Research Article

Fine-Scale Analysis of Mount Graham Red Squirrel Habitat Following Disturbance

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ABSTRACT Habitat destruction and degradation are major factors in reducing abundance, placing populations and species in jeopardy. Monitoring changes to habitat and identifying locations of habitat for a species, after disturbance, can assist mitigation of the effects of human-caused or -amplified habitat disturbance. Like many areas in the western United States, the Pinaleño Mountains of southeastern Arizona, USA, have suffered catastrophic fire and large-scale insect outbreaks in the last decade. The federally endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) is only found in the Pinaleño Mountains, and to assess effects of forest disturbance on habitat we modeled their potential habitat by identifying characteristics of cover surrounding their centrally defended middens. We classified high-spatial resolution satellite imagery into ground cover classes, and we used logistic regression to determine areas used by squirrels. We also used known midden locations in conjunction with slope, elevation, and aspect to create a predictive habitat map. 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 mature forests to the Pinaleño Mountains will rely on preservation of mixed conifer zones of the mountain and active restoration of 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 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. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2357–2364; 2007)

Anthropogenic habitat destruction and degradation reduce abundance, increasing risk of extinction due to demographic, genetic, and environmental stochasticity, and natural catastrophe (Shaffer 1981, Soulé 1987). Due to human impacts, the extinction rate is estimated at 48–11,000 times higher than the background rate (Baillie et al. 2004). Anthropogenic habitat destruction and degradation are major threats to >85% of threatened mammals, birds, and amphibians, and they have 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 sustained for conservation of species; therefore, identification of quality habitat and monitoring habitat disturbance are necessary for conservation and management.

The Pinaleño Mountains, southeastern Arizona, USA, are a microcosm of forests in the western United States, as recent increases of insect and fire disturbance (Koprowski et al. 2005, 2006) mimic forest conditions elsewhere (Allen et al. 2002, Lynch 2004). Holocene warming has restricted

spruce–fir and mixed conifer forests and their associated fauna to the highest elevations in the southwest (Lomolino et al. 1989). 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). Therefore, responses of tree squirrels to forest disturbance can be used to elucidate overall damage and quality of forests, such as those found in the Pinaleño Mountains, after disturbance.

The Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; MGRS), a federally endangered tree squirrel (U.S. Fish and Wildlife Service [USFWS] 1993), is found only at upper elevations in the Pinaleño Mountains. Mt. Graham red squirrels have persisted for >10,000 years, despite multiple large disturbances in the Pinaleño Mountains (Grissino-Mayer and Fritts 1995), but they now face anthropogenically amplified disturbances due to fire suppression. 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). However, MGRS have an estimated population of <300 squirrels, and this species is one of the most

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critically endangered mammals in North America; therefore, forest management practices must take into account MGRS habitat requirements. In 1988, USFWS established a refugium to restrict access to MGRS critical habitat (USFWS 1993). Mt. Graham red squirrels are territorial and defend middens to provide food for winter and in years of a poor cone crop (Finley 1969). Middens aid red squirrels in the protection of their food store by concentrating food while providing a cool, moist microclimate to delay cone opening and to prevent seed predators from accessing seeds (Smith 1968, Gurnell 1987). Generally, territories are circular, surrounding the midden for maximum foraging efficiency, and territories are critical to survival because squirrels gather most cones from territories for storage (Finley 1969, Rusch and Reeder 1978).

The positioning of middens and territories is likely to be a critical measure of the success of MGRS in the landscape. By investigating the factors that determine their position, we can accurately describe available habitat to make informed management and conservation decisions. Although past efforts identified MGRS habitat in the Pinaleño Mountains (Pereira and Itami 1991, Hatten 2000), an evaluation of current conditions after forest disturbance is needed for conservation. Additionally, the low spatial resolution of data generally used in models hampers the ability to capture fine-scale differences important to species, so we examined the extent to which high-resolution imagery predicts habitat. Our objectives were to 1) determine size and composition of forest patches that could contain MGRS middens, 2) relate patch characteristics and seedfall to midden occupancy, 3) combine spatial data for occupied middens to predict potential MGRS habitat, and 4) compare predicted habitat to areas previously described as highest quality by prior habitat models.

STUDY AREA

The Pinaleño Mountains rise from the relatively hot and dry surrounding desert at approximately 1,000 m to a cooler, moister environment at a maximum elevation of 3,267 m, and they form a sky island of forest surrounded by desert scrub. Precipitation came from 2 main pulses, snows from December to April and monsoon rains from July to September (total precipitation 1996–2003, 241.2 ± 23.9 mm [SE]; range = 77.8–438.1 mm). Our study area was located in the upper elevations of the range, and it was composed of 2 distinct forest types, spruce–fir forests (3,050–3,267 m) of Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*) and mixed conifer forests (2,870–3,050 m) of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), southwestern white pine (*P. strobiformis*), Engelmann spruce, and corkbark fir. Middens were surveyed mountain-wide by the Arizona Game and Fish Department (AGFD). Intensive monitoring was conducted on 252.5 ha of forest (72.1 ha of mixed conifer near Columbine Visitor Center; 180.4 ha of spruce–fir on Emerald, Hawk, and High peaks), as part of a long term monitoring program (Young 1995,

Koprowski et al. 2005). This intensively monitored study area contained 34% of all known middens. Catastrophic wildfires burned approximately 2,900 ha in 1996 (Clark Peak Fire; Froehlich 1996) and approximately 11,900 ha in 2004 (Nuttall Complex Fire; Koprowski et al. 2006) with parts of both fires burning into mixed conifer and spruce–fir forests. Also, large insect outbreaks damaged spruce–fir forests beginning in 1996 (Koprowski et al. 2005).

METHODS

Satellite Imagery

We acquired QuickBird satellite imagery (DigitalGlobe, Inc., Longmont, CO) in June 2003 for an area covering all potential habitat for MGRS by applying a 200-m buffer in ArcGIS 9.1 to the area delineated by the MGRS habitat map of Hatten (2000). We performed a Gram–Schmidt pansharpening to convert 2.4-m 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 we used principal components (PCs) analysis (PCA; Jensen 2005) of bands 1–4 (blue, green, red, and near infrared) of the Gram–Schmidt pansharpened multispectral image to reduce data dimensionality.

Our aim was to classify ground cover classes from the image to separate live, healthy trees from dead or dying trees. We used the isodata unsupervised classification procedure in ERDAS Imagine 8.6 (Leica Geosystems LLC, Norcross, GA) on several combinations of input layers, including the original 4 spectral bands, the NDVI layer, and the first 3 PCs from the PCA. Our most satisfactory classification resulted from a combination of the first 3 principal PCs from a PCA of bands 1–4 of the Gram–Schmidt pansharpened multispectral image. We mapped 9 separate land cover classes in the study area: 1) large healthy conifers; 2) small healthy trees or shrubs; 3) dying or dead trees; 4) cienega (a spring fed marsh or swamp), 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 were limited in extracting information from shadows, but by visually examining these areas, we deduced they were mostly composed of the unlit sides of live tree canopies, and we classified them as trees for analysis.

We selected 176 random locations to ground truth image classification. At each point, we recorded Global Positioning System (GPS) coordinates and we estimated, to the nearest 10%, canopy cover and the amount of damage due to fire and insect infestation (% of trees killed by each) within a 10-m radius around each point. We computed image-based canopy cover and damage measurements for all points in the study area. We determined canopy cover at each point from the percentage of 0.6-m pixels classified as trees within 10 m of that point. We determined damage severity for a given point by calculating the percentage of dead trees out of all trees within 10 m of that point. Because we could only verify accuracy of random points to within 10 m of their

corresponding locations in the satellite image, we determined and selected the best match for each ground truth point within the potential GPS error (10 m) of a point, and we 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 of MGRS midden sites have been monitored since 1986 by the AGFD (Hatten 2000). We monitored a subset of these middens more intensively by conducting ground surveys and recording midden occupancy quarterly (Koprowski et al. 2005) under permit from the University of Arizona Institutional Animal Care and Use Committee (05-031), the AGFD (SP796413), and the USFWS (TE041875-0). We used squirrel sightings and visible signs of activity to determine midden occupancy as either 1) occupied by an animal of unknown sex, 2) occupied by a male, 3) occupied by a female, or 4) unoccupied (Koprowski et al. 2005). We used occupancy data from 9 quarterly surveys around the image acquisition date of June 2003: summer 2002 (Jun–Aug), fall 2002 (Sep–Nov), winter 2002–2003 (Dec–Feb), spring 2003 (Mar–May), summer 2003, fall 2003, winter 2003–2004, spring 2004, and summer 2004. We assessed cone crop, directly related to and measured as seedfall, yearly (beginning in 1993) for 5 tree species eaten by MGRS (ponderosa pine, southwestern white pine, Douglas-fir, corkbark fir, and Engelmann spruce) from the same 28 plots (19 spruce-fir, 9 mixed conifer) distributed randomly within the intensively monitored areas. We randomly placed 3 0.25-m^2 seed traps within a 10×10-m plot at each location. We collected seeds for a given year from seed traps in spring of the following year. We separated by species and tallied conifer seeds contained in each trap (Koprowski et al. 2005, Rushton et al. 2006).

Midden Site and Land Cover

Midden site selection may be based on microclimate (appropriate conditions for cone storage) or on larger scale factors (productive territory). Hence, we examined 3 different-sized areas around a midden to determine which size best predicted MGRS site use. We chose a 10-m buffer distance to mimic previous field studies (Smith and Mannan 1994, Koprowski et al. 2005) and to 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 whether midden sites are selected at a larger scale. We created buffers around locations of our intensively monitored midden sites ($n = 389$) and counted the number of pixels of each of our 9 satellite image-determined land cover classes within the buffers, by using ArcGIS 9.1. We used random coordinates to identify nonmidden 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

We performed all statistical analyses with R (R Development Core Team, Auckland, New Zealand). Conditions around individual middens and random sites formed different combinations of the 9 land cover classes; each midden sat in the center of a circle with different amounts of each cover type. Because of the unit area sum constraint, we could not relate midden occupancy to the area of individual cover types. To avoid this problem and to reduce data dimensionality, we performed a PCA (Mardia et al. 1979) for all sites for each of the 3 buffer distances with the amounts of each cover type at each site as input. The end goal was to produce 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 (Mardia et al. 1979), the first 2 PCs of the PCA rotations for the 3 different buffer distances. To examine sex differences in site use, we compared middens in a stepwise linear discriminant analysis (Mardia et al. 1979) on the PC scores for middens of each sex. The only distinguishing variable was PC1 (error rate $= 0.42$), and it did not differ between the sexes ($t = -1.297$, $P = 0.21$), so we pooled occupied male and female middens for occupancy analyses.

Using logistic regression assuming binomial error structure (McCullagh and Nelder 1983), we investigated the relationship between midden occupancy and habitat characteristics. We used the first 4 PCs derived from land cover counts surrounding midden and random sites (PC1, PC2, PC3, and PC4) as independent predictor variables, and we defined site type (midden or random site) as the dependent variable. We used only middens occupied in June 2003, because these most closely correspond to the date of image acquisition. We performed analyses 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). We compared each midden set to each of the 4 sets of PCs for each of the 3 buffer distances, resulting in 12 models for each midden set.

We also used logistic regression (McCullagh and Nelder 1983) to investigate differences in individual midden quality by examining how often a midden was occupied. 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 9 seasons around satellite image acquisition. The dependent variable was the proportion of these seasons each midden was occupied (a pass-fail binomial response model).

Statistical Models of Seedfall

We took a 2-step approach to examine how cone availability is related to midden location. First, we created a multiple regression model (Ramsey and Schafer 2002) for seedfall. We created 28-m buffers and we tabulated land cover classes from satellite image classification for our seed plots and we generated PC scores with the same method as described above. We used in the analysis our independent predictor

variables for each seed trap site (PC1, PC2, PC3, yr, habitat, habitat × yr) and the log-transformed total seed counts (dependent variable) for the year before and the year of image acquisition. We used year in the model to account for differences between seed crops in mast and normal years as an indicator variable, with 0 as a normal year and 1 as a mast year. We used forward stepwise regression to identify the most parsimonious model. Second, we used the result from the multiple regression to predict seedfall at midden and random sites and compare seedfall to midden occupancy and turnover with the same method described above for models of occupancy (seedfall as the independent predictor variable).

Predictive Map

We generated logistic regression models, assuming binomial error structure (McCullagh and Nelder 1983), 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 9 land cover types from the classified image within a 28-m buffer for each 0.6-m cell in our classified satellite image. These counts of land cover type, and the PCA rotation we developed for occupancy models, allowed us to calculate PC scores for each cell. We used a 10-m digital elevation model (DEM) to generate elevation, slope, and aspect values for every cell in the study area. We divided aspect into 2 measures of energy: a north-to-south component [aspectNS = cos(aspect) × 90 + 90] and an east-to-west component [aspectEW = sin(aspect) × 90 + 90; Pereira and Itami 1991]. We used AGFD census results and selected the 144 active middens within the period from June 2001 to June 2004 as midden locations, and we created 320 random sites within the study area. We used the first 2 PCs (PC1 and PC2) and the DEM-derived characteristics (elevation, slope, aspectNS, and aspectEW) as independent predictor variables, and we used site type (midden and random) as the dependent variable. We also created 2 additional models to examine the effect of nonbiological parameters on our results. In the second model, we removed elevation from the list of independent predictor variables. Our 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 3 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 probability value, by calculating gain ({1 − [(% area > p)/(% 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

Of ground truth sites, >80% had satellite image-derived canopy cover within 10% of that observed in the field. We visually examined outliers (points >20% different), and we found our classification had overlap between classes, especially between shadow classes and ground cover due to tree shadows. In addition, the cienega–grass–aspen class had overlap with the small healthy tree or 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 >80% of our random points, somewhat lower accuracy than for canopy cover. Satellite image classification overestimated damage at lower damage levels, and it underestimated damage at higher damage levels. 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–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 of the buffered random and midden sites explained >80% of the variation in the first 4 PCs. The first PC emphasized the change from healthy small and large trees to more open areas of dead or dying trees and soil. The second PC emphasized the change from shadow to open areas of brighter soils. The first 2 PCs did not differ between buffers of 10 m and 28 m, 10 m and 56 m, or 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 rather than 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 1). The PC1–4 and PC1–3 models at 28 m (Table 2) best predicted occupancy. Squirrels were using midden sites with high numbers of healthy trees, with possibly some aspen, more than areas with high damage (high PC1). Squirrels located middens in denser forests over open areas of rock and soil (low PC2).

Our binomial model of proportion of occupied seasons [Logit(p) = −2.893 + (0.499 × PC1) + (−0.230 × PC2), where p is the probability a midden is occupied, $D^2 = 0.17$] 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 3 PCs and a year indicator variable to account for mast years [Fig. 1: Ln(seeds) = 2.57 + (0.263 × PC1) + (−0.205 × PC2) + (−0.334 × PC3) + (yr × 2.3), $F_{4, 51} = 55.7$, $P < 0.001$, $R^2 = 0.81$]. There was no interaction for seedfall between mast year and forest type. Similar to midden site selection models, higher seed production was found in areas of healthy (higher PC1), thicker (lower PC2) trees compared with open areas and areas with dying trees. A model of seedfall at occupied sites versus random sites explained midden site selection {Logit(p) = −15.43 + [4.22 ×

Table 1. The D^2 values for models examining habitat differences between occupied Mt. Graham red squirrel middens in 2003 and random sites in the Pinaleño Mountains, Arizona, USA. Principal components (PCs) axes from a principal components analysis of land cover counts derived from a classified satellite image.

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

ln(seeds)], where p is the probability a midden is occupied, $D^2 = 0.24$} as did a pass–fail binomial response model with the number of passes equal to seasons occupied out of 9 {Logit(p) $= -7.85 + [1.86 \times$ ln(seeds)], where p is the probability a midden is occupied, $D^2 = 0.14$}. 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 midden and random sites found that PC1, PC2, elevation, slope, and both components of aspect were significant predictors of midden location (Table 3). In each of the 3 models, much of the area classified as suitable, dense and healthy, falls outside the MGRS refugium (Fig. 2). For the all-inclusive model, our accuracy assessment showed that 90% of active middens occurred in areas with a probability score >0.3 (Fig. 2a). Only 21% of the study area was classified >0.3 in our probability map, for a gain of 77%, and known midden sites had higher relative scores than random sites (ROC plot, area under the curve [AUC] = 0.903). In the no-elevation model (Table 3), 77% of middens occurred within areas having a probability >0.3 (Fig. 2b). Suitable sites for middens made up 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). In the PC-only model (Table 3), 59% of middens occurred in areas with a probability >0.3 (Fig. 2c). Gain was only 48%, but the model prediction power was acceptable (ROC plot, AUC = 0.691). After the development of our models, the

Table 2. Results of 2 logistic regression models assuming binomial error structure comparing ground cover classes within 28-m buffers around Mt. Graham red squirrel midden sites and random sites, Pinaleño Mountains, Arizona, USA, 2003. Principal components (PC)1–4 are the first 4 bands from a principal components analysis of land cover counts derived from a classified satellite image.

Parameter	Estimate	SE	Z value	P
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:				
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
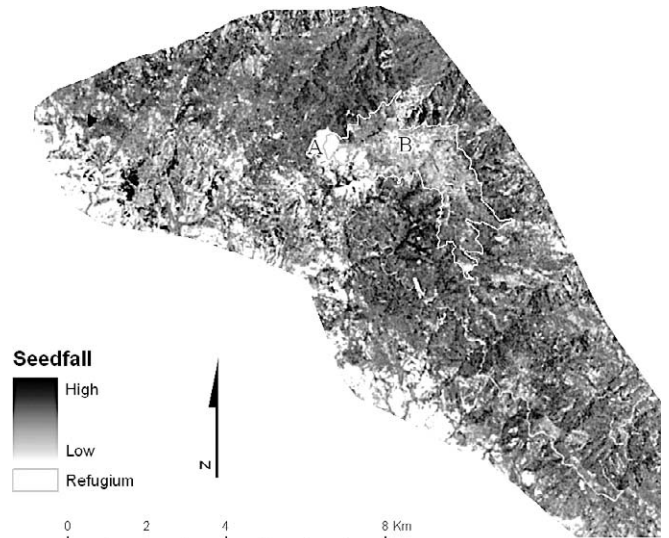
Figure 1. Seedfall predicted from principal components derived from high-resolution satellite imagery, taken June 2003, over potential Mt. Graham red squirrel habitat in the Pinaleño Mountains, Arizona, USA. Crown fire damage from the 1996 Clark Peak Fire (A) and severe insect damage in the late 1990s (B) show large reductions in seedfall compared with the surrounding forest.

Nuttall Complex fire burned into the upper elevations of the Pinaleño Mountains, destroying middens and burning areas classified as habitat in our models (Fig. 3).

DISCUSSION

Habitat for the Mt. Graham red squirrel has been reduced and constrained due to recent disturbances from fire and

Table 3. Results of nested binomial logistic regression models of Mt. Graham red squirrel midden locations, Pinaleño Mountains, Arizona, USA, 2003. We derived principal component (PC) axes from principal components analysis of ground cover class counts of Mt. Graham red squirrel midden sites versus random sites derived from high-resolution satellite imagery. We derived elevation, slope, and aspect from a 10-m digital elevation model. We divided aspect into 2 measures of energy based on the north–south and east–west direction the site faced.
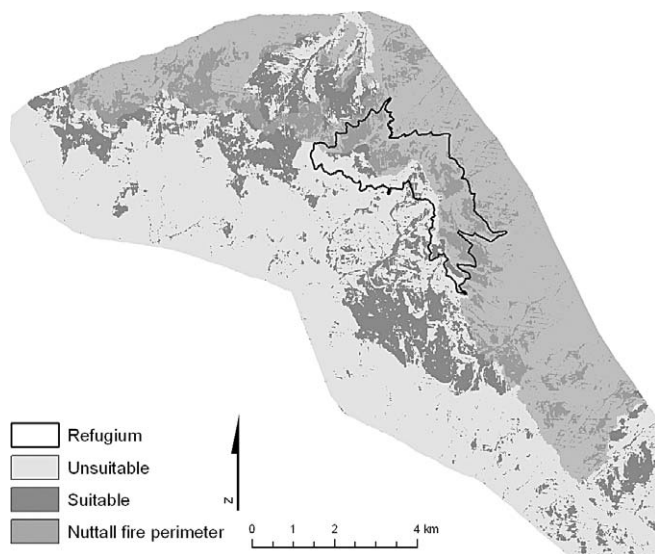
	Estimate	SE	Z value	P
Full model				
Intercept	−21.11	3.986	−5.29	<0.001
PC1	0.520	0.120	4.31	<0.001
PC2	−0.869	0.169	−5.11	<0.001
Elevation (m)	0.006	0.001	5.25	<0.001
Slope (degree)	−0.100	0.017	−5.75	<0.001
AspectEW	0.006	0.002	2.74	0.006
AspectNS	0.006	0.002	2.43	0.015
No-elevation model				
Intercept	−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 (degree)	−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
PC only model				
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
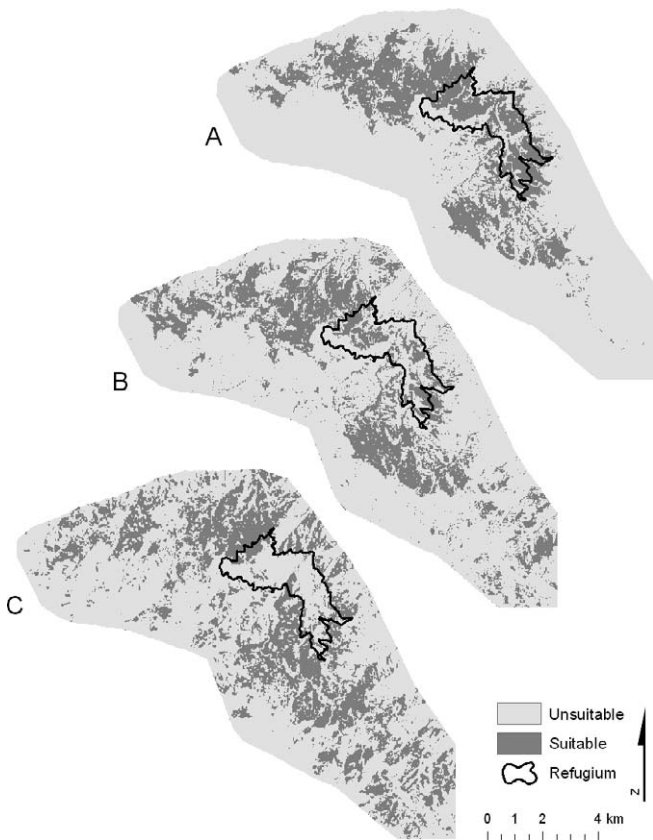
Figure 2. Mt. Graham red squirrel midden probability maps with areas of high midden probability (>0.3) compared with all potential area (<0.3) for the Pinaleño Mountains, Arizona, USA, 2003. The protected squirrel refugium is within the black boundary. Predictive parameters are (A) principal component (PC)1, PC2, elevation, slope, aspectEW (east–west facing of the site), and aspectNS (north–south facing of the site); (B) PC1, PC2, slope, aspectEW, and aspectNS; and (C) PC1 and PC2. PC1 and PC2 are the first 2 bands from a principal components analysis of land cover counts derived from a classified satellite image.

Figure 3. Suitable Mt. Graham red squirrel midden locations (p > 0.3) affected by the 2004 Nuttall Complex Fire in the Pinaleño Mountains, Arizona, USA. The probability model uses the predictive parameters principal component (PC1), PC2, slope, aspectEW (east–west facing of the site), and aspectNS (north–south facing of the site). Principal component 1 and PC2 are the first 2 bands from a principal components analysis of land cover counts derived from a classified satellite image.

insects, especially in the MGRS refugium where little habitat now remains. These disturbances killed trees and opened up the forest. However, midden sites are more likely to be found in areas of more live trees and denser forests, also areas where we predicted higher seedfall. Middens are located to maximize collection of 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 they provide a stable, observable site to analyze for habitat models, directly contributing to the success of this project. 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 habitat selection.

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 4 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 relative to the satellite imagery in heterogeneous areas or near cover type boundaries may have reduced the predictive power of our models. But without high spatial resolution, we would not have identified fine-scale patterns created by insect damage (Baker and Veblen 1990), and accurately localized seedfall predictions permitted a useful extrapolation to mountain-wide conditions.

Mt. Graham red squirrels use dense, healthy, mature forests for middens (Smith and Mannan 1994), conditions that now occur outside the MGRS refugium. We identified that selection statistically best occurred on a 28-m plot around middens, with strong selection on 56-m plots as well, indicating that selection also occurs on a territory scale rather than only at a microclimate level at the midden site. 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). Correspondingly, we found territories and middens more likely to be located and occupied in areas of high seedfall. Red squirrels spend significant energy collecting food (Smith 1968), and they 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 1968). Any reduction in territory quality, including, but not always, from thinning, may result in increased home range sizes

(Wolff and Zasada 1975, Sullivan and Moses 1986, Haughland and Larsen 2004), reduced survival, or abandonment of the midden.

In years before insect damage, seedfall in the Pinaleño Mountains would have shown large differences between spruce–fir and mixed conifer forests during mast and nonmast years (J. L. Koprowski, University of Arizona, unpublished data; Koprowski et al. 2005), which we did not find. 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). Mixed conifer forests of the Pinaleño Mountains contain the majority of squirrels, a reversal due to insect damage. Furthermore, spruce–fir forests exhibit stand-replacing fires every 200–400 years (Peet 1998), whereas mixed conifer forests have a 4-year interval of 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).

Our predictive maps are useful for comparison of past and future changes to habitable areas and for predicting the location of new middens (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 toward predicting high-elevation sites as more suitable and reduce probability scores of lower elevation mixed conifer sites that may be of higher quality. Mt. Graham red squirrels do occur at lower elevations than previously thought (Hatten 2000), and new middens continue to be found (J. L. Koprowski, unpublished data). Our model based solely on PCs indicates the degree of damage to high elevations, but it has lower predictive accuracy, illustrating that MGRS select areas with the right vegetation and 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 for 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 its effects on these ecosystems will be tested (Joyce et al. 2001). Our approach will facilitate fine-scale analysis of forests and modeling responses to disturbance. By creating models for indicator species, insight into ecosystem health and function is gained. By observing trends in habitat availability the recovery of an area after habitat disturbance can be identified by evaluating when a damaged area returns to a suitable classification, even before the indicator species has recolonized the area.

MANAGEMENT IMPLICATIONS

Current forestry practices prohibit thinning within 10 m of a MGRS midden during fuels reduction (U.S. Department of Agriculture Forest Service [USFS] 2000) but managers should be aware that squirrels are selecting on a territory scale as we identified, with strong evidence at 28-m and 56-m radii of selection. Therefore, further work needs to be done to ensure managers understand what triggers MGRS to select territories, and at what scale, so managers can make correct forest restoration decisions without hurting MGRS. After insect and fire disturbances in the Pinaleño Mountains, conservation efforts need to focus beyond spruce–fir forests, realizing that the critical habitat has been severely degraded. Therefore, a thorough survey of mixed conifer forests is needed to locate additional middens and to help start a reevaluation of where the most important MGRS habitat remains. Our results can be used to narrow the search area to the most probable locations for middens. Additionally, to ensure the future survival of this species, proper management will rely on the restoration of damaged spruce–fir and mixed conifer forests while protecting remaining stands of dense, mature forest.

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