

FOREST DISTURBANCE AND THE LONG TERM POPULATION PERSISTENCE  
OF THE MT. GRAHAM RED SQUIRREL: A SPATIALLY EXPLICIT MODELING  
APPROACH

by

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## ABSTRACT

We combined field data with high-resolution satellite imagery and a spatially explicit population model to predict long-term population dynamics of the endangered Mt. Graham red squirrel (MGRS: *Tamiasciurus hudsonicus grahamensis*), with the goal of examining effects of disturbance on MGRS population dynamics. We found that modeling MGRS dynamics improved with population specific data. Our results indicate that predation and competition potentially have large, adverse effects on population abundance. Habitat quality analysis indicates much of the spruce-fir forest is degraded to the point that it cannot support MGRS, therefore, the future of the species will rely on management in the mixed conifer zones. Our models predict that future populations will not show the variability exhibited in abundance over the past 20 years, likely due to degradation of spruce-fir forests, and that even low levels of fire and insect disturbance have the potential to drive MGRS population below critical population thresholds.

## CHAPTER I: INTRODUCTION

Mt. Graham red squirrels (MGRS: *Tamiasciurus hudsonicus grahamensis*) are restricted to upper elevation mixed conifer and spruce-fir forests of the Pinaleño Mountains of southeastern Arizona. The population has persisted for at least the last 11,000 years, surviving multiple large disturbances, including insect damage and large-scale catastrophic wildfires (Grissino-Mayer and Fritts, 1995). However, the population decreased dramatically in the mid-1900s leading to MGRS being listed as a federally endangered subspecies in 1987 (USDI Fish and Wildlife Service, 1993). Although the exact causes of the decline are unknown, a combination of factors including logging, the introduction of Abert's squirrels (*Sciurus aberti*), and increased use of the forest has been implicated in the decline (USDI Fish and Wildlife Service, 1993).

Despite the ability of fauna to survive past natural disturbance events in the Pinaleño Mountains (Grissino-Mayer and Fritts, 1995), the addition of anthropogenic disturbance (logging, recreation, astrophysical site construction) may reduce the ability of MGRS to persist (Fish and Wildlife Service, 1993; Heaney, 1995). Recently several large disturbances, including two large fires and a severe insect outbreak, have degraded areas of MGRS habitat (Froehlich, 1996; Koprowski et al., 2005; Koprowski et al., 2006).

The future survival of MGRS will depend on their ability to survive the damage to conifer forests from past and future disturbances. Therefore, accurate prediction of MGRS response to disturbance and ability to survive the natural or managed future of the forest is important for conservation of the subspecies (USDI Fish and Wildlife Service,

1993). Therefore, we created a spatially explicit population model (SEPM) for MGRS developed from population-specific life history data and validated the model with known MGRS population fluctuations. We used SEPMs because they provide an advanced empirically-based modeling efforts that creates predictions that can aid in management (Turner et al., 1995). Then we examined habitat heterogeneity in the Pinaleño Mountains from satellite imagery to reveal areas that are preferred for MGRS middens/territories. Finally we combined the SEPM with spatial differences in habitat quality to examine future potential population dynamics of MGRS in response to fire and insect disturbances.

## CHAPTER II: PRESENT STUDY

Detailed methods, results, and conclusions of this study are contained in the appendices attached. The major findings of this study follow.

Mount Graham red squirrels (MGRS: *Tamiasciurus hudsonicus grahamensis*) exhibit different life history characteristics than the species as a whole. We found a better fit of MGRS population dynamics with a spatially explicit population model populated with population specific data than when using general life history data. Our model indicated predation (mammalian and avian) and competition (from introduced Abert's squirrels) both have a high potential to affect MGRS population dynamics.

Through our analysis of land cover classification of MGRS middens we found that middens occur in areas of denser and healthier forest with greater seed production than unoccupied areas. Our analysis indicated insect damage and catastrophic wildfire have significantly reduced available midden/territory habitat and therefore the number of squirrels that could live in spruce-fir forests.

Our modeling efforts were improved by the inclusion of habitat heterogeneity, which allowed us to model disturbance. We predict that the future MGRS population will not fluctuate as much as in the past twenty years, most likely due to the loss of the spruce-fir forests. We discovered even low levels of insect damage and fire have the potential to drive the population to critical levels and that frequency of fires had a larger impact than the size of fires.

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**APPENDIX A: MODELING THE POPULATION DYNAMICS OF THE MT.  
GRAHAM RED SQUIRREL: CAN WE PREDICT ITS FUTURE IN A  
CHANGING ENVIRONMENT WITH MULTIPLE THREATS?**

**ABSTRACT**

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; MGRS) is among the most critically endangered mammals in the United States and is isolated on the periphery of the species' range, potentially increasing its conservation priority. To investigate potential threats to the population and provide a tool for land managers, we developed a spatially explicit population dynamics model. We tested model predictions using available range-wide data from the literature and fieldwork specific to the MGRS. An input data set using general mean life history values overpredicted MGRS abundance. However, we found significant correlation with known squirrel abundance using a general data set with curtailed fecundity and survival. A model with MGRS-specific data provided the best fit to observed population size. We investigated potential impacts of two major threats to the MGRS: competition from introduced Abert's squirrels (*Sciurus aberti*) and increased levels of predation. Predation and particularly competition could have significant effects on the future population of the MGRS. Careful attention must be used to model the viability of fringe populations as peripheral populations can have a different life history than populations found in the range core.

## INTRODUCTION

Effective management of any endangered population requires a thorough understanding of factors impacting population dynamics. These factors include not only proximal, human-driven causes of decline such as habitat loss, but also interspecific interactions and the relative contribution of innate life history characteristics that ultimately drive population dynamics. Red squirrels (*Tamiasciurus hudsonicus*) are common inhabitants of forests of North America (Steele, 1998). Their distribution in the western United States extends through the Rocky Mountains to a southern terminus in the arid lands of southeastern Arizona. At the terminus the distribution of red squirrels becomes fragmented into montane islands of high elevation forest in the Pinaleno Mountains, Graham County, Arizona, USA (Brown, 1984a). The southernmost population, the Mt. Graham red squirrel (*T. h. grahamensis*), is endemic to the Pinaleno Mountains, and as a peripheral population (Lesica and Allendorf, 1995; Vucetich and Waite, 2003) has greater conservation priority due to potentially unique characteristics.

The Mt Graham red squirrel (MGRS) is restricted to about 12,200 ha of coniferous forest from 2,362 m elevation to a summit of 3,267 m (Hatten, 2000). The area where the MGRS occurs is dominated by Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) at the highest elevations, with Douglas-fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*) becoming more frequent as elevation decreases (Hutton et al., 2003). Conifer seeds of these four species are the main food resource for MGRSs. The population is separated by > 100 km of low elevation desert scrub and grassland from populations of *T. h. lychnuchus*, the

nearest related subspecies (Brown, 1984b). MGRSs gained notoriety associated with efforts to construct an astrophysical complex in the late 1980s and the subspecies was protected under the United States' Endangered Species Act in 1987 (Fish and Wildlife Service, 1993; Istock and Hoffmann, 1994; Warshall, 1994). Despite > 15 yrs of legal protection, abundance remains low, down to 214 from a high of 562 squirrels in 1999, and the population faces several threats to the extent that it is considered critically endangered by the IUCN (Belitsky, 2000).

One threat to the MGRS is competition by Abert's squirrels (*Sciurus aberti*), an introduced tree squirrel (Fish and Wildlife Service, 1993). Abert's squirrels may competitively exclude MGRSs from some environments (Minckley, 1968; Gehlbach, 1981; Brown, 1984a; Hoffmeister, 1986; Fish and Wildlife Service, 1993; Hutton et al., 2003). Abert's squirrels may reduce food resources for MGRS (Nash and Seaman, 1977; Brown, 1984a; Edelman and Koprowski, 2005) because there is considerable dietary overlap between the species (Steele, 1998; Hutton et al., 2003). Abert's squirrels may also kleptoparasitise middens (larderhoards) of red squirrels (Ferner, 1974; Hall, 1981; Hutton et al., 2003) resulting in a direct loss of cached food resources. The impact on red squirrels may be significant since *Sciurus aberti* are known to reduce cone crops by as much as 74% due to herbivory and granivory (Larson and Schubert, 1970; Snyder, 1990; Allred et al., 1994).

Forest management can also impact the MGRS. Thinning operations that open forest canopy to reduce fire risk may change microclimates and increase predation (Hakkarainen et al., 1997; Carey, 2002; Thompson et al., 2003). A diversity of

mammalian and avian predators are known for the MGRS (Hoffmeister, 1956; Schauffert et al., 2002) and evidence across the geographic range of the species suggests that predation significantly impacts population size, accounting for 19-70% of mortality (Kemp and Keith, 1970; Rusch and Reeder, 1978; Wirsing et al., 2002).

Spatially explicit population models (SEPMs) have successfully been used to predict dynamics of squirrel populations (Rushton et al., 1999; Lurz et al., 2003), their spatial spread (Rushton et al., 1997; Lurz et al., 2001), and impacts of different management regimes (Rushton et al., 2002; Lurz et al., 2003). Furthermore, SEPMs can be used to explore site-specific management impacts (Lurz et al., 2003). Here we develop a SEPM to investigate dynamics of MGRSs in relation to the key population drivers. SEPMs require detailed information on life history patterns (Conroy et al., 1995; Ruckelshaus et al., 1997). Area or population specific data are not always available for some life history parameter ranges and general species data from comparable populations in other geographical locations are often used in population modeling of this type (Howells and Edward-Jones, 1997; Mladenoff and Sickley, 1998; South et al., 2000; Buenau and Gerber, 2004). However, it is unclear if data derived from studies of populations within a species' main distributional or 'core' range can adequately predict demography of fringe populations such as the MGRS population in the Pinaleno Mountains. This may be significant if these populations differ genetically and/or demographically, as is often the case in peripheral populations (see Hoffmann and Blows, 1994; Lomolino and Channell, 1995). Our objective was to create a SEPM that could be used for the conservation of the MGRS and use this model to evaluate potential threats.

To this aim, we collected life history data from literature that covers the entire geographical range of the red squirrel and data from surveys of the MGRS population. Using data on population fluctuations of MGRSs, we tested multiple life-history scenarios and performed an analysis to determine which life history set best describes the population dynamics of MGRSs. Using the best model, we investigated the potential effects of competition by introduced Abert's squirrels and increased predation levels linked to changes in forest management.

## **METHODS**

We used the previously successful approach of Rushton et al. (1997; 1999; 2000; 2002) and modeled: maximum dispersal distance, the maximum distance over which males would search to find a mate, adult mortality, juvenile mortality, fecundity (litter size), and the proportion of females breeding. We added an additional variable for cache size to represent the larder-hoarding strategy of *T. hudsonicus* (Gurnell, 1984).

### **Description of the Model**

The model had two main components: The first component was the Geographic Information System (GIS), which stored the position of home ranges in the landscape. Secondly, an individual-based population dynamics model simulated individual life histories and dispersal within the GIS-held landscape. Our population model was written in the programming language C and integrated with the GIS component through a UNIX-shell environment (Rushton et al., 1997; Rushton et al. 1999). The model was stage-

structured (Caswell, 2001), in so far as discrete stages were recognised in the population, but the life history processes of mortality, fecundity and dispersal were modelled stochastically at the level of the individual within the different age classes. Coordinates of each available midden in each year were used as the spatial reference point with which to model dynamics of individuals. We assumed squirrels would occupy home ranges centred on a midden site and an individual squirrel could occupy each midden within the landscape (Steele, 1998). Two age classes were modelled, adults and juveniles. We modelled the life history of each squirrel on a monthly time step. Middens known to have been destroyed by fire were removed from the available ‘midden pool’ following these events.

Reproduction occurred once a year in April (month 4: Koprowski, 2005). The proportion of females breeding was varied as a model input. Females were allowed to breed subject to the availability of a male within the maximum mating distance. This distance over which males were allowed to travel for mating was varied as an input. We estimated the number of young produced in each litter by drawing deviates from a Poisson distribution whose mean was varied as a model input (following Akçakaya et al., 1995; Rushton et al., 2000). The sex ratio of young was assumed to be 50:50 (Steele, 1998).

We modelled mortality in each month at the individual level for adults and juveniles. Probability of death for each individual was determined by sampling deviates from a uniform distribution in the range 0 to 1, with mortality occurring if the deviate was in the mortality range. Thus, for an individual subjected to adult mortality of 4.0%,

all deviates in the range 0 to 0.96 corresponded to the individual surviving, those greater than 0.96 and up to 1.0 to it dying.

Mortality and fecundity in tree squirrels are strongly linked to food supply (e.g. Koprowski, 1991), but their effects on population size and viability will be buffered by cached food. We modeled the size of the cache and its exploitation explicitly, with cache size varied as an input. Cache size was modeled in terms of months over which food stored in the cache would last. It was assumed that in good seed years squirrels create midden caches that are larger and effectively provide food for a longer period into the next season than would years with low seed production (Gurnell, 1984, 1987; Steele, 1998). We assumed adults would utilize other food sources when caches were depleted and therefore only modeled a direct food dependant mortality effect for juveniles (Barkalow et al., 1970; Koprowski, 1991). While food was available in a squirrel's midden, the associated juvenile squirrels were subjected to reduced mortality and adults to increased fecundity relative to periods of higher mortality and reduced fecundity when all stores had been consumed.

Most dispersal of young and sub-adult squirrels takes place in autumn so we modeled dispersal in August, September and October (months 8, 9, and 10). All young stayed in their mother's natal area until dispersal. We assumed for simplicity that the maximum dispersal distance modeled applied to both sexes. The dispersing animal sampled the landscape up to a maximum dispersal distance from their natal home range and settled at an existing empty midden location within the landscape. Any animal that could not find a home range was assumed to have perished in the landscape.

## **Parameterizing the Model**

Midden sites were derived from field surveys of the Pinaleño Mountains (Hatten, 2000; Buenau and Gerber, 2004). A total of 1293 known midden locations were available for squirrels in the simulation scenarios. We assessed midden occupancy from 1991 to 2004 by visiting the conspicuous cone scale piles (Finley, 1969) and noting sign of active cone caching and feeding (Rasmussen et al., 1975; Mattson and Reinhart, 1996). A 1996 fire in the Pinaleño Mountains severely damaged 39 middens, removing these sites as possible larderhoard locations (Froehlich, 1996), and we removed them as possible sites within the model simulation in the appropriate year.

Ranges for life history parameters and cone crops for the MGRS were obtained from yearly monitoring efforts, current work in the Pinaleño Mountains, and MGRS specific literature (see Table 1: Young, 1990; 1991; Young et al., 1992; Stromberg and Patten, 1993; Young et al., 1993; Young et al., 1994; Young et al., 1995; Kreighbaum and Van Pelt, 1996; Young et al., 1996; Young et al., 1997; 1998; Young et al., 1999; Koprowski et al., 2000, 2001; Koprowski et al., 2002, 2003; Miller and Yoder, 2008; Koprowski, 2005; Frank, 2008). Proportion of animals breeding was assessed by observation of individuals for evidence of lactation or scrotal testes. Fecundity (litter size) was assessed by repeated observation of juveniles emerging from nests. Beginning in 2001, squirrels were live-trapped, ear tagged, and radio-collared (reviewed in Koprowski, 2002; Koprowski, 2005). Weekly monitoring of animals by radio-telemetry permitted quantification of adult survival (proportion of adults surviving interval) and enabled us to monitor maximum distance moved by males to find a mate. Juvenile

dispersal distances were calculated from known dispersal movements by ear tagged juveniles from natal middens. Up to 1992, seed crops were assessed qualitatively as either 'poor' or 'good'. Seed production since 1993 was estimated from the same 28 (19 spruce-fir, 9 mixed-conifer) plots distributed among monitored areas (Koprowski et al., 2005). Three 0.25 m<sup>2</sup> seed traps were randomly placed within a 10 m x 10 m plot at each location. Seeds for a given year were collected from seed traps in spring of the following year. Conifer seeds contained in each trap were separated and tallied by species. Years were classified as 'poor' or 'good' by natural dichotomies (Table 2).

The same suite of life-history parameters was obtained from literature for red squirrel populations from central Arizona to Alaska (Hamilton, 1939; Layne, 1954; Smith, 1967; Wood, 1967; Smith, 1968b; Davis, 1969; Krasnowski, 1969; Wrigley, 1969; Kemp and Keith, 1970; Millar, 1970; Zirul, 1970; Davis and Sealander, 1971; Modafferi, 1972; Dolbeer, 1973; Ferron and Prescott, 1977; Kelly, 1978; Rusch and Reeder, 1978; Halvorson, 1982; Halvorson and Engeman, 1983; Erlein and Tester, 1984; Gurnell, 1984; Lair, 1985; LaPierre, 1986; Boutin and Schweiger, 1988; Sun, 1989; Klenner, 1990; Sullivan, 1990; Uphoff, 1990; Boutin and Larsen, 1993; Larsen and Boutin, 1994; Berteaux and Boutin, 2000; Humphries and Boutin, 2000; Anderson and Boutin, 2002; Wheatley et al., 2002; Haughland and Larsen, 2004). Values from this set were used in one instance in the specific MGRS life history collection where MGRS specific data were scarce (juvenile survival) but the one value available from the MGRS population was in the range of values from the general literature.

### **Running the Model**

We used Latin Hypercube Sampling (LHS) to generate suites of life history inputs from each parameter in the general red squirrel and MGRS specific data ranges (Table 3), following the methodology of Rushton et al. (2000). Five hundred sets of inputs were randomly generated based on a uniform distribution. For each set, values were randomly selected over the observed minimum to maximum range of each life history parameter to capture the whole universe of probable inputs. We randomly allocated 348 adult squirrels, the known population size in 1986, into the 1293 available middens with sex varied at random. An even sex ratio was assumed. We investigated persistence of red squirrels over 20 years for MGRS and general red squirrel inputs. The final population predicted at year 20 was used as a variable in a partial correlation analysis against the life history parameters used in each run to generate sensitivity analysis results for each life history collection.

We compared general input range based on *T. hudsonicus* literature and a MGRS specific range. We also created a series of curtailed general ranges to reflect reduced fecundity and survival found at the edge of a species range. The fit of model predictions based on these scenarios was compared to observed population census data (1987-2002).

The potential impact of Abert's squirrels on food availability was modeled by reducing the available cache size to individual red squirrels. Based on the best fit model (Table 4) we investigated possible reductions in food availability and thus cache size using observed reductions in cone crops due to Abert's squirrels (Larson and Schubert, 1970; Snyder, 1990; Allred et al., 1994). We simulated an increase in Abert's squirrel

competition through a reduction in the available cached food by 20, 56 and 74% (min, max, and midpoint of observed effect published in the literature). We also considered that Abert's squirrels might currently have an impact on MGRSs and predicted population size based on food cache increases of 20, 56 and 74% (potential but not maximal increases) should Abert's squirrels be removed from MGRS range.

Effects of increased predation on population size were investigated by imposing additional mortality on adults. Increases in predation rates by avian predators were simulated by increasing adult mortality for the months (Oct.-May) that raptors are known to have taken red squirrels on the mountain. The magnitude of likely increases in predation rates for the MGRS in the Pinaleno Mountains due to opening of the forest canopy as a result of fire prevention measures is unknown. We therefore explored two plausible scenarios covering increases of 5 and 10% in mortality rates as observed for another red squirrel population in response to high levels of predation (Wirsiing et al., 2002).

## **RESULTS**

### **Sensitivity Analysis**

The variables that were significant determinants of predicted population size depended on the life-history data set used in the model. Using the general life-history data set, adult mortality ( $f = 150.51$ ,  $p < 0.001$ ) and duration of cache ( $f = 30.87$ ,  $p < 0.001$ ) were the most significant life-history (model  $r^2 = 0.27$ ). For the MGRS-specific analyses (model  $r^2 = 0.67$ ) adult mortality ( $f = 561.19$ ,  $p < 0.001$ ) and duration of cache ( $f = 360.95$ ,  $p < 0.001$ ) were also significant. However, the results of the sensitivity analysis

using the MGRS life-history data set (Fig. 1) were also significant for three variables connected to reproduction for good years: juvenile mortality ( $f = 20.38$ ,  $p < 0.001$ ), fecundity ( $f = 24.13$ ,  $p < 0.001$ ), and proportion of females breeding ( $f = 29.07$ ,  $p < 0.001$ ). This indicates that the relative importance of life-history parameters differed between the two data sets. In effect the observed MGRS-specific data set indicate a constraining influence of variables linked to reproduction on population size.

### **Model Testing**

A general life history range (Table 1) vastly overpredicts MGRS numbers (Fig. 2a). Results from model simulations give a significant correlation of observed and predicted population estimates for the curtailed general range with reduced fecundity ( $r = 0.539$ ,  $p < 0.03$ : Table 4, Fig. 2a) and particularly the MGRS scenarios ( $r = 0.741$ ,  $p < 0.001$ : Table 1, Fig 2b).

### **Impacts of Aberts Squirrel and Predation on Population Size**

Competition for food and impacts of Abert's squirrels on seed or cone production has the potential to reduce population viability of MGRSs (Fig. 3). We also considered potential changes to another major life-history variable driving the red squirrel population dynamics in the Pinaleño Mountains – adult mortality. Based on plausible scenarios, both increased predation and competition from Abert's squirrels can have significant negative consequences. At the levels simulated, the potential impact of Abert's squirrels

competition is surprisingly high. Increases in predation of the MGRS led to considerably lower population levels (Fig. 4).

## **DISCUSSION**

What can modelling tell us about the population dynamics of MGRSs and future management? Firstly, strong agreement exists between predicted and observed population densities for squirrels from 1987 to 2002, but only for data generated on the Pinaleno Mountains, or where the generalized life history data were constrained at levels lower than the mean for the species over its full geographical range.

Results of sensitivity analyses were different for general life history and MGRS specific model runs. Whilst adult mortality and duration of cache size were significant predictors of population size for both sets of model runs, other reproductive parameters were significant predictors of population size for the MGRS population. This suggests that many aspects of the population dynamics of squirrels were of critical importance for the MGRS population. These results also suggest that MGRSs might be more susceptible to extinction since deviation in any one of the demographic variables is likely to result in changes in population size. We found large differences in fecundity and mortality for red squirrels (Table 5) and variation in life history patterns for populations at the edge of the species range in relation to the core range have been documented for other species (Aldridge and Brigham, 2001). Populations at the edge of their range may also show genetic (Vucetich and Waite, 2003), and morphological differences (Lesica and

Allendorf, 1995). Furthermore, abundance in peripheral populations is often lower and more variable than in core populations (Hengeveld and Haeck, 1982; Brown, 1984b).

The red squirrel gives us the unique opportunity to study a system where the core and fringe of the population are still extant. In many conservation situations we may be limited to data derived from previous studies focused on the core population. However, it is peripheral populations that are more likely to remain than core populations in cases of anthropogenic-caused extinctions (Lomolino and Channell, 1995). In modeling for conservation purposes we need to be concerned with how to model populations on the periphery of a species range and be aware of the differences between core and peripheral populations, since models that do not take into account local demographic patterns are unlikely to recapitulate system behavior or to be accurate predictors of the impact of management. Whilst previous modeling attempts worked well with general literature data for populations in habitats typical for the species' distribution range (e.g. Howells and Edward-Jones, 1997; Rushton et al., 1997; Mladenoff and Sickley, 1998; Rushton et al., 1999; South et al., 2000) our results indicate caution may have to be exercised when predicting dynamics of fringe populations.

Assessing the relative significance of current levels of predation and interspecific competition for the Mt Graham red squirrel is difficult because the two variables are confounded. We addressed this issue by estimating the proportion of known kills in the population over the period 2002-2005 and also by assessing how much of the total cone crop could have been removed by the competing Abert's squirrel and then manipulated the impacts of increases in competition or predation in the model proportionally. The

most interesting feature is that competition with the non-native has the potential for a much greater impact on squirrel population size than plausible increases in predation. This is a situation mirrored in the UK where the introduced gray squirrel (*Sciurus carolinensis*) poses a similar threat to the red squirrel (*Sciurus vulgaris*) and has led to extensive declines in range (Gurnell et al., 2004) whilst predation from reintroduced predators such as goshawks has had limited impact (Petty et al., 2003).

For conservation and management, our SEPM illustrates the most important need is to understand the relationships between MGRSs and its habitat at a local scale. Importantly the model emphasizes the need to understand the relationship of predation and resource availability, including interspecific competition, to MGRS mortality. MGRSs face a difficult future, as habitat is lost to a variety of disturbances. Insect damage has reduced available resources in large sections of the spruce-fir forest (Koprowski et al., 2005) and large catastrophic wildfires (such as in 2004: Koprowski et al., 2006) are still a threat (USDA Forest Service, 2000). Incorporating these processes into our initial model will lead to a more accurate tactical tool that will allow conservation managers to minimize the likelihood of extinction of the MGRS.

The MGRS appears to be a species that suffers from being endemic to a small isolated mountain range at the periphery of its range and subject to multiple threats from habitat loss, forest disturbance, and interspecific competition. In a sense, MGRSs are a paradigm for imperiled mammals. The conservation of many species will stand or fall based on our ability to manage multiple threats. European red squirrels are threatened by an introduced species and disease (Tompkins et al., 2002; Gurnell et al., 2004), Delmarva

fox squirrels (*Sciurus niger cinereus*) combat habitat degradation and fragmentation (United States Fish and Wildlife Service, 2003), large carnivores face threats of habitat loss and poaching in the Rocky Mountains (Noss et al., 1996), arctic foxes (*Alopex lagopus*) are imperiled by the loss of the wolf (*Canis lupus*), climate change, and increased red fox (*Vulpes vulpes*) density (Hersteinsson et al., 1989), and multiple threats are seen frequently for island populations (e.g. Cuaron et al., 2004). Our model has shown that future work should move some focus to monitoring the effects of competition and predation on the MGRS. Detailed raptor surveys and monitoring of the introduced Abert's squirrel, could aid the population by alerting managers of increased risks. Actions can then be taken against these threats. In addition, the relationship between resource availability (whether fresh cones are available in larderhoards) and life history is important. Careful monitoring of cone crops and the effects of climate, natural and anthropogenic influences on crop size are important for conservation of MGRS. We believe that modeling of the form reported here has a major role in determining the relative significance of different conservation threats and offers real opportunities for enhancing conservation through prioritizing potential intervention.

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Table A1, Life history parameters of Mt Graham red squirrels, Pinaleño Mountains, Arizona and literature averages for red squirrels across their range

Parameter	Mt. Graham Specific			Literature Average		
	Mean	Min	Max	Mean	Min	Max
Adult mortality (%) <sup>a</sup>	47	22	73	34.73	26.8	47
Juvenile mortality (%) <sup>b</sup>	50			61.82	25	81
Fecundity (num/litter)	2.35	1	5	3.69	1	7
Females breeding (%)	56	29	99	77.14	47	99
Max mate distance (m) <sup>c</sup>	418.7	92	923			
Dispersal distance (m)	460.5	0	1885	257	0	4500

<sup>a</sup> Estimates for Mt. Graham red squirrel adult mortality were generated from trapping efforts and telemetry data rather than overwinter survival or turnover.

<sup>b</sup> Only one mortality study was performed on juveniles of the Mount Graham red squirrel (Kreighbaum and Van Pelt, 1996).

<sup>c</sup> No maximum mate distance data were found in collected literature and our estimate represents maximum movements of radio-collared Mount Graham red squirrel males during the breeding season.

Table A2, Cone crop ratings from  
1987 to 2002, Pinaleño Mountains,  
Arizona.

Year	Crop Rating
1987	Poor <sup>a</sup>
1988	Poor <sup>a</sup>
1989	Poor <sup>a</sup>
1990	Good <sup>a</sup>
1991	Poor <sup>a</sup>
1992	Poor <sup>b</sup>
1993	Good <sup>c</sup>
1994	Poor <sup>c</sup>
1995	Poor <sup>c</sup>
1996	Poor <sup>c</sup>
1997	Good <sup>c</sup>
1998	Poor <sup>c</sup>
1999	Poor <sup>c</sup>
2000	Poor <sup>c</sup>
2001	Good <sup>c</sup>
2002	Poor <sup>c</sup>

<sup>a</sup> Based on Engelmann Spruce cone counts (Stromberg and Patten, 1993);

<sup>b</sup> Personal Communication with Vicki. L. Greer, University of Arizona;

<sup>c</sup> seed trap data

Table A3, Mount Graham red squirrel life history parameter ranges input for a sensitivity analysis of a spatially explicit population model (G=good; P=poor).

Parameter	General red squirrel		Mt. Graham red squirrel	
	Min	Max	Min	Max
Fecundity (G) (young/female)	3.7	7	2.6	5.0
Fecundity (P) (young/female)	1	3.6	1.0	2.5
Females breeding (G) (%)	47	79	56	99
Females breeding (P) (%)	79	99	29	56
Adult mortality (%)	26.8	47	22	73
Juvenile mortality (G) (%)	25	62	25	60
Juvenile mortality (P) (%)	62	81	60	81
Litter frequency (per year)	1	1	1	1
Dispersal distance (m)	0	4500	0	4500
Max mate distance (m)	92	923	92	923
Food cache size (months)	2	18	2	18

Table A4, Input parameter ranges for validation of spatially explicit red squirrel model for two data sets. The parameter range for the general red squirrel data set is the curtailed range that represents an average to poor range for the red squirrel.

Parameter	General red squirrel		Mt. Graham red squirrel	
	Good	Poor	Good	Poor
Fecundity (young/female)	3.69	2.77	3.0	2.35
Adult mortality (%)		0.34		0.46
Juvenile mortality (%)	0.61	0.81	0.50	0.81
Proportion breeding (%)	0.77	0.47	0.99	0.56
Cached food (months)	6	16	6	16
Max mate distance (m)		923m		923m
Dispersal distance (m)		4500m		4500m

Table A5, Comparison of critical life history traits for red squirrels generated from literature averages (min, max, and mean) and for studies of the endangered Mt. Graham red squirrel (MGRS). SD difference shows the deviation of the MGRS value and the literature mean.

	Min	Max	Mean	MGRS	SD difference
Adult mortality	26.8	47	34.73	47	1.66
Fecundity	2.77	5.4	3.69	2.35	1.46

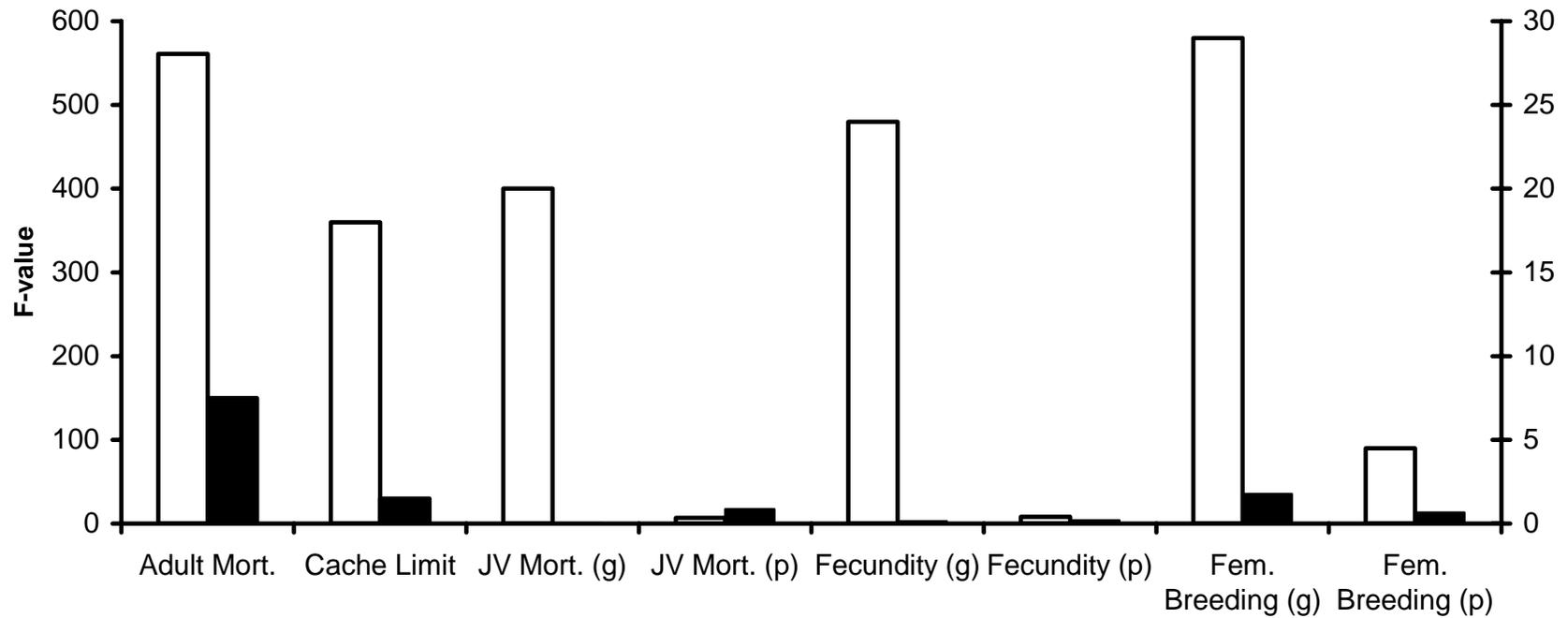


Figure A1. Plot of F-values (absolute value) of sensitivity analysis results for red squirrels, illustrating the relative importance of different life history parameters for a model populated by general red squirrel (filled bars) and Mt. Graham red squirrel (unfilled bars) life-history parameters. Adult mortality and cache size are plotted on the primary axis (left) and juvenile mortality, fecundity, and proportion females breeding are plotted on the secondary axis (right). In a good cone year parameters are indicated by a 'g' and in a poor cone year with a 'p'.

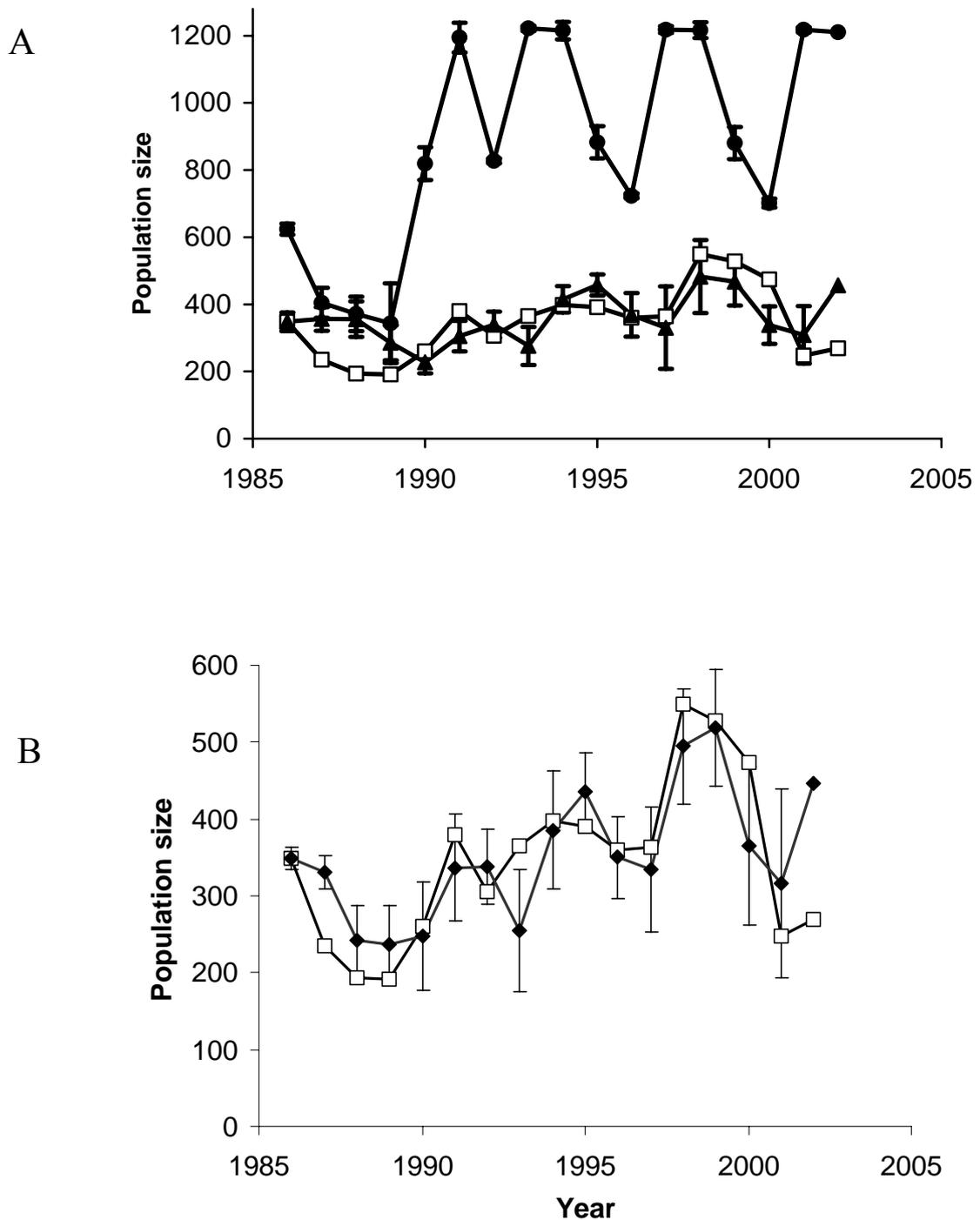


Figure A2, Spatially explicit population model predictions for red squirrels: a) Comparison of observed (open squares) and predicted population estimates (mean  $\pm 1$ SD) using general (closed circles) and a curtailed general (closed triangles:  $r = 0.539$ ,  $p < 0.03$ ) life history data sets and b) comparison of observed (open squares) and predicted population estimates (mean  $\pm 1$ SD) using Mt. Graham red squirrel specific (closed diamonds:  $r = 0.741$ ,  $p < 0.001$ ) life history ranges.

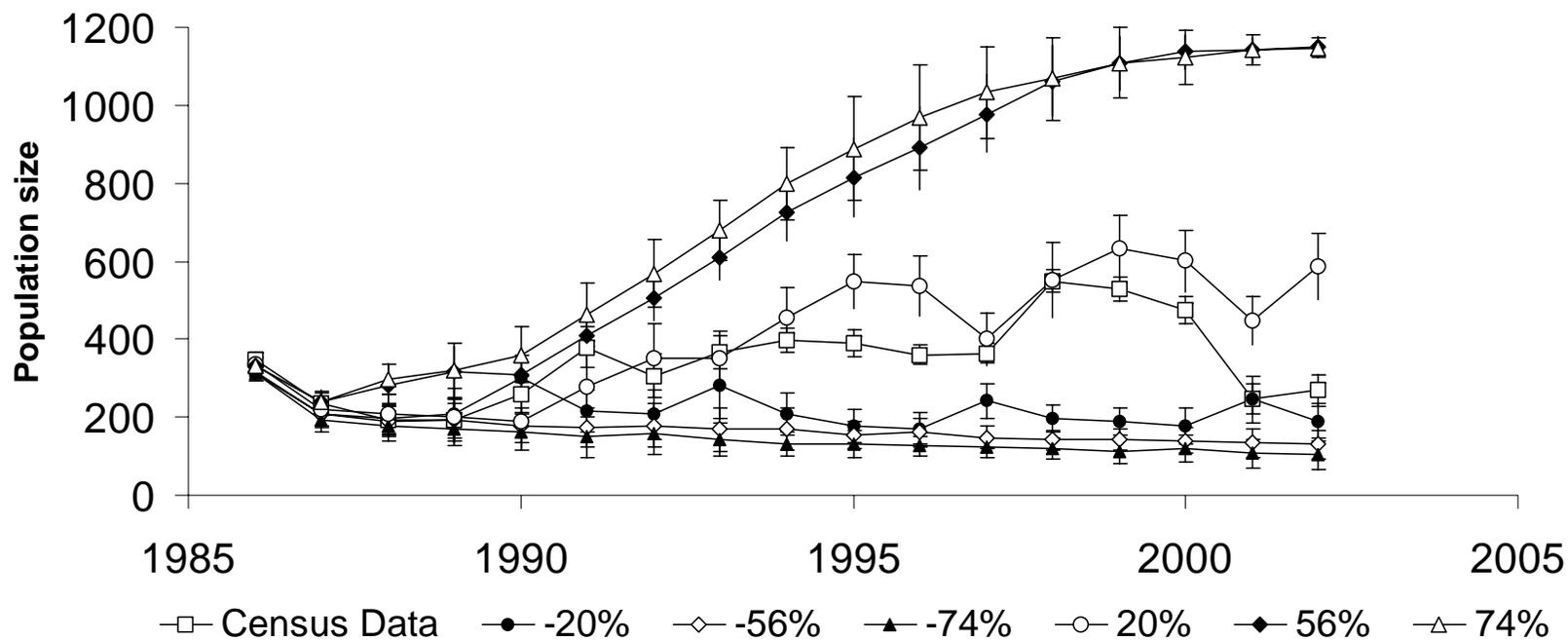


Figure A3, Spatially explicit population model predictions for Mt. Graham red squirrel population sizes (mean  $\pm$ 1SD) illustrating possible impacts of cache size reductions and increases from 1986 to 2002 due to Abert's squirrel foraging compared to observed population sizes (census data).

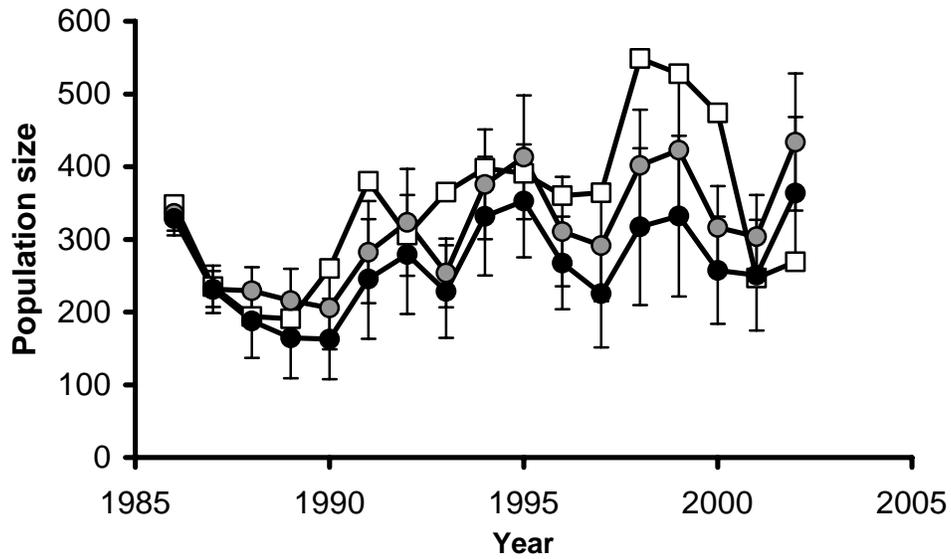


Figure A4, Observed (open squares) and predicted Mount Graham red squirrel population sizes (mean $\pm$ 1SD) illustrating the impact of increased predation levels of 5% (grey circles) and 10% (closed circles). Predictions generated by a spatially explicit population model developed for the Mt. Graham red squirrel.

## **APPENDIX B: FINE SCALE ANALYSIS OF MOUNT GRAHAM RED SQUIRREL HABITAT FOLLOWING DISTURBANCE**

### **ABSTRACT**

Habitat destruction and degradation are major factors in reducing abundance, placing populations and species in jeopardy. Mitigation of the effects of human caused or amplified habitat disturbance can be assisted by monitoring changes to habitat by disturbance and through identifying conditions that constitute habitat for a species. The Pinaleno Mountains of southeastern Arizona, USA have suffered catastrophic fire and large scale insect outbreaks in the last decade and are the only home of the federally endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*). We modeled potential Mt. Graham red squirrel habitat by identifying characteristics of cover surrounding their centrally defended larderhoards to assess effects of forest disturbance on habitat. We classified high spatial resolution satellite imagery into ground cover classes and used logistic regression to determine areas used by squirrels. We also used midden locations in conjunction with slope, elevation, and aspect variables to create a predictive habitat map for Mt. Graham red squirrels. Squirrels selected areas of denser forest with higher seedfall for midden sites. Among active middens, those in the densest and least damaged forests were occupied in more seasons than those in more fragmented and damaged areas. The future conservation of red squirrels and the return of healthy old-growth forests to the Pinaleno Mountains will rely on management in mixed conifer zones of the mountain and active restoration of highly damaged upper elevation spruce-

fir forests to return them to squirrel habitat. Our ability to evaluate the spectrum of fine- to coarse-scale disturbance effects (individual tree mortality to the area wide boundaries of a disturbance) with high-resolution satellite imagery shows the utility of this technique for monitoring future disturbances to habitat of imperiled species.

## **INTRODUCTION**

Anthropogenic habitat destruction and degradation reduce abundance, increasing risk of extinction through demographic, genetic, and environmental stochasticity, and natural catastrophe (Shaffer, 1981; Soulé, 1987). Due to human impacts, extinction rate is estimated at between 48 and 11,000 times higher than the background rate (Baillie et al., 2004). Anthropogenic habitat destruction and degradation is a major threat to >85% of threatened mammals, birds and amphibians and severely impacted 13 of 27 extinctions since 1984 (Baillie et al., 2004). A difficulty in reversing this trend is that landscapes are dynamic; natural disturbance is an integral part of ecosystem function (Knight, 1987). Habitat must be preserved to conserve species, however, identification of what constitutes quality habitat and monitoring habitat disturbance is necessary for conservation.

The low spatial resolution of data for parameters used in models hampers the ability to capture fine-scale differences important to species, so we examine the extent to which high-resolution imagery predicts habitat. Furthermore, the difficulty of identifying and measuring selection of habitat is critical to model accuracy and usefulness for conservation. We built models of the basic ecological needs of a species by using the

location of territories and conspicuous cone larderhoards, middens, of territorial Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*: MGRS) as indicators of squirrel presence. Middens are positioned to acquire, store, and protect resources, integrating needs of the species. MGRS are territorial and defend middens to provide food for winter and in years of a poor cone crop (Finley, 1969). Middens help red squirrels protect their food store by concentrating food, which facilitates repelling competitors, while providing a cool, moist microclimate that keeps cones closed, and prevents other seed predators from accessing seeds (Smith, 1968a; Gurnell, 1987). Generally territories are circular, surrounding the midden for maximum foraging efficiency and territories are critical to survival as squirrels gather most cones from them for storage (Finley, 1969; Rusch and Reeder, 1978).

Arboreal rodents are excellent indicators of forest productivity, stability, and connectedness (Carey, 2000; Steele and Koprowski, 2001), and tree squirrels are excellent models for studies in behavior, population ecology, and conservation (Steele and Koprowski, 2001). Responses of tree squirrels to forest disturbance can then be used to elucidate overall damage and quality of old-growth forests after disturbance. MGRS, a federally endangered tree squirrel (USDI Fish and Wildlife Service, 1993), are found only at upper elevations in the Pinaleño Mountains, southeastern Arizona. MGRS have an estimated population <300 squirrels and are one of the most critically endangered mammals in North America. In 1988, the USDI Fish and Wildlife Service established a refugium to restrict access to critical habitat (USDI Fish and Wildlife Service, 1993). MGRS inhabit high elevation spruce-fir forests of Engelmann spruce (*Picea engelmannii*)

and corkbark fir (*Abies lasiocarpa* var. *arizonica*), and mixed conifer forests of Douglas-fir (*Pseudotsuga menziesii*), pines (*Pinus ponderosa*, *P. strobiformis*), Engelmann spruce, and corkbark fir.

The Pinaleño Mountains are a microcosm of forests in the western US, as recent increases of insect and fire disturbance (Koprowski et al., 2005; Koprowski et al., 2006b) mimic forest conditions elsewhere (Allen et al., 2002; Lynch, 2004). Holocene warming has restricted spruce-fir and mixed conifer forests to the highest elevations in the southwest (Lomolino et al., 1989). MGRS persisted for >10,000 years despite multiple large disturbances in the Pinaleño Mountains (Grissino-Mayer and Fritts, 1995), but face anthropogenically amplified disturbances. Catastrophic wildfires burned in 1996 (Froehlich, 1996) and 2004 (Koprowski et al., 2006b), and large insect outbreaks damaged spruce-fir forests (Koprowski et al., 2005). Past efforts identified habitat on Mt. Graham (Pereira and Itami, 1991; Hatten, 2000), but an evaluation of current conditions following forest disturbance is needed for conservation.

MGRS middens meet a combination of basic ecological needs. By modeling midden locations we can accurately describe available habitat to make informed management and conservation decisions. Herein, we first classified ~110 km<sup>2</sup> of high-resolution satellite imagery to assess land cover in the Pinaleño Mountains. We combined the classified image with midden occupancy data to elucidate size and composition of forest patches used for middens. We used classified cover types to predict seedfall, and related patch characteristics and seedfall to midden occupancy. Finally, we combined spatial data for occupied middens to predict potential MGRS

habitat and evaluate use of high-resolution imagery for habitat analysis. Predicted habitat was compared to areas previously described as highest quality by prior habitat models to examine forest disturbance effects on habitat quality and availability to MGRS.

## **METHODS**

### **Satellite Imagery**

We acquired QuickBird satellite imagery (DigitalGlobe, Inc.) in June 2003 for an area covering all potential habitat for MGRS by applying a 200 m buffer in ArcGIS 9.1 (Environmental Systems Research Institute, 2005) to the area delineated by Hatten's (2000) MGRS habitat map. We performed a Gram-Schmidt pansharpening to convert 2.4m multispectral bands to the 0.6 m resolution of the panchromatic data. For finer discriminations of vegetation density, we calculated Normalized Difference Vegetation Index (NDVI: Tucker, 1979), and used principal components analysis to reduce data dimensionality (PCA: Jensen, 2005).

Our aim was to classify ground cover classes from the image that enabled us to separate live, healthy trees from dead or dying trees. We used the isodata unsupervised classification procedure in ERDAS Imagine 8.6 (ERDAS, 2003) on several combinations of input layers, including the original four spectral bands, the NDVI layer, and the first three principal components from the PCA. The most satisfactory classification resulted from a combination of the first three principal components from a PCA of bands 1-4 of the Gram-Schmidt pansharpened multispectral image. Nine separate land cover classes were mapped in the study area: 1) large healthy conifers, 2) small healthy trees or shrubs,

3) dying or dead trees, 4) cienega, grass, or aspen, 5) tan or light soil, 6) bright rock, 7) asphalt road, dark soil, or dark rock, 8) deep shadow or lake, and 9) shadow. We are limited in extracting information from shadows but by visually examining these areas we deduced they were mostly composed of the unlit backside of live tree canopies, and are used in analyses as trees.

We selected 176 random locations to ground truth image classification. At each point, we recorded GPS coordinates, and estimated, to the nearest 10%, canopy cover and the amount of damage due to fire and insect infestation (percentage of trees killed by each) within a 10 m radius around each point. Because we could only verify accuracy of random points to within 10 m of its corresponding location in the satellite image, we computed image based canopy cover and damage measurements for all locations  $\leq 10$  m from each random point. Canopy cover at each point was determined from the percentage of pixels classified as trees  $\leq 10$  away. Damage for a given point was determined by calculating the percentage of dead trees out of all trees  $\leq 10$  m from that point. Using these measurements, we determined and selected the best match for each ground truth point and computed accuracy by determining the difference between levels of damage and canopy cover from image classification and observed in the field.

### **Occupancy and Seedfall Data**

Location and condition MGRS midden sites have been monitored since 1986 by the Arizona Game and Fish Department (AGFD: Hatten, 2000). We monitored a subset of these middens more intensively by conducting ground surveys and recording midden

occupancy quarterly (see Koprowski et al., 2005). We used signs of activity to determine midden occupancy as occupied by an animal of unknown sex, occupied by a male, occupied by a female, or unoccupied (Koprowski et al., 2005). We used occupancy data near the image acquisition date, creating nine sets of seasonal occupancy data (summer 2002 (June – August), fall 2002 (September – November), winter 2002-03 (December – February), spring 2003 (March – May), summer 2003, fall 2003, winter 2003-04, spring 2004, and summer 2004). Cone crop, directly related to and measured as seedfall, was assessed yearly for five tree species known to be eaten by MGRS (*Pinus ponderosa*, *P. strobiformis*, *Pseudotsuga menziesii*, *Abies lasiocarpa* var. *arizonica*, *Picea engelmannii*) from 28 seed traps dispersed among our more intensively monitored areas (Koprowski et al., 2005; Rushton et al., 2006).

### **Midden Site and Land Cover**

Midden site use may be based on local microclimate (cone storage) or on a larger scale (productive territory). Hence we examined three different sized areas around a midden to determine which size best predicts MGRS site use. We chose a 10 m buffer distance to mimic previous field studies (Smith and Mannan, 1994; Koprowski et al., 2005) and reflect microclimate conditions at the midden. We selected 28 m and 56 m buffers to represent the smallest and largest known red squirrel territory reported in the literature (Steele, 1998) to evaluate if middens are selected within a productive area. We created buffers around locations of our intensively monitored midden sites (n = 389) and counted the number of pixels of each of our nine satellite image determined land cover

classes in ArcGIS 9.1 (Environmental Systems Research Institute, 2005). We used random coordinates to identify non-midden sites for comparison with those we knew to be occupied by selecting random sites ( $n = 660$ ) within the same study area and performing the same buffering and counting operation.

### **Statistical Models of Occupancy and Turnover**

All statistical analyses were performed in R (R Development Core Team, 2006). Conditions around individual middens and random sites comprised different combinations of the nine land cover classes; each midden sat in the center of a circle with different amounts of each cover type. Relating midden occupancy to the area of individual cover types was not possible because of the unit area sum constraint. To avoid this problem and to reduce data dimensionality, we performed a PCA for all sites for each of the three buffer distances. The end goal was to produce principal components (PCs) summarizing habitat composition around each of our midden and random sites.

To evaluate composition differences due to buffer distance, we compared, with a Procrustes rotation, the first two PCs of the PCA rotations for the three different buffer distances. To examine sex differences in site use, we compared middens in a stepwise linear discriminant analysis on the PC scores for middens of each sex. PC1 was the only distinguishing variable (error rate = 0.42) and did not differ between the sexes ( $t = -1.297$ ,  $p = 0.21$ ), so occupied male and female middens were pooled for occupancy analyses.

Using logistic regression assuming binomial error structure we investigated the relationship between midden occupancy and habitat characteristics. The first four PCs derived from land cover counts surrounding midden and random sites (PC1, PC2, PC3, PC4) were used as independent predictor variables and sites, with point type (middens and random sites) as the dependent variable. We only used middens occupied in June 2003. Analyses were undertaken with all independent variables in combination and with simpler models by removing the PC axis explaining the least variation (models: PC1-4 (all 4 PCs), PC1-3 (PC1, PC2, and PC3), PC1-2 (PC1 and PC2), and PC1). Each midden set was compared to each of the four sets of PCs for each of the three buffer distances resulting in 12 models for each midden set.

We also used logistic regression to investigate differences in individual midden quality by examining how often a midden was occupied and the amount of turnover at a midden site. We used the same PC sets as our independent variables (PC1-4, PC1-3, PC1-2, and PC1) but only for the 28 m buffer. We examined occupancy for every midden during the nine seasons around satellite image acquisition. The dependent variable was the proportion of these seasons each midden was occupied. We used general linear models with a Gaussian error structure to investigate two measures of turnover during the same nine seasons. Dependent variables were calculated by: 1) the proportion of nine seasons occupied by a distinct squirrel at a midden, and 2) the proportion of occupied seasons out of nine occupied by a distinct squirrel at a midden.

### **Statistical Models of Seedfall**

We took a two-step approach to examine how cone availability is related to midden location. First, we created a multiple regression model for seedfall. We created 28 m buffers and tabulated land cover classes from satellite image classification for 28 seed plots and generated PC scores with the same method as above. Our independent predictor variables for each seed trap site (PC1, PC2, PC3, year, habitat, habitat\*year) and the log-transformed total seed counts (dependent variable) for the year before and the year of image acquisition were used in the analysis. We used forward stepwise regression to identify the most parsimonious model. Second, the result from the multiple regression was used to predict seedfall at midden and random sites and seedfall was compared to midden occupancy and turnover with the same method as above models of occupancy and turnover.

### **Predictive Map**

We generated logistic regression models, assuming binomial error structure, to investigate the location of midden sites mountain-wide by comparing the relationship between habitat variables and occupied middens. We created counts of each of the nine land cover types from the classified image within a 28 m buffer for each cell in our study area. These counts of land cover type, and the PCA rotation we developed for occupancy models, allowed us to calculate PC scores for each cell. A 10 m digital elevation model (DEM) was used to generate elevation, slope and aspect values for every cell in the study area. Aspect was divided into two measures of energy: a north to south component

( $\text{aspectNS} = \cos(\text{aspect}) * 90 + 90$ ) and an east to west component ( $\text{aspectEW} = \sin(\text{aspect}) * 90 + 90$ ) (Pereira and Itami, 1991). We used AGFD census results and selected the 144 active middens within the period June 2001 to June 2004 as midden locations, and created 320 random sites within the study area. The first two PC bands and the DEM derived characteristics (PC1, PC2, elevation, slope, aspectNS, aspectEW) were used as independent predictor variables, and point type (midden and random) was used as the dependent variable. We also created two additional models to examine the effect of non-biological parameters on our results. In the second model, we removed elevation from the list of independent predictor variables. The third model used only satellite imagery (PC1 and PC2) to compare to past habitat predictions by Hatten (2000) and Pereira and Itami (1991). We used the three model results to create maps predicting the probability of a midden being in a particular cell of the study area. We assessed the accuracy of models by examining the percentage of training and test sites above a threshold value, by calculating gain ( $[1 - ((\% \text{ area} > p) / (\% \text{ middens in zone} > p))]$ , where  $p$  is a chosen threshold probability value), and by generating receiver operating characteristic (ROC) plots (Fielding and Bell, 1997; Guisan and Zimmermann, 2000).

## **RESULTS**

### **Satellite Imagery**

Over 80% of ground truth sites had satellite image-derived canopy cover within 10% of those observed in the field (Table 1). We visually examined outliers (points >20% different) and found our classification had overlap between classes, especially

between shadow classes and ground cover due to tree shadows. In addition, the cienega, grass, or aspen class had overlap with the small healthy tree and shrub class, leading to incorrect canopy cover estimates in some open areas such as shrub covered fields and open meadows. Damage level estimates derived from satellite imagery were within 20% of the field observations for over 80% of our random points; somewhat lower accuracy than for canopy cover (Table 1). Satellite image classification overestimated damage at lower damage levels and underestimated at higher levels of damage (Fig. 1). Our visual examination of outliers reiterated that the dying or dead tree class was overrepresented, with overlap between shadow and tree classes. Class overlap also occurred in open areas between the cienega, grass, or aspen class and the dying or dead tree class. The damage underestimate at higher damage levels and overestimate in open areas was caused by understory vegetation overlap with the dying or dead tree class.

### **Model Results**

Our PCA transformation (Table 2) of the buffered random and midden sites explained > 80% of the variation in the first 4 PCs (Table 3). The first PC emphasized the change from healthy small and large trees to more open areas of dead or dying trees and soil (Table 2). The second PC emphasized the change from shadow to open areas of brighter soils (Table 2). The first two PCs did not differ between buffers of 10 m and 28 m, 10 m and 56 m, and 28 m and 56 m (correlations = 0.997, 0.992, and 0.999, respectively, all  $p < 0.001$ , Procrustes rotation), so differences between models are due to selection by MGRS not due to differences in PCA classifications.

For our 12 occupied versus random site models the buffer distance of 28 m outperformed distances of 10 m and 56 m (Table 4). The PC1-4 and PC1-3 models at 28 m (Table 5) best predicted occupancy. Squirrels are using midden sites with high numbers of healthy trees, with possibly some aspen, more than areas with high damage (high PC1). Squirrels also use middens in denser forests preferentially to open areas of rock and soil (low PC2).

We did not find a strong relationship for either turnover measure of survival (distinct squirrels/total seasons;  $D^2 = 0.12$  and distinct squirrels/occupied seasons;  $D^2 = 0.03$ , for the best models). Our best binomial model of proportion of occupied seasons ( $D^2 = 0.17$ ; Table 6) resulted in a moderate relationship between the satellite image and midden quality. More middens were occupied across seasons in areas of healthy dense trees than in more open midden sites (high PC1 and low PC2).

The best prediction of total seedfall per site was from the first three PCs and a year indicator variable to account for mast years (Fig. 2:  $\text{Ln}(\text{seeds}) = 2.57 + (0.263 * \text{PC1}) + (-0.205 * \text{PC2}) + (-0.334 * \text{PC3}) + (\text{year} * 2.3)$ ,  $F_{4,51} = 55.7$ ,  $p < 0.0001$ ,  $R^2 = 0.81$ ). There was no interaction between seedfall and forest type. Higher seed production is found in areas of healthy (higher PC1), thicker (lower PC2) trees compared with open areas and areas with dying trees, similar to midden site selection models. A model of seedfall at occupied sites versus random sites explained midden site selection ( $D^2 = 0.24$ ; Table 7) as did a pass/fail binomial response model with the number of passes equal to seasons occupied out of nine ( $D^2 = 0.14$ ; Table 7). Occupied middens were found in

areas of the mountain with high seedfall, and occupied middens with more activity over the period near image acquisition were in areas of higher seedfall.

### **Midden Location Probability Maps**

A comparison of training and random sites found that PC1, PC2, elevation, slope, and both components of aspect were significant predictors of midden location (Table 8). In each of the three models, much of the area classified as suitable, dense, healthy, old growth, fall outside the MGRS refugium (Fig. 3). For the all-inclusive model, our accuracy assessment showed that 90% of active middens fell in areas with a probability score  $> 0.3$  (Fig. 3a). Only 21% of the study area was classified above 0.3 in our probability map for a gain of 77% and known midden sites have higher relative scores than random sites (ROC plot, AUC = 0.903, Fig. 4a). In the no-elevation model (Table 8) 77% of middens fell within areas with a probability  $> 0.3$  (Fig. 3b). Suitable sites for middens comprised 24% of the study area leading to a gain of 68%, and the model also had a low false positive rate (ROC plot, AUC = 0.856, Fig. 4b). In the PC only model (Table 8) 59% middens fell in areas with a probability  $> 0.3$  (Fig. 3c). Gain was only 48%, but the model prediction power was acceptable (ROC plot, AUC = 0.691, Fig. 4c). Following the development of our models the Nuttall Complex fire burned into the upper elevations of the Pinaleño Mountains destroying middens and burning parts of habitat classified as suitable in our models (Fig. 5).

## **DISCUSSION**

Conspicuous sites, such as den (Gilbert and Pierce, 2005) or resting sites (Zielinski et al., 2006), can simplify models of potential habitat. However, applicability of a model can be reduced if the simplification does not integrate factors critical to overall habitat selection. We modeled MGRS midden locations, because middens are located to maximize collecting quality cones, maintain microclimate conditions for storage, and permit defense from neighbors. Hence, middens are ecological integrators, combining multiple aspects of the ecology of an animal, and provide a stable, observable site, to analyze for habitat models. Assessment of basic biological requirements is an easy, accurate approach to habitat modeling.

Use of satellite imagery and environmental characteristics makes our study repeatable and changes in habitat availability can be monitored over time (Zielinski et al., 2006). Our use of high-resolution satellite imagery allowed us to examine forest conditions at the level of individual trees; however, classification inaccuracies due to having only four spectral bands created some overlap between classes and inconsistent estimates of damage. Advancement in classification techniques that allow height representations and neighborhood analysis may improve future classification. Any misregistration of midden locations by GPS errors with satellite images in heterogeneous areas or near cover type boundaries may have reduced the predictive power of our models. Without high spatial resolution we would not have identified fine-scale patterns created by insect damage (Baker and Veblen, 1990) and seedfall predictions were highly accurate.

MGRS use dense, healthy, old growth forests for middens (Smith and Mannan, 1994), conditions that now fall outside the MGRS refugium. We identified that selection occurred on a 28 m plot around middens, indicating that selection also occurs on a territory scale rather than only at the midden site (Smith and Mannan, 1994). Adult squirrels can survive on a variety of foods (Gurnell, 1987; Steele and Koprowski, 2001) but years of large population increases are linked to high seedfall (Gurnell, 1987; Becker, 1992).

Current forestry practices use 10 m buffers for thinning operations (USDA Forest Service, 2000). Red squirrels density can be reduced after forest thinning (Wolff and Zasada, 1975; Sullivan and Moses, 1986), but is not always (Haughland and Larsen, 2004). Fuel reduction is essential to protect forests from catastrophic fire (Parsons and DeBenedetti, 1979) and insects (Covington and Moore, 1994; but see also Moreau et al., 2006). Moreover, managers must understand what triggers MGRS to select territories. Any reduction in territory quality may result in increased home ranges (Wolff and Zasada, 1975; Haughland and Larsen, 2004), reduced survival, or dispersal. We found territories and middens more likely located and occupied in areas of high seedfall. Red squirrels spend significant energy collecting food (Smith, 1968a), and defend areas large enough to supply food for a year (Rusch and Reeder, 1978). Territory size is inversely related to food density (Rusch and Reeder, 1978) and increased territory size would result in higher energy expenditures for food gathering (Smith, 1968a). Red squirrels select cones based on caloric value and distance from their midden (Elliot, 1988). Therefore, management for MGRS should maximize food quality near middens.

Our habitat prediction maps indicate little habitat within the insect damaged MGRS refugium remains; therefore conservation efforts need to focus beyond spruce-fir forests. In years prior to insect damage, seedfall in the Pinaleño Mountains would have shown large differences between spruce-fir and mixed conifer forests during mast and non-mast years (Koprowski unpublished data, Koprowski et al., 2005), which we did not see. Mixed conifer forests may provide a diverse food supply, but with less variation. However, seedfall in spruce-fir forest is now very low and only a few squirrels inhabit these areas (Koprowski et al., 2005; Koprowski et al., 2006a). Mixed conifer forests of the Pinaleño Mountains contain the majority of squirrels, a reversal due to insect damage.

Spruce-fir forests exhibit stand-replacing fires every 200-400 years (Peet, 1998), whereas mixed conifer forests have a 4 year interval, with cool surface fires that kill few cone bearing trees (Grissino-Mayer and Fritts, 1995). However, mixed conifer forests are overgrown due to fire suppression and are now susceptible to stand replacing fires (Cole and Landres, 1996). In 2004, the Nuttall Complex Fire severely burned much of the spruce-fir and mixed conifer forests of the Pinaleño Mountains. Proper management will rely on the restoration of damaged spruce-fir and mixed conifer forests while protecting remaining stands of old-growth.

Our predictive maps are useful for comparison of past and future changes to habitable areas as well as to guide location of new middens (see Guisan and Zimmermann, 2000). Although the model that included all parameters had the highest gain and AUC, it is not the most biologically meaningful. Many known middens are found at higher elevations, which would bias the model towards predicting high elevation

sites as suitable while reducing probability scores of lower mixed-conifer sites that may be higher quality. MGRS occur at lower elevations than previously thought (Hatten, 2000), and new middens continue to be found (Koprowski, unpublished data). A thorough survey of mixed conifer forests where forests are less damaged is needed to locate additional middens. Our results can narrow the search area. Our model based solely on PCs indicates the degree of damage to high elevations but has lower predictive accuracy illustrating MGRS select areas with the right vegetation and of lower solar input.

We demonstrated that high-resolution satellite imagery can be used to evaluate the fine- to coarse-scale effects of disturbance over large geographic areas. Similar approaches can be used for other species of concern within the same geographic area, increasing management efficiency. Increased threats of forest disturbance impose an escalating need to evaluate damage to forests and habitat availability of resident species. Increased temperatures due to climate change will push forests higher on mountains (Smith et al., 2001), and human activities, such as fire suppression, will require forest restoration (Allen et al., 2002). As forest disturbance increases, the ability of science to accurately predict the effects to these ecosystems will be tested (Joyce et al., 2001). Our approach will facilitate fine-scale analysis of forests and modeling responses of to disturbance. By creating models for indicator species insights into ecosystem health and function are gained by observing trends in habitat availability so that recovery following disturbance can be identified by evaluating when a damaged area returns to a suitable classification, even before the indicator species has recolonized the area.

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Table B1, Percent canopy cover and damage accuracy assessment of classified high-resolution satellite imagery of the Pinaleño Mountains, Arizona. Number of points within percentage and overall accuracy for original values at GPS determined point and then for the best point out of a 10m radius around a GPS point.

	At point		Best of Moving Window	
	Number	Accuracy	Number	Accuracy
<b>Canopy cover</b>				
5%	42	23.86%	123	69.89%
7.5%	53	30.11%	131	74.43%
10%	69	39.20%	142	80.68%
12.5%	82	46.59%	148	84.09%
15%	97	55.11%	157	89.20%
17.5%	114	64.77%	161	91.48%
20%	122	69.32%	165	93.75%
<b>Damage</b>				
10%	31	17.61%	89	50.57%
12.5%	40	22.73%	103	58.52%
15%	49	27.84%	122	69.32%
17.5%	62	35.23%	135	76.70%
20%	72	40.91%	145	82.39%

Table B2, Rotation for first three principal components of ground cover class counts derived from satellite imagery of midden and random sites in the Pinaleño Mountains, Arizona. Sites were buffered by 10 m, 28 m, and 56 m.

	PC1			PC2			PC3		
	10 m	28 m	56 m	10 m	28 m	56 m	10 m	28 m	56 m
Deep shadow, lake	0.140	-0.134	-0.126	0.421	-0.472	-0.492	-0.325	-0.297	-0.293
Shadow	0.010	-0.010	-0.027	0.553	-0.556	-0.564	-0.347	-0.354	-0.341
Healthy large conifers	-0.507	0.487	0.475	0.131	-0.128	-0.134	-0.080	-0.048	-0.011
Small healthy shrubs or trees	-0.531	0.510	0.494	-0.020	-0.015	-0.027	0.083	0.101	0.122
Dying or dead trees	0.374	-0.400	-0.419	0.247	-0.185	-0.129	0.173	0.161	0.156
Cienega, grass, aspen	-0.291	0.349	0.380	-0.142	0.121	0.133	0.339	0.271	0.181
Tan or light soil	0.147	-0.102	-0.081	-0.520	0.527	0.528	-0.305	-0.307	-0.312
Bright rock	-0.004	0.030	0.039	-0.351	0.314	0.283	-0.662	-0.717	-0.757
Asphalt road, dark soil or rock	0.440	-0.435	-0.431	-0.154	0.162	0.170	0.290	0.256	0.232

Table B3, Variation explained by each new band following a Principal Component Analysis of ground cover class counts derived from high-resolution satellite imagery around buffered midden and random sites in the Pinaleno Mountains, Arizona.

	Buffer Distance (m)		
	10	28	56
PC1	0.350	0.400	0.430
PC2	0.249	0.273	0.279
PC3	0.127	0.129	0.129
PC4	0.109	0.088	0.073
PC5	0.076	0.062	0.053
PC6	0.045	0.027	0.020
PC7	0.029	0.015	0.010
PC8	0.013	0.005	0.003
PC9	0	0	0

Table B4,  $D^2$  values for models examining habitat differences between occupied Mt. Graham red squirrel middens and random sites in the Pinaleño Mountains, Arizona.

Buffer	PC1-4	PC1-3	PC1-2	PC1
10m	0.307	0.288	0.252	0.137
28m	0.336	0.327	0.246	0.123
56m	0.294	0.290	0.229	0.118

Table B5, Results of two logistic regression models assuming binomial error structure comparing ground cover classes within 28m buffers around Mt. Graham red squirrel midden sites and random sites, Pinaleño Mountains, Arizona. PC1-4 are the first four bands from a Principal Component Analysis of ground cover counts derived from a classified satellite image. Models are PC1-4 ( $D^2 = 0.34$ ) and PC1-3 ( $D^2 = 0.33$ ).

Parameters	Estimate	Standard Error	Z value	<i>p</i>
PC1-4 Model:				
Intercept	-6.852	1.0655	-6.43	<0.001
PC1	1.618	0.3556	4.55	<0.001
PC2	-1.442	0.3569	-4.04	<0.001
PC3	-1.622	0.4768	-3.40	<0.001
PC4	0.564	0.4962	1.13	0.254
PC1-3 Model 2:				
Intercept	-6.633	0.9965	-6.65	<0.001
PC1	1.549	0.3395	4.56	<0.001
PC2	-1.338	0.3168	-4.22	<0.001
PC3	-1.580	0.4545	-3.47	<0.001

Table B6, Results of logistic regression model ( $D^2 = 0.17$ ) with binomial error structure using number of seasons occupied as a pass variable and number of seasons not occupied as a fail variable for Mt. Graham red squirrel middens, Pinaleno Mountains, Arizona. PC1 and PC2 are the first two bands from a Principal Component Analysis of ground cover counts derived from a classified satellite image.

Parameter	Estimate	Standard Error	Z value	<i>p</i>
Intercept	-2.893	0.112	-25.69	<0.001
PC1	0.499	0.035	13.96	<0.001
PC2	-0.230	0.085	-2.68	0.007

Table B7, Results of logistic regression models comparing occupancy of Mt. Graham red squirrel middens to seedfall in the Pinaleño Mountains, Arizona. One model examines occupied sites versus random sites ( $D^2 = 0.24$ ) and the second is a pass/fail binomial model with the number of passes equal to seasons occupied out of 9 ( $D^2 = 0.14$ ). Seedfall data derived from a comparison of seed plots and high-resolution satellite imagery.

Parameter	Estimate	Standard Error	Z Value	<i>p</i>
Occupied vs. Random				
Intercept	-15.43	3.78	-4.07	<0.001
Ln(seeds)	4.22	1.13	3.72	<0.001
Turnover				
Intercept	-7.85	0.50	-15.66	<0.001
Ln(seeds)	1.86	0.15	11.72	<0.001

Table B8, Results of nested binomial predictive models of Mt. Graham red squirrel midden location (see Fig. 3). PC parameters derived from principal component analysis of ground cover class counts of Mt. Graham red squirrel midden sites vs. random sites derived from high-resolution satellite imagery. Elevation, slope, and aspect were derived from a 10m digital elevation model. Aspect divided into two measures of energy.

	Estimate	Std. Error	z-value	<i>p</i>
<b>Full Model</b>				
Intercept	-21.11	3.986	-5.29	<0.001
PC1	0.520	0.120	4.31	<0.001
PC2	-0.869	0.169	-5.11	<0.001
Elevation (m)	0.006	0.001	5.25	<0.001
Slope (deg.)	-0.100	0.017	-5.75	<0.001
AspectEW	0.006	0.002	2.74	0.006
AspectNS	0.006	0.002	2.43	0.015
<b>No Elevation model</b>				
Intercept	-0.571	0.415	-1.37	0.169
PC1	0.171	0.087	1.95	0.050
PC2	-0.787	0.148	-5.30	<0.001
Slope (deg)	-0.118	0.016	-7.35	<0.001
AspectEW	0.007	0.002	3.09	0.001
AspectNS	0.005	0.002	2.49	0.012
<b>PC Only model</b>				
Intercept	-1.633	0.23560	-6.934	<0.001
PC1	0.193	0.07058	2.747	0.006
PC2	-0.627	0.10663	-5.885	<0.001

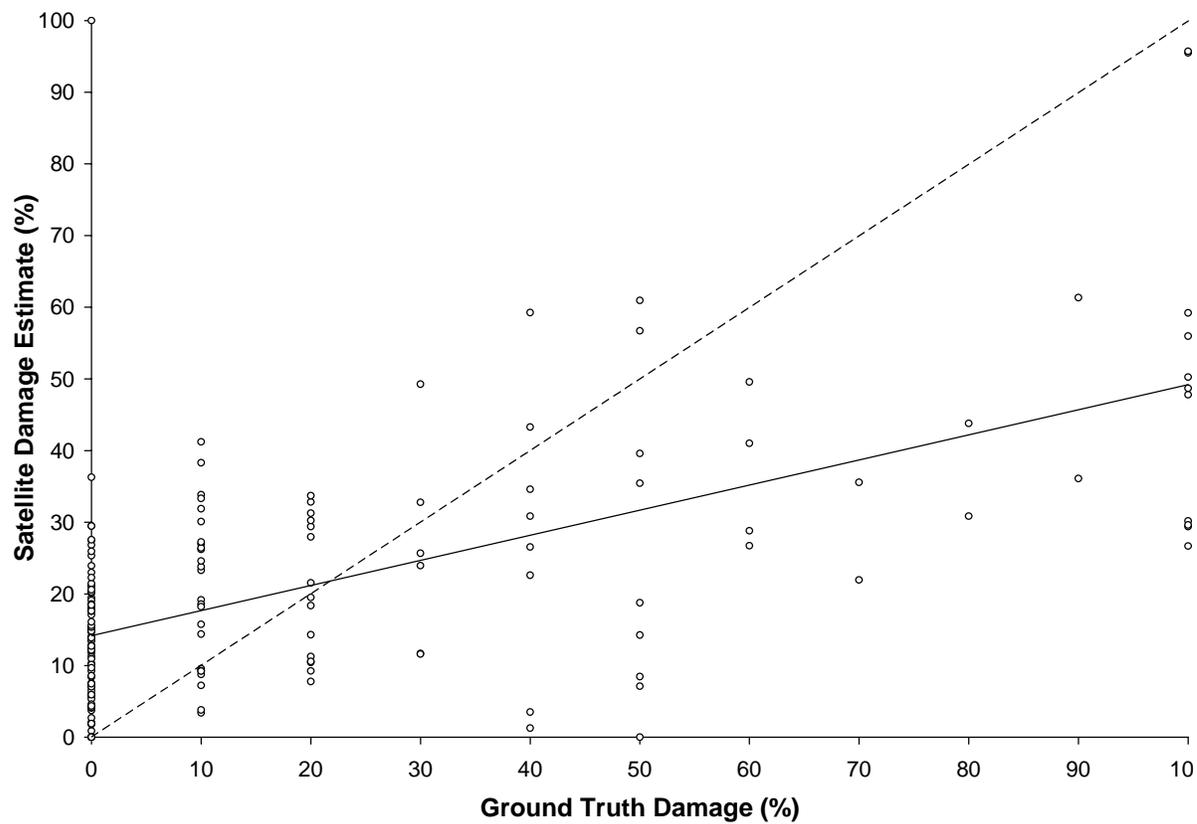


Figure B1, Ground truth damage levels compared to levels computed from a high-resolution satellite image (Quickbird) for the Pinaleño Mountains, Arizona. The 1:1 line (dashed line) and fitted line (solid line) are added.

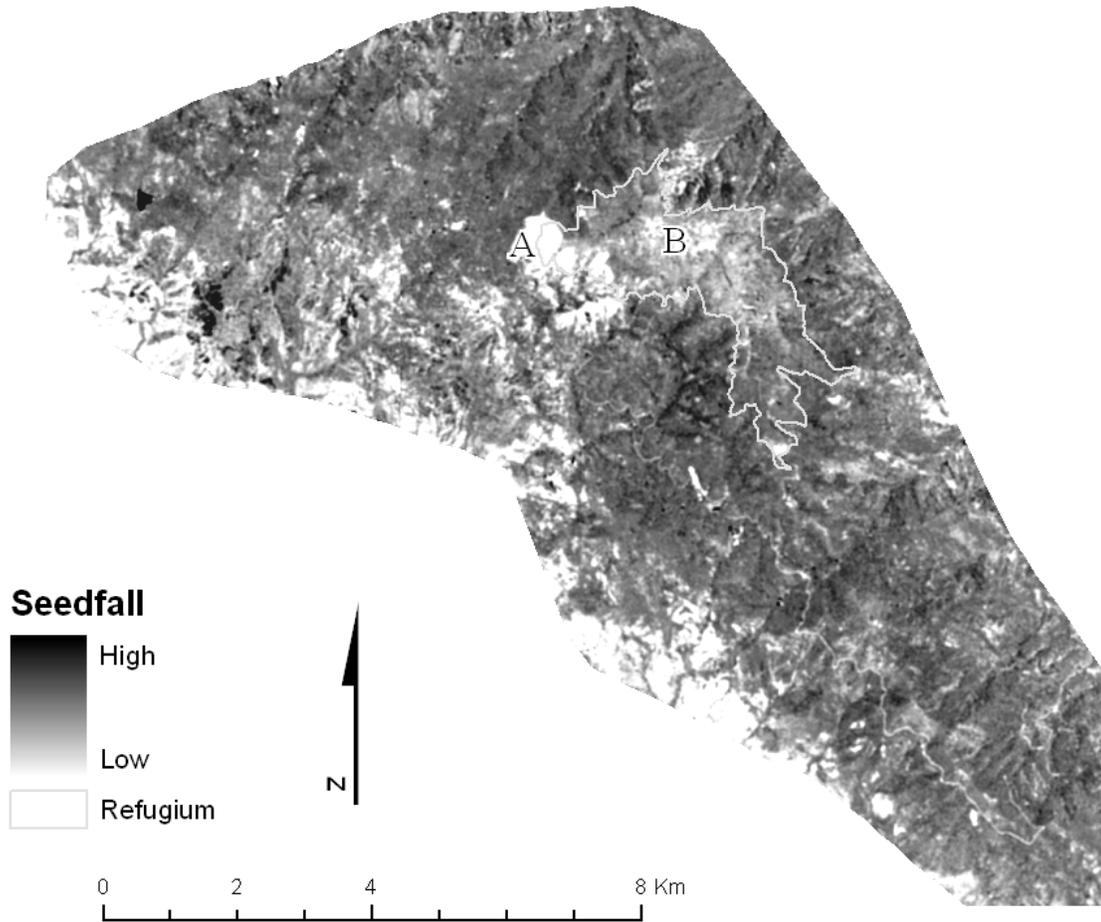


Figure B2, Seedfall predicted from principal components derived from high-resolution satellite imagery over potential Mt. Graham red squirrel habitat in the Pinaleno Mountains, Arizona. Crown fire damage from the Clark Peak Fire (A) and the most extensive insect damage (B) show large reductions in seedfall compared to the surrounding forest

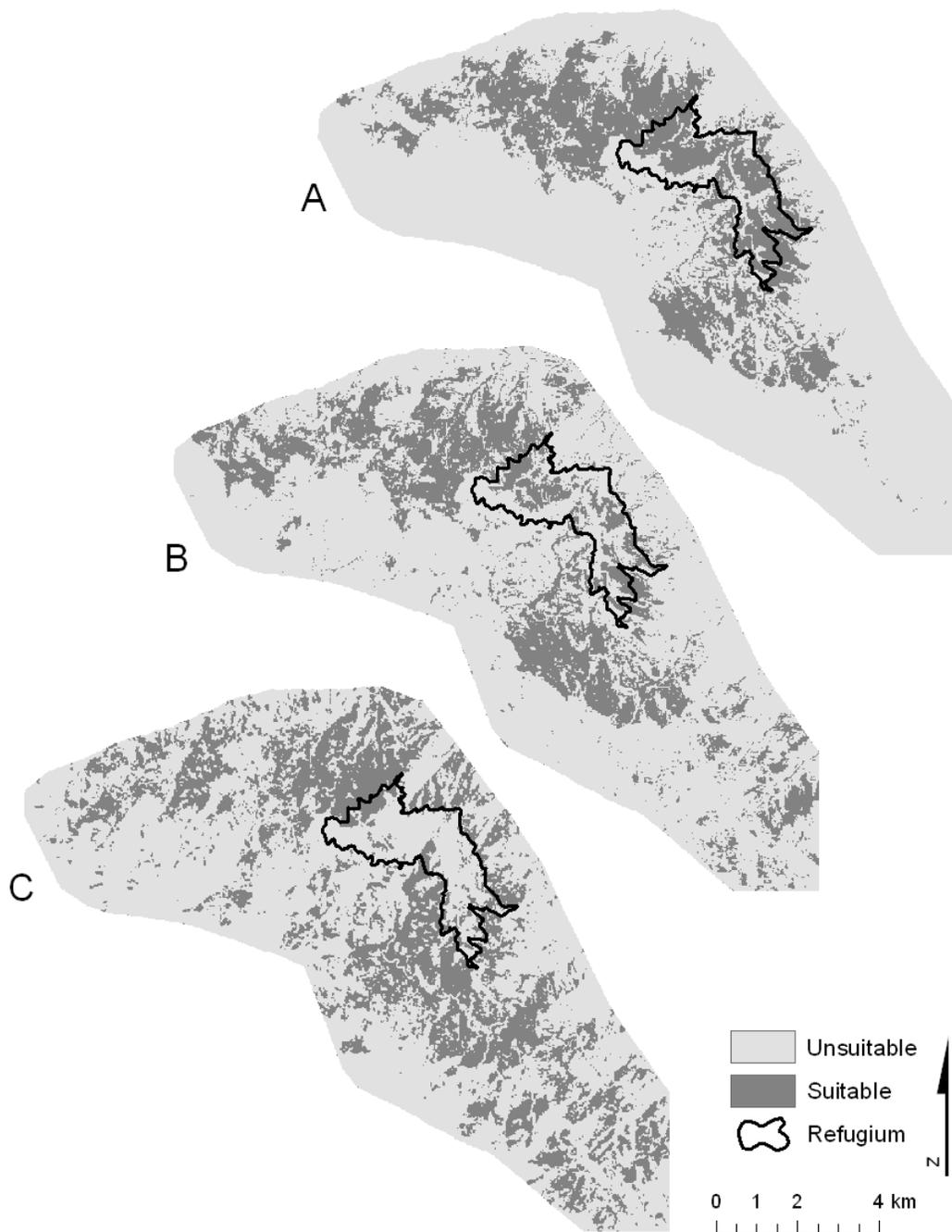


Figure B3, Mt. Graham red squirrel midden probability maps with areas of high midden probability ( $>0.3$ ) compared to all potential area ( $<0.3$ ) for the Pinaleno Mountains, Arizona. The protected squirrel refugium is within the black boundary. Predictive parameters are a) PC1, PC2, elevation, slope, aspectEW, and aspectNS, b) PC1, PC2, slope, aspectEW, and aspectNS, and c) PC1 and PC2.

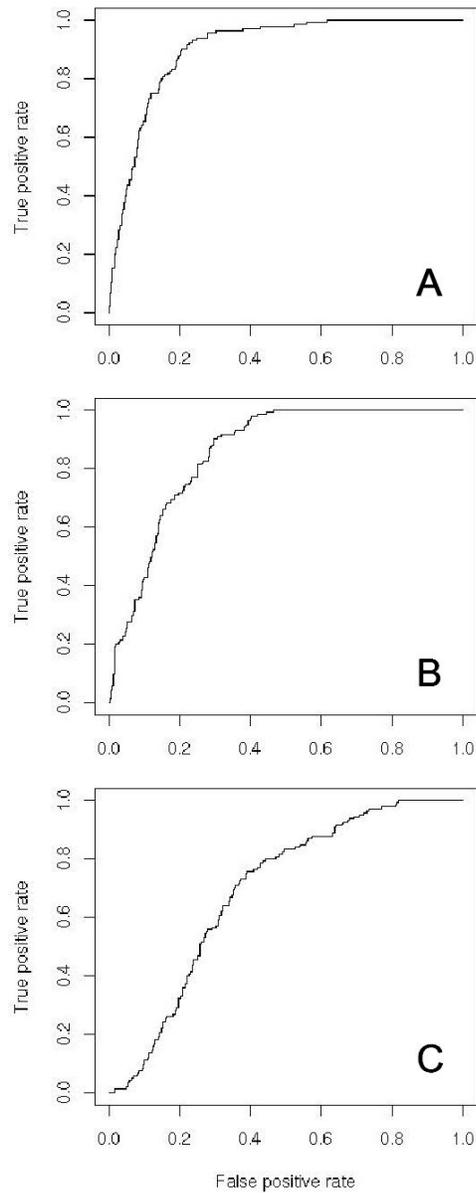


Figure B4, ROC plot of models generated for Mt. Graham red squirrel midden locations in the Pinaleno Mountains, Arizona, (Figure 3) based on a) PC1, PC2, elevation, slope, aspectEW, and aspectNS, b) PC1, PC2, slope, aspectEW, and aspectNS, and c) PC1 and PC2. Area under the curve is a) 0.903, b) 0.856, and c) 0.691.

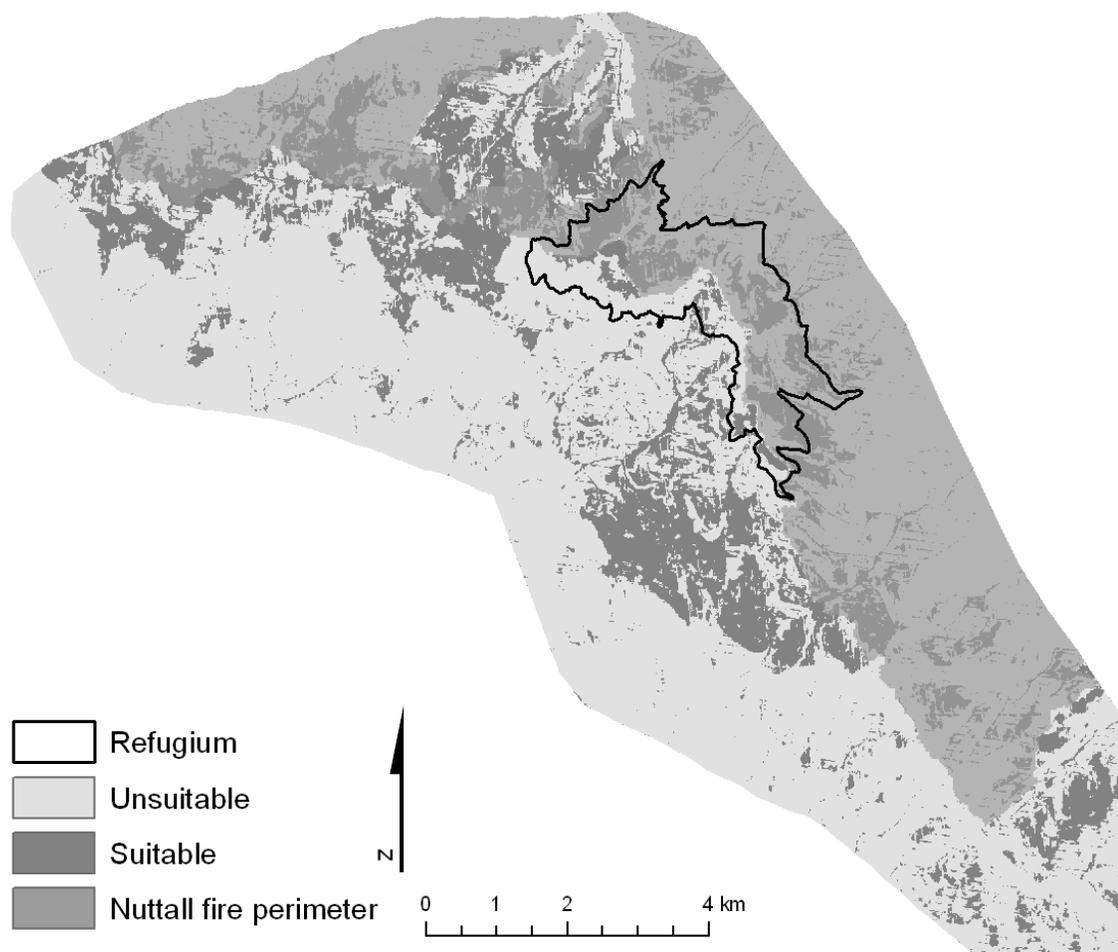


Figure B5, Suitable Mt. Graham red squirrel midden locations ( $p > 0.3$ ) affected by the 2004 Nuttall Complex Fire in the Pinaleno Mountains, Arizona. The probability model uses the predictive parameters: PC1, PC2, slope, aspectEW, and aspectNS.

## **APPENDIX C: HABITAT HETEROGENEITY, DISTURBANCE, AND THE FUTURE OF A HEALTHY FOREST INDICATOR**

### **ABSTRACT**

Difficulties in conservation and management of forest ecosystems arise from dynamics of forests and challenges in understanding disturbance. Disturbances, especially fire and insect outbreaks, have increased in occurrence and severity due to climate change and forest management. Developing tools to understand disturbance is an important step in being responsible land stewards. Herein, we use the Pinaleno Mountains of southeastern Arizona and the endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) as a study system to combine spatially explicit population models with spatial models of habitat heterogeneity. We parameterized the model with estimates of extent, frequency, and severity of insect outbreaks and fire and used the number of Mt. Graham red squirrel populations dropping below critical population thresholds to characterize the effects of these disturbances. We determined future disturbances, even at low levels, are likely to have a detrimental effect on Mt. Graham red squirrel population size. This model framework can be used to predict effects of future disturbance on habitat quality and population persistence for species in general. Our technique will help with adaptive management, allowing the effects of disturbance to be evaluated in small scales and at the species level.

## INTRODUCTION

Management and conservation of ecosystems requires balancing the needs of multiple species and evaluating the availability of particular habitats. Understanding responses to changes wrought on a landscape by disturbance is therefore critical to adapting management decisions (Vogt et al., 1997), especially for imperiled species and forested ecosystems (DeStefano, 2002). Forests constantly change due to physical and biological disturbance (Knight, 1987), resulting in a shifting mosaic of conditions. Disturbances can degrade or destroy mature forests, thereby modifying availability of successional stages, and hence habitat available to individual species (Whittaker, 1975).

In the last 20 years, large fires have increased due to longer fire seasons, resulting in allocation of over \$1.5 billion annually for control of fires in the United States (Whitlock, 2004; Westerling et al., 2006). Although low severity fires may have minimal impacts on forest structure and composition, severe fires kill most trees, radically altering biological communities. Starting in the early 1900s, most western U.S. forest fires have been suppressed (Pyne, 1982). Such alteration of natural processes has often had unexpected and undesirable results (Davis and Halvorson, 1996), such as promoting an increase in small diameter trees that can act as ladder and ground fuels and magnify the effects of fire (Parsons and DeBenedetti, 1979; Cole and Landres, 1996). Ultimately, climate change may be the overarching driver behind changes to fire regimes (Westerling et al., 2006). For species that depend on mature forests, increases in wildfire severity equate to reductions in habitat.

Insect damage to forests also has increased in frequency and exhibited novel behavior in recent years due to climate changes (Swetnam and Lynch, 1989; Swetnam and Lynch, 1993; USDA Forest Service, 2006). Insect outbreaks can kill large canopy trees, and reduce basal area and stand density (McMillin et al., 2003). Defoliators can stunt growth, top-kill trees, and make trees susceptible to death by bark beetles (Wickman et al., 1981). Fire suppression creates conditions that favor insect outbreaks (Cole and Landres, 1996). Disturbances, such as fire and insect outbreaks, will have large and costly impacts on forests, therefore, understanding the potential changes to the habitat of species is critical to making informed management decisions in many terrestrial ecosystems.

As forest disturbance increases, the ability of science to accurately predict effects of disturbance on forested ecosystems will be tested (Joyce et al., 2001), and new approaches will be needed. Spatially explicit population models (SEPMs) can be used to evaluate threats to population persistence due to disturbance (Liu et al., 1995; Wennergen et al., 1995) and, with appropriate testing and evaluation, provide an effective tool to evaluate management alternatives (Dunning et al., 1995). SEPMs are particularly effective tools for exploring disturbance because they link complex landscape conditions with population dynamics (Rushton et al., 1997), permitting evaluation of future disturbances and management actions. Remote sensing can provide high spatial resolution satellite images that allow evaluation of health of individual trees and of habitat quality (Wood et al., 2007). Linking such fine resolution data with SEPMs may

provide a framework that can be used in managing for a range of species in different ecosystems.

We chose the isolated Pinaleño Mountains in southeastern Arizona as a study system for evaluating and testing models linked to habitat heterogeneity. The Pinaleño Mountains are a microcosm of western forests and provide an ideal study animal, the federally endangered Mt. Graham red squirrel (MGRS: *Tamiasciurus hudsonicus grahamensis*), in an isolated and easily bounded system. Our objectives were to 1) modify a SEPM for MGRS (Rushton et al., 2006) by including current habitat quality as evaluated from high-resolution satellite imagery (Wood et al., 2007); 2) evaluate the viability of MGRS from disturbances ranging from intermittent small fires to large-scale catastrophic fires and from minimal insect damage to severe large-scale outbreaks.

## **METHODS**

### **The Pinaleño Mountains and Mt. Graham Red Squirrels as a Study System**

In the Southwest, Holocene warming has restricted boreal forests and their associated fauna to highest elevations (Lomolino et al., 1989). Climate change, combined with drought, will likely continue to alter upper elevation forests through increased wildfires and insect outbreaks (Lynch, 2005). In the Pinaleño Mountains, a recent increase in insect and fire disturbance (Koprowski et al., 2005; Koprowski et al., 2006b) mimics forest conditions elsewhere in the western U.S. (Allen et al., 2002; Lynch, 2004). The 1996 Clark Peak fire burned almost 3,000 ha (Froehlich, 1996), and the 2004 Nuttall Complex Fire burned almost 12,000 ha (Koprowski et al., 2006b), both severely

damaging high elevation forests in the Pinaleno Mountains. Many areas with high fuel loads still exist. In 1996, insect outbreaks began radically degrading spruce-fir forests (Koprowski et al., 2005), and mixed-conifer forests still have potential for insect outbreaks.

MGRS are found only in upper elevation spruce-fir forests, dominated by Engelmann spruce (*Picea engelmannii*) and Corkbark fir (*Abies lasiocarpa* var. *arizonica*), and in more diverse mixed-conifer forests with Douglas-fir (*Pseudotsuga menziesii*), Ponderosa pine (*Pinus ponderosa*), White pine (*P. strobiformis*), Engelmann spruce, and Corkbark fir (U.S. Fish and Wildlife Service, 1993). Like other red squirrels in coniferous forests, MGRS defend territories surrounding middens, central larderboards used for storing cones (Steele, 1998). Middens are important for over-winter survival because they provide cool, damp environments that delay cone opening, and prevent MGRS competitors from accessing seeds (Smith, 1968a; Finley, 1969; Steele and Koprowski, 2001).

A long-term MGRS monitoring program has been in place since 1989 (Young, 1995) and provides habitat and population specific data that can be used to parameterize effects of disturbance on the MGRS population. Arboreal rodents are excellent indicators of forest productivity, stability, and connectedness (Carey, 2000; Steele and Koprowski, 2001), and tree squirrels are excellent models for studies in behavior, population ecology, and conservation (Steele and Koprowski, 2001). The Pinaleno Mountains and MGRS provide an excellent system for developing models to evaluate effects of disturbance on forested ecosystems.

### **Validating a Population Model Incorporating Habitat Heterogeneity**

In the MGRS population model of Rushton et al. (2006), it was assumed that habitat was uniform and that middens were of equal quality. We modified the model to allow for variation in midden quality as age and composition of trees surrounding middens changed available resources. We assumed that the amount of cones squirrels could hoard in their middens varied with forest type, tree density, and cone crop in a given year. Thus, in good cone years, squirrels can collect more resources and provide a store that would last longer than in poor cone years. Specifically, spruce-fir forests mast approximately every 4 years, where as Douglas-fir and pines in mixed-conifer forest provide a less variable seed crop (Burns and Honkala, 1990; Rushton et al., 2006). For squirrels in spruce-fir forest, we provided a maximum of a 20-month supply of cones in a mast year and a 4-month supply in a bad year. In mixed-conifer forest we provided a maximum of 8 or 6 months of cones in good and bad years, respectively. Midden storage was capped at 24 months, because cones lose nutritional value and degrade in 2 years (Smith, 1968b; Wheatley et al., 2002; Frank, 2008). We tracked midden quality by assigning each midden a score and used this value to adjust food available to a squirrel occupying a specific midden. A higher score indicated a squirrel could store all or almost all of the potential months of food while lower scores caused squirrels to store a smaller fraction of the available cones, added in August when cones mature by increasing the number of months of food available in a midden. In our model, resident squirrels dispersed if the midden quality dropped to where they could store <40% of the available cones, governed by the same rules as for juveniles in the original model (see Rushton et

al., 2006). We did not have habitat quality data from the start of our validation period, therefore, we assumed all middens had equal quality and squirrels could store the total amount of available cones each year. In simulations, following the Clark Peak fire year, we adjusted midden scores within the fire boundary and in 2001, following the peak of insect damage, we updated all midden scores, with scores based on seedfall as determined from a map generated from high-resolution satellite imagery (Wood et al., 2007). We used a Jenks natural breaks classification in ArcGIS 9.1 (2005) to divide seedfall levels into 10 classes and assigned the respective scores to middens as a proxy for habitat quality, where midden score divided by ten equaled the fraction of available cones a squirrel could store.

Our revised model (Figure 1) incorporated MGRS specific life history data, spatial patterning of middens, and habitat variability between middens. We validated our model with the same process as the original model (Rushton et al., 2006). We randomly allocated 348 squirrels, the known population size in 1986, with sex and age structure varied at random, to middens. We ran this model 20 times with masting history from 1986 to 2003 (see Table 2 in Rushton et al., 2006), averaged final population numbers, and calculated correlation of the model to actual population sizes.

### **Future Habitat Variability and Predictions of Population Size**

To predict future MGRS population fluctuations, we simulated changes in resources due to variability of cone crops. We used a binary good vs. bad distinction to separate out years of high resource abundance from average or bad years. We predicted

masting events of Engelmann spruce/corkbark fir and good Douglas-fir years and adjusted maximum available cones, which we measured in how many months the store would last, for each forest type separately. In the model, base levels, the low/normal year level of available cones, were set to 4 months for middens in spruce-fir forest and 6 months for those in mixed-conifer forest, to reflect more constant food supplies in mixed-conifer forests and extremely low cone production in spruce-fir forests in non-mast years. An Engelmann spruce/corkbark fir masting event increased the number of cones a squirrel could store to 14 months in spruce-fir forest and 3 months in mixed-conifer forest. A good Douglas-fir year increased available cone months by 3 in mixed-conifer forest but zero in spruce-fir forest. Good years, treated separately for each forest type, were predicted by comparing a sampling deviate from a uniform distribution  $[0, 1)$  to a calculated probability, the time since last mast input into the normal cumulative probability function (mean = 4, standard deviation = 2; Harding et al., 2008).

We updated midden quality scores to reflect damage from the 2004 Nuttall Complex Fire with fire severity classes derived from a comparison of high-resolution satellite images taken pre- and post-fire (Villarreal 2007). This fire severity map had high, medium, and low/no fire classes and we reduced modeled midden quality scores (the habitat heterogeneity addition to the model) within the Nuttall Complex Fire boundary by 10, 5, and 0 classes, respectively. To establish a baseline we ran our population model for 100 years, with 40 replicates with the same future resource predictions, so fluctuations due to future resources patterns were not hidden by variation separate resource patterns.

## **Insect Outbreaks**

We defined three parameters, extent, frequency, and severity, to parameterize insect outbreaks. Since most MGRS are restricted to mixed-conifer forests, we primarily used literature on Douglas-fir tussock moth (*Orgyia pseudotsugata*) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae*), the two largest threats, to obtain values to populate the model. In the event of an outbreak, we assumed the entire 114-km<sup>2</sup> study area would be affected. Outbreaks in mixed-conifer forests are related to prolonged drought, allowing several years of favorable conditions for insect population expansion (Martinat, 1987), so we used Palmer Drought Severity Index (PDSI) reconstructions from tree rings to estimate outbreak frequency (Cook et al., 2004). We used 20-year low pass filter values, to remove short term events that would not have led to an outbreak, from 1500 A.D. to 2000 A.D. (downloaded from NOAA Paleoclimatology Branch <http://www.ncdc.noaa.gov/paleo/paleo.html>, grid point 105, southeastern Arizona) and selected events that peaked below a PDSI of -1. There were 7 for a recurrence interval of 77 years, so we modeled the chance of an outbreak at 1 per 77 yrs.

During an outbreak, areas having higher basal area experience higher tree mortality (Negrón, 1998; Negrón et al., 1999). To calculate basal area across the mountain, we used basal area (BA, m<sup>2</sup>/ha) from random sites (n = 192) generated in other studies (Edelman and Koprowski, 2005; Merrick et al., 2007). We used multiple regression to determine the relationship between basal area and the first two principal components (PC1 and PC2) generated from a Principal Components Analysis on counts of land cover classes surrounding middens and random sites (Wood et al., 2007). We

used this regression to predict basal area for all known middens ( $BA = 53 + (2.57 * PC1) + (-6.57 * PC2)$ ,  $R^2 = 0.24$ ). Estimates of BA were then classified into 10 categories (1-10) by the Jenks natural breaks method in ESRI ArcGIS 9.1 (2005) with higher scores representing higher basal area. We used fire severity estimates, classified as high, medium, or low/no fire severity (Villarreal 2007), to adjust basal area after the Nuttall Complex Fire. For middens within the fire perimeter we reduced basal area scores by 8, 4, and 2 for high, medium, and low/no fire severity, respectively. These values were used to adjust the amount of mortality of trees (see below) experienced in an outbreak.

Empirical evidence indicates that insect outbreak severity ranges from very little mortality to up to 80% mortality of trees in the worst cases (Swetnam et al., 1995). We examined multiple levels of severity and modeled scenarios of 20 to 80% maximum tree mortality per outbreak in increments of 10%. For each outbreak, we used BA scores to adjust tree mortality at each midden site, and reduced midden quality scores by the corresponding percentage. For example, with a maximum tree mortality of 50%, a basal area score of 10 would result in a 50% reduction of midden quality, where as a basal area score of 6 would result in 6/10 of the maximum tree mortality ( $0.6 * 50\%$ ), and a 30% reduction of midden quality. Following disturbance, surviving trees experience a growth spurt due to release from competition so we modeled an increase in cone production 10 and 20 years after an insect outbreak (Simard and Payette, 2005). Quality scores of middens in disturbed areas were increased by up to 1 at 10 years and up to 2 at 20 years, but could not exceed their original quality scores. We ran each tree mortality scenario for 100 years, conducted 100 replicates and examined only modeled populations

experiencing insect outbreak. We calculated the proportion of theoretical populations dropping below critical population thresholds (100, 50, 20, and 0 squirrels) to examine the effect of plausible levels of insect damage severity on the population persistence of MGRS. Using logistic regression for binomial counts in JMP IN 5.1 (SAS Institute, Cary, NC, USA), we modeled the change in the odds of the MGRS population decreasing to  $\leq 50$  individuals with an increase in severity of insect damage. We used number of populations below and above 50 individuals as the dependent variable and severity level as the independent variable.

### **Forest Fire**

We parameterized wildfire through frequency, severity, and size. We used fire frequencies from spruce-fir to mixed-conifer forest fire intervals; 300, 100, 50, 15, and 4 years (Grissino-Mayer and Fritts, 1995). We ran simulations with the chance of fire in a given year as the inverse of the mean fire interval. Fire location was determined by creating a random point within the Pinaleno Mountains and using it as the center of a circular fire perimeter. We simulated fires of 100, 500, 1,000, 2,500, 5,000 and 10,000 ha. We used FlamMap3 (Finney et al., 2004) to generate two estimates of crown fire severity. FlamMap is a fire behavior model that predicts potential fire behavior based on physical and vegetative site characteristics. Data were downloaded for the Pinaleno Mountains from the Landfire project (Rollins and Frame, 2006) through the National Map interface (<http://gisdata.usgs.net/website/landfire/>). We ran simulations with average fuel moistures from June 2006 (for all fuel models, fuel moistures of 3%, 4%,

4%, 65%, 65%, for 1 h, 10 h, 100 h, herbaceous, and woody fuels respectively) and created low- and high-severity scenarios by increasing wind speed (32.2 to 64.4 km/h). Resulting crown fire activity (CFA) maps rated areas as low, medium, or high activity, and we assigned these classes to middens in corresponding areas. Midden quality scores inside a fire perimeter were not changed for middens in areas of low CFA, but reduced by 20% and 50% for medium and high CFA, respectively. We increased midden quality scores following fires (see insect outbreaks). We ran all combinations of mean fire interval (5 levels) and extent (6 levels) at each low and high CFA. Each trial was run for 100 years and replicated 100 times. To evaluate model results, we calculated percentage of simulations dropping below critical levels (100, 50, and 20 squirrels) for each combination. We performed a logistic regression, with populations below and above 50 individuals as the dependent variable and fire severity, extent, and mean interval as independent variables. We included an interaction between mean fire interval and extent, and a squared fire interval term to ensure a non-significant lack of fit test for the model.

## **RESULTS**

### **Validation**

Adding habitat variability improved the fit for the modified population model ( $r^2 = 0.76$ ,  $p < 0.0001$ ) versus the original model ( $r^2 = 0.55$ ,  $p < 0.001$ ), and with known population fluctuations (Figure 2). Model predictions based on a single future resource sequence demonstrate a narrow range of population sizes with little chance of population

numbers dropping to near extinction (Figure 3). However, these results do not incorporate future disturbance.

### **Simulations**

Even with low levels (20%-40%) of tree mortality associated with an insect outbreak, there was a high probability that numbers of MGRS would drop below 100 (Figure 4). At 50% maximum tree mortality, over 20% of predicted population sizes declined to below 100 squirrels, and at 60% maximum tree mortality, at least 30% of populations declined to < 50 squirrels and had a substantial chance of dropping below 20 individuals (Figure 4). At extreme (> 60%), but not unprecedented levels of tree mortality, almost all populations of squirrels fall below critical levels (Figure 4). A 1% increase in insect outbreak severity increased the odds of dropping below 50 individuals by 43% (95% C.I. 30% to 57%; overall model:  $r^2 = 0.79$ ,  $\chi^2 = 526$ ,  $p < 0.0001$ ).

Our model found that the MGRS population would be at a high risk of extinction for many plausible scenarios of fire size, frequency, and severity (Figure 5). The odds of declining below 50 individuals were significantly affected by mean fire interval and severity with interactions between extent and interval (Table 1; overall model:  $r^2 = 0.22$ ,  $\chi^2 = 504$ ,  $p < 0.0001$ ). Specifically, the odds of declining to a critical level increased at shorter fire intervals relative to longer intervals. Mean fire interval continues to play a large role in the chance of persistence for MGRS as extent and mean fire interval interact, with a relative increase in the chance of extinction at short fire intervals and larger extents of burned areas. The importance of the effect of mean fire interval on population

size of MGRS is illustrated by the shape of the probability surfaces (Figure 5); a rapid curved increase in the number of populations declining below critical levels as fire interval decreases but a linear increase as fire size increases.

## **DISCUSSION**

Our addition of a dynamic habitat model to a population model improved model fit. We can successfully capture changes in habitat quality due to disturbance and relate these to population processes, and provide insights for evaluating different conservation strategies and management options (Larson et al. 2004). Disturbances can be incorporated into models at scales allowing evaluation of patterns and probabilities of dropping below critical thresholds generated by different disturbances, prudent as climate change increases the chance of extreme disturbance events (Dale et al., 2001). We used population thresholds because we were interested in assigning probabilities of an event having a severe effect on the population rather than determining the reduction in number of squirrels. Population models are more appropriate for ranking and evaluating alternatives rather than producing population numbers (Turner et al., 1995). Our modeling approach has potential for broad-scale application, as it is easy to use and modify for evaluation of future disturbances on populations. The linkage of a population model to a GIS creates a framework that allows for modification of modeled habitat quality (Larson et al., 2004).

Changes to factors critical in determining dynamics of disturbance will require updates to assumptions used in predictive models. Combinations of disturbance are

difficult to understand; disturbances may affect ecosystems in nonlinear ways or cause synergistic responses (Turner and Bratton, 1987). Incorporating the connection between disturbances relies on a knowledge that permits one to parameterize relationships. We chose to model 2 disturbances separately so that we could evaluate each disturbance independently. Climate change may affect interactions between disturbances and contribute to difficulty in modeling multiple disturbances in the future (Dale et al., 2001).

The insect damage variables we included (extent, severity, and timing of insect outbreaks) may not be valid in the future. Increases in aridity and temperature in the southwestern United States (Weiss and Overpeck, 2005) will likely increase frequency of extreme climatic events. More extreme droughts will also increase severity of insect outbreaks, a pattern already documented. Severity of recent outbreaks could not have been maintained historically (Swetnam et al., 1995). Increased temperatures from global climate change would quicken developmental rates of forest insects and decrease winter mortality, increasing the potential for forest disturbance and altering its course (Ayres and Lombardero, 2000). Introductions of non-native species, such as spruce aphids (Lynch, 2004), have potential to further alter timing and severity of insect outbreaks. In our system, increases in severity of insect outbreaks rapidly exacerbated risk of extinction, and similar damage compounded with amplified severity from climate change may dramatically affect many systems.

Modified climate and associated changes in insect damage would likely increase fire frequency, size, and severity (Ayres and Lombardero, 2000; Flannigan et al., 2000). Drought reduces fuel moisture and increases fire severity and tree mortality. For the

southern Rockies, drought stress is predicted to worsen due to global climate change (Dale et al., 2001). In our system, odds of dropping below critical levels of abundance of MGRS increased with the square of fire frequency, and we found an interaction between fire frequency and extent. Changes from climate alteration move both extent and frequency of fires towards situations with increased chance of dropping below critical population sizes for MGRS. In addition, climate change may alter conditions required for establishment of plant species, therefore disturbance can also result in altered opportunities for recovery from disturbance and forest type (Flannigan et al., 2000).

In the Pinaleno Mountains, adding habitat heterogeneity and modeling future conditions led to novel conclusions about MGRS and suggests important areas for management and conservation actions. The MGRS population will follow different patterns due to loss of high quality habitat in spruce-fir forests (Wood et al., 2007). Our predictions show a population without large fluctuations exhibited over at least the last 20 years. More stable cone supplies in mixed-conifer forests can maintain some squirrels, but the majority of the population existed in spruce-fir forests, where big pulses of resources led to large increases in population sizes. Following insect disturbance, MGRS exist in damaged spruce-fir forests at low numbers and do not respond to masting events with large population fluctuations (Zugmeyer, 2007). In addition to fewer seeds, spruce-fir forests exhibited lower squirrel-edible mushroom yields following insect outbreaks (Koprowski et al., 2005). However, remaining live trees in most spruce-fir forests were destroyed in the Nuttall Complex Fire.

MGRS face acute vulnerability from both insect outbreaks and fire. Even at low levels of fire and insect damage, the population can drop below critical levels. Disturbances in the Pinaleno Mountains are not separate; the future will see a multi-pronged attack with complicated interactions and with cumulative effects much more severe than from a single disturbance. Mixed-conifer forests have over 100 years of fuel accumulation, increasing likelihood of catastrophic fire (Grissino-Mayer and Fritts, 1995). Opening of the forest may not prevent catastrophic fires, as climate fluctuations dry forests and fires catastrophically burn drought-stressed forests whether open or closed canopy (Whitlock, 2004). Squirrels in heavily insect damaged areas of spruce-fir forests experience higher mortality than squirrels in mixed-conifer forests, perhaps caused by opening up of the forest, increasing the success of avian predators (Zugmeyer, 2007). Known MGRS middens are generally located in flatter areas, characterized by mature forests and denser areas (Smith and Mannan, 1994; Wood et al., 2007). These gentle slopes have less potential for crown fires, minimizing our measure of fire severity but due to tree density are potentially subject to increased levels of insect damage (Negron, 1998; Negron et al., 1999). Squirrels may be forced into marginal, steeper areas by disturbance. Areas around these middens would be more likely to experience severe fire.

The chances of MGRS surviving multiple disturbance events are likely to be lower than we predict, considering the multitude of other factors that could be implicated in their decline including competition from introduced Abert's squirrels, new forest pests, other introduced species, predation, disease, development, the potential for changing dynamics due to anthropogenic influences and climate change (Swetnam and Lynch,

1993; USDI Fish and Wildlife Service, 1993; Koprowski et al., 2005; Rushton et al., 2006), and other unforeseen factors. Together, these could create a reality more severe and dire than our estimates. We can, however, use our simplified approach to examine factors discretely and assess the magnitude of individual threats. The added benefit of our model is its ability to be used to evaluate the immediate future and contribute to adaptive management (Murray and Marmorek, 2003). Once the magnitude of damage due to a disturbance event in the Pinaleno Mountains is known, our MGRS model can be used to evaluate the potential consequences of that disturbance to the endemic squirrel. Mitigation can be planned and potential management actions evaluated.

The basic framework we developed can be used to evaluate other species in multiple ecosystems (Larson et al. 2004). We modeled a small mammal but the potential exists to use the same techniques at multiple scales. Remote sensing technologies exist that allow for large-scale habitat analysis (e.g. Kinnaird et al. 2003) and as technologies improve, an examination of microhabitats important to smaller sized and ranging organisms (Entwistle and Stephenson, 2000) will become possible. The ability to monitor small organisms over large areas is critical to conservation. For example, small mammals are underrepresented in conservation efforts yet critical to ecosystem function (Entwistle and Stephenson, 2000). The ability to model future responses of species to disturbance is important, as global climate change will likely increase severity and frequency of disturbance worldwide (Dale et al., 2001). To mitigate these changes, conservation biologists and managers must have tools available to evaluate landscape impacts on species of interest and to evaluate multiple management possibilities.

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Table C1, Odds, from a logistic regression for binomial counts, of the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) population, Pinaleno Mountains, southeast Arizona, falling below 50 individuals for future fire scenarios. Extents ranged from 100 ha to 10,000 ha, intervals from 4 years to 300 years, and severity was rated as low or high.

Term	Odds ratio	Std Error	$\chi^2$	p value
ln(extent)	0.96	0.093	0.16	0.688
ln(interval)	0.19	0.203	65.08	<0.001
High fire severity	1.19	0.064	7.36	0.007
ln(interval) * ln(extent)	0.87	0.050	7.14	0.008
ln(interval) <sup>2</sup>	0.76	0.081	11.92	<0.001

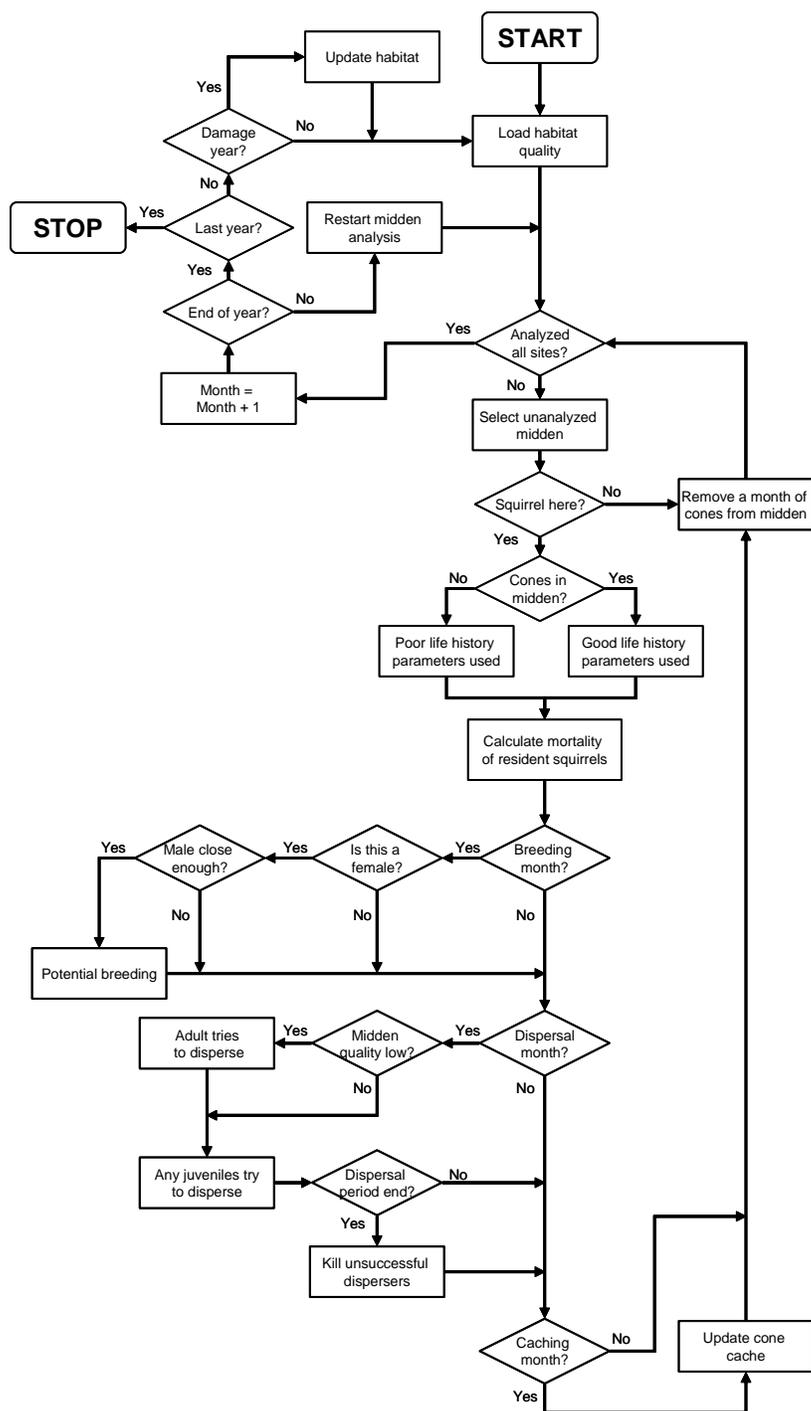


Figure C1, A flow chart illustrating a spatially explicit Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) stochastic population model incorporating habitat heterogeneity and disturbance.

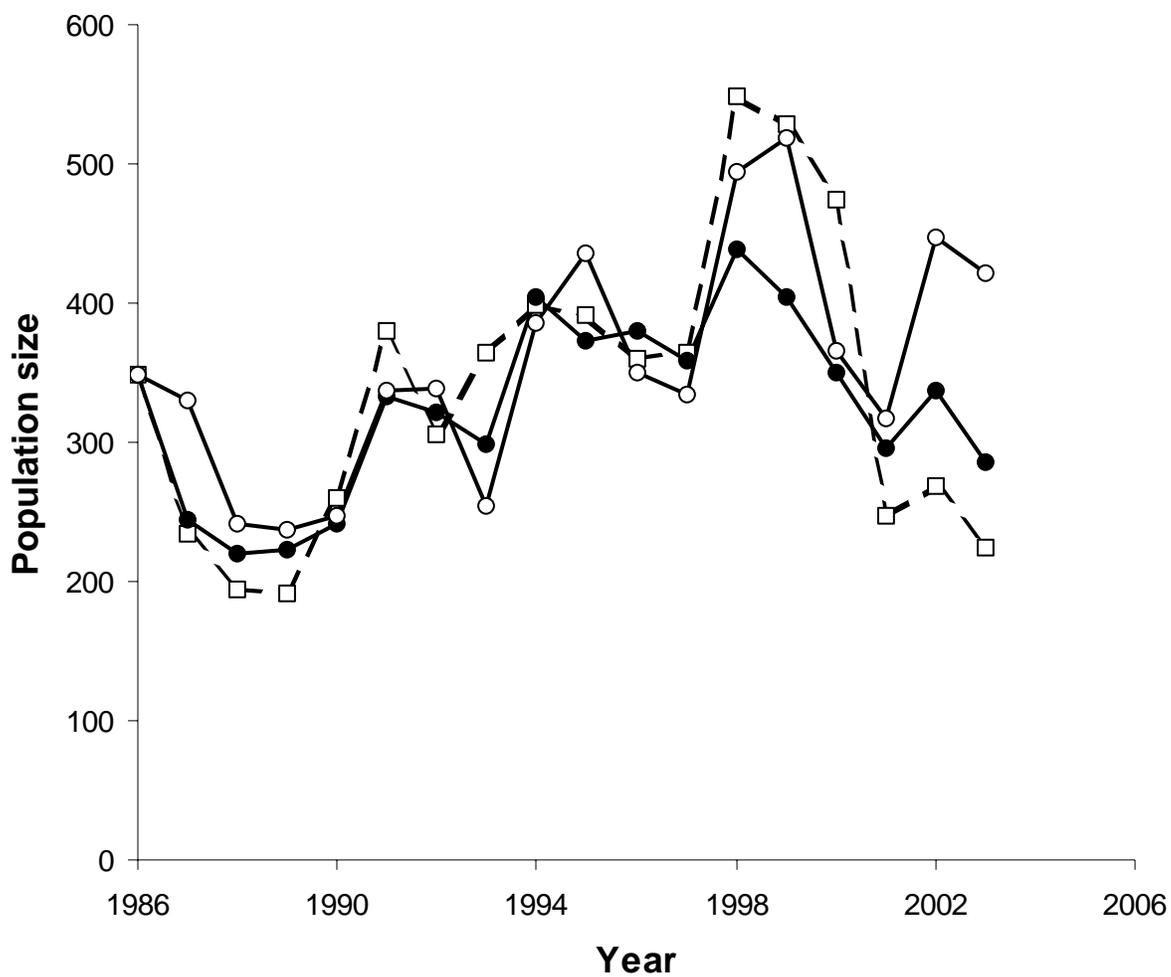


Figure C2, Revised spatially explicit Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) population model incorporating habitat heterogeneity (closed circles;  $R^2 = 0.76$ ) compared to model without habitat heterogeneity (open circles;  $R^2 = 0.54$ ; see Rushton et al., 2006) and census data (open squares, dashed line) for 1986 – 2003.

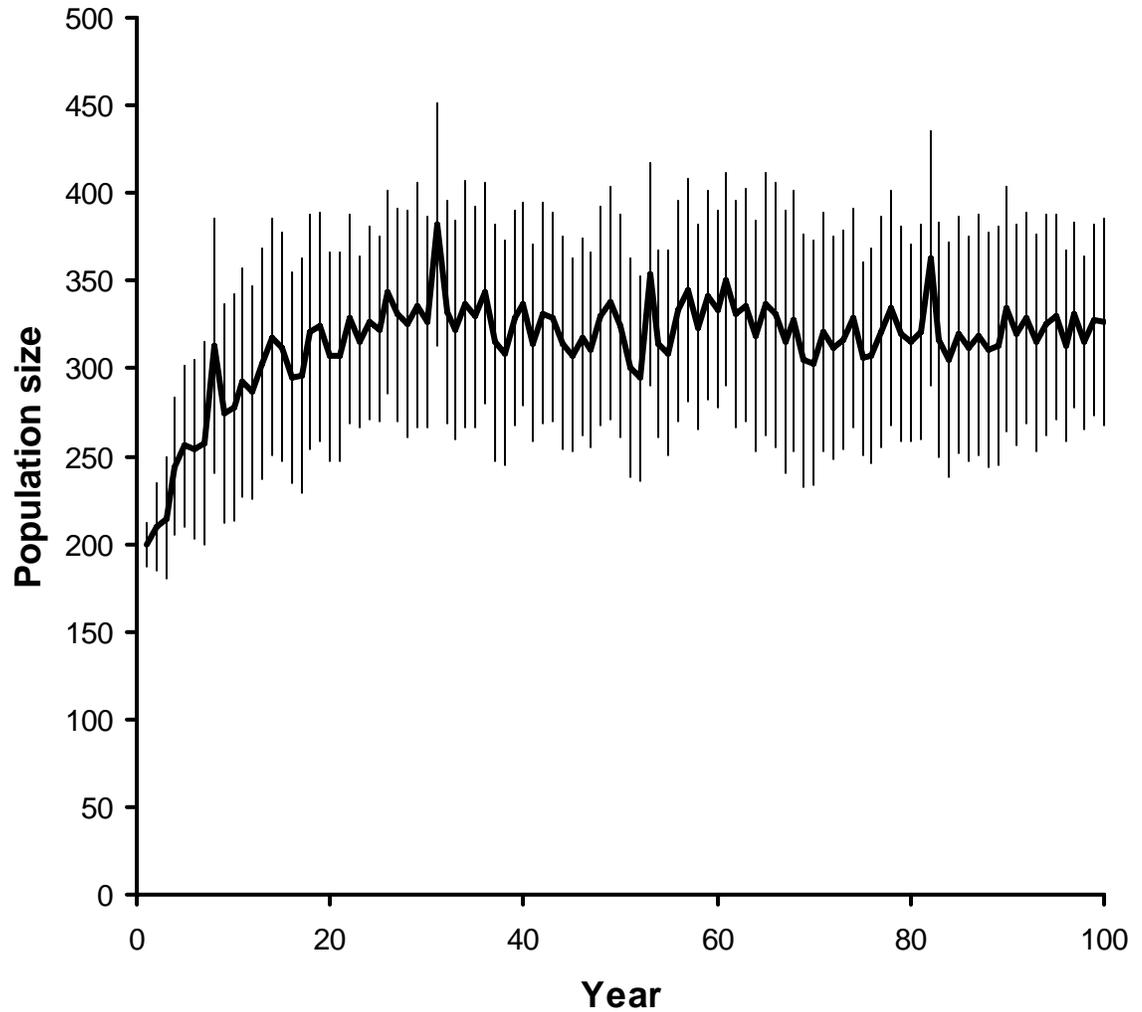


Figure C3, Future spatially explicit population model predictions of population size ( $\pm 1SE$ ) for the Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) over the next 100 years generated for a single predicted masting sequence without disturbance. Population size does not exhibit large fluctuations as seen prior to large scale insect damage in the spruce-fir forests of the Pinaleno Mountains, Arizona.

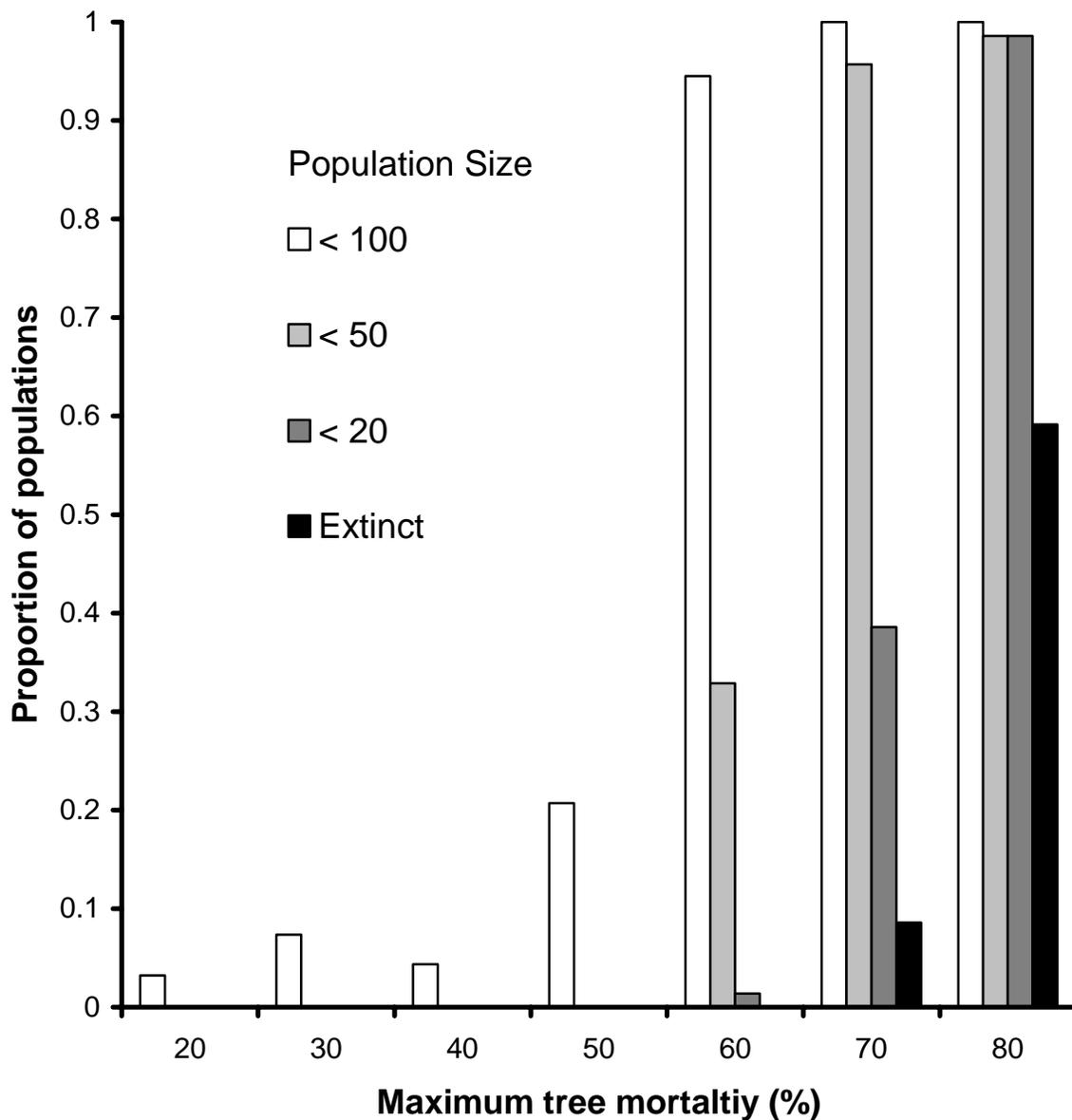


Figure C4, Percentage of Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) populations dropping below critical thresholds at different levels of insect outbreak severity. Estimates generated from a Mt. Graham red squirrel spatially explicit population model incorporating future insect disturbance where insect outbreak severity was measured by the maximum tree mortality a site would sustain in an outbreak.

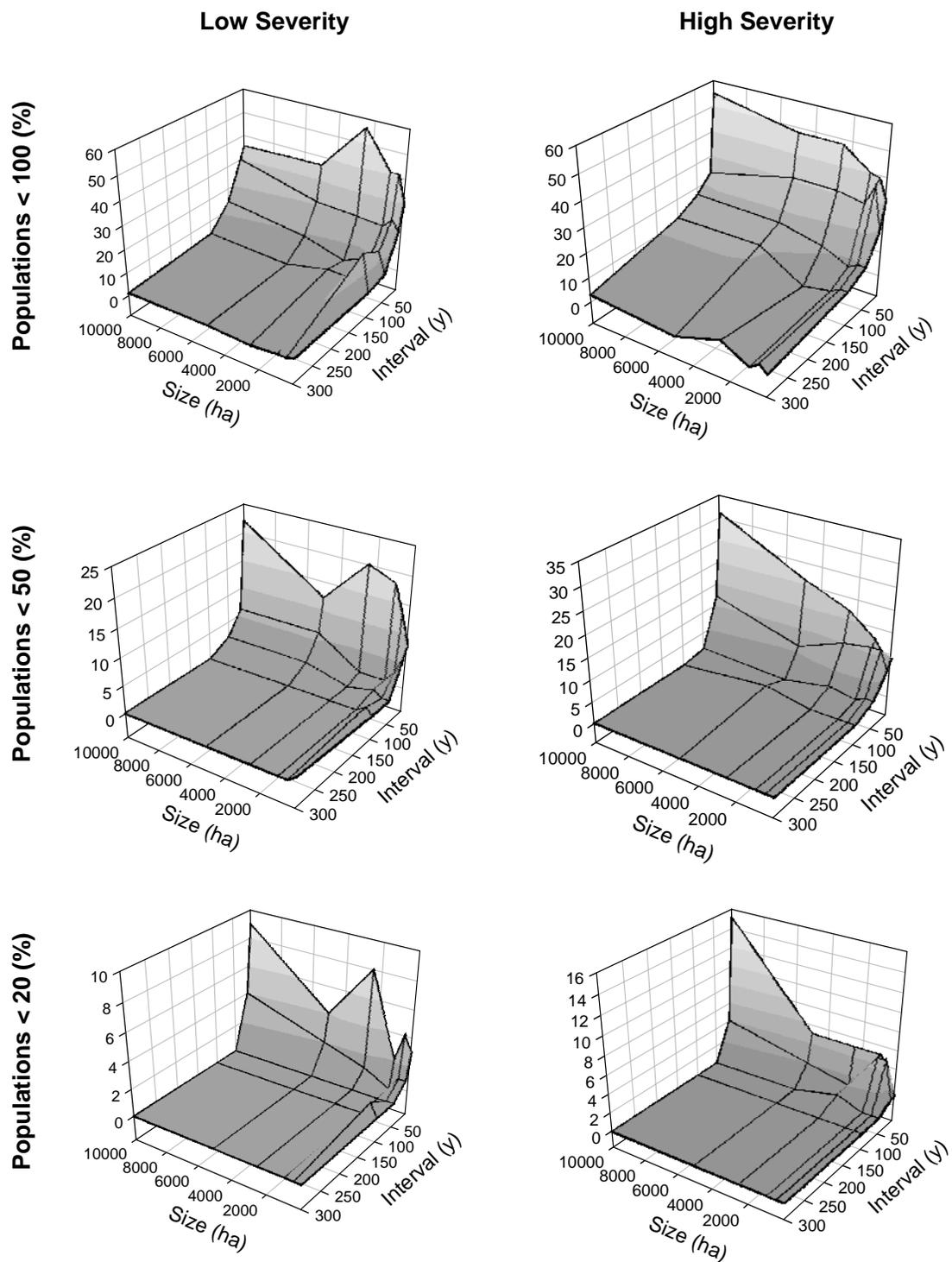


Figure C5, Percentage of Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) populations dropping below critical population thresholds at combinations of mean fire intervals and fire sizes over the next 100 years. Estimates generated from a Mt. Graham red squirrel spatially explicit population model incorporating wildfire.