

Altered Species Interactions and Implications for Natural Regeneration in Whitebark Pine Communities

Shawn T. McKinney, National Park Service, Inventory and Monitoring Program, Sierra Nevada Network;
Diana F. Tomback, Department of Integrative Biology, University of Colorado Denver; Carl E. Fiedler, College of Forestry and Conservation, University of Montana, Missoula

Background

Whitebark pine (*Pinus albicaulis*) decline has altered trophic interactions and led to changes in community dynamics in many Rocky Mountain subalpine forests (McKinney and Tomback 2007). Here we discuss how altered species interactions, driven by disproportionate whitebark pine mortality, constrain the capability of whitebark pine forests to contribute genetic material to subsequent generations. The degree to which whitebark pine forests are reproductively limited, however, depends in large part on tree species composition and forest structure. The results of these changed dynamics have several important implications for restoration decisions.

Seed Production

Whitebark pine cone production was positively correlated with live whitebark pine basal area (BA) and negatively correlated with whitebark pine tree mortality at the site-level in the U.S. Rocky Mountains (McKinney and others 2009; Table 1). White pine blister rust (*Cronartium ribicola*) damages and kills whitebark pine trees by girdling branches and trunks (McDonald and Hoff 2001), and therefore reduces seed production within trees and forest stands. Thus, blister rust directly constrains the ability of individual trees and forest stands to contribute propagules, and hence genetic material, to subsequent generations. This reduction in regeneration potential is further aggravated by altered interactions between whitebark pine and two key vertebrate species resulting from disproportionate whitebark pine mortality.

Table 1. Pearson's correlation coefficients of whitebark pine forest characteristics from 24 sites in the central and northern Rocky Mountains, USA. Correlations are based on site-level mean values and are all significant at $\alpha = 0.01$.

Site variable	Cone production (ln[no./ha.] ²)	Tree mortality (%)
Basal area (ln m ² /ha)	0.81	-0.78
Cone production (ln[no./ha.] ²)		-0.71

Predispersal Seed Predation

The North American red squirrel (*Tamiasciurus hudsonicus*) is a highly efficient, voracious consumer of conifer seeds. Squirrels cut down conifer cones and store them in large, conspicuous piles, called middens. Red squirrels preferentially select tree species based on cone energy content, foraging first on the highest energy species before moving on to the next highest energy species (Smith 1970, Hutchins and Lanner 1982). This adaptation is significant to the fate of whitebark pine because it has the greatest cone energy content of all sympatric species in U.S. Rocky Mountain upper subalpine forests (McKinney and others 2009). Due to their high foraging efficiency and central-place foraging lifestyle, red squirrels can greatly diminish cone crops at a local level. Indeed red squirrels are the primary predispersal seed predator of whitebark pine in the Rocky Mountains, taking more than 80 percent of the cone crop (Hutchins and Lanner 1982, McKinney and Tomback 2007).

Predispersal cone predation within a given forest is directly associated with red squirrel residential status. Squirrels remove proportionately more cones in forests where they reside (mixed conifer stands) versus whitebark pine-dominated stands where they simply feed and move on. In U.S. central and northern Rocky Mountain forests, the proportion of total squirrel detections comprised of active middens was significantly correlated with whitebark pine predispersal cone predation ($r = 0.65$, $P < 0.05$) (McKinney and Fiedler 2010). As cone production increases, squirrel predation increases at both tree- and stand-levels; however, the strength of the relationship between production and consumption is dependent on whitebark pine relative abundance (McKinney and Tomback 2007, McKinney and Fiedler 2010) (Figure 1). Predispersal cone predation decreases linearly with increasing proportion of total stand basal area comprised of whitebark pine (Figure 2). Therefore as whitebark pine becomes an increasingly dominant structural component, conditions for squirrel residence become less favorable, and cone predation declines.

Whitebark pine dominant forests provide suboptimal red squirrel habitat; conversely, squirrels thrive in mixed conifer forests containing whitebark pine. The reason for the disparity between the two forest types in squirrel residential status appears due to a higher degree of uncertainty in annual cone crops (Reinhart and Mattson 1990), and uncertainty appears

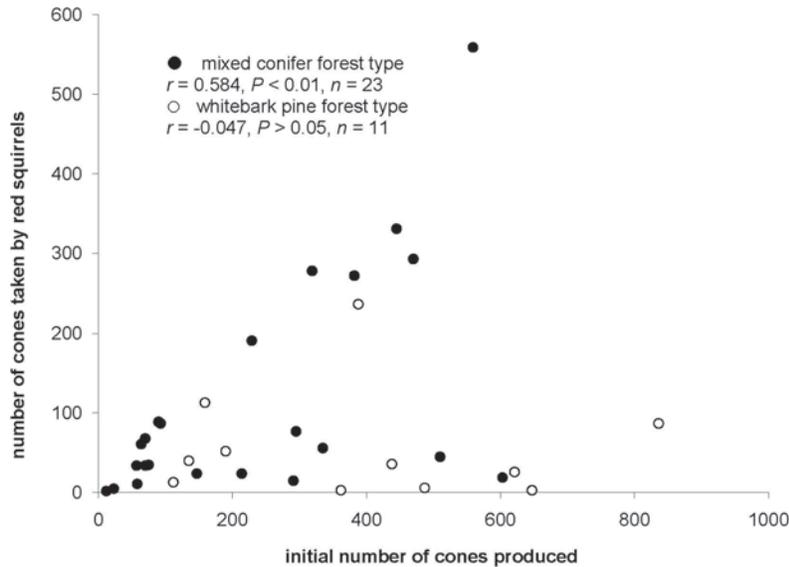


Figure 1. Correlation between red squirrel predispersal cone predation and whitebark pine cone production in two forest types (mixed conifer and whitebark pine dominant) in the Rocky Mountains, USA. Forest type defined by whether whitebark pine comprised > 50 per cent of total basal area; sites were classified as mixed conifer if condition was not met. Number of initial cones (x-axis) is the number of cones counted in late June to early July (McKinney and Fiedler 2010).

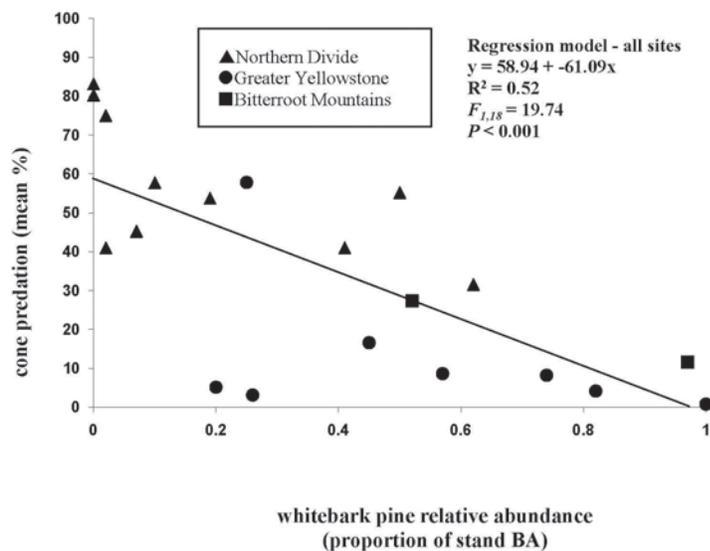


Figure 2. Simple linear regression analysis of the relationship between red squirrel mean predispersal cone predation (percentage of initial cone crop lost) and the relative abundance of whitebark pine at 20 subalpine forest sites in the Rocky Mountains, USA (McKinney and Fiedler 2010).

to be inversely related to tree species diversity. Squirrels, however, still prefer whitebark pine cones to sympatric conifers and will disperse into whitebark pine dominant forests to harvest cones, especially after disturbances such as wildfire (McKinney and Tomback 2007, McKinney and Fiedler 2010). However, because squirrel residence is low and ephemeral in whitebark pine dominant forests, overall cone consumption is low compared to mixed conifer forests containing whitebark pine. Hence whitebark pine dominant forests will likely have a larger proportion of their annual initial cone crop available for seed dispersal relative to mixed conifer forests.

Although squirrels appear to favor whitebark pine seeds, their residential status is dependent on forest structure and tree species composition (Mattson and Reinhart 1997, Fisher and Bradbury 2006). Squirrels need enough cones to store in order to survive long boreal winters (Steele 1998), and over time this requirement is best met in mature mixed conifer forests; those with high basal area and tree species diversity. These conditions are rarely met in forests where whitebark

pine makes up greater than 50 per cent of stand basal area (McKinney and Fiedler 2010). Indeed, red squirrel occurrence in whitebark-dominated stands is often transient, with a higher degree of cones eaten *in situ* and a lower degree of active middens relative to mixed conifer forests (McKinney and Fiedler 2010).

Seed Dispersal

Clark's nutcracker (*Nucifraga columbiana*) and whitebark pine are coevolved mutualists (Tomback 1982), whereby the pine is obligately dependent upon the bird for dispersal of its large, wingless seeds. In late summer and early fall, nutcrackers extract ripe whitebark pine seeds from cones, transport seeds in a specialized sublingual pouch, and cache them in the ground at an average depth of 2.5 cm (Tomback 1982). In early summer, nutcrackers forage in subalpine forests and assess the developing cone crop (Vander Wall 1988). This behavior presumably alerts birds to imminent seed shortages

(Vander Wall and others 1981). Depending on the severity of cone crop failure, nutcrackers either emigrate regionally or from large geographic areas in search of food (Davis and Williams 1957, 1964, Bock and Lepthien 1976).

The frequency of nutcracker occurrence in a whitebark pine forest is strongly associated with the number of available cones. The proportion of total observation hours with at least one Clark's nutcracker sighting increased linearly with increasing whitebark pine cone production across 24 research sites in the U.S. Rocky Mountains (Figure 3). Furthermore, because nutcracker occurrence is strongly associated with cone production, it is also positively correlated with live whitebark pine basal area and negatively correlated with whitebark pine tree mortality (Table 1). This suggests that these measurable site variables (BA and mortality) can be important indicators of cone production, and thus, bird occurrence.

Cone production is also a strong predictor of the probability of nutcracker seed dispersal (Figure 4). It appears that by the time seed dispersal behavior initiates (late summer to early fall), nutcrackers have decided whether or not to settle in an area, and this decision is largely determined by the

size of the existing cone crop. Moreover, the combined results indicate that there is a threshold of whitebark pine cone production below which there is a rapid decline in both the frequency of nutcracker occurrence (Figure 3) and probability of seed dispersal (Figure 4).

Continued degradation of cone production capacity within whitebark pine forests coupled with the tendency of nutcrackers to emigrate when cone crops are small, could result in fewer seed dispersal events in many whitebark pine forests. This outcome is especially troubling because high-mortality stands have lower cone abundance (McKinney and Tomback 2007); yet harbor a higher relative frequency of rust-resistant trees than similar stands with low mortality simply because most non-resistant trees in high-mortality stands have succumbed to blister rust (Hoff and others 1994). If nutcrackers are rare or absent in high-mortality stands, the putative resistance in the surviving trees would have little chance to be passed on to the next generation. Thus, identifying whether a threshold exists in whitebark pine cone production necessary to elicit seed dispersal by nutcrackers is an important question for restoration planning.

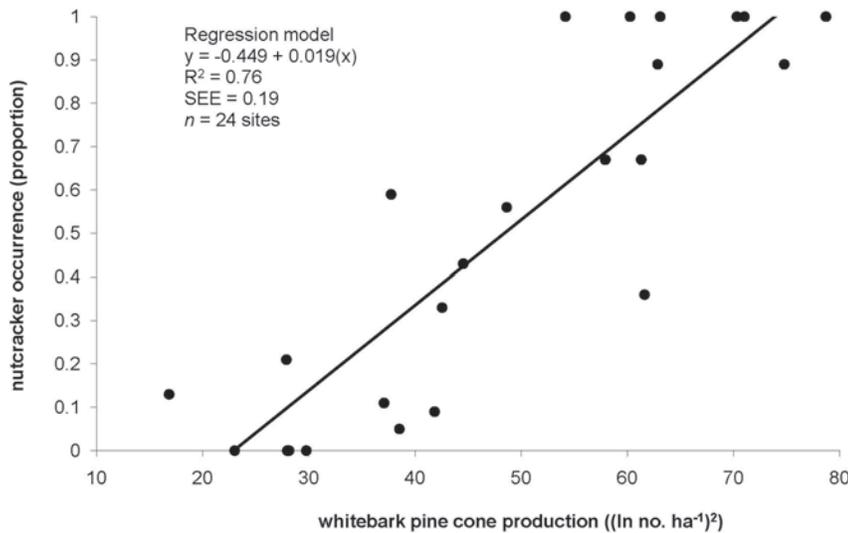


Figure 3—Simple linear regression analysis of the proportion of total observation hours (all years combined) with ≥ 1 Clark's nutcracker present as a function of mean, transformed whitebark pine cone production in Rocky Mountain forest sites, USA. SEE indicates the standard error of the estimate (proportion) (McKinney and others 2009).

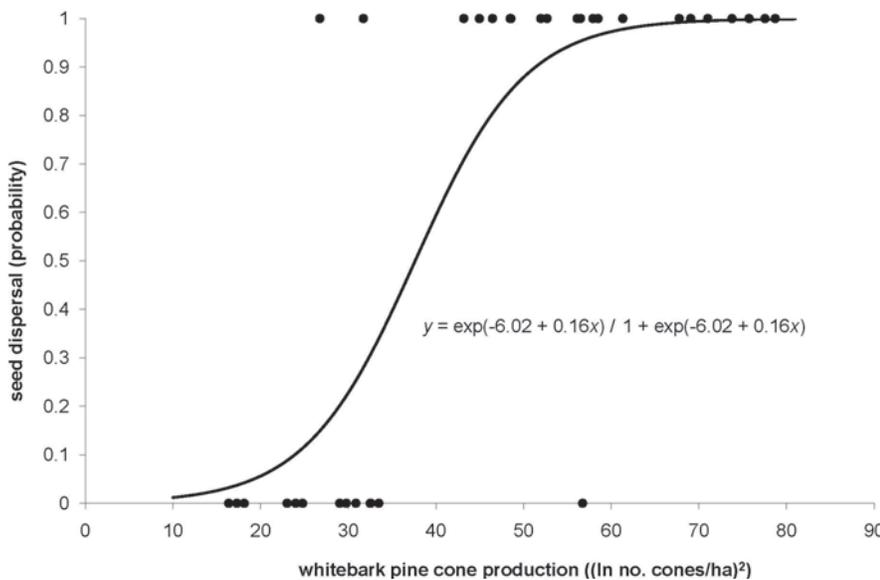


Figure 4—Binary logistic regression analysis of Clark's nutcracker seed dispersal (1 = dispersed, 0 = not dispersed) as a function of mean annual whitebark pine cone production in Rocky Mountain forest sites, USA ($n = 34$). The solid line represents the probability function derived from the prediction equation. A solid circle along the y-axis "1" indicates that a site had a seed-dispersal event recorded and a circle along the "0" line indicates that none was recorded (McKinney and others 2009).

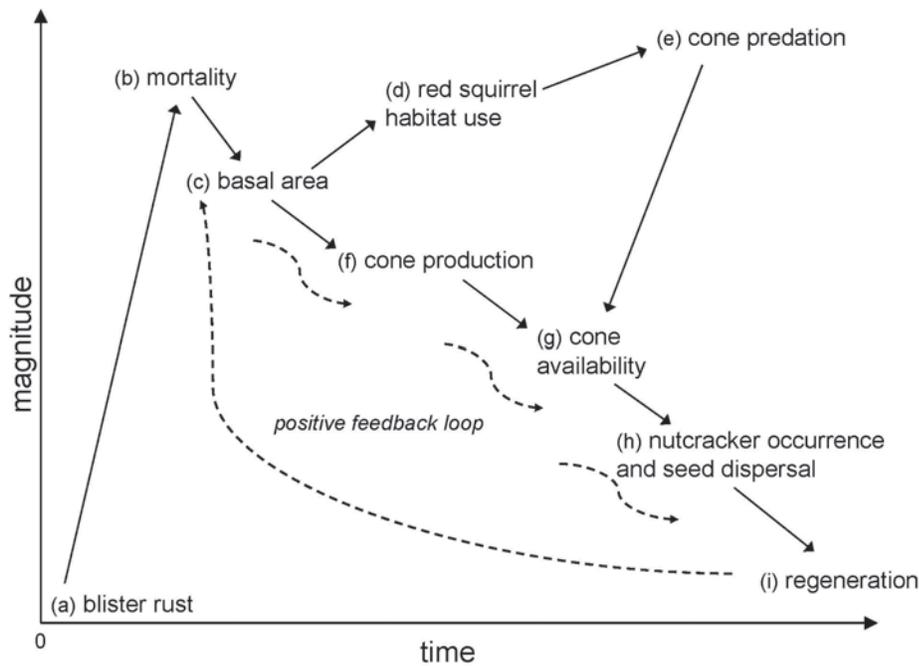


Figure 5—Analytically-based model depicting the series of processes between blister rust invasion of a whitebark pine forest and the creation of a positive feedback loop hastening the decline of whitebark pine within the forest. The arrow preceding a component represents the direction of influence of its associated component. For example, basal area (c) declines with increasing tree mortality (b). All components except (d) and (h) refer specifically to whitebark pine. For example, basal area (c) indicates resulting effects of whitebark pine basal area declining. Data are from 24 forest sites ranging in size from two to seven ha located in the central and northern Rocky Mountains, USA (2001-2006).

Management Implications

An analytically-based model is presented in Figure 5 that depicts the series of processes that occur following the arrival of blister rust within a whitebark pine stand. These processes erode community composition and function, culminating in the creation of a positive feedback cycle. It is difficult to identify exactly where in the cycle active management intervention is needed. Uncertainty is due to differing management goals and priorities between jurisdictions, and to the complexities inherent in the habitat and landscape context of the forest in question. We can, however, point to empirical data that may indicate a particular forest has entered this cycle. The seed dispersal model (Figure 4) can be used to estimate the level of cone production where seed dispersal can be expected. Decisions regarding an acceptable level of uncertainty need to be made first, however. For example, if we set a cutoff probability of seed dispersal to 0.70 (we want to be 70 percent sure some seeds will be dispersed), 94.7 percent (18/19) of all the dispersed sites were correctly classified by the model and predicted to have seed dispersal. Based on the logistic equation, a whitebark pine forest has a predicted seed dispersal probability ≥ 0.70 when average cone production ≥ 700 cones ha^{-1} ($(\ln \text{cones } \text{ha}^{-1})^2 \geq 42.9$; Figure 4).

We have shown that specific habitat conditions of a forest are crucial elements in predicting the number of cones available for nutcrackers, nutcracker seed dispersal probability, and thus, the potential to contribute genetic material to future generations through natural regeneration. We propose that altered interspecific interactions result in a positive feedback mechanism whereby increased whitebark pine mortality leads to higher rates of predispersal seed predation, fewer seed dispersal events, and reduced regeneration. Without management intervention, these trends portend

accelerated decline and possible extinctions of some whitebark pine populations.

Acknowledgments

We thank the following sources for funding the research presented in this paper: U.S. Forest Service Rocky Mountain Research Station, U.S. National Park Service, Cooperative Conservation Initiative grant, McIntire-Stennis Research Program grant, and the College of Forestry and Conservation, University of Montana. We are grateful to Vern Peters (The King's University College) and Les Chow (National Park Service) for thoughtful reviews and helpful comments that improved the document.

Literature Cited

- Bock, C. E.; L. W. Lephien. 1976. Synchronous eruptions of boreal seed-eating birds. *The American Naturalist*. 110: 559-571.
- Davis, J.; L. Williams. 1957. Irruption of the Clark Nutcracker in California. *The Condor*. 59: 297-307.
- Davis, J.; L. Williams. 1964. The 1961 Irruption of the Clark's Nutcracker in California. *The Wilson Bulletin* 76: 10-18.
- Fisher, J. T.; S. M. Bradbury. 2006. Understorey protection harvest expedites recolonisation of boreal forest stands by North American red squirrels. *Forest Ecology and Management*. 234: 40-47.
- Hoff, R. J.; S. K. Hagle; R. G. Krebill. 1994. Genetic consequences and research challenges of blister rust in whitebark pine forests. Pages 118-126 in W. C. Schmidt and F. K. Holtmeier, editors. *Proceedings—International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our Knowledge*. General Technical Report INT-GTR-309. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, UT, USA.

- Hutchins, H. E.; R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. *Oecologia*. 55: 192-201.
- Mattson, D. J.; D. P. Reinhart. 1997. Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. *Journal of Applied Ecology*. 34: 926-940
- McDonald, G. I.; R. J. Hoff. 2001. Blister rust: an introduced plague. Pages 193-220 in D. F. Tomback, S. F. Arno, and R. E. Keane, editors. *Whitebark pine communities: ecology and restoration*. Island Press, Washington, DC.
- McKinney, S. T., and D. F. Tomback. 2007. The influence of white pine blister rust on seed dispersal in whitebark pine. *Canadian Journal of Forest Research*. 37: 1044-1057.
- McKinney, S. T.; C. E. Fiedler; D. F. Tomback. 2009. Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. *Ecological Applications*. 19: 597-607.
- McKinney, S. T.; C. E. Fiedler. 2010. Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer. *Oecologia*. 162: 697-707.
- Reinhart, D. P.; D. J. Mattson. 1990. Red squirrels in the whitebark zone. In Schmidt, W.C.; McDonald, K.J., eds. *Proceedings-Symposium on whitebark pine ecosystems: Ecology and management of a high-mountain resource*. Gen. Tech. Rep. INT-270, U.S. Dept. Agric.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs*. 40: 349-371.
- Steele, M. A. 1998. *Tamiasciurus hudsonicus*. *Mammalian Species*. 586: 1-9.
- Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. *Journal of Animal Ecology*. 51: 451-467.
- Vander Wall, S. B. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. *The Condor*. 90: 621-631.
- Vander Wall, S. B.; S. W. Hoffman; W. K. Potts. 1981. Emigration behavior of Clark's Nutcracker. *The Condor*. 83: 162-170.

The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.
