreaks can change the probability of fire occurrence, potential for crown fire, rate of fire spread, and burn severity patterns and variability
- Climate influences fire and beetle interactions differently due to species composition and landscape configuration.
- Wildland fire influences blister rust by changing the distribution, and abundance of its two hosts - five-needle pines and *Ribes* spp.
- Literature review illustrates that the effects of blister rust infection on MPB outbreaks are variable.
- These modeled simulations indicate that the presence of MPB and WPBR reduces the basal area of pine species. Fire, while reducing pines in the short term, appears to ensure their long-term persistence by eliminating competitors.
- Climate has an enormous influence on all disturbance agents and regimes.
- Topography influences the rate of fire, MPB and rust spread, while water and radiation balance, and microclimatic conditions, influence host vulnerability.

Implications

- At landscape scales, effects of long-term and coupled disturbance regimes can lead to complex feed-backs and nonlinear responses causing landscape trajectories to differ significantly.

- 17. Keane, Robert E.; Holsinger, Lisa M.; Loehman, Rachel A.; Mahalovich, Mary F.; Tomback, Diana F. 2015. Restoring whitebark pine (*Pinus albicaulis*) ecosystems in the face of climate change. Gen. Tech. Rep. RMRS-GTR-XXX. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station XXX p.**

Background & Objectives

The recently developed range-wide strategy for whitebark pine restoration failed to fully address projected effects of climate change on existing whitebark pine populations and restoration efforts. In this report, the authors present guidelines for restoring whitebark pine under future climates using the range-wide restoration strategy structure. For each of the original strategy's guiding principles and suggested restoration actions, this publication provides additional information and guidance for developing and implementing restoration plans which account for predicted changes in climate. Information used to adjust whitebark pine restoration guidance for climate change impacts came from a comprehensive literature review and results from a spatially explicit, ecological process model.

Main Findings

- The major finding from this effort is that whitebark pine can remain on upper subalpine high mountain landscapes in new climates with the help of restoration efforts.

Implications

- The paper is written as a general guide to be used by public land management agencies in collaboration with the range-wide strategy to address climate change impacts when planning, designing, implementing, and evaluating fine-scale restoration activities for whitebark pine.

18. Hansen, Andrew J., and Linda B. Phillips. 2015. Which tree species and biome types are most vulnerable to climate change in the US Northern Rocky Mountains? *Forest Ecology and Management*. Pages 68-83. <https://dx.doi.org/10.1016/j.foreco.2014.11.008>

Background & Objectives

The goal of this modeling effort was to assess components of vulnerability of tree species and biome types to projected future climate, based on two IPCC emissions scenarios, within the Great Northern Landscape Conservation Cooperative in the US Northern Rockies and the ecosystems surrounding Glacier and Yellowstone/Grand Teton National Parks.

Main Findings

- In the Greater Yellowstone predicted biome shifts include conifer forest types decreasing from 82% of the current area to 26% and scrub types increasing from 0% to 48% of the area.
- Based on the model the proportion of the landscape predicted to maintain suitable climate for whitebark pine based on the characteristics of sites that are currently occupied by whitebark pine decreases from 20% to 0.5–7.0% by 2070–2100
- Whitebark pine had the highest vulnerability score of any forest species, based on: tree species demographic response to climate change, changes in disturbance regimes and interactions with pests and competing tree species, species exposure, sensitivity, potential impact, and adaptive capacity including demographic, life history, genetic, and habitat dynamics factors for past, current, and/or future periods.

Implications

- The results provide information for future climate vulnerability assessments.
- This information provides guidance for management approaches under predicted future climate scenarios.
- Provides methods to use bioclimatic envelope studies to assess vulnerability in other ecosystems.
- Management strategies for species deemed most vulnerable should be stratified geographically based on the locations of current and projected suitable habitats.

19. Schaming TD. 2016. Clark's Nutcracker Breeding Season Space Use and Foraging Behavior. PLoS ONE 11(2): e0149116. doi:10.1371/journal.pone.0149116

Background & Objectives

The objectives of this study were to examine Clark's nutcracker breeding season home range size, territoriality, habitat selection, and foraging behavior in the southern Greater Yellowstone Ecosystem.

Main Findings

- Clark's nutcrackers select Douglas fir for home ranges.
- 83% of radio-tagged Clark's nutcrackers remained on the study area through the end of the breeding season
- No aggressive territorial interactions were observed and territories overlapped considerably
- Clark's nutcrackers selected Douglas-fir habitat in two years with contrasting (little whitebark seed crop versus abundant whitebark seed) food availability and breeding status (nonbreeding versus breeding season).
- Nutcrackers infrequently use whitebark pine communities during the breeding season, and were observed in whitebark primarily in July - September eating seeds.
- Spring use of whitebark habitat is dependent on timing of snowmelt.

Implications

- Clark's nutcrackers alter their habitat use depending on demographic and/or environmental conditions, such as breeding condition or whitebark pine cone crop.
- Considering the entire life history of a species is fundamental to developing effective conservation strategies.
- Douglas-fir habitat is the most important breeding season habitat for Clark's nutcrackers.
- In the Greater Yellowstone Ecosystem, Clark's nutcracker populations may be more likely to be retained year-round when whitebark pine restoration efforts are located adjacent to Douglas-fir habitat.
- It is possible that Clark's nutcrackers may decline or become extinct locally, but could then recolonize an area once habitat improves, providing they survive elsewhere.
- Douglas-fir stands may provide a critical alternative seed source in the Greater Yellowstone Ecosystem, helping the Clark's nutcrackers to meet their foraging requirements and may be critical to long-term population viability.

20. Jennifer G. Klutsch, Betsy A. Goodrich, William R. Jacobi. 2015. Post-fire regeneration dynamics in whitebark pine (*Pinus albicaulis*) forests in Wind River and Absaroka Mountains, Wyoming, USA . J. For. Res. DOI 10.1007/s11676-015-0064-6.

Background & Objectives

This project assessed regeneration densities and site factors associated with regeneration success in burned and adjacent non-burned areas at six high elevation locations in northwest Wyoming where stand-replacing fires occurred 8–32 years prior.

Main Findings

- Whitebark pine regeneration density was greater and seedlings were older in non-burned compared to burned areas.
- Within burns, north aspects had more regeneration than south aspects.
- Greater seed source densities and other species' regeneration were positively related to whitebark pine regeneration densities in burned areas.
- South facing slopes or grass covered areas had very little to no regeneration.
- Whitebark pine seedlings in burned and non-burned areas were spatially correlated with logs and bases of trees.

Implications

- Authors recommendations include:
 - Plant whitebark in areas that have *V. scoparium* and do not have extensive grasses, next to microsites and in areas that are north facing where there are relatively wet, cool, and sheltered conditions.
 - Promote and maintain mature whitebark pine as seed sources.
 - Some planting sites may require removing competing tree species and grasses.
 - Interplanting whitebark with competing advanced regeneration may be useful to initial establishment, but co-occurring species may also have to be removed later.

21. Barbara J. Bentz, Celia Boone, and Kenneth F. Raffa. 2015. Tree response and mountain pine beetle attack preference, reproduction and emergence timing in mixed whitebark and lodgepole pine stands. *Agricultural and Forest Entomology*. 17, 421–432

Background & Objectives

This paper reported on monitoring mountain pine beetle attacks, adult emergence timing and reproductive capacity in lodgepole and whitebark (*Pinus albicaulis*) pines growing in mixed stands at relatively high elevation. The study sites included Fish Creek and Union Pass. MPB were monitored from June 2007 - September 2007. Phloem monoterpene chemistry of trees prior to and during attack was compared within and between species.

Main Findings

- Beetles attacked lodgepole pine more frequently.
- Lodgepole pines resisted attacks more frequently.
- The proportion of whitebark pines within a stand that were attacked tended to increase as the availability of lodgepole pine decreased.
- Lethal attacks between whitebark and lodgepole were equal.
- Brood production and adult emergence timing did not differ between tree species.
- Both whitebark and lodgepole contain compounds in the phloem that affect mountain pine beetle attack and reproductive success.
- Unattacked and attacked whitebark pine tissue contained 3.8–4.2 times more α -pinene and 2.9–4.7 times more myrcene, each of which are exploited by MPB for pheromonal communication, than lodgepole pine.

Implications

- This study begins to explain MPB host selection, range expansion and host tree defensive response.
- This topic will greatly benefit from further understanding of *Pinus* chemotype evolution.

22. Régnière, J., St-Amant, R., Bentz, B.J., Powell, J.A. 2015. Individual-based modeling: Mountain pine beetle seasonal biology in response to climate. *Simulation Modeling of Forest Landscape Disturbances*, pp. 135-164

Background & Objectives

This paper reports results from an integrated model of phenology and cold tolerance to evaluate climate influences on the invasiveness of MPB.

Main Findings

- Winter survival and the ability of adults to overcome host defenses explained 98.6 % of the variation in MPB population growth between years and locations. Along an elevation gradient, thermal regimes that resulted in univoltinism and larval overwintering were optimal for MPB population growth.
- Warm summers at the lowest modelled elevations accelerated development, resulting in adult emergence in the year of attack.
- Low overall population fitness resulted from poor phenological synchrony.

Implications

- This model illustrates the importance of accounting for the interactions between temperature, cold-hardiness, and life-stage-specific phenological characteristics.
- This model explains the role of weather in the current MPB expansion.
- According to this model and climate change predictions, MPB population growth in Alberta and northern BC will continue to increase.
- Thermal conditions across the boreal forest into eastern Canada will not be as favorable for population growth.
- The MPB could extend its range south into pine forests of Mexico.

23. Perkins, D. 2015. Facilitation of *Pinus albicaulis* seedling regeneration by *Vaccinium scoparium*. For *Ecol and Mgmt* 349 (2015) 55-65.

Background & Objectives

This paper explores the possible facilitative effects of *Vaccinium scoparium* and *Carex spp* on *Pinus albicaulis* seedlings. The author reports on observational studies, transplant experiments, and fertilization experiments to look at the effects of neighboring plants on whitebark seedling growth, survival and nutrient uptake.

Main Findings

- Observational studies at five previously burned sites showed a positive association between whitebark pine seedlings and low huckleberry.
- Transplant studies showed the best survival of PIAL seedlings occurred when planted with VASC or when planted in bare ground with shade cloth, but not with *Carex sp*.
- Fertilization studies conducted in the field showed no significant response to any of the fertilization treatment.
- Greenhouse studies showed greater root growth and root nodules on seedlings planted with VASC, suggesting an enhancement of mycorrhizal associations.

Implications

- There appears to be a facultative effect of *Vaccinium scoparium* on whitebark seedlings and specifically a detrimental effect of *Carex spp* that cannot be eliminated through scarification of soils prior to planting.
- Planting of whitebark pine seedlings in VASC or bare soil sites is likely to be more successful than *Carex* sites, and in all sites the use of microsites to provide shading was recommended.

24. Hansen, A., Ireland, K., Legg, K., Keane, R., Jenkins, M, and Pillet, M. 2016. Complex Challenges of Maintaining Whitebark Pine in Greater Yellowstone under Climate Change: A Call for Innovative Research Management, and Policy Approaches. Forests 7, 54.

Background and Objectives

Climate suitability is projected to change for numerous native plant species. This paper examines the effects of climate and 5 other factors that make whitebark pine especially vulnerable to climate change in the coming decades. These factors include competition, fire, bark beetles, white pine blister rust, and seed dispersal as well as climate. The review of the status of whitebark pine in light of these variables is used as a basis for making recommendations for whitebark pine and other subalpine species that may be affected by climate change. This paper also essentially provides a critique of the GYA Whitebark Pine Strategy and its implementation based on these climate-driven variables.

Main findings

- Assessing the risk of climate change to WBP populations in the GYE is difficult due to the complex array of interacting ecological factors
- Climatically-suitable habitats for WBP are projected to decrease, while suitability in current WBP locations may increase for subalpine fir, potentially increasing competitive effects. While fire generally mediates competition on whitebark pine limited studies have been conducted in the subalpine.
- Climate suitability is expected to increase for both MPB and blister rust.
- While increases in fire may lead to more suitable sites for WBP regeneration, it is unclear if nutcracker-based seed dispersal will be available due to decreases in seed sources which may result in abandonment of sites by nutcrackers or insufficient seed to disperse.
- More research is needed on all aspects described above - Climate suitability models do not address or identify micro-refugia which likely will provide continued habitat for whitebark pine, additional studies are needed to identify these locations; the plasticity of WBP in a changing climate is unknown and the tolerances of WBP to warmer and drier conditions is unknown; the effects of a changing fire regime on WBP competitive relationships is not adequately understood.
- Use of “core habitats” with likely continued habitat suitability is recommended for restoration sites, while also maximizing seed dispersal in future suitable habitats using rust-resistant seedlings.

Implications

- A modified framework for managing WBP in the GYE is recommended based on projected future climate suitability that incorporates the consideration of sites that are predicted to continue to be suitable, to deteriorate, and to become suitable in the future – some of these sites are alpine locations which are not currently forested.
- High levels of uncertainty on future climates suggest the need for a highly adaptive strategy in regard to WBP. Components of this adaptive strategy include placement of treatments, expanding monitoring efforts to gauge response to WBP treatments, and the use of modeling to project potential long-term outcomes of treatments.

25. Lynn M. Resler, Yang Shao, Diana F. Tomback & George P. Malanson. 2014. Predicting Functional Role and Occurrence of Whitebark Pine (*Pinus albicaulis*) at Alpine Treelines: Model Accuracy and Variable Importance, *Annals of the Association of American Geographers*, DOI:[10.1080/00045608.2014.910072](https://doi.org/10.1080/00045608.2014.910072)

Background and Objectives

Whitebark pine plays a central role in tree island development at some Rocky Mountain alpine treeline ecotones (ATEs or treelines). Using data from three different Rocky Mountain sites (including site locations include Alberta, Canada, Flathead National Forest, and the Beartooth Plateau, Custer National Forest) the authors examine the utility of four different predictive models using generalized linear models, classification and regression trees, random forests and support vector machines to determine if any one model or combination thereof was most useful in predicting the relative role of whitebark pine in tree island development.

Main findings

- The keystone role of whitebark pine in the facilitation of tree island development varies spatially.
- Comparing the results from different models enables the assessment of relative predictive capacity and provides for better variable selection and appropriateness.
- The most important variables determining the functional role of whitebark pine in the combined model were growing season temperature and slope curvature.
- Whitebark pine was the initiator (starting conifer) in 55% of the tree islands sampled (a total of 180 tree islands). Of the 1,149 total whitebark sampled on the three sites 40.9% were growing within the 180 tree islands. The majority of the WBP were solitary trees on two of the three sites.

Implications

- Models can be used to help determine where whitebark pines most greatly influence tree island formation.
- This information can be used in combination with other data to influence restoration and establishment of whitebark pine in or near alpine treeline ecotones.

26. Leirfallom, SB., Keane, RE., Tomback, DF., and Dobrowski, SZ., 2015. The effects of seed source health on whitebark pine (*Pinus albicaulis*) regeneration density after wildfire. *Can J. For Res.* 45:1597-1606.

Background and objectives

Whitebark pine populations are declining over much of its range due to a combination of factors including MPB, white pine blister rust, and successional replacement due to fire exclusion. Due to high mortality in cone-bearing trees, seed production may be inadequate for natural regeneration following disturbance such as fire. The objective of this study is to determine the relationship between whitebark pine seed source health and regeneration following disturbance. The study examined 15 burns ranging from 5 to 23 years old.

Main findings

- This study found a positive relationship between seed source health and seedling density in adjacent burns with sparse natural regeneration when the adjacent whitebark had 50% or more damage or mortality.
- Regeneration was present throughout most burns, but closer to seed sources had higher probabilities of seedling occurrence.
- Additional factors that influenced regeneration within a burn included vegetation cover and solar radiation.
- Study also found that 73% of seedlings germinated between 5 and 10 years after fire with only 13% germinating in the first 4 years following fire and that 54% of seedlings were found within 0.5 meters of a microsite feature such as a rock, log, stump or snag.

Implications

- In burned areas where more than 50% of adjacent seed source is damaged or dead low seed availability may limit whitebark pine regeneration potential.
- Seedling and sapling mortality is likely to increase over time due to WPBR, influencing the target amount of natural regeneration necessary to reforest a site, the degree of blister rust resistance varies, and should also be considered in natural regeneration target densities.
- Burned areas continue to provide the most favorable conditions for natural whitebark pine seedling regeneration; decreased regeneration potential is not cause to suppress high-elevation fire, however fire suppression on a small scale that leads to protection of healthy seed source stands or plus trees is part of the best fire management response in whitebark pine forests.

27. Hickey, JA, Meddens, AJH, and Kolden, CA., 2015. Recent tree mortality in the western United States from bark beetles and forest fires. *For. Sci.* 62.

Background and Objectives

Quantifying and understanding the effects of the two major disturbance agents that kill trees, fire and beetles, is important to understand the effects of disturbance. In turn tree mortality and its effects include reduction in carbon sequestration, changes in water quantity and changes in erosion and sedimentation rates. This study uses mortality area (canopy area of killed trees) to characterize disturbance in time and space. Fire mortality data are derived from two sources: Monitoring Trends in Burn Severity (MTBS) data and data derived from LANDSAT imagery. Bark beetle mortality area was derived using an updated data set produced by Meddens et al (2012) based on USDA Forest Service Aerial Detections Surveys (ADS) in 1997-2010.

Main findings

- Bark-beetle cause canopy mortality area in the past 3 decades was approx. 6.6 million hectares (0.64-7.8 percent of forested area in Western US) and fire-caused mortality was 2.7-5.9 million hectares (2.9-6.3%) of forested area.
- In several forest types mortality area exceeded 20% of the total forest area of that type.
- Mortality vector varied geographically with California, Idaho and Montana having high levels of mortality due to fire, while Colorado and Montana had high levels of beetle-caused mortality.
- Beetle-caused mortality occurred more consistently while fire-caused mortality is more temporally sporadic.

Implications

- Study found that fires are a more typical disturbance in lower elevation forests and beetles more common in high elevation forests; however the authors note that the fire return interval in high elevation forests is generally longer than the period addressed in this study.
- Additional research is suggested to reduce uncertainties and address anticipated changes in the relative importance of these forest disturbance processes.