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Appendix A. Parameter estimation.

## Appendix A: Parameter estimation

This appendix contains the methods and sources of how the model parameters were estimated. We assume seed distribution and storage into caches by the Clark's nutcracker (Tomback, 1982). Efforts were made to estimate parameters using data from the high-elevation white pine species *P. albicaulis* (whitebark pine), *P. flexilis* (limber pine), and *P. aristata* (Rocky Mountain bristlecone pine). However, where data were unavailable we used data from other, non-high-elevation, white pines; *P. monticola* (Western white pine) and *P. strobiformis* (Southwestern white pine). Finally, estimates derived from other, closely related pine species such as *P. ponderosa* (ponderosa pine), *Abies amabilis* (Pacific silver fir), *Pseudotsuga menziesii* (Douglas fir), and *Tsuga heterophylla* (western hemlock) were used if white pine species data were completely lacking.

Below is a summary description of how the model stages were determined. For a full description with references please see the main paper. The six model stages are defined as: 1) seeds, 2) primary seedlings, 3) secondary seedlings, 4) saplings, 5) young adults, and 6) mature adults. We initially define the seed stage as 0 – 1 years (i.e. no seed bank). Primary seedlings ( $SD_1$ ) are defined as 1 – 4 year olds. We define secondary seedlings ( $SD_2$ ) as seedlings as 5 years until they reach a height of definable dbh ( $\sim 20$  years old). Saplings (SA) are defined as trees 21 years ( $>1.37$  m) until reproductive age, which we set at 40 years, since high-elevation white pines have first reproductive output between ages 30 – 50. Young adults (YA) are defined as reproductive trees ages 41 – 90 years and mature adults (MA) as greater than 90 years old with full reproductive capacity (Table 1).

Based on this stage structure, the mean diameter at 1.37 m (dbh) for saplings, young adults, and mature adults was estimated to be 2.05, 12.5, and 37.0 cm respectively (Table 2).

### Primary seedlings ( $SD_1$ ) § *Linear model components*

The probability of primary seedlings (ages 1 – 4) surviving through their fourth growing season ranges from 0.22 – 0.58 (Tomback, 1982, calculated from primary data in Maher

and Germino (2006) and Shepperd et al. (2006)). The survival rates of *P. albicaulis* from Maher and Germino (2006) are from seedlings in ideal microsites within approximately 5 m from tree islands with annual mortality of 0.249 in the upper forest to 0.107 at tree line. Shepperd et al. (2006) recorded an annual mortality of 0.335 for *P. ponderosa* in Colorado. We use maximum likelihood estimation (MLE) for SD<sub>1</sub> mortality using survivorship data from Tomback et al. (2001). The MLE of yearly survivorship was 0.848 (95% confidence interval of 0.785 – 0.899). This estimate corresponds to approximately a 50% ( $0.848^4 = 0.52$ ) probability of surviving to the end of the fourth growing season. Thus, SD<sub>1</sub> mortality,  $m_2 = 1 - 0.848 = 0.152$ , with a residence time of 4 years (Table 2).

### Secondary seedlings (SD<sub>2</sub>) § *Linear model components*

Using primary data from Shepperd et al. (2006) for *P. ponderosa*, the MLE of the yearly SD<sub>2</sub> survivorship was 0.895 with a 95% confidence interval of 0.772 – 0.966. Thus, SD<sub>2</sub> mortality,  $m_3 = 1 - 0.895 = 0.105$  and  $R_3 = 16$  (Table 2). This is consistent with low mortality observed by Maher and Germino (2006) for *P. albicaulis* in a 2 year data set for seedlings > 5 years.

### Saplings (SA) § *Linear model components*

Sapling annual mortality ranges from 0.003 – 0.04 for high-elevation white pines (Hamilton Jr., 1986; Kobe and Coates, 1997; Moore et al., 2004; Dixon, 2002). Because survivorship data for high-elevation white pines of this stage was lacking, we were unable to use maximum likelihood to estimate SA mortality. We assume a sapling mortality,  $m_4 = 0.02$ , which was used previously by Ettl and Cottone (2004).

### Young and mature adults (YA & MA) § *Linear model components*

Previous estimates of yearly mortality of both young and mature adults are 0.01 because of a combination of competition, and in the case of mature adults, advanced age (Edmonds et al., 1993; Mast and Veblen, 1994; Monserud and Sterba, 1999; Battles et al., 2008). Survivorship data for adult stages of high-elevation white pines are rarely collected

so we use data from [Edmonds et al. \(1993\)](#) for various conifer species in the maximum likelihood estimation. Yearly YA survivorship MLE was equal to 0.985 with a 95% confidence interval of 0.977 – 0.991. Therefore  $m_5 = 1 - 0.985 = 0.015$  and  $R_5 = 50$  (Table 2).

Mature adults were estimated to have a slightly higher annual survivorship of 0.995 with a 95% confidence interval of 0.984 – 1.0. Thus, MA mortality was equal to  $m_6 = 1 - 0.995 = 0.005$ . Since there is no stage beyond MA,  $R_6 = \infty$ , these individuals either survive with a probability of  $s_6$ , equation (18), or they die with probability  $m_6 = 0.005$  (Table 2). Additionally, mature adults cannot transition to a higher stage.

## Seedling recruitment parameters § *Nonlinear model components*

The seed germination equation (29) contains two *reduction factors*,  $r_{ALs}(\vec{x}_6)$  and  $r_{cache}(\vec{x}_6)$ , ranging from  $0 \rightarrow 1$  that depend upon the size of the population (and time) and thus exhibit nonlinear behavior. The two factors are calculated prior to the application of the linear map for survivorship and transition (see § *Linear model components*).

The first reduction factor,  $r_{ALs}$  (Fig. 1a), represents available light and was estimated using equation (28). This factor reflects the effect of canopy cover on germination probability at ground level and was modified from [Keane et al. \(1996\)](#) for shade intolerant species.

The second reduction factor,  $r_{cache}$  (Fig. 1b), represents the propensity of birds to cache seeds (as opposed to consuming them). Clark’s nutcrackers typically consume what is necessary to fulfill their caloric requirements and cache the remainder ([McKinney et al., 2009](#)). This depends on the total number of available seeds ( $x_1$ ) in the population for birds to consume; when seeds are abundant, birds cache more and *vice versa*. For a given time step,  $r_{cache}$  was calculated using a modified function from (see Fig. 2b in [Keane et al., 1990](#)) with seeds per bird ( $SpB$ ) as the independent variable, see equations (26) and (27), rather than cones per bird ([Keane et al., 1990](#), assume  $\sim 60$  seeds/cone). Previous studies estimated  $r_{cache}$  for whitebark pine as  $\sim 0.37$  ([Cottone, 2001](#)).

## Fecundity parameters § *Nonlinear model components*

Observations from [Scott and McCaughey \(2006\)](#) for *P. albicaulis* and data from [Burns et al. \(201X\)](#) for *P. flexilis* and *P. aristata* document reduced numbers of cones per tree in dense stands as compared to more open stands. Therefore, density-dependence resulting from crown crowding was incorporated into the model by scaling  $C_{max}$  by the reduction factor,  $r_{cones}$  (see equation (31)). The adjusted number of cones per tree is then multiplied by the seeds per cone,  $S_{cone}$  ([Owens et al., 2008](#)), which is assumed to be constant, to obtain the total number of seeds produced per tree, equation (33).

## Viability cost parameters § *Survivorship & transition vs disease*

Survivorship of infected stages was determined by multiplying the susceptible survivorship by a viability cost reduction factor,  $c_i$ . Numerous studies have shown that rust infection rapidly kills small trees, but that large trees can survive for many years after infection. Data derived from [Kegley and Sniezko \(2004\)](#) for *P. monticola* in SD<sub>1</sub> individuals was used to calculate the reduction factor  $c_2 = 0.01$ . Secondary seedlings have similarly low survivorship with infection ([Kolpak et al., 2008](#)). Based on calculations from data from [Kolpak et al. \(2008\)](#), we assume the infection cost to survivorship for SD<sub>2</sub>,  $c_3 = 0.13$  (equation (40)).

Annual survivorship was estimated at 0.993 for trees with dbh  $\geq 7$  cm for infected *P. albicaulis* in Crater Lake National Park (data from [Murray and Rasmussen \(2000\)](#)) and 0.998 for infected *P. strobiformis* in New Mexico (primary data from [Conklin \(2004\)](#)). The effect of rust infection on survivorship was therefore modeled as a function of dbh. For stages taller than 1.37 m (i.e. SA, YA, MA), survivorship of infected stages was determined by a function modified from [Keane et al. \(1996, 1990\)](#); see equation (41) and Fig. 1d.

## Fecundity cost parameters § *Fecundity and disease*

Infection with WPBR can severely reduce the fecundity of individual pine trees. According to [McKinney and Tomback \(2007\)](#) infected individuals are only 12.5% as fecund as

uninfected individuals, in agreement with [Ettl and Cottone \(2004\)](#), who estimated an infected fecundity of 12% (mean of infected stages grouped). We set the infection cost to fecundity as  $C_f = 0.125$  for infected YA and MA stages ( $x_{11}$ ,  $x_{12}$ ).

## Infection parameters § *Infection*

Infection probability was estimated from data from [Conklin \(2004\)](#) (for *P. strobiformis* in sites in New Mexico) and [Burns \(2006\)](#) (for *P. flexilis* and *P. aristata* in sites in Colorado) ranged between 0 – 0.6. Furthermore,  $\beta$  ranged from 0 – 0.03 in mature, adult *P. albicaulis* in Montana ([Smith et al., 2008](#)) and from 0.13 – 0.18 in primary seedlings of *P. monticola* ([Kinloch et al., 2008](#)). [McDonald and Hoff \(2001\)](#) recommend a yearly infection probability of  $\beta = 0.016$  for high-elevation white pines and will be used as a lower limit in analyses. The highest infection probability calculated from primary data was  $\beta = 0.2$  ([Burns, 2006](#)) and will be used as an upper limit in analyses.

We again used maximum likelihood to estimate infection probability ( $\beta$ ) using comparable data sets from [McDonald and Hoff \(2001, Table 10.2 and 10.3; p. 205–207\)](#), and from [Conklin \(2004\)](#). Only data from high-elevation white pines (*P. albicaulis*, *P. monticola*, and *P. strobiformis*) were included in the analysis. This resulted in an MLE for  $\beta = 0.044$  and a 95% confidence interval from 0.037 – 0.052 (Table 2), which is in accordance with the other estimates in high-elevation white pines.

Infection probability also varies with climate, microclimate, topographic position, and spatial distribution of hosts which together combine to define site rust hazard ([Kendall and Keane, 2001](#); [Scott and McCaughey, 2006](#)). We recognize that estimating infection probability from survey data is biased toward larger trees because infected young trees may have already died and would not be counted, while infected adults would remain standing to be surveyed. To avoid this bias, we examined survey data from recently-infected areas that had little to no mortality ([Conklin, 2004](#)) to assess the potential for stage-dependent infection probability. Larger trees have a larger surface with which to intercept spores and may therefore have a greater likelihood of infection ([Smith and Hoffman, 2001](#); [Conklin, 2004](#); [Smith et al., 2008](#)). On the other hand,

younger trees are often easier to infect under a given spore load. We did not find a consistent pattern of infection probability among trees of the sizes in the six stages defined in this model, and therefore assumed a constant infection probability across all stages (see equation (44) and Table 2).

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