PLANT-ANIMAL INTERACTIONS - ORIGINAL PAPER

Tree squirrel habitat selection and predispersal seed predation in a declining subalpine conifer

Shawn T. McKinney · Carl E. Fiedler

Abstract Differential responses by species to modern perturbations in forest ecosystems may have undesirable impacts on plant-animal interactions. If such disruptions cause declines in a plant species without corresponding declines in a primary seed predator, the effects on the plant could be exacerbated. We examined one such interaction between *Pinus albicaulis* (whitebark pine), a bird-dispersed, subalpine forest species experiencing severe population declines in the northern part of its range, and *Tamiasciurus hudsonicus* (red squirrel), an efficient conifer seed predator, at 20 sites in two distinct ecosystems. Hypotheses about squirrel habitat preferences were tested to determine how changes in forest conditions influence habitat use and subsequent levels of predispersal cone predation. We performed habitat selection modeling and variable ranking based on Akaike's information criterion; compared the level and variance of habitat use between two forest types (*P. albicaulis* dominant and mixed conifer); and modeled the relationship between *P. albicaulis* relative abundance and predispersal cone predation. *T. hudsonicus* did not demonstrate strong habitat preference for *P. albicaulis*, and thus, declines in the pine were not met with proportional declines in squirrel habitat use. *P. albicaulis* habitat variables were the least important in squirrel habitat selection. Squirrel habitat use was lower and varied more in *P. albicaulis*-dominant forests, and predispersal cone predation decreased linearly with increasing *P. albicaulis* relative abundance. In Northern Rocky Mountain sites, where *P. albicaulis* mortality was higher and abundance lower, squirrel predation was greater than in Central Rocky Mountain sites. In ecosystems with reduced *P. albicaulis* abundance, altered interactions between the squirrel and pine may lead to a lower proportion of *P. albicaulis* contributing to population recruitment because of reduced seed availability. Reducing the abundance of competing conifers will create suboptimal squirrel habitat, thus lowering cone predation in *P. albicaulis* and ensuring more seeds are available for avian dispersal.

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S. T. McKinney · C. E. Fiedler
College of Forestry and Conservation,
University of Montana, Missoula, MT 59812, USA

Present Address:
S. T. McKinney (✉)
National Park Service Inventory and Monitoring Program,
Sierra Nevada Network, P.O. Box 700-W,
El Portal, CA 95318, USA
e-mail: shawn_mckinney@nps.gov

Introduction

Human-induced changes to forest ecosystems can alter plant-animal interactions, leading to disproportionate effects on certain plant species. Both the loss of animal seed dispersers, whether from forest fragmentation (Cordeiro and Howe 2003), overhunting (Meehan et al. 2002), or invasive species (McKinney et al. 2009), and the introduction of animal seed predators (Christian 2001) have induced plant declines and shifts in community composition. What is not well known is how declines in plant abundance–without corresponding declines in animal abundance–might affect plant-animal interactions. Specifically, if a plant species is declining but a seed predator remains intact, will the

effects on the plant be exacerbated? The issue becomes especially compelling when the plant in question is a foundation tree species and thus regulates population and community dynamics, and tempers ecosystem processes (Ellison et al. 2005).

North American and Eurasian arboreal squirrels (*Tamiasciurus* and *Sciurus* genera) and members of the genus *Pinus* have an evolutionary relationship dating back to the late Pliocene (ca. 1.7 Ma; Hafner 1984; Axelrod 1986). The evolution of tree squirrel adaptations for specialized feeding on pine seeds, and *Pinus* cone and seed morphologies to inhibit seed predation, is well documented (Smith 1970; Elliott 1974; Benkman et al. 1984). Arboreal squirrels can exert significant ecological and evolutionary effects on seeds, tree population dynamics, and forest structure by directly influencing seed fate (Steele et al. 2005). Despite this predation pressure, the distribution of *Pinus* has generally been increasing in both North America and Eurasia (Axelrod 1986; Willis et al. 1998), underscoring the ability of pines to adapt to challenges posed by efficient seed predators.

Many coniferous forests are currently facing insect epidemics, exotic species invasions, and altered disturbance regimes that negatively and disproportionately affect *Pinus* species. How changes in tree species composition will affect interactions between *Pinus* seed producers and tree squirrel seed predators will likely depend on the squirrel's food choices and habitat preferences. For example, North American arboreal squirrels selectively harvest cones from tree species with the highest cone energy content (Smith 1968, 1970). Tree species selection based on cone energy content is also documented in Eurasian squirrels, with selection apparently dependent upon forest composition (Lurz et al. 1995; Molinari et al. 2006).

We studied *Tamiasciurus hudsonicus* [North American red squirrel (Erxleben) family Sciuridae] habitat use in Rocky Mountain *Pinus albicaulis* [whitebark pine (Engelmann) family Pinaceae, subgenus *Strobus*] forests to understand how seed producer and seed predator relationships are influenced by differential *Pinus* mortality. The species' geographical ranges are sympatric in the Rocky Mountains where both maintain a boreal affinity. Furthermore, both species are present in late Pleistocene deposits (ca. 0.8–0.5 Ma; Kurtén and Anderson 1980; Baker 1990), suggesting a prolonged ecological interaction.

P. albicaulis occurs in nearly pure stands on the coldest and driest sites where few other tree species can grow, and in mixed-species stands on less severe, lower elevation sites (Arno and Hoff 1990). Its seeds are retained in indehiscent cones (McCaughey and Schmidt 1990) and are dispersed in late summer and early fall by Clark's nutcracker (*Nucifraga columbiana*), a coevolved mutualist with the pine (Tomback 1982). Nutcrackers consume unripe seeds in early to mid-summer, however, acting as seed predators and competing with tree squirrels (Hutchins and Lanner 1982). Where squirrels outcompete nutcrackers for seeds, the evolution of cone and seed traits that facilitate nutcracker seed dispersal is constrained (Siepielski and Benkman 2007). The pine is considered a foundation species of subalpine forest ecosystems (Ellison et al. 2005) because it: (1) regulates snowmelt and stream flow (Farnes 1990); (2) moderates local environments, allowing for establishment of shade-tolerant conifers (Callaway 1998) and diverse understory communities; and (3) provides an important food source for many birds and mammals, including grizzly bears (*Ursus arctos*) that poach cones from squirrel middens (Mattson et al. 1991).

P. albicaulis is faced with multiple challenges to its long-term persistence, including the exotic fungal pathogen, *Cronartium ribicola*, which causes white pine blister rust (Hoff et al. 1980), mountain pine beetle (*Dendroctonus ponderosae*) upsurges (Logan and Powell 2001), and successional replacement by shade-tolerant conifers (Arno 1980). Fire exclusion has also prevented creation of forest openings favorable both to nutcracker seed-caching and later germination and development of shade-intolerant seedlings (Brown et al. 1994; Murray et al. 2000). Declines in *P. albicaulis* are occurring nearly rangewide, but are most severe in the Northern Rocky Mountains, where tree mortality and blister rust infection levels reach 90% in some stands (Keane et al. 1994; Kendall and Keane 2001).

T. hudsonicus is a territorial granivore and central-place forager (Elliott 1988). Territories are maintained by a single adult that cuts conifer cones and stores them in middens (Smith 1981). Within Rocky Mountain coniferous forests, mean territory sizes (no. ha^{-1}) reported here and in the literature are similar: 0.4–1.5 in Alberta, Canada (Rusch and Reeder 1978; Larsen and Boutin 1994); 0.7–1.1 in Wyoming and Montana, US (Mattson and Reinhart 1997; the present study); and 1.3 in Colorado, US (Gurnell 1984). Squirrels favor habitat conditions that ensure a dependable supply of cones and fungi (mixed conifer forests with high basal area), allow for adequate cone storage (cool and moist forest floor), and provide suitable nesting sites, and cover from predators (closed, tall canopies; Rothwell 1979; Steele 1998). However, suboptimal habitats that do not possess all of these characteristics can be temporarily used during periods of population growth (Rusch and Reeder 1978). Individuals may disperse into suboptimal conditions, cut cones to eat in situ, and attempt to form a new territory. Strong philopatry, increased predation risk with increasing dispersal distance, and lower survival contribute to transient squirrel occurrence in suboptimal habitats (Larsen and Boutin 1994). Thus, the relative proportion of active middens (indicating residence) versus cones cut and eaten in situ (indicating transience) can be used as an index of

habitat quality, with greater midden use indicating better habitat conditions. Reinhart and Mattson (1990) found fewer resident squirrels in nearly pure stands of *P. albicaulis* compared to mixed conifer stands containing *P. albicaulis*. They speculated that *P. albicaulis*-dominant forests are not hospitable habitat because of lower basal area and tree diversity, greater cone crop variability, and harsher environmental conditions compared to mixed species forests.

T. hudsonicus is the main predispersal seed predator of *P. albicaulis* in the Northern Rocky Mountains–taking more than 80% of the cone crop and greatly diminishing the number of seeds available for nutcracker dispersal (McKinney and Tomback 2007). This predation limits *P. albicaulis* regeneration potential because cone abundance significantly influences the probability of nutcracker seed dispersal (McKinney et al. 2009). The squirrel may prefer *P. albicaulis* cones in Rocky Mountain upper subalpine forests because of their high energy content (*P. albicaulis* = 27.7 Kcal per cone, next highest *Abies lasiocarpa* = 15.7 kcal per cone; Tomback 1982; Smith 1970). Thus, a tradeoff may exist between selection at the tree level (*P. albicaulis* for its high energy cones) and the stand level (habitat conditions suitable for survival and reproduction).

The purpose of this study was to determine how changes in forest conditions influence *T. hudsonicus* habitat use and subsequent *P. albicaulis* predispersal cone predation. Our secondary objective was to interpret findings and suggest management options for increasing the likelihood of *P. albicaulis* natural regeneration. We compared forest characteristics and squirrel habitat use between two forest types (*P. albicaulis* and mixed conifer) and two ecosystems—one in the Northern Rocky Mountains where *P. albicaulis* is suffering sharp declines, and one in the Central Rocky Mountains where it is not. Previous studies have related *T. hudsonicus* activity and abundance to forest structure and habitat type in both US Rocky Mountain (Mattson and Reinhart 1997) and Canadian boreal forests (Fisher and Bradbury 2006). To our knowledge, no previous study has investigated the relationship of forest compositional change with habitat use and associated predispersal cone predation by squirrels.

How squirrels respond to *P. albicaulis* declines could greatly influence the potential for pine regeneration, which leads to two hypotheses and subsequent predictions of squirrel habitat use. Specifically:

1. If squirrels have a strong habitat preference for *P. albicaulis*, then (a) specific *P. albicaulis* habitat variables will rank high in importance in squirrel habitat selection; (b) habitat use will be lower in forests with lower *P. albicaulis* relative abundance; and therefore, (c) cone predation will remain constant across varying levels of *P. albicaulis* relative abundance.

2. Alternatively, if squirrels do not have a strong preference for *P. albicaulis*, but rather use the pine opportunistically, then (a) specific *P. albicaulis* habitat variables will rank low in importance in squirrel habitat selection; (b) habitat use will not decline with lower *P. albicaulis* relative abundance; and therefore, (c) cone predation will increase proportionally with declining *P. albicaulis* relative abundance (fewer cones with unchanged squirrel abundance).

Materials and methods

Study area and sampling design

We conducted research from June to September 2004–2006, within two distinct geographic areas in the Rocky Mountains, USA. Research within the Northern Divide Ecosystem (NDE) of northwestern Montana took place in Glacier National Park and the Flathead National Forest (48.8–48.3°N, 113.3–114.4°W). Elevation of research sites ranged from 1,806 to 2,181 above sea level. In the Greater Yellowstone Ecosystem (GYE) of southwestern Montana and northwestern Wyoming, research was conducted within Yellowstone National Park and the Gallatin and Shoshone National Forests (45.1–44.8°N, 109.5–110.6°W). Elevation of sites ranged from 2,546 to 2,978 m above sea level. Forest communities at research sites comprised *P. albicaulis*, *Pinus contorta* (lodgepole pine), *A. lasiocarpa* (subalpine fir), *Picea engelmannii* (Engelmann spruce), and *Pseudotsuga menziesii* (Douglas-fir) in various combinations and relative abundances.

Individual research sites were selected based on the presence of cone-bearing *P. albicaulis*, while multiple research sites within ecosystems were selected to capture variation in tree species composition and structure and in the altitudinal range of *P. albicaulis* and *T. hudsonicus* co-occurrence (NDE $n = 10$ sites, GYE $n = 8$ sites). We established sites by delineating rectangular boundaries that were 100 m wide by $\geq$200 m long within contiguous forest stands (site area: minimum = 2 ha, maximum = 7 ha, mean = 2.6 ha). The actual size of a site was determined by the density of cone-bearing *P. albicaulis*. To obtain an adequate sample of trees to calculate means and estimate variation, forests with low densities of cone-bearing *P. albicaulis* (e.g., 1 ha^{-1}) required larger sampling areas. Forest sites with low densities of cone-bearing *P. albicaulis* were characterized by a larger relative abundance of other conifer species (Table 1). Sites were subdivided into 1-ha squares (100 m × 100 m) to provide better sampling control.

Table 1 Site-level parameter values of Rocky Mountain *Pinus albicaulis* forests used to evaluate *Tamiasciurus hudsonicus* habitat use

Location	Forest type[a]	Total basal area ($m^2 ha^{-1}$)	*P. albicaulis* relative abundance[b] (% BA)	Tree diversity (Simpson's)	Elevation (m)	Mean (±SE)					
						Latitude (dd)	Longitude (dd)	Aspect (°)	Slope (°)	Canopy height (m)	Canopy cover (%)
NDE	*P. albicaulis*	8.0	62.2	2.26	2,181 (2)	48.316	−113.315	177 (4)	15 (0)	6.6 (0.4)	19 (3)
	Mixed	5.5	49.6	2.07	2,116 (3)	48.482	−113.341	257 (3)	25 (0)	8.2 (0.5)	21 (4)
	Mixed	34.2	2.5	1.05	2,136 (4)	48.708	−113.654	213 (10)	8 (1)	12.4 (0.6)	85 (4)
	Mixed	21.3	1.7	1.37	2,169 (2)	48.713	−113.648	201 (8)	5 (1)	10.7 (0.8)	45 (6)
	Mixed	18.9	0	1.97	1,887 (15)	48.524	−114.393	130 (51)	15 (4)	25.1 (1.7)	67 (4)
	Mixed	9.5	0	1.65	1,806 (11)	48.530	−114.391	91 (17)	13 (1)	21.4 (3.5)	47 (11)
	Mixed	44.1	10.1	1.71	2,103 (35)	48.422	−113.392	229 (16)	23 (3)	12.9 (1.6)	84 (8)
	Mixed	3.2	41.3	3.42	2,060 (8)	48.529	−114.106	166 (9)	26 (2)	7.4 (0.4)	18 (2)
	Mixed	4.0	6.6	3.29	2,080 (20)	48.183	−113.268	227 (11)	30 (1)	9.2 (0.6)	26 (4)
	Mixed	23.8	19.4	3.16	1,837 (22)	48.541	−114.392	163 (62)	15 (6)	23.8 (4.7)	77 (13)
	P. albicaulis	15.0	100.0	1.00	2,814 (6)	45.056	−110.588	197 (9)	24 (2)	11.7 (0.8)	46 (6)
	P. albicaulis	25.5	57.3	2.21	2,864 (3)	44.810	−110.429	266 (33)	24 (2)	12.8 (0.8)	47 (7)
	P. albicaulis	30.2	73.9	1.68	2,911 (2)	45.065	−109.937	200 (17)	13 (2)	14.3 (0.9)	54 (7)
	P. albicaulis	30.4	81.7	1.47	2,899 (5)	44.940	−109.563	140 (21)	10 (2)	11.8 (1.5)	71 (5)
	Mixed	40.3	25.0	3.80	2,546 (4)	45.062	−110.608	158 (31)	20 (1)	18.4 (0.8)	92 (4)
	Mixed	41.8	19.7	2.24	2,744 (4)	45.037	−109.939	205 (4)	20 (1)	15.5 (1.1)	84 (3)
	Mixed	37.5	45.1	2.27	2,755 (3)	44.817	−110.443	311 (7)	17 (1)	16.3 (0.9)	68 (5)
	Mixed	16.8	25.7	2.30	2,978 (4)	44.935	−109.503	113 (42)	9 (2)	8.5 (0.8)	52 (6)
BME	*P. albicaulis*	29.3	97.2	1.06	2,561 (5)	46.505	−114.239	271 (28)	20 (1)	11.7 (0.5)	56 (4)
	P. albicaulis	15.3	52.4	2.22	2,389 (3)	46.507	−114.218	218 (52)	20 (2)	12.9 (0.3)	54 (5)

NDE Northern Divide Ecosystem, northwestern Montana; *GYE* Greater Yellowstone Ecosystem, southwestern Montana and northwestern Wyoming; *BME* Bitterroot Mountains Ecosystem, west-central Montana

[a] Forest type defined by whether *P. albicaulis* comprised >50% of total basal area (*BA*); sites were classified as mixed conifer if condition was not met

[b] Sites with zero values failed to have live *P. albicaulis* recorded by transect sampling, though cone trees were present and selected using alternative methodology (see text)

Field methods

We generated random numbers for azimuth degree and distance and followed them from a corner of each 1-ha square until we encountered a cone-bearing *P. albicaulis* tree within the site. Selected cone trees were ≥25 m apart with a minimum of 1 and maximum of 4 sampled trees ha^{-1} (cone trees per site: minimum = 4, maximum = 16, mean = 10.6). We marked cone trees with metal identification tags and logged tree coordinates with a handheld Global Positioning System unit (± 10 m; Garmin International, Olathe, KS.) for later relocation. We focused on estimating predispersal cone predation by squirrels, and not total seed consumption, because the probability of nutcracker seed dispersal is largely influenced by the number of cones available at that time (McKinney et al. 2009). Previous research in our study region identified squirrel cone predation to initiate between late June and early July, and nutcracker seed dispersal to begin in late August (Hutchins and Lanner 1982; McKinney and Tomback 2007); we therefore chose our cone count survey dates accordingly.

Initial ovulate cone counts were conducted between 29 June and 15 July of each year. We used tripod-mounted spotting scopes with 10–60× zoom eyepieces (Leica, Solms, Germany) and handheld tally devices to count cones. Two to three observation points that allowed for unobstructed views of a tree's canopy were used to census cones on each tree. We returned to the same observation points between 19 August and 4 September of each year and counted the remaining cones. Because cones are indehiscent at maturity and rarely fall to the ground without vertebrate assistance, we were able to ascribe cone loss to one of two species. Nutcrackers extract seeds while the cone remains attached to the branch, leaving a characteristic dished-out cone after seed harvesting, and rarely dislodge cones from branches (Hutchins and Lanner 1982; Tomback 1998). Squirrels use their sharp teeth and strong temporal muscles to either cut branch tips and drop individual or whorls of cones, or to cut the base of a single cone and eat it

in situ (Smith 1970; Hutchins and Lanner 1982). Because *T. hudsonicus* was the only mammal in the study area capable of cutting cones from the canopy, we attributed the difference between the initial and final cone numbers to squirrel predation (McKinney and Tomback 2007). Percent predispersal cone predation for each site was calculated annually and overall (i.e., within a year and all years combined) as the sum of cones lost to squirrels (by year, all years) divided by the sum of initial cone counts (by year, all years), multiplied by 100.

We established two 10×50-m (500-m^2) belt transects along random azimuths within each hectare of each research site to collect tree- and site-level data. We measured eight variables to assess their relative importance in squirrel habitat selection. Two of these variables were specific *P. albicaulis* habitat parameters that could influence squirrel use: cone-bearing *P. albicaulis* trees (no. ha^{-1}) and *P. albicaulis* tree mortality (%). Six were more general site descriptors or habitat parameters that previous studies have shown to be important to squirrels (see "Introduction"): total tree basal area (m^2 ha^{-1}), tree species diversity (Simpson's index), canopy cover (%), canopy height (m), slope (°), and a site index (elevation × latitude interaction). All trees with diameter at breast height (DBH; 1.4 m) ≥ 7 cm were recorded by species and DBH (± 0.1 cm); canopy cover (± 5%) was estimated at each transect midpoint with a convex forest densitometer in four cardinal directions; and canopy height (± 1 m) and site slope ($\pm 1°$) were measured with a clinometer. We calculated basal area (BA; m^2 ha^{-1}) from the DBH for each tree and summed BA by transect, species, and research site. The four canopy cover readings at each transect were averaged, converted into percent canopy cover, and then used to calculate the site mean. We inspected all living *P. albicaulis* trees ≥ 7 cm DBH for the presence of ovulate cones and blister rust infection symptoms. A tree was identified as infected if it exhibited active or inactive branch or stem cankers (Hoff 1992). We estimated percent crown kill (± 5%) for all infected trees, considering the crown to extend from the top of the tree down to the lowest branches (McKinney and Tomback 2007).

At each research site, we used two strip transects (Eberhardt 1978) 50 m wide by the length of the site to survey for signs of two types of *T. hudsonicus* activity–active middens and fresh cones. Active middens were identified by the presence of recently cut cones, cone scales, or chewed cone cores on or within larger multiple year accumulations of cone debris (Finley 1969). Hence active middens were evidence of current *T. hudsonicus* residence. Fresh cones were defined as *P. albicaulis* cone debris of the current year that was not on, in, or within 5 m of a midden (Côté and Ferron 2001). Current-year status was determined by debris having purple cone scales, white cores, white seed coats, and

softness. Since the seeds of the fresh cone category were eaten in situ and not connected with an active midden, fresh cones provide no evidence of a squirrel's residence. One person ran a transect tape and maintained a consistent azimuth while each of two researchers surveyed for active middens and fresh cones within 25 m on either side of the transect line. Detections were recorded at 50-m interval lengths, summed for each category, and divided by the total area sampled to calculate the mean number of middens and fresh cones per square meter. We calculated the proportion of total squirrel activity by each detection category for each site. Given the large size and conspicuous nature of an active midden (Finley 1969), and our search intensity, we assumed a detection probability of a squirrel's residence ≈ 1 (Burnham et al. 1980).

In 2006, extra resources allowed us to sample two additional research sites in the Bitterroot Mountains of west-central Montana (46.5°N, 114.2°W, 2,389–2,561 m). These sites were intermediate in latitude and elevation to the NDE and GYE sites. Data were collected using the same design and sampling protocols employed at the NDE and GYE sites.

Data analyses

Prior to analyses, we summarized data at the site level and calculated a Simpson's diversity index value for each site based on total tree species BA. A significance level of $P = 0.05$ was assumed for subsequent hypothesis testing, tests for violations of assumptions were investigated, and all necessary data transformations were made. We used S-Plus 7.0 (Insightful 2005), SPSS 10.0 (SPSS 1999), and Microsoft Excel (Microsoft 2003) for all statistical analyses and computations.

T. hudsonicus habitat use: site-level comparisons

Active middens (number per hectare for each site) served as the response variable for the squirrel habitat selection analysis. We fit exponential and gamma distributions to the midden data and compared their log-likelihoods to determine which error distribution best fit the data. Because several sites had zero values for middens, a value of 0.5 was added to each site's midden count and the adjusted value natural-log transformed (Sokal and Rohlf 1995) before calculating log-likelihoods. We evaluated eight variables for their relative importance in squirrel habitat selection (Table 1). We used generalized linear models with gamma error distribution and identity link for all possible combinations of these eight variables. Thus, $2^8 = 256$ possible models, including a null model (intercept only), were analyzed. Iterations were terminated due to singularities in 32 of the 256 models; therefore, these failed models were not used in

the subsequent analysis. We used an information-theoretic approach to rank models based on Akaike's information criterion (AIC) corrected for small sample sizes (AIC$_c$) and on calculated Akaike weights (Burnham and Anderson 2002). We estimated the relative importance of each variable by summing the Akaike weights of all models within which the variable occurred and dividing by the number of models it occurred in; a higher weight for a variable was interpreted as having more support from the data (Burnham and Anderson 2002).

Linear regression was used to model the relationship between predispersal cone predation (percentage of total cones lost all years) and the relative abundance of *P. albicaulis* (proportion of total BA) across all research sites ($n = 20$) and test the hypothesis that cone predation does not change with declining *P. albicaulis* relative abundance. To determine whether higher squirrel residency is associated with higher predispersal cone predation, we used correlation analysis and quantified the relationship between the proportion of total squirrel detections comprising active middens and percent cone predation.

T. hudsonicus habitat use: forest type comparisons

Research sites were classified into forest cover types based on the predominant tree species occupying the site (UFFES 1998), i.e., *P. albicaulis* forest type if *P. albicaulis* was the dominant species and constituted >50% of the total site BA, and mixed forest type if these conditions were not met. Because we were concerned only with trees of cone-bearing size, BA was computed for trees ≥9.0 cm. We used multivariate ANOVA (MANOVA) to determine if forest types differed in population mean vectors for forest structure, composition, and site slope. Forest structure was represented by the dependent variables total BA, canopy cover, and canopy height. Forest composition was calculated as the proportion of total BA represented by *P. albicaulis*. Canopy cover and canopy height were natural log-transformed to meet assumptions of normality.

We evaluated four aspects of squirrel habitat use to determine whether and how habitat use varies with *P. albicaulis* relative abundance (i.e., forest type). First, we used correlation analysis to compare the strength of the linear association of squirrel predispersal cone predation (total number of cones taken) and the number of cones initially produced between each forest type for each year. We then calculated t-values to determine whether the correlation for each forest type was different from zero. Second, the number of active middens and fresh cone detections were summed and their proportions calculated for each forest type. We used a χ^2-test to determine if the relative proportion of detections that were residential (middens) and transient (fresh cones) were affected by forest type. Third, we used a two-tailed

independent samples t-test to determine whether the two forest types differed in population mean predispersal cone predation (percentage of total cones lost all years) by squirrels. Cone predation was square root transformed to meet assumptions of normality. Fourth, we calculated the coefficient of variation (%) for predispersal cone predation based on the annual means of each forest type to see if variation in predation changed with forest type.

Forest conditions: an ecosystem comparison

We compared forest conditions between the two ecosystems by using a MANOVA test to confirm if observed sharp *P. albicaulis* declines in the NDE were reflected in greater population mean vectors for mortality, blister rust infection, and rust-induced crown kill (mean % by site). Crown kill was natural log-transformed to meet assumptions of normality. One-tailed independent samples t-tests were used to determine whether absolute and proportional *P. albicaulis* BAs were lower and population mean cone predation higher in NDE forests.

Results

T. hudsonicus habitat use: site-level comparisons

The parameters and associated site-level values used in the squirrel habitat selection analysis are reported in Table 1. Total BA received the most support from the data as an important variable for squirrel habitat selection, with an average Akaike weight 2 times greater than the variables *P. albicaulis* cone-bearing trees and *P. albicaulis* tree mortality (Table 2). Indeed, all six general habitat variables ranked higher than either of the specific *P. albicaulis* habitat variables. Even though the two *P. albicaulis* variables ranked lowest in habitat-selection modeling, squirrel predispersal cone predation proved sensitive to changes in *P. albicaulis* relative abundance at the site level. Predispersal cone predation decreased in a linear fashion with increasing *P. albicaulis* relative abundance across the 20 research sites (Fig. 1). Furthermore, higher squirrel residency was associated with a higher proportion of the cone crop taken by squirrels. The proportion of total squirrel detections comprising active middens was positively and significantly correlated with predispersal cone predation at the site level ($r = 0.652$, $P < 0.05$).

T. hudsonicus habitat use: forest type comparisons

The two forest types were significantly different in population mean vectors for forest structure, composition, and site slope (MANOVA Wilks' λ $F_{5,14} = 7.794$, $P = 0.001$).

Table 2 Relative importance of eight predictor variables in estimating *T. hudsonicus* habitat selection (number of active middens ha^{-1}) in 20 Rocky Mountain, USA subalpine forest sites

Rank	Variable	Average Akaike weight[a]
1	Basal area (m^2 ha^{-1})	0.35353
2	Site index (elevation × latitude)	0.29099
3	Tree diversity (Simpson's index)	0.28374
4	Canopy cover (%)	0.28153
5	Canopy height (m)	0.20702
6	Site slope (°)	0.18713
7	*P. albicaulis* cone trees (no. ha^{-1})	0.18359
8	*P. albicaulis* mortality (%)	0.17751

All possible combinations of the variables ($2^8 = 256$ models) were used in maximum likelihood analyses, with Akaike's information criterion corrected for small sample sizes to weight the relative support for each model

[a] Relative importance of predictor variables was estimated by summing the Akaike weights across all the models in the set where a variable occurred, dividing by the number of models it occurred in, and multiplying by 100
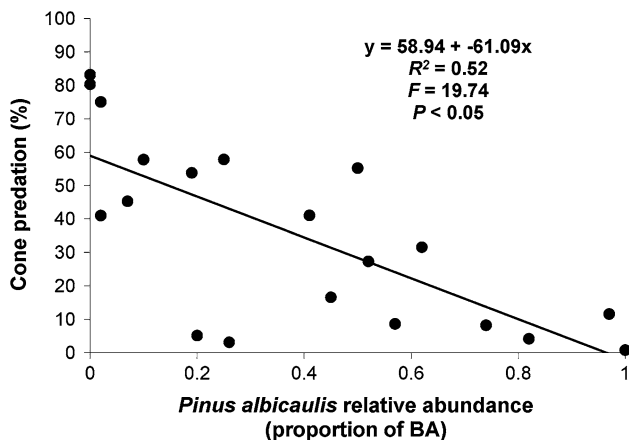

Fig. 1 Simple linear regression analysis of the relationship between *Tamiasciurus hudsonicus* mean predispersal cone predation (percentage of initial cone crop lost) and the relative abundance of *Pinus albicaulis* at 20 subalpine forest sites in the Rocky Mountains, USA, 2004–2006. *BA* Basal area

However, univariate test results showed that the two forest types were not different in population mean values for forest structure and topography, but were different in composition (Table 3).

Squirrel habitat use was strongly influenced by forest type. In mixed conifer forests, squirrels responded to increased cone production by harvesting more cones, and the correlation between the number of cones taken by squirrels and the number of cones initially produced was positive (Fig. 2) and significantly different from zero ($t = 3.29$, df = 21, $P < 0.01$). Spatio-temporal fluctuations in squirrel density could explain the weak relationship evidenced in

some of the mixed forest stands, however. No such relationship existed in *P. albicaulis* forests where the correlation between the number of cones produced and those harvested did not differ from zero ($t = 0.14$, df = 9, $P > 0.05$; Fig. 2).

The relative proportion of *T. hudsonicus* detections that were residential (middens) and transient (fresh cones) were significantly different between forest types ($\chi^2 = 6.72$, df = 1, $n = 126$ total detections, $P = 0.01$), with the mixed conifer type having a resident to transient ratio nearly 3 times greater than the *P. albicaulis* type (Table 4). Moreover, higher residency resulted in higher mean predispersal cone predation in mixed conifer forests (two-tailed *t*-test $t_{18} = 3.248$, $P = 0.004$; Table 4). Higher predispersal cone predation in mixed conifer forests was also associated with lower year-to-year variation in predation. The coefficient of variation for cone predation over the 3 years of the study was 6.5 times higher in the *P. albicaulis* type than in the mixed conifer type (Table 4).

Forest conditions: an ecosystem comparison

We assessed differences in forest health conditions between ecosystems by documenting mortality, blister rust infection, and crown kill of 4,496 *P. albicaulis* trees (NDE = 2 404, GYE = 2 092) at 18 research sites over a 3-year period (Fig. 3). Population mean vectors for these three parameters differed between ecosystems (MANOVA Wilks' λ $F_{3,14} = 9.806$, $P = 0.001$), with pair-wise comparisons confirming greater mortality ($F_{1,16} = 12.663$, $P = 0.003$), infection ($F_{1,16} = 10.403$, $P = 0.005$), and crown kill ($F_{1,16} = 14.633$, $P = 0.001$) in NDE forests (Fig. 3). The poorer health conditions in NDE forests were associated with significantly fewer live *P. albicaulis*. There was on average 7.5 times greater BA and 2.7 times greater relative abundance of *P. albicaulis* in GYE than NDE forests (Table 5). Moreover, the fewer live *P. albicaulis* trees in the NDE experienced greater mean predispersal cone predation, more than 4.3 times higher, than GYE trees (Table 5).
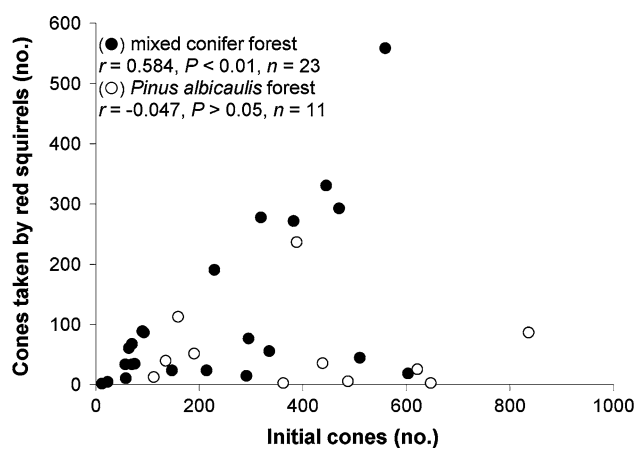
Discussion

The results of our study support the hypothesis that *T. hudsonicus* does not have a strong habitat preference for *P. albicaulis*, but rather uses the pine opportunistically, and is therefore relatively unaffected by declining *P. albicaulis* populations. Mean predispersal cone predation decreased linearly with increasing *P. albicaulis* relative abundance (Fig. 1), indicating that as the pine becomes a more dominant stand component, conditions become less hospitable for squirrels and proportionally fewer cones are depredated.

Table 3 Forest parameter means (±SE) and ANOVA results for subalpine forest sites classified by forest type—Rocky Mountains 2004–2006
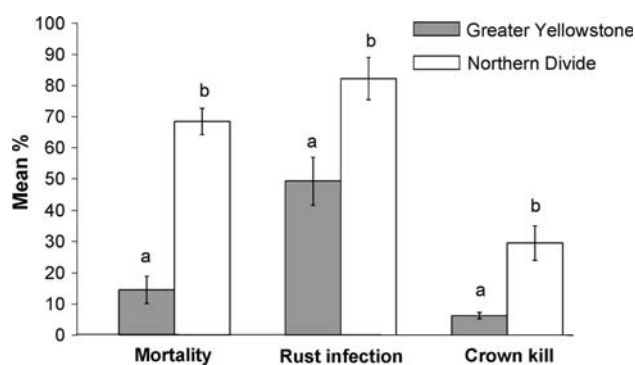
Forest parameter	Forest type		ANOVA results		
	Pinus albicaulis	Mixed conifer	*df*	*F*	*P*
Total basal area (m^2 ha^{-1})	21.9 (3.43)	23.1 (4.18)	1, 18	0.036	0.851
Canopy cover[a] (%)	49.6 (5.9)	59.1 (7.2)	1, 18	0.234	0.635
Canopy height[a] (m)	11.7 (0.9)	14.6 (1.7)	1, 18	0.901	0.355
Site slope (°)	17.9 (2.02)	17.5 (2.11)	1, 18	0.023	0.882
P. albicaulis relative abundance (% BA)	75.0 (7.15)	19.0 (4.88)	1, 18	43.667	<0.001

Forest type defined by whether *P. albicaulis* comprised > 50% of total basal area; sites were classified as mixed conifer if condition was not met

[a] Canopy cover and height were natural-log transformed for ANOVA, with untransformed means reported

Fig. 2 Correlation between *T. hudsonicus* predispersal cone predation and *P. albicaulis* cone production in two forest types in the Rocky Mountains 2004-2006

Fig. 3 *P. albicaulis* forest health attributes (mean ± SE) in two ecosystems in the Rocky Mountains, 2004-2006. *Different lowercase letters* indicate significant differences (ANOVA, *P* < 0.05) between ecosystems

Similarly, squirrel habitat use was greater in forests with lower *P. albicaulis* relative abundance as evidenced by higher squirrel residence, greater mean predispersal cone predation, and lower annual variation in predation in mixed conifer forests (Table 4). Cone predation also significantly increased with increasing *P. albicaulis* cone production in mixed conifer forests, but showed no response to increasing cone availability in *P. albicaulis* forests (Fig. 2). These

relationships show that squirrels thrive in mixed conifer forests that include *P. albicaulis* and vigorously harvest the pine's high energy cones. Thus, as *P. albicaulis* abundance diminishes in mixed conifer forests the proportion of the total cone crop taken by squirrels increases sharply, leaving few seeds available for avian dispersal.

Our results corroborate those from previous studies concluding that the persistence of *T. hudsonicus* populations within coniferous forests requires conditions that produce

Table 4 *T. hudsonicus* habitat use (resident vs. transient) at 20 subalpine forest sites classified by forest type—Rocky Mountains, 2004–2006

Forest type	Proportion of total squirrel activity by detection category[a]		Predispersal cone predation (percentage of *P. albicaulis* cones taken by squirrels)	
	Active middens (resident)	Fresh cone debris (transient)	Mean (SE)[b]	Coefficient of variation[c]
Pinus albicaulis (*n* = 7)	0.19	0.81	13.2 (4.4)	85.5
Mixed conifer (*n* = 13)	0.41	0.59	47.3 (7.2)	13.0

Forest type defined by whether *P. albicaulis* comprised >50% of total basal area; sites were classified as mixed conifer if condition was not met

[a] Relative proportions of squirrel activity differed by forest type (χ^2-test, *P* < 0.05); an active midden equates to residency status, fresh cone debris does not

[b] Predation was significantly higher in mixed conifer type (two-tailed *t* test, *P* < 0.05)

[c] Calculated based on annual predation means by forest type

Table 5 Ecosystem comparison of *P. albicaulis* variable means (±SE) and results of one-tailed independent samples *t* test for research sites—Rocky Mountains, 2004–2006

Variable	Ecosystem		Two-sample *t*-test results		
	Northern Divide[a]	Greater Yellowstone[b]	df	t	P
Basal area (m^2 ha^{-1})	1.9 (2.04)	14.5 (2.44)	16	2.747	0.007
Relative abundance (% BA)	19.4 (7.32)	53.6 (10.51)	16	5.020	<0.001
Cone predation (%)	56.4 (5.63)	13.1 (6.61)	16	5.483	<0.001

Values are for *P. albicaulis* trees only

[a] Northern Divide sites (*n* = 10) were in northwestern Montana

[b] Greater Yellowstone sites (*n* = 8) were in southwestern Montana and northwestern Wyoming

enough seeds for them to survive long winters while providing cover and escape from predators (Table 2; Smith 1981; Rush and Reeder 1978). Furthermore, our finding of decreasing cone predation with increasing *P. albicaulis* relative abundance (Fig. 1) lends strong support to the notion that squirrels select the tree species with the highest cone energy content (Smith 1970), but require the more diverse, and hence more stable, food supply of mixed species forests for residential status (Reinhart and Mattson 1990). Interestingly, comparisons showed that the two forest types differed only in the dependability of an annual cone crop (Table 3). Thus the disparity in habitat suitability between forest types appears to be due to a lack of alternative conifer seed sources and the uncertainty associated with highly variable annual cone production in *P. albicaulis*-dominant forests. In this study, for example, the average year-to-year difference in *P. albicaulis* cone production within sites was 87% relative to mean cone production (i.e., the absolute difference between 2 years, divided by the mean of the 2 years, multiplied by 100). Hence forests with multiple conifer species should have a lower likelihood of total cone crop failure compared to *P. albicaulis*-dominant forests.

These findings have important implications for the persistence of *P. albicaulis* in the face of multiple health threats. Previous researchers have suggested that historically (i.e., pre-blister rust invasion), *P. albicaulis*-dominant forests were likely the primary seed sources contributing to regeneration because of lower cone predation (e.g., Hutchins and Lanner 1982). Our results indicate that squirrels appear unaffected by declining *P. albicaulis*, remaining abundant in mixed conifer forests but unable to thrive in *P. albicaulis*-dominant stands. Predation influences on *P. albicaulis* regeneration potential may be accentuated at a landscape scale because disproportionate tree mortality is converting some Rocky Mountain *P. albicaulis* forests to late-successional mixed-conifer forests. When taken across a broad landscape such as the NDE, the number of seeds available for avian dispersal, and thus natural regeneration, will also decrease. Thus, a lower proportion of the historical range of *P. albicaulis* will likely contribute to population

recruitment because of anthropogenic factors that have changed habitat conditions and altered interactions between the squirrel and pine.

Management implications

Both modeling and field studies provide evidence that without fire, *A. lasiocarpa* will eventually replace *P. albicaulis* in many Rocky Mountain ecosystems, and that replacement will be accelerated by mortality from blister rust and pine beetle (Keane 2001). Our results show that *T. hudsonicus* can greatly diminish cone crops where *P. albicaulis* tree damage and mortality are severe. In the Northern Rocky Mountains NDE, where mortality is high and *P. albicaulis* abundance low, direct management intervention will likely be needed to augment severely diminished potential for natural regeneration. The most comprehensive treatments would be required in the mixed conifer forest type where *P. albicaulis* mortality, rust infection, and successional replacement are the most dramatic. Here, allowing some natural lightning-ignited fires to burn, and applying silvicultural cuttings that remove encroaching shade-tolerant *A. lasiocarpa* and *P. engelmannii*—followed by planting rust-resistant seedlings—may be the only way to maintain *P. albicaulis* in the landscape (Schoettle 2004; Mahalovich et al. 2006).

Conversely, reports from other researchers show that blister rust has not yet caused extensive damage in the *P. albicaulis* forest type (e.g., Keane 2001). Given that squirrel predation was also the lowest there, these forests can serve as seed sources for natural regeneration by nutcrackers and thus require less intensive management (e.g., allowing for wildland fire only).

Different complications arise in the management of *P. albicaulis* in the Central Rocky Mountains–GYE. The seeds of *P. albicaulis* are an important source of nutrition for grizzly bears in this region, where the bear has just been delisted as a threatened and endangered species. Bears obtain seeds by raiding squirrel middens (Mattson and Reinhart 1997), and our study documents that middens are

significantly more likely to occur in the mixed conifer forest type. Our surveys in the GYE show that *P. albicaulis* mortality is low (15%), but that current rust infection levels of nearly 50% portend future increases in mortality. *P. albicaulis* declines to current levels in the NDE would have serious ramifications for the bear's status in the future. Because grizzly bears rely on squirrels to access *P. albicaulis* seeds, converting stands to *P. albicaulis* type, as outlined above for the NDE, would not be a prudent option. Planting rust-resistant seedlings prior to severe decline, and allowing high-elevation fires to burn when possible, are the most feasible options in the GYE.

Here we demonstrate that factors causing disproportionate declines in a conifer species without corresponding effects on a primary seed predator can further accelerate the tree's decline. The specific relationships between producer and consumer are dependent on conditions and processes occurring at both site and ecosystem levels. Management treatments proposed to comprehensively address these relationships must account for specific conditions at each level.

References

Arno SF (1980) Forest fire history in the northern Rockies. J For 78:460–465

Arno SF, Hoff RJ (1990) *Pinus albicaulis* Engelm. Whitebark Pine. In: Burns RM, Honkala BH (eds) Silvics of North America, vol I. Conifers: agriculture handbook 654. US Department of Agriculture, Washington, DC, pp 268–279

Axelrod DI (1986) Cenozoic history of some western American pines. Ann Miss Bot Gard 73:565–641

Baker RG (1990) Late quaternary history of whitebark pine in the Rocky Mountains. In: Schmidt WC, McDonald KJ (eds) Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General technical report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, pp 40–48

Benkman CW, Balda RP, Smith CC (1984) Adaptations for seed dispersal and the compromises due to seed predation in limber pine. Ecology 65:632–642

Brown JK, Arno SF, Barrett SW, Menakis JP (1994) Comparing the prescribed fire program with presettlement fires in the Selway-Bitterroot Wilderness. Int J Wild Fire 4:157–168

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information theoretic approach, 2nd edn. Springer, New York

Burnham KP, Anderson DR, Laake JL (1980) Estimation of density from line transect sampling of biological populations. Wild Monogr 72:1–202

Callaway RM (1998) Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. Oikos 82:561–573

Christian CE (2001) Consequences of a biological invasion reveal the importance of mutualism for plant communities. Nature 413:635–639

Cordeiro NJ, Howe HF (2003) Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proc Natl Acad Sci 100:14052–14056

Côté M, Ferron J (2001) Short-term use of different residual structures by three sciurid species in a clear-cut boreal landscape. Can J For Res 31:1805–1815

Eberhardt LL (1978) Transect methods for population studies. J Wild Manage 42:1–31

Elliott PF (1974) Evolutionary responses of plants to seed-eaters: pine squirrel predation on lodgepole pine. Evolution 28:221–231

Elliott PF (1988) Foraging behavior of a central-place forager: field tests of theoretical predictions. Am Nat 331:159–174

Ellison AE, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486

Farnes PE (1990) SNOTEL and snow course data describing the hydrology of whitebark pine ecosystems. In: Schmidt WC, McDonald KJ (eds) Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General technical report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, pp 302–304

Finley RB Jr (1969) Cone caches and middens of *Tamiasciurus* in the Rocky Mountain region. Misc Publ Univ Kans Mus Nat Hist 51:233–273

Fisher JT, Bradbury SM (2006) Understory protection harvest expedites recolonisation of boreal forest stands by North American red squirrels. For Ecol Manage 234:40–47

Gurnell J (1984) Home range, territoriality, caching behaviour and food supply of the red squirrel (*Tamiasciurus hudsonicus fremonti*) in a subalpine lodgepole pine forest. Anim Behav 32:1119–1131

Hafner DJ (1984) Evolutionary relationships of the nearctic Sciuridae. In: Murie JO, Michener GR (eds) The biology of ground dwelling squirrels. University of Nebraska Press, Lincoln, pp 3–23

Hoff RJ (1992) How to recognize blister rust infection on whitebark pine. For Serv Res Note INT-RN-406

Hoff RJ, Bingham RT, McDonald GI (1980) Relative blister rust resistance of white pines. Eur J For Pathol 10:307–316

Hutchins HE, Lanner RM (1982) The central role of Clark's nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201

Insightful (2005) S-Plus 7.0 for Windows. Insightful. Seattle

Keane RE (2001) Successional dynamics: modeling an anthropogenic threat. In: Tomback DF, Arno SF, Keane RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, pp 159–192

Keane RE, Morgan P, Menakis JP (1994) Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, USA. Northwest Sci 68:213–229

Kendall KC, Keane RE (2001) Whitebark pine decline: infection, mortality, and population trends. In: Tomback DF, Arno SF, Keane

RE (eds) Whitebark pine communities: ecology and restoration. Island Press, Washington, DC, pp 221–242

Kurtén B, Anderson E (1980) Pleistocene mammals of North America. Columbia University Press, New York

Larsen KW, Boutin S (1994) Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75:223–241

Logan JA, Powell JA (2001) Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). Am Entomol 47:160–172

Lurz PWW, Garson PJ, Rushton SP (1995) The ecology of squirrels in spruce dominated plantations: implications for forest management. For Ecol Manage 79:79–90

Mahalovich MF, Burr KE, Foushee DL (2006) Whitebark pine germination, rust resistance, and cold hardiness among seed sources in the Inland Northwest: planting strategies for restoration. For Serv Proc RMRS-P-43

Mattson DJ, Reinhart DP (1997) Excavation of red squirrel middens by grizzly bears in the whitebark pine zone. J Appl Ecol 34:926–940

Mattson DJ, Blanchard BM, Knight RR (1991) Food habits of Yellowstone grizzly bears, 1977–1987. Can J Zool 69:1619–1629

McCaughey WW, Schmidt WC (1990) Autecology of whitebark pine. In: Schmidt WC, McDonald KJ (eds) Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General technical report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, pp 85–96

McKinney ST, Tomback DF (2007) The influence of white pine blister rust on seed dispersal in whitebark pine. Can J For Res 37:1044–1057

McKinney ST, Fiedler CE, Tomback DF (2009) Invasive pathogen threatens bird-pine mutualism: implications for sustaining a high-elevation ecosystem. Ecol Appl 19:597–607

Meehan HJ, McConkey KR, Drake DR (2002) Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. J Biogr 29:695–712

Microsoft (2003) Microsoft Office Excel 2003: Microsoft. Redmond

Molinari A, Wauters LA, Airoldi G, Cerinotti F, Martinoli A, Tosi G (2006) Cone selection by Eurasian red squirrels in mixed conifer forests in the Italian Alps. Acta Oecol 30:1–10

Murray MP, Bunting SC, Morgan P (2000) Landscape trends (1753–1993) of whitebark pine (Pinus albicaulis) forests in the West Big Hole Range of Idaho/Montana, USA. Arct Antarct Alp Res 32:412–418

Reinhart DP, Mattson DJ (1990) Red squirrels in the whitebark zone. In Schmidt WC, McDonald KJ (eds) Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. General technical report INT-270. U.S. Department of Agriculture, Rocky Mountain Research Station, Ogden, Utah, pp 256–263

Rothwell R (1979) Nest sites of red squirrels (*Tamiasciurus hudsonicus*) in the Laramie Range of southeastern Wyoming. J Mammal 60:404–405

Rusch DA, Reeder WG (1978) Population ecology of Alberta red squirrels. Ecology 59:400–420

Schoettle AW (2004) Developing proactive management options to sustain bristlecone and limber pine ecosystems in the presence of a non-native pathogen. In: Shepperd WD, Eskew LG (eds) Silviculture in Special Places: Proceeding of the national silviculture workshop. Proceedings RMRS-P-34, U.S. Department of Agriculture, Rocky Mountain Research Station, Fort Collins, pp 146–155

Siepielski AM, Benkman CW (2007) Selection by a predispersal seed predator constrains the evolution of avian seed dispersal in pines. Funct Ecol 21:611–618

Smith CC (1968) The adaptive nature of social organization in the genus of tree squirrel *Tamiasciurus*. Ecol Monogr 38:30–63

Smith CC (1970) The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol Monogr 40:349–371

Smith CC (1981) The indivisible niche of *Tamiasciurus*: an example of nonpartitioning of resources. Ecol Monogr 51:343–363

Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. Freeman, New York

SPSS (1999) SPSS 10.0 for Windows. SPSS. Chicago

Steele MA (1998) *Tamiasciurus hudsonicus*. Mammal Spec 586:1–9

Steele MA, Wauters LA, Larsen KW (2005) Selection, predation, and dispersal of seeds by tree squirrels in temperate and boreal forests: are tree squirrels keystone granivores? In: Forget PM, Lambert JE, Hulme PE, Vander Wall SB (eds) Seed fate: predation, dispersal and seedling establishment. CABI, Wallingford, pp 205–221

Tomback DF (1982) Dispersal of whitebark pine seeds by Clark's nutcracker: A mutualism hypothesis. J Anim Ecol 51:451–467

Tomback DF (1998) Clark's nutcracker (*Nucifraga columbiana*). In: Poole A, Gill F (eds) The birds of North America, no. 331. The Birds of North America, Philadelphia

University of Florida Forest Extension Service—UFFES (1998) Forest terminology for multiple-use management. SS-FOR-11

Willis KJ, Bennett KD, Birks JB (1998) The late Quaternary dynamics of pines in Europe. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 107–121