

Resiliency in masting systems: Do evolved seed escape strategies benefit an endangered pine?

VERNON S. PETERS,† MATTHEW S. GELDERMAN,¹ AND DARCY R. VISSCHER

Department of Biology, The King's University, 9125 50th Street, Edmonton, Alberta T6B 2H3 Canada

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Abstract. Satiation of predispersal seed predators by mast years has been demonstrated in many intact ecosystems. When disease causes mortality of seed-bearing trees in an ecosystem, the abundance of food sources may alter seed predator behavior and abundance, and the ecosystem services derived from mutualistic seed dispersers. We used the endangered limber pine (*Pinus flexilis*) to examine whether the benefits of interannual variation in cone production vary depending on the severity of white pine blister rust (*Cronartium ribicola*) infections, the abundance of seed predator populations, and stand characteristics. We compared infection level, cone production, cone predation, and abundance of red squirrels (*Tamiasciurus hudsonicus*) in 17 stands over two mast years and two nonmast years. Stands were selected from a southern and northern ecosystem within Alberta's montane ecoregion, with varying forest composition and history of blister rust infection. Considerable variability in interannual cone production, and proportionately greater cone escape (those remaining in stands) in the 2010 mast year led to 10 times greater cone escape overall in the mast year than in nonmast years. Model selection using Akaike's information criterion (AIC) suggests that both cone escape and proportion cone escape from seed predators depended primarily on temporal variability in cone production among mast vs. nonmast years, basal area of canopy trees within stands, squirrel abundance, and ecosystem differences. Several two-way and three-way interactions between masting, ecosystems, and predator abundance were selected by AIC for inclusion into the best model of the a priori candidate set for both the cone escape model and proportion cone escape model. Our study suggests that masting confers temporal resiliency in seed escape in declining limber pine ecosystems, even under varying disease and seed predator threats. These findings also suggest that evolved seed escape strategies may be resilient to a variety of ecological conditions, including low reproductive capacity. Nonetheless, proximate ecological conditions may determine the fate of declining species, as predator behavior differed between ecosystems, and greater net cone escape in favorable stands may be necessary to attract mutualistic seed dispersers.

Key words: Alberta; cones; disease; dispersal; escape; limber pine; masting; nutcrackers; predation; resiliency; squirrels.

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¹ Present address: Forestry Division, Department of Agriculture and Forestry, Bag 900-39, 9621 96th Avenue, Peace River, Alberta T8S 1T4 Canada.

† **E-mail:** vern.peters@kingsu.ca

INTRODUCTION

Reproduction is a risky business, even in plants. While many tree species have evolved mast

seeding as an effective strategy of escaping seed predators (Janzen 1971, Silvertown 1980), masting does not guarantee greater regeneration because of ecological interactions including

seedling predation (Ida and Nakagoshi 1996, Sato 2000), unsuitable seedbeds (Peters et al. 2005), competition for resources (Houle 1995, Negi et al. 1996), and insufficient seed dispersal mutualists (Herrera 1985, McKinney et al. 2009). Masting has been linked to dispersal syndromes, and tree species engaged in mutualistic associations with vertebrates may exhibit lower interannual variability in seed production than species dispersed by abiotic means (Herrera et al. 1998). When other community-level interactions, such as disease, cause the rapid decline of a species and directly diminish the reproductive capacity of infected survivors, even minor variations in interannual seed production may increase opportunities for dispersal if proportionately more seed remains after seed predation.

The rapid decline of limber pine (*Pinus flexilis*), James, and other five-needled pines in North America (Tomback 2011) provides an ideal system for studying the ecological interactions between masting, seed predators, disease, habitat quality, and mutualists. Limber pine, a long-lived foundation species, occurs in conifer-dominated xeric montane or subalpine ecosystems (Schoettle and Rochelle 2000) where most species mast and show high degrees of synchrony and periodicity (Koenig and Knops 1998). High seed years in limber pine have been reported to occur intermittently every two to four years (ASRD and ACA 2007); however, no scientific studies have investigated their geographic synchrony or the degree of cone failure following large crops. A long-term coevolution has occurred between conifer cone traits and red squirrels (*Tamiasciurus hudsonicus*), Erxleben (Benkman 1995, Wheatley 2007). Limber pine seed dispersal adaptations, which include large seed size and gravity-assisted dispersal, represent a compromise between avoiding red squirrels and facilitating dispersal by limber pine's primary seed disperser, Clark's nutcracker (*Nucifraga columbiana*), Wilson (Linhart and Tomback 1985, Siepielski and Benkman 2007). Cone predation rates have been reported in a single limber pine population when squirrels are present (Benkman et al. 1984) and when both squirrels and nutcrackers are present (Lanner and Vander Wall 1980); however, no study on limber pine has quantified cone escape (those remaining in stands) among populations or relative to temporal variation in cone production.

Limber pine that has declined rapidly throughout its range due to high mortality caused by white

pine blister rust (WPBR; *Cronartium ribicola*), Fisch, mountain pine beetle (*Dendroctonus ponderosae*), Hopkins, and limited regeneration opportunities (Tomback 2011). As a result, limber pine is listed as endangered in Alberta, Canada, which is the northern edge of its range (AESRD 2015). Seed production in white pines is directly reduced by WPBR in two multiplicative ways: (1) Initially, WPBR kills upper branches where most of the cones are produced (McCaughy 1994) and (2) mortality of cone-bearing trees in severe infestations reduces the number of trees and the cumulative cone production per ha (10,000 m²) below thresholds required to attract dispersal mutualists (McKinney et al. 2009). Since mast years are required to attract Clark's nutcracker in healthy whitebark pine (*Pinus albicaulis*), Engelm., ecosystems (Tomback et al. 2001, McKinney et al. 2009), WPBR-induced declines in seed production, particularly in mast years, may disrupt the balance between seed predators and mutualists.

Threats to limber pine cause habitat degradation and forest fragmentation, which have been observed to disrupt disperser mutualisms in other tree species (Cordeiro and Howe 2003); however, the impacts of such habitat changes on the temporal dynamics of seed predator populations and seed escape are not well known. A few studies on other conifer species have investigated the effect of habitat alteration on seed escape from red squirrels, but their focus has been on spatial differences in disease-altered landscapes (McKinney and Fiedler 2009) and spatial and temporal differences in partial retention harvesting systems (Peters et al. 2003). Since most flowering species exhibit supra-annual variation in seed production (Koenig and Knops 2000), temporal differences in seed escape may limit regeneration opportunities to individual years. The evolutionary trade-offs that may have led to seed crops that satiate seed predators without overwhelming dispersers (Herrera et al. 1998) may break down in declining species. This may occur when alternate food sources sustain seed predator populations, but seed predators switch to declining species when they mast (i.e., type III functional feeding response). In such systems, seed predators may consume proportionately similar amounts of the seed crop in both low and high seed years.

We investigated the importance of interannual variation in cone production to seed dispersal and

seed predator escape in stands with varying WPBR infection levels from two ecosystems, including the northern-most populations of limber pine in North America (ASRD and ACA 2007). These northern populations warrant focused study because the nature and strength of interspecific interactions and differences in community composition and selection pressures have been known to engender greater variation in demographic characteristics in a variety of peripheral ecosystems (Tomback et al. 2005b). Our objective was twofold: (1) to determine which factors predict the number of cones remaining following predation and available for mutualistic seed dispersers (i.e., cone escape), thereby addressing proximate seed limitation issues for an endangered species, and (2) to test which factors predict seed predator satiation (proportion of cones remaining after predation), thereby addressing ultimate questions of masting advantages. We addressed these objectives by determining whether supra-annual variability in cone production in an endangered species assists in cone escape from seed predators (temporal escape hypothesis), whether cone escape depends on the severity of infection among stands (seed limitation–spatial escape hypothesis), and how habitat density and composition determine cone escape (habitat quality hypothesis). We hypothesized that, in stands with an extended history of WPBR (southern ecosystem, approximately 50 yr of WPBR presence; Gatreau 1963), cone escape is lower due to the negative effects of disease on cone production. We further hypothesized that the proportion of cones escaping predation will increase with WPBR infection levels because reduced habitat quality and cone availability will support fewer squirrels. These hypotheses suggest that the benefits of supra-annual variation in seed production are conserved, even when plant populations decline and differences in the availability of seed for dispersers relative to infection level are reduced, provided there are concurrent declines in habitat quality that affect the abundance of the principal seed predator.

METHODS

Stand selection and experimental design

Limber pine is a long-lived foundation species in xeric montane or subalpine ecosystems

(Schoettle and Rochelle 2000). Our study compared stands from two distinct geographical regions of the Montane Ecoregion in the Rocky Mountains of Alberta, Canada. Our southern ecosystem (49.60° N, 114.20° W) extended east of the Rockies to include the Porcupine Hills formation, and contained stands of either limber pine or limber pine–Douglas fir (*Pseudotsuga menziesii*; Mirb), Franco, mixtures that occurred on the tops of ridges. Our northern ecosystem, approximately 400 km away, included the northern-most populations of limber pine in North America (52.10° N, 116.40° W; Appendix S1) proximal to Kootenay Plains and Abraham Lake. There, limber pine occurred in pure stands or in association with white spruce (*Picea glauca*; Moench), Voss, and/or lodgepole pine (*Pinus contorta*; Douglas), Loudon, on plains or forests at the base of larger mountains. Stands ranged in elevation from 1300 to 1504 m in the south and from 1391 to 1447 m in the north. White pine blister rust surveys in each area in 2003 (according to methods in Smith et al. 2013) indicated 1% live tree infestation in the northern ecosystem ($n = 3$ study stands sampled) and 38% infection in the southern ecosystem ($n = 3$ study stands; a subsample of stands from Smith et al. 2013). Further characterization in 2008 and 2009 revealed that the southern ecosystem had 2.9 times as much dead limber pine basal area (Appendix S1), and more WPBR cankers on dead trees (4.0 vs. 0 cankers; Smith et al. 2013), than the northern ecosystem.

We selected study stands that varied in forest composition, disease, and squirrel density. We sampled eight and nine forest stands in the southern and northern ecosystems, respectively. Most of our sampling was driven by stand-level considerations (i.e., independent populations of squirrels between stands) and has attributes that were both readily characterized at the stand level, and highly variable between stands (disease, forest composition [Appendix S1], and squirrel density). To ensure that stands were large enough to support several squirrels, we sampled only stands >5 ha. This allowed us to test whether seed predation was related to squirrel density, rather than just presence or absence of squirrels. Stands were separated by 3–15 km in the southern ecosystem with unsuitable intervening habitat for red squirrels (cereal crop or pasture), and stands were separated by 300 m to

10 km in the northern ecosystem, with adjacent forest habitat for squirrels. Dispersal barriers such as cliff ridges and large mountain rivers were assumed to reduce squirrel dispersal in the three stands situated <2 km apart in the northern ecosystem. As a rough estimate of independence between squirrel populations among stands, the variability in midden densities among close stands was compared with the densities observed in further stands. In each year, squirrel populations showed more variation in density among proximal stands than among distant stands, suggesting squirrel densities were linked to local, stand-level attributes. Owing to the different physical and forest structural attributes of the two ecosystems, squirrel populations were more isolated and potentially subject to local extinction events in the southern ecosystem.

Stand characterization

A central transect was laid out within each stand. Commencing 50 m from the forest edge, four plots were located along the transect at randomly selected distances of 80–120 m between adjacent plots. Each plot center was permanently marked and its Universal Transverse Mercator coordinates were marked with a handheld Global Positioning System unit (± 3 m, Garmin Etrex Legend). At each plot, we recorded slope aspect with a compass, and slope grade (%) with a clinometer (Appendix S1). At three sampling points situated 15 m from each plot center (chosen randomly from the four cardinal directions), a basal area prism, a standard device used by foresters to estimate basal area/hectare (a basal area factor two prism was selected, given the open stand conditions), was used to characterize the forest cover. The number of live and dead individuals of each tree species was recorded. The basal area of standing dead stems in each stand (Appendix S1) was used as a proxy to detailed WPBR infection survey data that were available for three stands in each of our ecosystems (Smith et al. 2013). The causes of mortality were quantified in this subsample of stands according to the methods in Tomback et al. (2005a).

Cone production and predation

Limber pine cone surveys were initiated in 2007 (two stands in each ecosystem, $n = 4$), expanded in 2008 to include additional stands (five and six

stands in total in the southern and northern ecosystems, respectively, $n = 11$), and further expanded in 2009 and 2010 (eight and nine stands in total in the southern and northern ecosystems, respectively, $n = 17$). In 2007, only 10 live trees per stand were selected for cone surveys. Between 2008 and 2010, the 10 trees nearest to each plot center ($n = 4$ plots per stand, and thus 40 trees per stand in most cases) that were of cone-bearing size (diameter at breast height >8 cm; dbh = 1.3 m) were selected in each stand for cone counts and tagged. Trees that had lost most of their needles and appeared close to death were not chosen. Thus, cone counts were recorded for a total of 40, 440, 679, and 678 trees for 2007, 2008, 2009, and 2010, respectively. The 2007 data were used only to indicate cone production, while counts from 2008 to 2010 were used in detailed statistical analyses. The height (m) of each sample tree was measured with a clinometer, and the dbh (cm) was measured with a dbh tape.

Ovulate (seed producing) cone counts were recorded annually between June 15 and July 10, a period when all maturing green third-year cones could be distinguished from aborted cones (V. Peters, *personal observation*) and cone caching by squirrels had not commenced. We used the mean number of ovulate cones produced per tree to record the size of cone crop. To compare inter-annual variability of cone production in limber pine to other studies of masting species, we used the commonly accepted coefficient of variation (CV), which provides an index of proportional variability (yearly cone production) independent of the mean (yearly cone production; McArdle and Gaston 1995). Coefficient of variation values were calculated individually for the 11 stands where cone crops were recorded for the full three-year period (2008–2010). A single CV value from these 1320 counts was also calculated for this period. CV values are presented as a percentage ($CV = [\text{standard deviations}/\text{mean}] \times 100$), both for our data and for comparisons with values reported in the literature.

Natural cone opening and seed fall occurred primarily in the last week of August (D. Langor, *personal communication*), but we waited until September 14–21 to complete final cone counts. All remaining cones were open at this time, suggesting no further cone predation would occur. Mature cones may persist for many years on the

branch, so we only counted cones that had one year of leader growth extending beyond the most recent terminal bud scar (Morgan and Bunting 1992). This is readily visible in limber pine, because leaders are stout and terminal bud scars are conspicuous (V. Peters, *personal observation*). Current-year cones were also readily differentiated from old cones by color; new cones were bright brown and retained a greenish hue, which was lost in cones retained for one or more years after maturation. New and old cones on each tree were counted using binoculars (7–10 times zoom). Counts were made from several unobstructed vantage points of each tree's canopy. Like McKinney and Fiedler (2009), we ascribed the difference in cone counts primarily to red squirrel predation, because cones rarely fall without vertebrate clipping, while nutcrackers primarily remove seed while the cone remains attached to the tree (Tomback and Kramer 1980) and we found no evidence of cone removal by other mammal species in eight cone bait stations that we monitored with infrared motion cameras (V. Peters, *unpublished data*). Cone removal by squirrels was interpreted as a complete loss of propagules from the tree, because squirrels are total seed predators and germination of seeds from buried cones does not occur in the midden (V. Peters, *personal observation*). Cones remaining on the tree are a good outcome for the tree, and both attract and are used by the mutualistic seed disperser, the Clark's nutcracker. Since we have no data on nutcrackers, we use "cone escape" henceforth, to refer to and interpret the benefits of these remaining cones.

Red squirrel abundance

We used strip transects that recorded active middens (Mattson and Reinhart 1996) as an index of the abundance of resident squirrels. Call surveys (Rusch and Reeder 1978) were abandoned after our squirrel population census in 2008 because individuals were not heard in many stands despite visuals on squirrels, and the presence of active middens. Active middens were identified by the presence of recently cut cones (green or bright brown), fresh green scales, and tunnels within multi-year accumulations of cone debris, while inactive middens generally had substantial overgrowth, noticeably duller scales, and caved-in tunnels or no evidence of

tunnels. The annual status of middens was recorded in June of the year following the cone crop because recent accumulations of cone debris were most visible at this time. Notably, midden data reflect the survivorship of territory-holding squirrels that survived the winter, rather than a precise estimate of the number of squirrels that actually harvested cones in the fall. Midden data were thus paired with cone removal data from the preceding year's cone crop and the current year's cone removal data to test in which year midden counts best predicted the relationship between squirrel abundance and cone escape. Squirrel density per stand was determined by summing the number of active middens in each strip transect and dividing by the total area sampled (ha) per stand.

Data analysis

We conducted two separate but related analyses. First, to test whether masting confers an adaptive advantage to seed dispersal in disease-altered landscapes, cone escape was selected as a response variable for statistical analyses. Cone density thresholds determine nutcracker foraging attraction (McKinney et al. 2009); consequently, factors that are likely to determine the number of cones produced (disease, ecosystem productivity), and the temporal variability in cone escape (masting and seed predator density) collectively determine cone escape. Secondly, to test whether masting conferred an adaptive advantage to seed predator escape in disease-altered landscapes, the proportion of cones escaping seed predators was selected for analyses. Proportion cone escape is the key response variable related to masting benefit because it alters the reproductive allocation among years.

Model identification

Broadly construed, our models address hypotheses related to issues of seed limitation, seed predation, and habitat quality for an endangered species (Table 1). We looked at our data to help determine which variables and interactions between variables were appropriate for hypothesis tests (Fig. 1). We tested a larger set of specific hypotheses that we identified a priori as possibly altering both the number and proportion of cones escaping seed predators (Table 2). Cone escape and proportion cone escape are used to refer to

Table 1. Hypothesized relationships between cone escape and proportion cone escape in declining limber pine stands.

| Name | Hypothesis | Reason | How hypothesis is tested |
|-----------------|--|--|---|
| Seed limitation | Spatial escape: cones are less available in WPBR ecosystems with high infections | WPBR infections reduce cone production so ecosystems and stands with greater disease provide fewer cones for dispersers | Ecosystem model: stands in N vs. S Disease model: proportion dead limber pine |
| Masting | Temporal escape: masting confers proportionately higher cone escape from predators in mast years | Seed predators are satiated in mast years, and populations are depressed in nonmast years | Masting model: mast vs. nonmast years Predator model: squirrel density in stands |
| Habitat quality | Proportionately higher cone escape occurs in marginal seed predator habitat | WPBR reduces the proportion of limber pine in stands, and total basal area, lowering the density of seed predators supported | Habitat quality model: total basal area in stands |

Notes: The base of the models tested is presented showing only the individual covariates. WPBR, white pine blister rust.

the specific response variables tested in the models in Table 2 and in the description of results.

Model names are based on the independent variable and combination of variables tested in Table 2, which were abbreviated to models A through I. The units for each independent variable are as follows (also listed in Table 3): (A) Ecosystem (ECOS) is a factor (northern and southern); (B) disease is the proportion of limber pine stems that were dead (PDLP) in each stand; (C) habitat quality is an index of total basal area of all tree species (half the total m²/ha; BATO); (D) predator (PRED) is the density of squirrel middens (middens/ha), tested with both the current year's cone/proportion cone escape and with the preceding year's escape (to account for the temporal nature of predation); and (E) masting (MAST) is a dichotomous factor indicating whether or not it was a mast year (0/1). Nonmast years (2008, 2009) were combined in the nonmast variable. In analyses of the number of cones escaping for dispersers, the number of new cones produced (COST) was not modeled as a predictor of cone escape because the two variables are non-orthogonal. In analyses of the proportion of cones escaping seed predators, the number of new cones (COST) was modeled as a predictor variable in model F and models G–I. All individual variables were tested in a global model (G) and series of models testing two- and three-way interactions (H and I).

Statistical analysis

For both analyses, we used a generalized linear model framework to fit our models. As the number and proportion of cones remaining at each

tree within a stand is not statistically independent, we used a mixed-model approach and included stand identity as a random effect via a random intercept in all models (Zuur et al. 2009). Further, we used Akaike's information criterion (AIC) to determine which model was the most parsimonious from our a priori candidate model set (Akaike 1973, Burnham and Anderson 2002). Following the identification of the top candidate model, we inspected model residuals to confirm that errors were homogeneous and independent with respect to model covariates and location. We analyzed the number of limber pine cones that escaped predation using a two-step procedure. First, we compared four competing model forms using a standardized model with respect to independent variables. Using AIC, we compared Poisson, zero-inflated Poisson, negative binomial, and zero-inflated negative binomial model forms (Table 4). Secondly, using the model form identified in the previous step, we compared a series of a priori models based on our hypotheses on the role variables play in determining escape (Table 2).

We then analyzed the proportion of cones that escaped predation with a binomial model. However, before our analysis, we noted that a percentage of trees did not produce cones in a given year (i.e., zero values), and this rate varied among years (44.1%, 34.1%, and 6.0% in 2008, 2009, and 2010, respectively). These trees were excluded from analyses of proportion cones remaining, while trees that produced cones, but had zero cones removed, were included as "true" zeros in analyses of proportions. In visual comparisons of actual cone production and cone

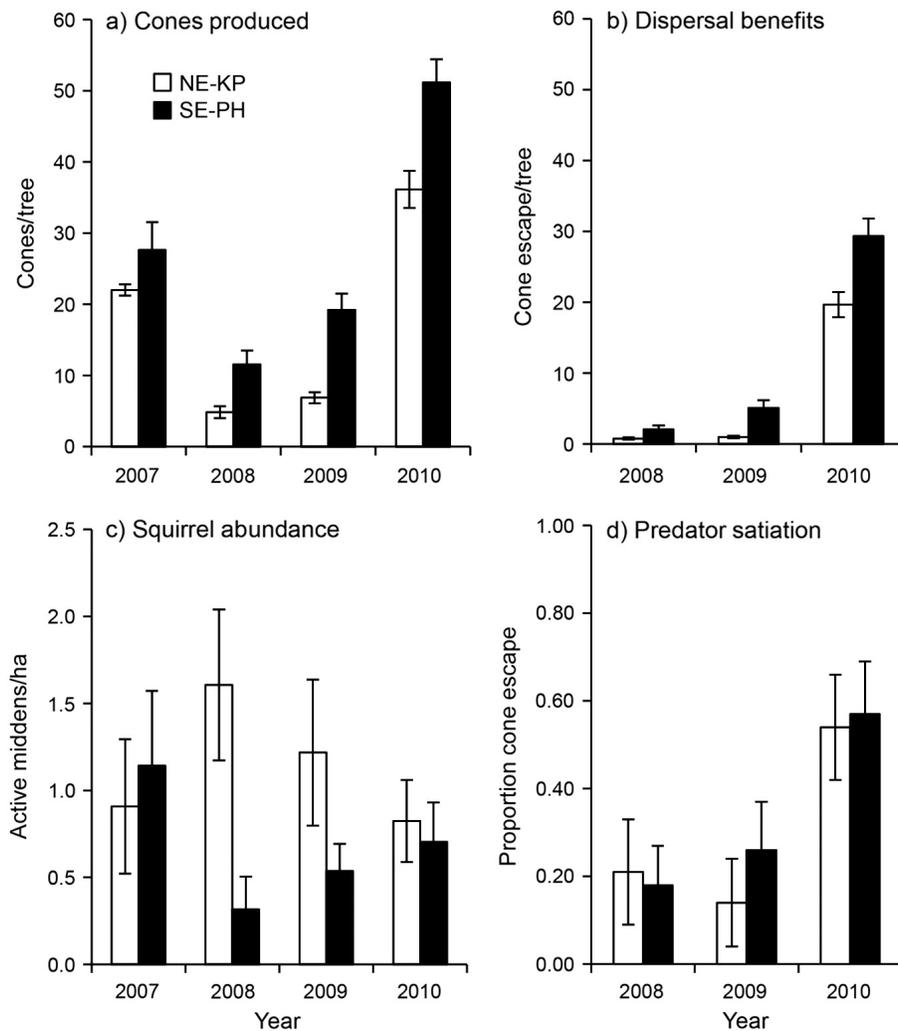


Fig. 1. Annual mean variation in cone production relative to cone escape, predator abundance, and proportion cone escape in the southern and northern limber pine ecosystems (± 1 SE, $n = 5$ and 6 stands, respectively, in 2007–2008, and eight and nine populations, respectively, in 2009–2010). Mast years occurred in 2007 and 2010, while intervening years were classified as nonmast years. Midden counts are paired with the preceding year's cone crop (-1 yr).

escape, trees that did not produce cones in a given year were included in means along with trees that bore cones (Fig. 1). All analyses were conducted in the *glmmADMB* and *lme4* packages in R (Bates et al. 2015, R Development Team 2015, Skaug et al. 2016).

Variation in predictor variables

To facilitate comparisons between mast and nonmast years and generalize stand-level findings in AIC analyses to the study ecosystems,

results in Fig. 1 are presented as means with standard error bars. To understand differences in predictor variables between ecosystems, stand attributes such as the proportion of dead limber pine, total basal area of live trees (Appendix S1), cone production per tree, and the density of active red squirrel middens were quantified using means and standard errors. These variables served principally as predictor variables in subsequent hypotheses tests. In all analyses, WPBR severity was replicated at the stand level

Table 2. Model comparisons of hypotheses tested of covariates affecting cone escape and proportion cone escape models.

| Model name | Model ID | Model† | k_i | Cone escape | | | df | Proportion cone escape | | |
|-----------------|----------|-------------|-----------|---------------|--------------|-------------------|-----------|------------------------|--------------|-------------------|
| | | | | AIC | Δ AIC | AIC _{wi} | | AIC | Δ AIC | AIC _{wi} |
| Ecosystem | A | ECOS | 5 | 8791.7 | 740.6 | 0 | 3 | 1629.5 | 292.6 | 0 |
| Disease | B | PDLP | 5 | 8791.6 | 740.5 | 0 | 3 | 1628.0 | 291.2 | 0 |
| Habitat quality | C | BATO | 5 | 8773.9 | 722.8 | 0 | 3 | 1616.1 | 279.2 | 0 |
| Predator | D | PRED | 5 | 8740.1 | 689.0 | 0 | 3 | 1610.1 | 273.2 | 0 |
| Masting | E | MAST | 5 | 8112.5 | 61.5 | 0 | 3 | 1359.5 | 22.6 | 0 |
| Cones | F | <i>COST</i> | | | | | 3 | 1593.2 | 256.3 | 0 |
| Global | G | ‡ | 9 | 8074 | 23 | 0 | 8 | 1341.0 | 4.1 | 0.039 |
| Interaction | H_1 | § | 10 | 8065.7 | 13.7 | 0.001 | 9 | 1341.1 | 4.2 | 0.038 |
| Interaction | H_2 | ¶ | 11 | 8066.1 | 15.1 | 0 | 10 | 1337.7 | 0.88 | 0.198 |
| Interaction | H_3 | # | 12 | 8058.1 | 7.1 | 0.020 | 11 | 1337.5 | 0.66 | 0.221 |
| Interaction | H_4 | | 13 | 8052.9 | 1.9 | 0.271 | 12 | 1337.8 | 0.92 | 0.195 |
| Top | I | †† | 14 | 8051.0 | 0 | 0.708 | 13 | 1336.8 | 0 | 0.308 |

Notes: We included stand identity as a random effect in all models (not shown). Bold text indicates the top model of those evaluated per Akaike weight. k_i is the number of estimated parameters, AIC is Akaike’s information criteria, Δ AIC is the difference from the model with the minimum value, and wi (Δ AIC weight) is used to determine the most parsimonious model in the candidate set.

† Model: The number of cones at the start (*COST*), prior to predation, was included only in models of proportion cone escape and thus italicized in the model column.

Interaction models and top model included the following variables:

‡ ECOS + PDLP + PRED + MAST + BATO + (*COST*).

§ ECOS + (PDLP × PRED) + MAST + BATO + (*COST*).

¶ ECOS + BATO + (PDLP × PRED) + (MAST × PRED) + (*COST*).

ECOS + BATO + (PDLP × PRED) + (MAST × PRED) + (ECOS × PRED) + (*COST*).

|| ECOS + PDLP + BATO + (MAST × PRED × ECOS) + (*COST*).

†† ECOS + BATO + (PDLP × PRED) + (MAST × PRED × ECOS) + (*COST*).

Table 3. The individual variables tested and their coefficients in the most parsimonious model among the candidate set (model I; Table 2) for cone escape and proportion cone escape.

| Name | Abbreviation | Cone escape | | | Proportion cone escape | | |
|-----------------------------|--------------------|-------------|--------|----------|------------------------|--------|----------|
| | | Coefficient | SE | <i>P</i> | Coefficient | SE | <i>P</i> |
| Fixed effects | | | | | | | |
| Intercept | INT | −0.091 | 0.459 | 0.843 | −1.958 | 0.569 | 0.006 |
| Ecosystem | ECOS | 1.939 | 0.693 | 0.005 | 1.122 | 0.848 | 0.186 |
| Disease | PDLP | 1.826 | 2.462 | 0.458 | 3.254 | 3.070 | 0.289 |
| Habitat quality | BATO | −0.123 | 0.026 | <0.001 | −0.157 | 0.301 | <0.001 |
| Predator | PRED | 0.021 | 0.1655 | 0.900 | 0.296 | 0.085 | 0.326 |
| Masting | MAST | 3.252 | 0.2372 | <0.001 | 3.242 | 0.399 | <0.001 |
| Initial cones | <i>COST</i> | | | | −0.001 | <0.001 | 0.974 |
| Interactions | | | | | | | |
| Disease × Predator | PDLP × PRED | −2.771 | 1.425 | 0.052 | −3.211 | 2.452 | 0.190 |
| Ecosystem × Predator | ECOS × PRED | −1.372 | 0.392 | <0.001 | −0.962 | 0.633 | 0.129 |
| Mast × Predator | MAST × PRED | 0.255 | 0.244 | 0.296 | −0.647 | 0.391 | 0.100 |
| Mast × Ecosystem | MAST × ECOS | −1.023 | 0.332 | 0.002 | −0.972 | 0.510 | 0.057 |
| Mast × Predator × Ecosystem | MAST × PRED × ECOS | 0.551 | 0.402 | 0.170 | 0.470 | 0.607 | 0.439 |
| Random effects | | | | | | | |
| Stand | STND | 1.059† | 1.029‡ | | 1.051† | 1.025‡ | |

Notes: The unit descriptions for the variables are as follows. Ecosystem, 0 or 1 (the southern ecosystem was designated as 1); disease, proportion dead limber pine; habitat quality, an index of basal area of all species combined based on counts obtained with a prism with a basal area factor of two (half the actual m²/ha); predator, middens/ha; masting, 0 or 1 (mast years designated as 1); initial cones: number of cones; stand: each stand assigned a unique number.

† Value is the variance.

‡ Value is the standard deviation.

Table 4. Model selection for the appropriate model form to model count data (Poisson or negative binomial and inclusion of zero inflation).

| Models | k_i | AIC | Δ AIC | AIC _{wi} |
|----------------|-------|-----------|--------------|-------------------|
| ZINB (null) | 9 | 8073.98 | 0.00 | 0.74 |
| NB (null) | 8 | 8076.08 | 2.10 | 0.26 |
| ZIP (null) | 7 | 14,422.42 | 6348.44 | 0.00 |
| Poisson (null) | 7 | 16,726.92 | 8652.94 | 0.00 |

Notes: k_i is the number of estimated parameters, AIC is Akaike's information criteria, Δ AIC is the difference from the model with the minimum value, and w_i (Δ AIC weight) is used to determine the best model. A standardized minimal null model was used to compare the forms. The abbreviations for model form are as follows: zero inflation (ZI), negative binomial (NB), and Poisson (P).

($n = 17$), with nine and eight stands, respectively, in the southern and northern WPBR ecosystems. Testing WPBR effects at the stand level rather than at the ecosystem level was necessary because the two ecosystems differed in the density of limber pine trees independently of WPBR, with higher basal areas of limber pine in the southern ecosystem even after experiencing greater mortality (mean of 33% vs. 10% mortality, respectively; Appendix S1). To reduce the confounding effect of density, the proportion of dead limber pine out of all standing live and dead limber pine was used to test the effect of WPBR infection on cone escape.

RESULTS

Modeling results of cone escape

In all, 1797 limber pine cone measurements were taken between 2008 and 2010, across 17 stands that captured both the number of cones produced (Fig. 1a) and the number remaining, following predation. Overall, more cones escaped predation in the 2010 high cone year (24.3 ± 1.5 cones/tree when averaged across all trees), which was 16.1 and 7.1 times greater than the number of cones remaining in nonmast years (2008 and 2009, respectively; Fig. 1b). Mast years thus led to a net benefit in the number of cones available for attracting avian seed dispersers in both ecosystems (Fig. 1b). The number of cones remaining following squirrel predation ranged from 0 to 308 cones per tree (median = 2). Counts of zero cones comprised 36.7% of the total observations, 56.7% in a nonmast year

(56.0% and 57.3% for northern and southern ecosystems, respectively), and 15.0% in a mast year (19.5% and 10.3% for northern and southern ecosystems, respectively). We found that it was important to account for zero inflation when modeling the number of cones remaining and the error distributions were best fit with a negative binomial model (Table 4).

Comparison of models A through E, each of which tested single factors alone, to the global model (G) and to interaction models (H and I) suggested that the most parsimonious model from within the candidate set was model I ("top model," I, AIC_{wi} = 0.708, Table 2). Model I included whether the present year was a mast year, the study ecosystem, the total basal area of conifers, an interaction between dead limber pine and the number of squirrel middens, and a three-way interaction between mast years, squirrel middens, and study ecosystem. There was little support, as evidenced by AIC weights for models without interactions (A–G) or for models with only two-way interactions (H_1 – H_3 , Table 2). There was marginal support for model H_4 , which included the three-way interaction between mast years, squirrel middens, and study ecosystem, but omitted the two-way interaction between dead limber pine and squirrel abundance (Δ AIC = 1.9, AIC_{wi} = 0.271; Table 2). The top model also showed that more cones escaped in the mast year, that cone escape was greater overall in the southern ecosystem, and that cone escape decreased with stand basal area (Figs. 1, 2, Table 3). Cone escape decreased with squirrel abundance, when midden data were paired with cone removal data from the preceding year's cone crop; there was more support for this treatment of predator abundance than when midden counts were paired with the current year's cone removal data.

Modeling results of proportion cone removal

Cone removal ranged from 0% to 100%. More trees had all their cones removed in nonmast years (34.7%) than in the mast year (14.1%). Averaged across both ecosystems, a substantially higher proportion of cones escaped in the 2010 mast year (0.535) than in nonmast years (0.217 and 0.194 in 2008 and 2009, respectively; Fig. 1d).

Comparison of models A through E, each of which tested single factors alone, to the global model (G) and interaction models (H and I)

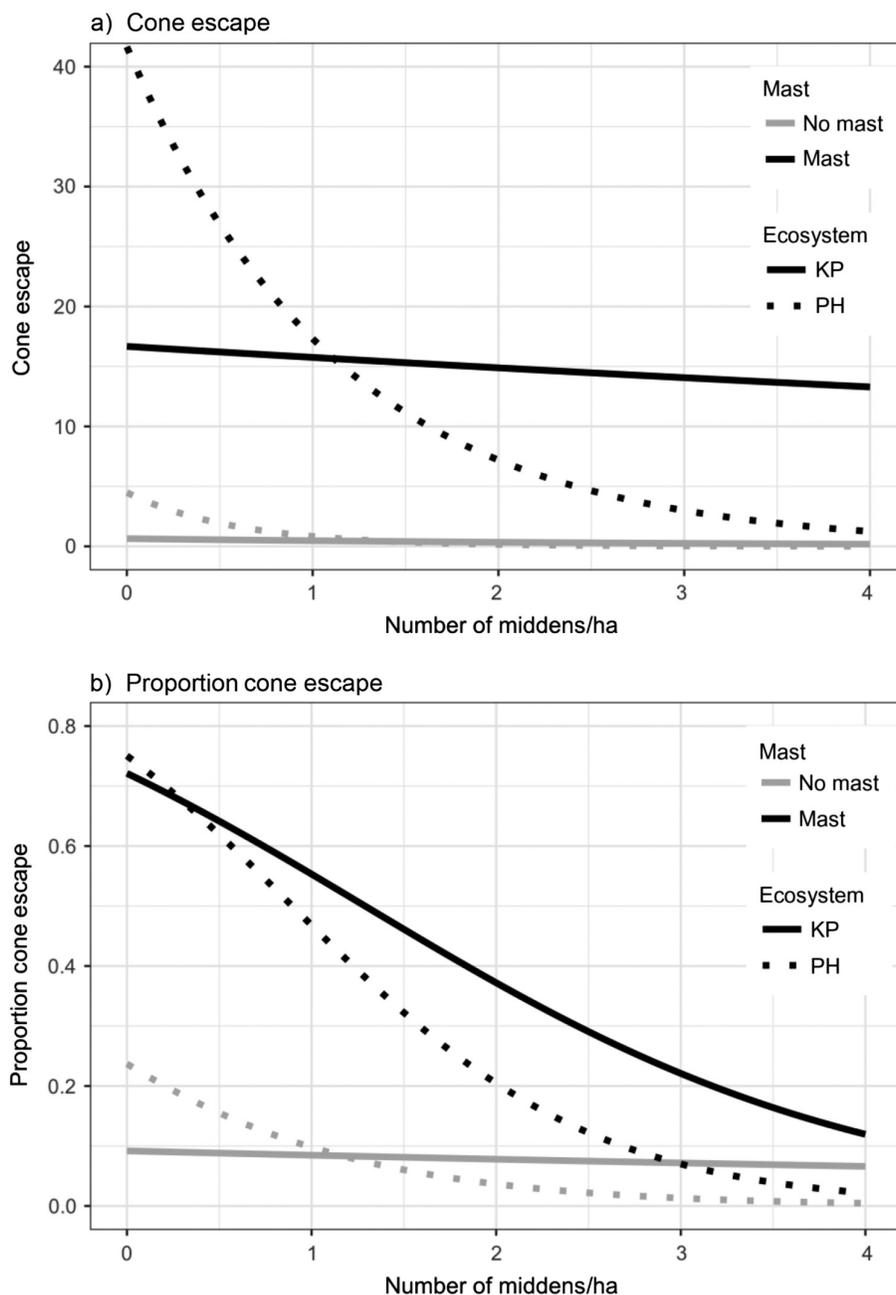


Fig. 2. Model predictions for (a) cone escape (number of cones) modeled with zero inflation and negative binomial error and (b) proportion cone escape (proportion of cones remaining) modeled with binomial error, as a function of potential seed predation pressure, indexed by the number of active squirrel middens per hectare, from the most supported model for each response variable (model I in Table 2). The black lines indicate cone escape during a mast year, while gray lines are nonmast years. The northern Kootenay Plains (KP) ecosystem is given as a solid line, while the southern Porcupine Hills ecosystem is given as a dashed line. All other variables were held at their average in the dataset (index of total basal area = 4.6, and proportion of dead limber pine = 0.12); model 2b also number of cones at the start = 31.0.

suggested that there was the most evidence for interaction model I (i.e., the most parsimonious model for both cone escape and proportion cone escape). Of the candidate models tested, the top AIC model (I, $AIC_{wi} = 0.308$, Table 2) had marginally more support than interaction models H_2 , H_3 , and H_4 ($AIC_{wi} = 0.198$, 0.221 , and 0.195 , respectively). The top model showed that the proportion of cones escaping was best explained when mast years, numbers of squirrels, and ecosystem were included in the model, along with two-way interactions between ecosystem and mast years, ecosystem and squirrel abundance, mast years and squirrel abundance, and a three-way interaction between ecosystems, squirrel abundance, and mast years. The top model also showed that stand basal area, the number of initial cones in the stand, and disease added information to the model. Estimates of the fitted model parameters for the top candidate model are given in Table 3.

Seed limitation hypothesis—cone availability in WPBR-altered ecosystems

Our results show that disease alone did not influence cone availability, but an interaction between WPBR infection levels and squirrel densities adds information to both cone escape and proportion cone escape estimates in AIC models. This relationship was tested across a broad range of WPBR levels among stands, which ranged from 0% to 43% dead limber pine (Appendix S1). Live limber pine remained the dominant species and structural element in most study stands (seven stands in each ecosystem), despite WPBR-induced mortality over time. The southern ecosystem retained higher densities of limber pine (35.2% more basal area) than the northern ecosystem, despite a long-term presence of WPBR at high levels. Cone production was 69.8% greater in the southern ecosystem between 2008 and 2010, despite a higher proportion of dead limber pine. The combined effect of more live limber pine and greater seed production per tree in the more diseased southern ecosystem can be crudely estimated as resulting in 2.30 times as many cones produced per hectare (1.35 times as many trees per hectare \times 1.70 times as many cones per tree). This finding is counterintuitive and suggests that WPBR had a smaller effect on limber pine cone production than inherent

differences in ecosystem productivity between the studied ecosystems.

Masting hypothesis—interannual variation in cone crops and escape

We found considerable support for our hypothesis that masting confers temporal benefits in both cone escape and proportion cone escape from seed predators. First, limber pine cone production showed considerable interannual variability. The overall CV value from 2008 to 2010 was 193.4 and ranged between 132.7 and 242.5 for individual stands. Second, due to higher cone production and lower rates of cone predation in the 2010 mast year, more cones escaped and proportionately more cones escaped predation than in nonmast years (Figs. 1, 2). Thirdly, masting caused the greatest decline in the AIC, relative to other univariate models (Table 2), and added information to the top model in several two-way and three-way interactions with other variables (Table 3). Changes in the proportion of cones escaping predators were captured better by the categorical variable masting than it was by the number of cones produced by trees (ΔAIC from the top model I was 22.6 vs. 256.3, respectively; Table 2).

Few trees retained cones post-predation in nonmast years (26.7%) and a few stands did not have any cones available for dispersers after cone predation in one (one stand in each ecosystem) or both of the low cone years (two stands from the southern ecosystem). However, in the 2010 mast year, 80% of trees retained cones for dispersers, and cones were readily available for dispersers in all of the stands after cone predation.

Model predictions of cone escape remained sensitive to changes in seed predator densities. When the average values from each ecosystem were added uniquely to the model, it predicted that in the northern ecosystem (1.0 middens/ha, proportion dead lp, 0.07; and basal area total, $4.0 \text{ m}^2/\text{ha}$), we would expect 0.5 cones and 17.8 cones would escape in a nonmast and a mast year, respectively. In the southern ecosystem (0.6 middens/ha, proportion dead lp, 0.19; and basal area, $5.3 \text{ m}^2/\text{ha}$), we would expect 1.5 and 22.9 cones would escape in a nonmast and a mast year, respectively. In order to reduce the number of mast year cones escaping in the southern ecosystem to that of the northern ecosystem,

squirrel densities only need to increase from 0.6 to 0.82. These densities are well within the range of predator densities observed in many stands in both ecosystems (Fig. 2a) and may influence the attraction of nutcrackers at a stand or ecosystem level. Of greater conservation concern, model predictions in Fig. 2b suggest that beyond predator densities of 3.0 middens/ha, the evolutionary benefits of masting may be lost in southern ecosystems, when the proportion of cones escaping in mast years diminish below levels observed in nonmast years. This scenario appears rare, as predator densities were lower than this threshold in all but one stand, and future mortality of infected limber pine in southern ecosystems will likely lower the capacity of stands to support current squirrel densities.

Habitat quality hypothesis

Comparison of habitat model C to the top model (I) shows that basal area of tree species needs to be considered simultaneously with other factors, to understand the overall effects of habitat quality. In our top model (Table 3), basal area negatively impacted cone availability. This result likely reflects the overriding positive effect of basal area and other conifer species on squirrel abundance, which in turn negatively impacts limber pine cone availability. We found that squirrel populations were 85% greater in the northern vs. southern ecosystems (Fig. 1c), which had a proportionally higher ratio of other conifer species to limber pine (Appendix S1). This suggests that limber pine could escape proportionately higher predation risks in dense stands when alternative conifer food sources are available.

Resiliency: interactions between escape, masting, predators, and ecosystems

In analyses of both cone escape and proportion cone escape, several interactions between squirrel abundance, ecosystem, and mast year were observed to affect escape. To understand these dynamics, we have modeled predictions for the three-way interaction between squirrel abundance, masting, and ecosystem, while holding basal area and PDLP at their mean values (Fig. 2). Fig. 2a shows that while more cones escape in mast years, predation risk varies greatly between ecosystems, altering the benefits

of masting spatially. Squirrel abundance has a disproportionately negative effect in mast years in the southern ecosystem, and any gains in cones produced due to site quality in the southern ecosystem can be negated by seed predators. The proportion of cones escaping predators also declines more rapidly with predator density in the southern ecosystem (Fig. 2b). Different temporal patterns of squirrel abundance between the northern and southern ecosystems may help explain this result (Fig. 1c). In the southern ecosystem, squirrel populations declined (3.5-fold and twofold, respectively) during the nonmast years of 2008 and 2009 from populations observed in the mast year of 2007 (Fig. 1c). In the northern ecosystem, squirrels displayed the opposite pattern, increasing 80% and 40% in abundance in the nonmast years (2008 and 2009, respectively; Fig. 1c) and exhibiting the lowest abundance in the two high cone years (2007 and 2010). This suggests that squirrel population dynamics and diet are more dependent on temporal patterns of limber pine cone production in southern ecosystems, which are predominated by limber pine (Appendix S1).

DISCUSSION

Masting facilitates temporal escape in limber pine

Our results suggest that masting not only facilitates seed predator escape in an endangered species, but it can do so across a range of cone production levels, seed predator densities, and disease conditions directly contributing to the decline of the masting species. Limber pine's overall CV value of 193.4 was considerably higher than the threshold CV of 40 (standardized to a percentage) used by Kelly (1994) to delineate nonmasting species from those with marked supra-annual variability. Limber pine's overall CV value (193.4) fits within the highest 10% and 15% of datasets reviewing supra-annual seed production among species (Herrera et al. 1998, Kelly et al. 2001, Greene and Johnson 2004). Our estimate of limber pine's CV value may be less accurate than those reported for other species in the preceding studies due to our shorter duration of study (three years vs. four or more years; Herrera et al. 1998). Supra-annual variability has been linked to seed dispersal syndromes, with the greatest variability observed in nonzoochorous

species (dispersed by abiotic means; Herrera et al. 1998). Limber pine showed greater supra-annual variability than observed in many dyszoochorous species (dispersed by scatter hoarders), where seed predator escape likely selects for high interannual variability (Tomback 1982, Herrera et al. 1998). In whitebark pine ecosystems, which also rely on the Clark's nutcracker as a scatterhoarding mutualist, mast crops are critical for attracting birds at regional levels (Tomback et al. 2001, McKinney et al. 2009).

The evolutionary benefits of masting for seed predator escape may decline when disease does not alter habitat quality sufficiently to depress seed predator populations. Our study suggests that the benefits of masting (i.e., proportionately higher cone escape) could be lost in more severely diseased southern limber pine ecosystems if seed predator densities exceed 3.0 squirrels/ha (Fig. 2b). This occurred when model predictions were fit to the data, and basal area and PDLP were held at their mean values. In additional model predictions, habitat quality (basal area) had a greater effect than disease (PDLP). Lowering total basal area by 50% (index of BATO = 2.3, vs. its overall average of 4.6), while holding PDLP at its overall average (0.12), increased cone escape in both ecosystems. This suggests that cone escape in limber pine is aided by low basal area, a condition that naturally occurs on the xeric site types it occupies and that will be perpetuated with further mortality caused by disease.

Northern ecosystems, with lower seed production and lower WPBR infections, show that the benefits of masting can be conserved in high-quality habitats that support many seed predators, when seed predator populations are maintained by alternative conifer food sources (i.e., white spruce, lodgepole pine). Additionally, alternative reproductive strategies, namely persistent aerial cone banks in lodgepole pine, may maintain seed predator populations in nonmast years in the northern ecosystem.

Several key factors may have contributed to the proportionately greater cone escape we observed in mast vs. nonmast years across our limber pine study system. Firstly, interannual variation in cone production was high in our study, which frequently contributes to a higher proportion of seed escape in the mast year in

boreal (Peters et al. 2005), temperate (Crawley and Long 1995), and tropical ecosystems (Sun et al. 2007). Masting theory suggests that episodic and synchronized seed production may have evolved to alternately starve and satiate seed predator populations, thereby providing opportunities for regeneration (Janzen 1971, Tomback 1982). The high proportion cone escape we observed in the 2010 mast year (0.535) provides new insight to the predatory role of red squirrels in limber pine ecosystems, and supports our hypothesis that predator satiation occurs even while a species declines. Secondly, in mixed conifer stands, red squirrel populations may be less dependent on limber pine cone production than on white spruce, as is the case in boreal ecosystems (Kemp and Keith 1970, Peters et al. 2005). Thirdly, masting does not appear to be temporally synchronous among conifer species in montane environments in the northern Rockies (white spruce, Douglas fir, and limber pine all had high seed crops in 2007 but only limber pine masted in 2010; V. Peters, *personal observation*).

Predation threats—temporal and spatial considerations

Our results indicate that red squirrel populations display different temporal dynamics in two disease-altered ecosystems, and present different predation threats to limber pine. These are important contributions to our understanding of red squirrel predation; while known to be high (74–90%, Lanner and Vander Wall 1980, Benkman et al. 1984), previous studies were restricted to single limber pine populations and did not account for interannual variation. In the southern ecosystem in Alberta, red squirrel populations appear to be dependent on limber pine mast years, declining in low cone years because of limited limber pine cone resources, and peaking in mast years, displaying a response to mast crops that is widely reported in boreal ecosystems dominated by white spruce (Kemp and Keith 1970, Wheatley et al. 2002, Peters et al. 2003, Boutin et al. 2006). Conversely, the lowest squirrel densities occurred in the two limber pine mast years in the northern ecosystem, even though interannual variation in limber pine seed crop was synchronous between ecosystems. Contrasting temporal seed predator population dynamics likely contributes to the interaction between mast

years and squirrel density. Cone escape and proportion cone escape declined more rapidly in mast years than in nonmast years as squirrel abundance increased (Fig. 2a, b). These effects were more pronounced in the southern ecosystem, as indicated by the more rapid decline in both response variables with squirrel abundance (Fig. 2a, b).

Several aspects of our approach to estimating squirrel abundance are important to consider when interpreting squirrel population dynamics and cone predation. Our estimates of squirrel abundance only reflect the survivorship of territory-holding adults observed by cone feeding evidence from the fall and winter of each of these years, rather than the overall abundance of all juveniles and adults. Previous studies in boreal ecosystems have found that the greatest mortality of squirrels occurs during the winter of cone failure years among young squirrels that fail to occupy a good territory after dispersing from natal territories (Kemp and Keith 1970). Our treatment of squirrel abundance data, pairing observations of late winter midden use (i.e., 2008) with the preceding years cone crop (i.e., 2007), reflected the biology of squirrels responsible for predation during a particular year. Statistical analyses supported this approach, more than using squirrel midden counts (taken in spring) to predict the current year's escape, later that fall.

A closer comparison of cone availability and forest composition between the two ecosystems may help explain the predation threats squirrels present relative to habitat quality. Habitats that supply a dependable supply of cones, high basal areas for cone storage, and cover from predators are favored by red squirrels (Rothwell 1979, Steele 1998). In the northern ecosystem, either white spruce (a masting species) or lodgepole pine (a species that retains cones over multiple years) co-occur in most of the limber pine stands, and predominate in the adjacent forest, providing intermittent or stable food sources, respectively, to squirrels (Wheatley et al. 2002). White spruce stands support higher densities of squirrels than other stand types in most studies, while lodgepole pine facilitates high annual rates of juvenile production (Wheatley et al. 2002). Mixed conifer stands with whitebark pine support more squirrels than pure whitebark pine stands (0.41 vs.

0.19 middens/ha) and have proportionately higher cone predation (0.47 vs. 0.13; McKinney and Fiedler 2009). In the southern ecosystem, all stand types provide intermittent and unstable food sources across years. Douglas fir and limber pine (both of which are masting species) co-occur in half the stands, and limber pine dominates the remaining half. Temporally fluctuating cone resources may be one trigger for the local dispersal of red squirrels to higher-quality territories in the spring (Fisher et al. 2005); thus, squirrel dispersal would be facilitated more in the northern ecosystem, which is embedded within a continuous forest matrix. In contrast, the southern ecosystem is an agricultural and ranching matrix with limber pine stands occurring on isolated rocky outcrops. The intermittent food supply and lack of a colonizing pool of squirrels proximal to study stands in the southern ecosystem likely explains the rapid decline of red squirrels in the cone failure of 2008 and the limited increase in numbers in the high cone year of 2010. Based on the variables tested in this study, we can only document the variation in squirrel abundance and predation relative to differences in forest density, composition, and seed availability.

The proportionately greater effect of predators on cone escape in the southern vs. northern ecosystem (Fig. 2a) suggests that the per capita cone take by squirrels is greater in severely diseased stands. White pine blister rust appeared to lower the suitability of southern ecosystems to support red squirrel populations by reducing limber pine basal area through WPBR-induced mortality. This provided few direct benefits for seed escape in limber pine. Contrary to our seed limitation hypothesis, and findings by McKinney and Fiedler (2009) in whitebark pine stands, disease does not inherently allow for proportionately greater cone escape in limber pine; effects were contingent on ecosystem and predator density (Fig. 2b). Our study suggests that while disease lowers the suitability of limber pine stands to support squirrels, the remaining squirrels exert stronger predatory pressure and reduce the proportion of cones escaping for dispersers. These results suggest that as stands decline and become suboptimal for red squirrel foraging, the species exhibits a type III functional feeding response (Holling 1965) on limber pine cones (i.e., individual squirrels increase

their consumption of limber pine cones). Such responses occur in white spruce-dominated systems when red squirrels consume proportionally more cones in intermediate cone years (Fletcher et al. 2010) and when habitat patches experience numerical responses in seed predator densities to seed supply (Kitzberger et al. 2007). In studies on whitebark pine, cone production at the stand level declined with increasing WPBR levels, because diseased individuals died and were removed from the cumulative reproductive effort (McKinney et al. 2009).

In our study, the more diseased southern ecosystem had greater live limber pine basal area, and higher cone production per tree, suggesting that cone production per hectare and site quality was likely greater than in northern ecosystems. Overall, environmental influences on seed production appeared to have greater effects on cone escape than disease. Masting provided proportionally greater cone escape regardless of community-level effects such as disease, predator density, and stand composition, ensuring that cones remain available for dispersers across a wide range of ecological conditions.

Evolutionary constraints and ecological realities for the conservation of limber pine

For declining conifers where both numerical responses of seed predators occur and nutcracker-assisted dispersal is a functional response to seed availability, supra-annual variability becomes critical for recruitment opportunities. Despite predator satiation, the actual amount of seed that escapes predispersal seed predators may still be inadequate to attract nutcrackers or other seed dispersers in diseased stands. Thresholds above 1000 cones per ha are necessary for attracting nutcrackers to whitebark pine (McKinney et al. 2009, Crone et al. 2011). This threshold is not known for limber pine, but is a concern in provincial recovery plans (AWLPRT 2014). To address these conservation biology concerns about seed dispersal, it was critical to examine cone escape, and not just the proportion cone escape (which is typically used in studies testing the evolutionary advantages of mast seeding), as a response variable. This distinction was supported statistically; in our candidate models for cone escape, the three-way interaction between masting, squirrel abundance,

and ecosystem was supported much more strongly than in proportion cone escape models, where two-way interactions between masting and predators (H_2) and ecosystem and predators (H_3) drove model performance (Table 2). Notably, seed predation by red squirrels has constrained the evolution of cone morphology in limber pine and may drive the seed dispersal mechanism more than the mutualism with nutcrackers (Siepielski and Benkman 2008).

The contextual nature to WPBR effects on cone production and predation for two declining species resulted in greater spatial effects in whitebark pine ecosystems (McKinney and Fiedler 2009), and a combination of temporal and spatial effects in limber pine ecosystems (present study). We expect that changes in forest composition may predispose limber pine to altered seed predation risks in other portions of its range, where disease has a more pronounced effect on cone production. The effect of seed predation on declining species may also be contingent on the synchrony of mast seeding among co-occurring species, whether seed predators respond to altered food availability or habitat conditions, and whether mutualist-dispersal systems are affected by the species decline. In short, predispersal predation provides little indication of the success of the overall regeneration process, as numerous factors related to post-dispersal predation, secondary caching, the regeneration niche, or stand dynamics determine the importance of seed availability to regeneration (Janzen 1971, Crawley 1997).

Economies of scale

Kelly (1994) concluded that factors affecting seed production operate in terms of economies of scale. When the success of pollination, dispersal, and seed escape interact with seed production, economies of scale become the major determinants of interannual variation in seed production in plants (Herrera et al. 1998). As hypothesized, predator satiation occurred across a broad range of stand conditions in both ecosystems, despite differing levels of habitat alteration by WPBR. However, economies of scale may break down when a masting species declines more rapidly than seed predator populations, or when alternate food sources are unavailable to reduce predation pressure on a masting species, as occurred in our southern limber pine ecosystem. Our data also

suggest that a masting species can escape predators by being a minor component of the forested landscape, reflective of a type III functional response (Holling 1965). Such was the case in the northern ecosystem where squirrel habitat remains largely intact due to the abundance of other conifer species, and alternative food sources are available. Studies in multi-species masting systems show that high-value prey species experience low predation during mast years due to swamping effects (Kitzberger et al. 2007). Greater dispersal distances between patches of limber pine habitat may contribute to the different temporal dynamics observed in squirrel populations between the ecosystems, and raise landscape connectivity and metapopulation issues that are beyond the scope of the current study.

The evolutionary determinants of reproductive behavior are complex and may be juxtaposed with new ecological realities that may tip in favor of one community-level interaction. Additionally, the strength of community-level interactions combined with abiotic factors may select which masting species may decline most rapidly. For example, both limber pine and whitebark pine are listed as endangered in Alberta, both show marked interannual variation in seed production, and both experience high seed predation by red squirrels. However, limber pine is less dependent on the Clark's nutcracker for primary dispersal because cones open, while whitebark pine cones remain closed. Vanderwall (2001) classify this dispersal syndrome as "nut presentation" for secondary dispersers. Assuming that threats and other biological attributes are similar (i.e., percent adult and seedling survivorship in the face of WPBR, and seed production), the limber pine appears less vulnerable to dispersal failure.

CONCLUSION

In the endangered limber pine, masting facilitates predispersal cone escape in disease-altered ecosystems with differences in seed predator densities. Cone escape in time, more than cone escape in space, appears to facilitate the seed dispersal mutualism with Clark's nutcracker. Concerns remain that altered species interactions may affect the recovery prospects of limber pine because cone predation by squirrels removes the majority of seed in most years, potentially

restricting regeneration opportunities to mast years when cone production may be sufficient to attract dispersal mutualists. Our study suggests that there is temporal resiliency in seed escape in limber pine ecosystems, even under different disease, productivity, and seed predator threats. While our results are contingent on the stronger effects of site productivity than disease in southern ecosystems, and the availability of alternative food sources from other conifer species in northern ecosystems, a fundamental principle of masting benefits remains. Our modeled predictions show that masting conferred proportionately more cone escape from predators, and ensured more cones were available to attract dispersers under most stand conditions. Proportionately greater cone escape in low- vs. high-productivity ecosystems at increasing seed predator densities provides a hopeful example of how masting could remain beneficial as disease causes stand decline, and more broadly for the conservation of masting species under altered environmental conditions. Further study of seed escape in other masting species may reveal whether other compensatory mechanisms facilitate seed escape when masting species reach critically low levels.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1928/full>