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RESEARCH ARTICLE

Impact of forest management on the communication distance of an endangered tree squirrel

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Abstract

Long-distance acoustic signals mediate important social interactions between animals, and the structure of the environment can influence sound transmission to affect communication distance. Anthropogenic disturbances such as fire suppression alter forest structure and can potentially affect acoustic interactions by altering sound attenuation patterns. In the spruce-fir and mixed-conifer forests of the Pinaleño Mountains, Arizona, USA, that harbor endangered Mount Graham red squirrels (*Tamiasciurus fremonti grahamensis*), numerous historical anthropogenic disturbances have altered forest characteristics and contributed to habitat degradation and loss. In this study, we assessed how recent forest management treatments influenced the attenuation of red squirrel territorial rattle vocalizations. In June 2023–August 2023, we broadcast and recorded rattles 5.4 m above the forest floor at various distances (1, 10, 20, and 40 m) to mimic hypothetical senders and receivers. We used on-the-ground measurements and lidar to quantify forest structure relative to patterns of sound attenuation in 3 treatments: thinning, understory fuel reduction, and untreated control plots. Across all treatments, we found that increasing tree basal area resulted in higher attenuation, with rattles being approximately 6 dB lower in amplitude in the most dense compared to the least dense plots, equivalent to a doubling in squirrel communication distance. Additionally, rattles on untreated control plots experienced more attenuation than thinned (~3 dB) and fuel-reduced

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(~1.5 dB) plots. A lidar-derived measure of canopy structure was a better predictor of rattle attenuation than lower resolution on-the-ground measurements. In the short-term, forest thinning may facilitate development of acoustic social neighborhoods that increase squirrel fitness, though alternative costs of more open forests exist. More generally, our results indicate that forest management can affect the efficacy of acoustic communication and that integration of signaling and sensory ecology with remote sensing can inform wildlife conservation.

KEYWORDS

acoustic communication, audible distance, environmental attenuation, forest management, lidar, Mount Graham red squirrel, remote sensing, *Tamiasciurus fremonti grahamensis*

Ecological restoration aims to restore biodiversity to ecosystems degraded primarily by human activities. However, inconsistent outcomes of restoration projects (Jones et al. 2018, Atkinson et al. 2022) indicate that new perspectives are required to better understand variation in success rate. In animals, integrating knowledge of behavior can improve habitat restoration (Hale et al. 2020). For example, vulnerable populations of willow flycatchers (*Empidonax traillii*) exhibit conspecific attraction and recolonize areas of variable habitat quality if conspecific songs are broadcast experimentally (Schofield et al. 2018). Such knowledge of animal behavior is increasingly being incorporated into planning and improving restoration efforts (Hale et al. 2020).

Acoustic communication is a widespread behavior that mediates key social interactions in many animals (Bradbury and Vehrencamp 1998). The efficacy of acoustic signal propagation depends on properties of the environment (Marten and Marler 1977), with attenuation arising from atmospheric and ground absorption, and reflection of sound by vegetation (Marten and Marler 1977, Marten et al. 1977, Waser and Brown 1986). In forested ecosystems, vegetation contributes significantly to signal attenuation (Wiley and Richards 1978, Richards and Wiley 1980, Blumenrath and Dabelsteen 2004). Despite a large body of work on the effects of vegetation structure on sound propagation, few studies have assessed the impact of forest restoration and management on the efficacy of animal communication (Green et al. 2020, Brzozowski et al. 2023, Boycott et al. 2023), especially in relation to the mechanisms underlying animal sensory worlds or umwelten (von Uexküll 1934, Dusenbery 1992). Integration of sensory mechanisms into conservation is critical to understanding species-specific responses to restoration and developing effective management recommendations (Van Dyck 2012, Blumstein and Berger-Tal 2015, Fernández-Juricic 2016).

North American red squirrels (*Tamiasciurus* spp.) are forest-dependent species that defend exclusive territories centered around food hoards termed middens (Steele 1998). Red squirrels commonly produce rattle vocalizations (Smith 1978) to reinforce territory boundaries and avoid costly physical encounters (Smith 1978, Lair 1990, Siracusa et al. 2017*a*). In some populations, rattles encode individual identity and facilitate neighbor recognition (the dear enemy effect; Fisher 1954) to reduce agonistic interactions (Digweed et al. 2012, Wilson et al. 2015). Neighborhood familiarity mediated through vocalizations results in fitness benefits, including increased survival, reproductive success, and recruitment (Siracusa et al. 2021). The spatial scale of social neighborhoods is associated with the propagation distance of rattles (Dantzer et al. 2012, Siracusa et al. 2021), directly implicating the acoustic environment in demographic rates.

Mount Graham red squirrels (*T. fremonti grahamensis*) are an endangered subspecies isolated in the mixed-conifer and spruce-fir forests of the Pinaleño Mountains (Dził Nchaa Sí'an) of southeastern Arizona, USA

(Sanderson and Koprowski 2009). Like other *Tamiasciurus* species, Mount Graham red squirrels produce territorial rattles to defend middens (Lair 1990, Siracusa et al. 2017*a*). Fire suppression, livestock grazing, logging, and other anthropogenic disturbances since Euro-American settlement have altered forest characteristics on the mountain (Grissino-Mayer and Fritts 1995, Vankat 2013). Dendrochronology studies indicate that mixed-conifer forests have experienced a 14-fold increase in tree density since the beginning of fire suppression in the early twentieth century (60–860 trees/ha from 1870–1970; O'Connor et al. 2017). Such increases in tree density and understory fuel loads are associated with a series of insect outbreaks (Wilson et al. 1999; Lynch 2009, 2019; Lynch and O'Connor 2013; Negrón et al. 2009; and O'Connor et al. 2015) and severe crown fires that have contributed to habitat loss and degradation over recent decades (Anderson and Shafer 1991, Koprowski et al. 2006, Swetnam et al. 2009, O'Connor et al. 2014, Merrick et al. 2021). In 2012, the Pinaleño Ecosystem Restoration Project (PERP) initiated experimental forest management treatments with the objective of restoring historical forest conditions and decreasing fire severity by reducing stand densities and fuel loads and changing understory species composition (U.S. Forest Service 2010). Habitat loss via high-intensity fire is the primary threat to the persistence of Mount Graham red squirrels (Koprowski et al. 2006, Blount and Koprowski 2012). Since 2004, over half of their known middens have been affected by 3 major fires with moderate-high severity burns, with 34% of middens affected by the 2017 Frye Fire (Merrick et al. 2021) that burned >19,000 ha of forest, including almost all of the remaining spruce-fir forest and most of the mixed-conifer forest (Merrick et al. 2021). Although PERP's actions to reduce the threat of habitat loss are necessary for the long-term persistence of Mount Graham red squirrels, forest treatments may have shorter-term negative impacts on red squirrel habitat quality (Merrick et al. 2007, Wood et al. 2007). While the long-term goal of PERP is intended to aid in Mount Graham red squirrel recovery by reducing the frequency and severity of such disturbance events, understanding the short-term impacts of forest management on red squirrel ecology and behavior are needed to better inform conservation efforts.

Given the potential importance of rattles to Mount Graham red squirrel sociality and fitness, the goal of this study was to determine how forest structure and PERP treatments affect the propagation of rattles. We assessed the attenuation of rattles across plots of differing living tree area densities among PERP treatments and incorporated data from aerial light detection and ranging (lidar) as an additional method to quantify vegetation structure. We expected that differences in sound attenuation would result primarily from differences in vegetation structure, and that rattles broadcast in areas of higher tree basal area would attenuate more rapidly. We contextualized our findings by estimating receiver hearing sensitivities and modeling sound attenuation over ecologically relevant distances.

STUDY AREA

The Pinaleño Mountains (Dził Nchaa Sí'an) of southeastern Arizona are a Madrean sky island mountain range rising to 3,267 m at High Peak (Mount Graham) and surrounded by Sonoran-Chihuahuan desert. Forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), corkbark fir (*Abies lasiocarpa* var. *arizonica*), white fir (*A. concolor*), and southwestern white pine (*P. strobiformis*; Johnson 1988, Vankat 2013). Mount Graham red squirrel critical habitat was designated by the United States Fish and Wildlife Service in spruce-fir forest above 3,048 m (55 FR 429 1990). However, following fires and insect infestations, little spruce-fir forest remains and Mount Graham red squirrels mostly occupy mixed-conifer forests between 2,375 m and 3,048 m (Koprowski et al. 2005, Merrick et al. 2021). Our study area was in mixed-conifer forest with the highest Mount Graham red squirrel population density, a 2,300-ha area, ranging from 2,800 m to 3,000 m in elevation (U.S. Forest Service 2010). Average annual precipitation from 1993–2023 was 575.23 mm (197.35–981.45 mm; Western Regional Climate Center 2024). Average maximum summer temperature from 1992–2023 was 26.81°C (17–30°C), and average minimum winter temperature was 0.25°C (−14–9°C; Northeast Regional Climate Center 2024).

METHODS

Plot design

We conducted sound attenuation experiments on vegetation plots within the PERP area from 3 treatments: 1) fuel-reduced (removal of understory trees <22.86 cm diameter at breast height [DBH] followed by piling and burning), 2) thinned (removal of trees <45.72 cm DBH and either masticated and scattered in the understory or hand-piled without burning prior to the Frye fire), and 3) control areas (no PERP or other treatment for at least 10 years prior to the 2017 Frye Fire; Agee and Skinner 2005, Keifer et al. 2006, Battaglia et al. 2008, Martinson and Omi 2013). All treatments were completed between 2014 and 2017 (prior to the Frye Fire), and control plots had not received any forest treatment for at least 10 years before the Frye Fire and following the Frye Fire. Plots >10 years in age display fuel loads and conditions similar to untreated units in montane conifer forests throughout the western United States (Keifer et al. 2006, Battaglia et al. 2008, Martinson and Omi 2013, Dodge et al. 2019). We used stratified random sampling to select 30 plots (10 plots/treatment; Figure 1A and B) on southwest facing slopes of similar low grade across various burn severity classes (15 low, 10 moderate, and 5 high; see Hefty et al. 2024) to capture variation in tree densities (see below) and maximize the spatial coverage of the study area. All plots were at least 60 m apart and at least 60 m from the edge of the treatment area. We measured a variety of forest characteristics in June 2020–July 2020 following sampling designs of Hudak et al. (2011) and Dodge et al. (2019; see Hefty et al. 2024). Of specific interest, the diameter of living trees at breast-height (excluding trees <10 cm DBH) within 11.3 m of the 0.4-ha plot center. We chose the 10-cm threshold to distinguish between mid- to overstory trees from understory trees and seedlings or saplings (typically <12 cm DBH; U.S. Forest Service 2023). We inventoried seedlings and saplings separately. We subsequently used the vegetation plot DBH to estimate the living tree basal area density (m^2/ha), yielding a wide range of living basal area (mean = 33.51 m^2/ha, SD = 22.72 m^2/ha, range = 0.00-87.15 m^2/ha).

Rattle propagation experiment

To obtain stimuli for the sound attenuation experiment, we placed 9 autonomous recording units (ARUs; Wildlife Acoustics model SM4, Maynard, MA, USA) at currently occupied middens on the Pinaleño Mountains between June 2022–March 2023. All ARUs fell within control areas outside of PERP forest treatments, ranging from approximately 300–700 m away from the nearest treatment area boundary. We randomly selected 20 recordings from each ARU with high signal to noise ratios for inclusion in our call library and randomly selected 1 rattle per animal for use in rattle playback experiments. We used Avisoft SASLab Pro (version 5.3.01; Avisoft Bioacoustics, Glienicke/Nordbahn, Germany) to high-pass filter (500 Hz; finite impulse response [FIR] filter = time domain filter, number of taps = 128, Hamming window, sample rate = 32 kHz) to remove background noise and normalized all recordings to their peak amplitude. We then extracted the rattle note with the maximum amplitude from each call and created a playback stimulus file by replicating the note 50 times with 0.5 seconds of silence between replicates (Figure S1, available in Supporting Information). We inserted a 1-kHz tone of 1-second duration in the beginning of the file as an internal reference. We analyzed acoustic properties of playback files using Raven Pro (version 1.6.5; Cornell Lab of Ornithology, Ithaca, New York, USA). Because we aimed to specifically assess the effect of forest structure on sound amplitude and frequency, synthesized stimuli derived from biologically relevant signals enabled strong control and within-site replication to balance internal and external validity. We randomly selected 1 file at each playback site. In June 2023–August 2023, we broadcast stimuli from a speaker (Ultrasonic Dynamic Speaker, ScanSpeak, Avisoft Bioacoustics) via a power preamplifier (UltraSoundGate Player 416H, Avisoft Bioacoustics) affixed to an overlook stand (Model 269HDBU, Manfrotto, Cassola, Italy) 5.4 m above the forest floor. The height represented the lower heights of calling squirrels observed from our focal recordings. We broadcast signals from the center of each plot in 4 cardinal directions at the maximum amplitude levels permitted by the audio equipment

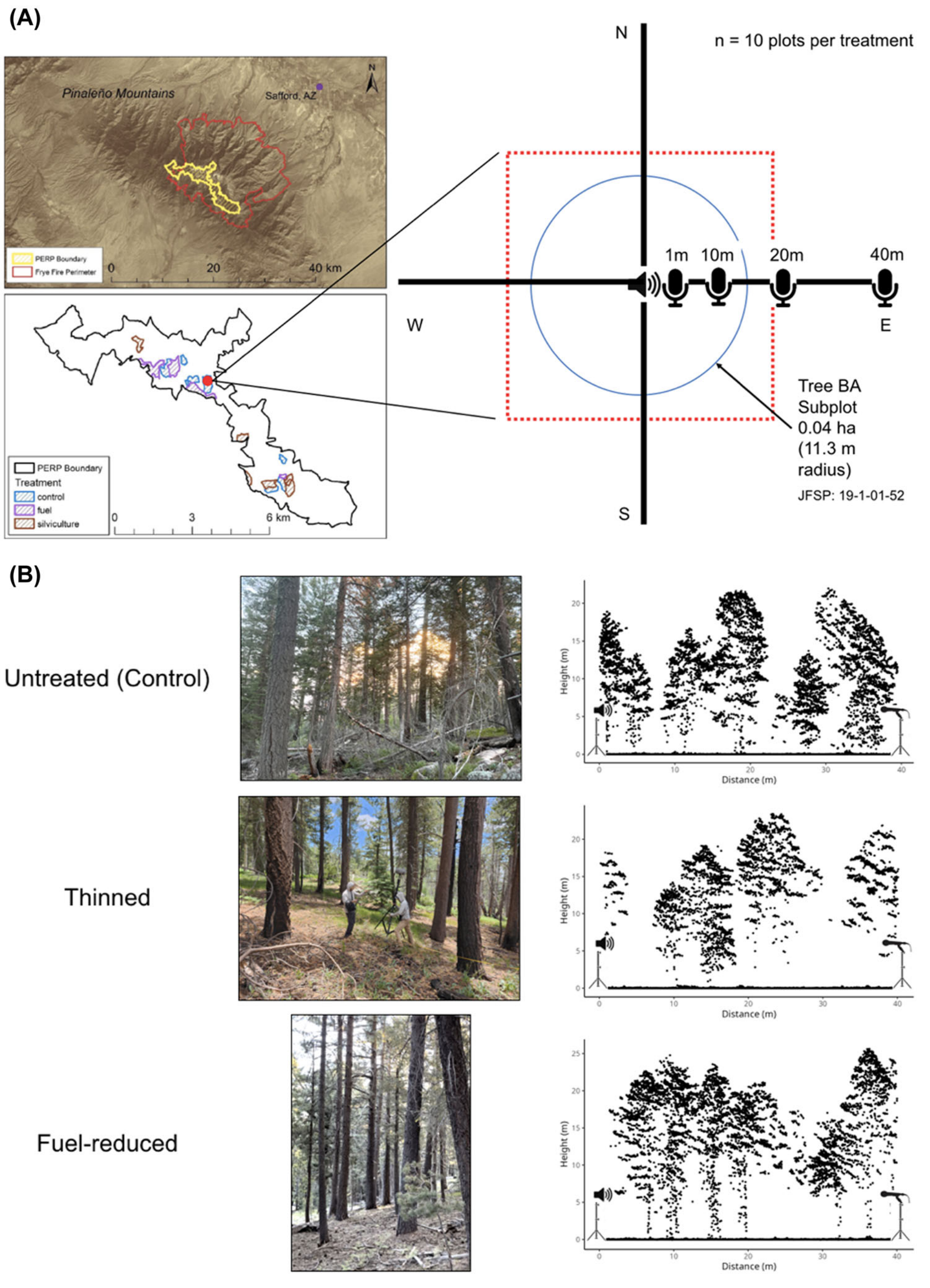

FIGURE 1 (A) Left: The Pinaleño Ecosystem Restoration Plan (PERP) aims to reintroduce low severity, high frequency fires back into the Pinaleño Mountains (red boundary) in Arizona, USA, by thinning stands and removing understory fuels (yellow boundary, Hefty et al. 2024). Right: Plot design from Hefty et al. (2024), with playback transects overlayed (10 plots/treatment). (B) Middle: Photographs taken in 2023 along a transect from plots in each PERP treatment type. Right: Example of a lidar point cloud from each playback transect pictured from 2018 data. Each point is a return, where the laser bounced back to the reading instrument. On the left end of the points is the center of a plot, and the right end is 40 m, the distance of the playback transects. This data includes 5 m on both sides of the transect line. Illustrations of a tripod with a speaker at 0 m and a tripod with a speaker at 40 m, both at 5.4 m height, represent the height and maximum distance that playbacks were conducted along transects.

to ensure high signal to noise ratios, and relativized the resulting recordings to 104 dB (the greatest peak amplitude values of our recordings; see Results). We used a laptop (Windows 10, version 21H2; Dell Latitude 7220, Round Rock, TX, USA) running Avisoft RECORDER (version 5.2.14) and recorded stimuli at 1 m, 10 m, 20 m, and 40 m with a portable audio recorder (Mix Pre 6 II, sampling rate 48 kHz, 16 bits; Sound Devices, Reedsburg, WI, USA) and microphone (MKH 8060, 50 Hz–25 kHz flat frequency response; Sennheiser, Wedemark, Germany) to quantify sound attenuation. Of these recording distances, the 1-m and 10-m distances were within the measured plot area, and we assumed similar structure between 10-40 m and tested this assumption (see Analyses). We high-pass filtered (50 Hz) the recordings to remove background noise and measured the root mean square (rms) amplitude (20 ms averaging time) and peak frequency of each of the 50 replicates using automated detection in Avisoft SASLab Pro and averaged per distance per plot.

Lidar

We used lidar point clouds from the 2018 Kaibab LiDAR Project (U.S. Geological Survey 2018) to quantify forest characteristics along playback transects at each plot (Figure 1B). The lidar dataset met the minimum recommended system specifications for forest analyses, including a nominal pulse density of ≥3 pulses/m^2, minimum side overlap of 50%, and a scan angle within 14° of nadir (Mitchell et al. 2012). Lidar devices, usually placed on an aircraft flying repeatedly over a transect, determine distance between the sensor and target surfaces by measuring the elapsed time between emission of a laser pulse and arrival of the reflection of that pulse at the device's receiver, with resulting spatial data estimating any high and low vegetation along with the ground surface (Lefsky et al. 2002). Lidar is increasingly used to measure forest structure and is capable of estimating properties such as stand density, leaf area, canopy structure, tree height, and tree biomass (Dubayah and Drake 2000, Lefsky et al. 2002, Beland et al. 2019). We extracted the lidar metric canopy relief ratio (CRR), a quantitative descriptor of whole-canopy density and diversity, defined as the mean height of returns minus the minimum height divided by the maximum height minus the minimum height (Parker and Russ 2004). Higher values of CRR correspond to increased variation in canopy cover, whereas smaller values represent lower variation. We used the lidR package (Roussel et al. 2020, Roussel and Auty 2024) in R (R Core Team 2017) to process lidar point clouds, and the metrics_dispersion() function in the lidRmetrics package (Tompalski 2023) to estimate CRR.

Analyses

Factors contributing to rattle attenuation

We evaluated the specific environmental factors contributing to rattle attenuation, including the role of living tree basal area, lidar-derived CRR, distance, and forest treatment type. We found that basal area and the lidar metric CRR were correlated; however, the relationship was weak ($R^2 = 0.12$, $P < 0.001$; Figure S2, available in Supporting Information), indicating that each vegetation metric may explain unique rattle attenuation patterns. As such, we conducted 2 analyses to assess rattle attenuation, one with on-the-ground estimates of vegetation using living basal area ($m^{2/}$ha) and a separate model using lidar-derived CRR using generalized linear mixed models (GLMM; lme4 package; Bates et al. 2015) in R (R Core Team 2017). In the basal area model, we included the log-transformed synthesized stimuli sound pressure level (an absolute measure of amplitude) as the response variable and microphone distance (1 m, 10 m, 20 m, 40 m), basal area (living basal tree area, m^2/ha), and PERP forest treatment (control, fuel reduction, thinning) as main effects. We tested for an interaction between basal area and distance because we expected living basal area to have more pronounced effects at farther distances. Treatment type could potentially interact with both basal area and distance to further influence attenuation. Therefore, we included all 2- and 3-way interactions between main effects.

In the CRR model, we tested the relationship between rattle attenuation and vegetation using the lidar-derived CRR. To do so, we included the log-transformed synthesized stimuli sound pressure level as the response variable and microphone distance (1 m, 10 m, 20 m, 40 m), and PERP forest treatment (control, fuel reduction, thinning) as main effects, and all 2- and 3-way interactions, as above. Analysis of variance and *post hoc* Tukey tests indicated that background noise did not vary among sites (range = 18.07–59.82 dB, $F_{29,\ 60} = 1.19$, $P = 0.28$). Nevertheless, we included background noise as a random effect in the GLMM to control for the wide range of background noise amplitudes. Rattles varied among playback files (Figure S1; peak frequency mean = 4,451.39 Hz, SD = 1,901.58, 90% bandwidth mean = 8,381.94 Hz, SD = 2,299.04). Therefore, we included playback file as random effects in the GLMM to control for sound file variation. To test our assumption of similar forest structure within and beyond 10 m of the plot center, we used a GLMM with distance and forest treatment as main effects and plot as a random effect with CRR as the response variable. Distance had no relationship with CRR ($\chi^2 = 1.66$, df = 1, 464, $P = 0.20$), indicating that forest structure was similar across transect distances. The Frye Fire from 2017 burned through our study area, and we evaluated how fire severity correlated with living tree basal area and CRR to quantify how our measures of forest structure captured this variation. Fire severity was correlated with basal area ($F_{1,\ 465} = 56.9$, $P < 0.001$) and marginally with CRR ($F_{2,465} = 2.54$, $P = 0.08$). Therefore, to control for spatiotemporal autocorrelation (Kéry and Royle 2020) of burn severity throughout our study area, we included fire severity as a random effect in both models.

Given that our plots contained standing dead trees (Figure S3, available in Supporting Information), we ran a third GLMM identical to the living basal area and CRR models but with standing dead tree basal area in place of those forest structure metrics, to evaluate how standing dead trees influence rattle propagation. Finally, we evaluated how rattle frequency was influenced by forest structure using a GLMM with peak frequency as the response variable, living basal area, distance, and treatment as main effects, and plot ID, playback file, and fire severity as random effects. For all models, we verified assumptions of normality and homoscedasticity by visual inspection of q-q and residual plots. We computed effect sizes (η^2) and 95% confidence intervals in the effectsize package for R (Ben-Shachar et al. 2020); η^2 represents the variation explained by a particular model term and the confidence interval is an indication of the variability of the effect (Steiger 2004, Norouzian and Plonsky 2018). We used the car package (Fox and Weisberg 2019) to calculate *P*-values with likelihood ratio tests.

Communication distance estimation

To contextualize our results, we integrated estimates of Mount Graham red squirrel hearing sensitivities with our attenuation models. We first modeled rattle attenuation via spherical spreading and excess attenuation along each transect by fitting a logarithmic decay model (Jacobsen 1987) in R for our observed amplitude values at 1 m, 10 m, 20 m, and 40 m. We then extrapolated amplitude values beyond 40 m using the line of best fit equation. To estimate the communication distance (also known as audible distance or active space) of red squirrel rattles, we used the line of best fit equation to calculate the distance (m) at which sound attenuation intersected a conservative estimate of receiver hearing sensitivity in squirrels and other rodents (30 dB; Hamill et al. 1989, Dent et al. 2018) based on the average attenuation within each PERP treatment. We also assessed communication distance using 5 plots with the lowest tree basal areas, and 5 plots with the highest tree basal areas. Finally, PERP prescribes a maximum untreated buffer of 61 m around known middens because Mount Graham red squirrels select territories in untreated areas. In thinned treatment plots, the untreated buffer could result in pronounced attenuation for 61 m and less attenuation beyond the buffer, thus creating heterogeneous and complex acoustic environments around squirrel middens. We evaluated the influence of treatment buffers on attenuation and communication distance of a rattle that travels through an untreated area for 61 m, and beyond through thinned treatment area. To do so, we calculated treatment buffer attenuation by quantifying the average amplitude value of a rattle that propagated through 61 m of untreated forest, extrapolated from a logarithmic decay attenuation function. We used the amplitude value at 61 m as the initial value in the thinned forest attenuation function to estimate attenuation beyond 61 m in thinned areas.

RESULTS

Factors contributing to rattle attenuation

On each of the 30 plots, we conducted playbacks at 4 distances in each cardinal direction. We found several lines of evidence that rattle attenuation was influenced by forest structure from our basal area model (Table 1). Attenuation of synthesized rattles was influenced by receiver distance (Figure 2), treatment (Figure 3), and the living tree basal area × distance interaction (Figure 2). The interaction indicated that living basal area per hectare had a greater effect on rattle attenuation at farther distances. All other factors in the model did not influence attenuation (Table 1). Random effects explained little variation (plot $\sigma^2 = 0$; playback file $\sigma^2 < 0.0001$; fire severity $\sigma^2 = 0$).

Based on our CRR model, we found rattle attenuation was influenced by forest stand structure (Table 2). We found attenuation increased with distance and CRR and a distance × CRR interaction indicated that CRR had pronounced effects on attenuation at farther distances and less attenuation at closer distances (Figure 2). All other factors in the CRR model did not influence rattle attenuation (Table 2), and random effects explained little variation (plot $\sigma^2 = 0$; playback file $\sigma^2 < 0.0001$; fire severity $\sigma^2 < 0.0001$). We found no evidence that standing dead trees influenced rattle attenuation (Table S1, available in Supporting Information). On average, recordings in the plots with the densest stands were approximately 6 dB lower in amplitude than recordings in the most open plots (Figure 2). The difference in amplitude between recordings in low and high CRR was 8 dB (Figure 2). On average, recordings in control plots were 3 dB lower than recordings in thinned plots and 1 dB lower than those in fuel plots (Figure 3).

Peak frequency generally decreased over distance ($\chi^2 = 249.42$, df = 1, 444, $P < 0.001$; Table S2, available in Supporting Information). We found a distance × living basal area interaction ($\chi^2 = 35.61$, df = 1, 444, $P < 0.001$) and a

TABLE 1 Attenuation of Mount Graham red squirrel territorial rattle vocalizations were influenced by distance, stand density, and wildfire restoration treatment in the Pinaleño Mountains in Arizona, USA, 2023. We present the results of likelihood ratio tests (Type II Wald χ^2 tests) from a generalized linear mixed model and effect sizes (η^2; 95% confidence interval) from the basal area model (living tree basal area [m^2/ha]). Random effects of plot, fire severity, and playback file ID explained little variation (plot $\sigma^2 = 0$; playback file $\sigma^2 < 0.0001$; fire severity $\sigma^2 = 0$). Significant model terms are indicated by an asterisk (*).

Model terms	χ^2	df	P	η^2	95% CI
Distance*	2,411.05	1, 460	<0.001	0.560	[0.51, 1.00]
Treatment*	7.34	2, 296	0.025	0.004	[0.00, 1.00]
Living tree basal area	3.09	1, 384	0.079	0.001	[0.00, 1.00]
Distance × treatment	3.63	2, 460	0.160	0.002	[0.00, 1.00]
Distance × living tree basal area*	5.03	1, 460	0.025	0.010	[0.00, 1.00]
Treatment × living tree basal area	2.76	2, 234	0.250	0.002	[0.00, 1.00]
Distance × treatment × living tree basal area	0.56	2, 460	0.760	0.001	[0.00, 1.00]

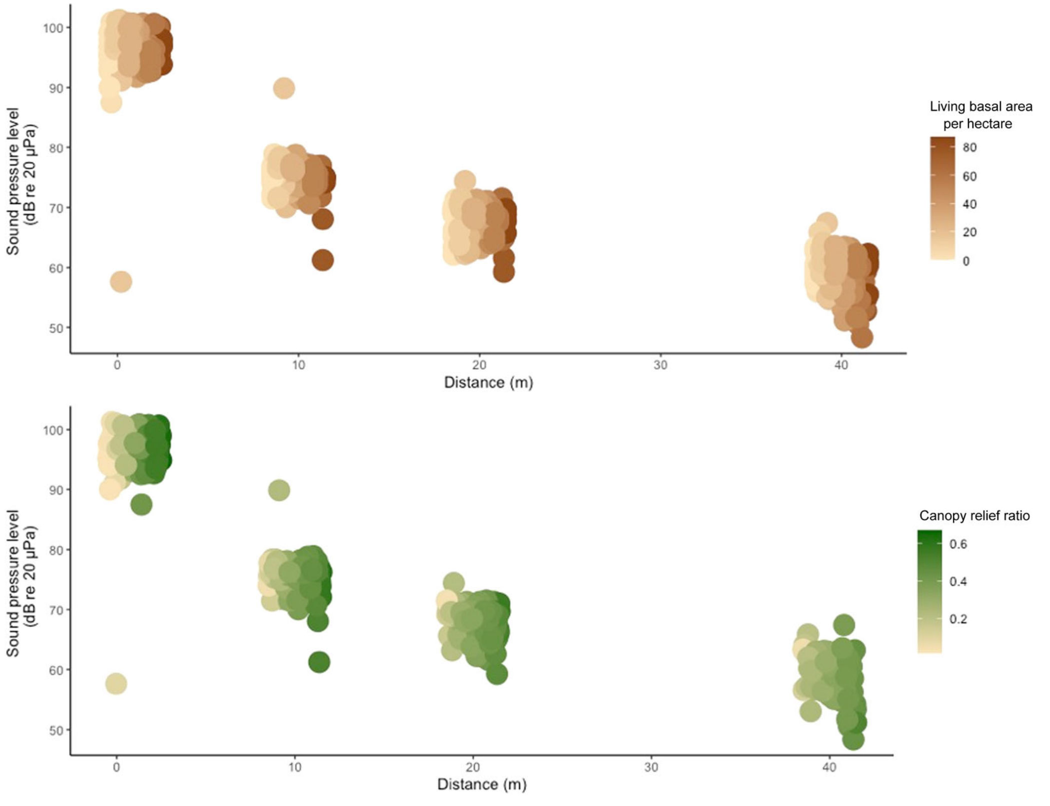

FIGURE 2 Influence of living tree basal area (m^2/ha), a vegetation-plot measure (brown shading), and canopy relief ratio, a lidar metric of canopy density and diversity (green shading), on Mount Graham red squirrel rattle attenuation values as measured as average amplitude (dB) at each plot at 1-m, 10-m, 20-m, and 40-m distances in the Pinaleño Mountains in Arizona, USA. Each dot corresponds to the amplitude of the synthesized rattle at each distance per transect. Lidar data were collected in 2018, vegetation-plot data were collected in 2020, and rattle attenuation was measured in 2023.

distance × treatment interaction (χ^2 = 12.39, df = 2, 444, P = 0.002), and a 3-way distance × treatment × living basal area interaction (Table S2, χ^2 = 7.46, df = 2, 444, P = 0.02) indicated greater effects on rattle frequency at farther distances and in plots with higher stand densities (i.e., control plots).

Communication distance estimation

Amplitude attenuation curves indicated that rattles propagating through areas with the lowest tree basal areas (0–14.2 m^2/ha) had an average communication distance of 1,202 m (Figure 4A). In contrast, communication distance of rattles propagating through areas with the highest tree basal areas (57.8–87.1 m^2/ha) were approximately halved (587 m; Figure 4A). Beyond these distances, amplitudes fell below the estimated hearing threshold of receivers (30 dB). Rattles had an average communication distance of 713 m in control treatments, compared to 1,082 m in fuel-reduced treatments and 1,083 m in thinned treatments (Figure 4B). Finally, given that PERP treatments leave a maximum radius of 61 m around the midden, we modeled how rattles attenuated through areas similar to forest conditions that typify control plots and then propagated into thinned, treated areas. Under this scenario, we found the communication distance was 311 m farther than if rattles propagated solely through forests resembling control plot conditions (Figure 5).

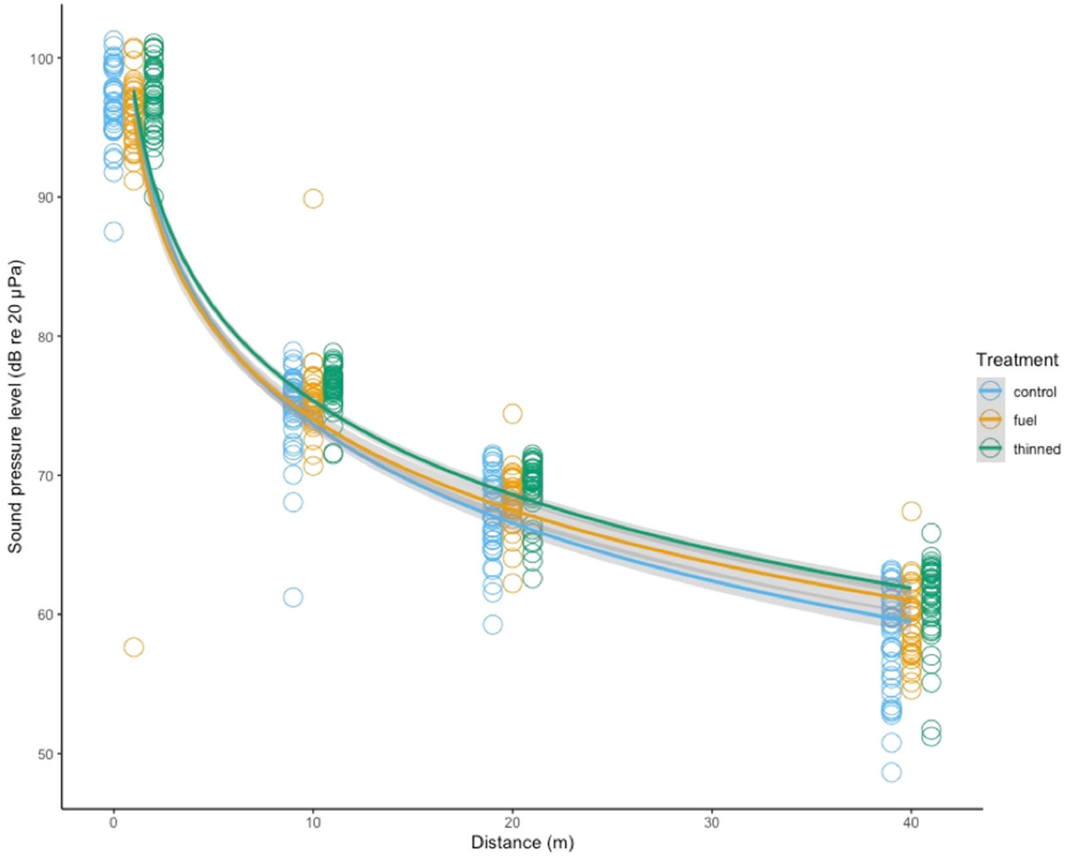

FIGURE 3 Average amplitude (dB) of recorded Mount Graham red squirrel rattles at each distance from the speaker of 1 m, 10 m, 20 m, and 40 m in the Pinaleño Mountains in Arizona, USA, 2023. Each dot corresponds to the amplitude of the standardized rattle at each distance. Attenuation curves display the average loss of amplitude of standardized rattles over distance in each treatment. Each color represents the Pinaleño Ecosystem Restoration Project (PERP) treatment that took place in that plot, with control meaning no treatment. Fuel plots underwent the removal of understory fuel loads such as downed trees, stumps, and understory vegetation (including trees under 22.86 cm diameter at breast height). Thinned plots underwent the removal of trees under 45.72 cm diameter at breast height.

DISCUSSION

Tree squirrels are strong indicators of forest structure (Carey 2000, Steele and Koprowski 2001) because of their dependence on mature trees for seeds, nest sites, and cover (Gurnell 1987, Steele and Koprowski 2001). In particular, red squirrels rely on large trees with high canopy cover to ensure cool microclimates for food storage in middens (Steele 1998) that in turn are defended using territorial rattle vocalizations (Smith 1978, Lair 1990, Siracusa et al. 2017*a*). Our results update the known communication distance of red squirrel rattles, previously estimated as 130 m based on audible distance by humans (Smith 1978). Even in the densest forest of our study area, the communication distance of rattles was >4 times farther, reaching 587 m using a conservative estimate of hearing sensitivity. We contextualize the importance of this distance relative to forest management to inform future studies on red squirrel behavior and conservation.

Because the efficacy of acoustic communication depends on the structural environment and red squirrel rattles influence fitness, understanding the impacts of forest management on sound attenuation is fundamental to Mount

TABLE 2 Attenuation of Mount Graham red squirrel territorial rattle vocalizations were influenced by distance and canopy density in the Pinaleño Mountains in Arizona, USA, 2023. We present the results of likelihood ratio tests (Type II Wald χ^2 tests) from a generalized linear mixed model and effect sizes (η^2; 95% confidence interval) from the lidar-derived canopy relief ratio (CRR) model. Random effects of plot, fire severity, and playback file ID explained little variation (plot $\sigma^2 = 0$; playback file $\sigma^2 < 0.0001$; fire severity $\sigma^2 < 0.0001$). Significant model terms are indicated by an asterisk (*).

Model terms	χ^2	df	*P*	η^2	95% CI
Distance*	2,505.19	1, 466	<0.001	0.20	[0.15, 1.00]
Treatment	5.12	2, 300	0.077	0.003	[0.00, 1.00]
CRR*	6.83	1, 421	0.009	0.002	[0.00, 1.00]
Distance × treatment	1.97	2, 465	0.370	0.003	[0.00, 1.00]
Distance × CRR*	20.79	1, 466	<0.001	0.030	[0.01, 1.00]
Treatment × CRR	1.95	2, 361	0.380	0.003	[0.00, 1.00]
Distance × treatment × CRR	1.16	2, 466	0.560	0.003	[0.00, 1.00]

Graham red squirrel conservation. Our findings indicate that rattles experienced less attenuation in areas of lower living tree basal area, through thinned and fuel-reduced forest, and through more open canopy (lower CRR). For some variables, effect sizes were small and variable over the 40 m distance that we conducted our playback experiments. However, when we extrapolated values to ecologically relevant distances, the magnitude of the effect sizes were more pronounced, as evidenced by a near doubling in audible distance between areas with the highest and lowest tree basal area (Figure 4). Thus, our attenuation experiment conducted along 40-m transects represents a conservative estimate of how rattles interact with the habitat following forest restoration. In interaction with distance, CRR likely explained differences in attenuation better than tree basal area because the metric more directly estimated canopy vegetation, the main source of environmental attenuation on rattles. Furthermore, rattles in control plots had an average communication distance of roughly 300 m less than fuel-reduced or thinned PERP plots. Similar to amplitude, peak frequency of rattles decreased more over distance in plots with higher tree basal areas and CRR values. Greater attenuation of higher frequencies is expected because shorter wavelengths experience more absorption and reflection from vegetation than the longer wavelengths that characterize low-frequency sounds (Marten and Marler 1977). The lack of an effect from standing dead trees on rattle attenuation further emphasizes the importance of living canopy vegetation on rattle transmission through the forest. Furthermore, differences in sound propagation were not likely influenced by background noise as our analysis indicated no difference among plots or treatments. Altogether, our results indicate a strong effect of forest structure on the propagation of red squirrel rattles.

Although historical fire intervals and forest structure in the Pinaleño Mountains are complex (Grissino-Mayer and Fritts 1995), current management efforts are reducing stand densities to conditions that were likely similar to those in which squirrels have persisted since the last glaciation (Anderson and Shafer 1991, Hope et al. 2016), at least in mixed-conifer forests in the Pinaleños (O'Connor et al. 2017). Our data indicate that such thinning can increase the propagation distance of red squirrel rattles, which may have implications for red squirrel fitness. Greater acoustic familiarity with neighbors reduces the number of intruders (Siracusa et al. 2017*b*), rattle rates (Siracusa et al. 2019), and time spent in vigilance (Siracusa et al. 2019) while increasing the probability of adult survival and juvenile recruitment (Siracusa et al. 2021). Given that Mount Graham red squirrel territories are up to 10 times larger than other congeners (~3.0 ha; Leonard and Koprowski 2009, Blount and Koprowski 2012), thinning may be particularly important in maintaining communication distances and reducing the energetic costs associated with defense of large territories. For example, Mount Graham red squirrels in untreated, denser stands may be more

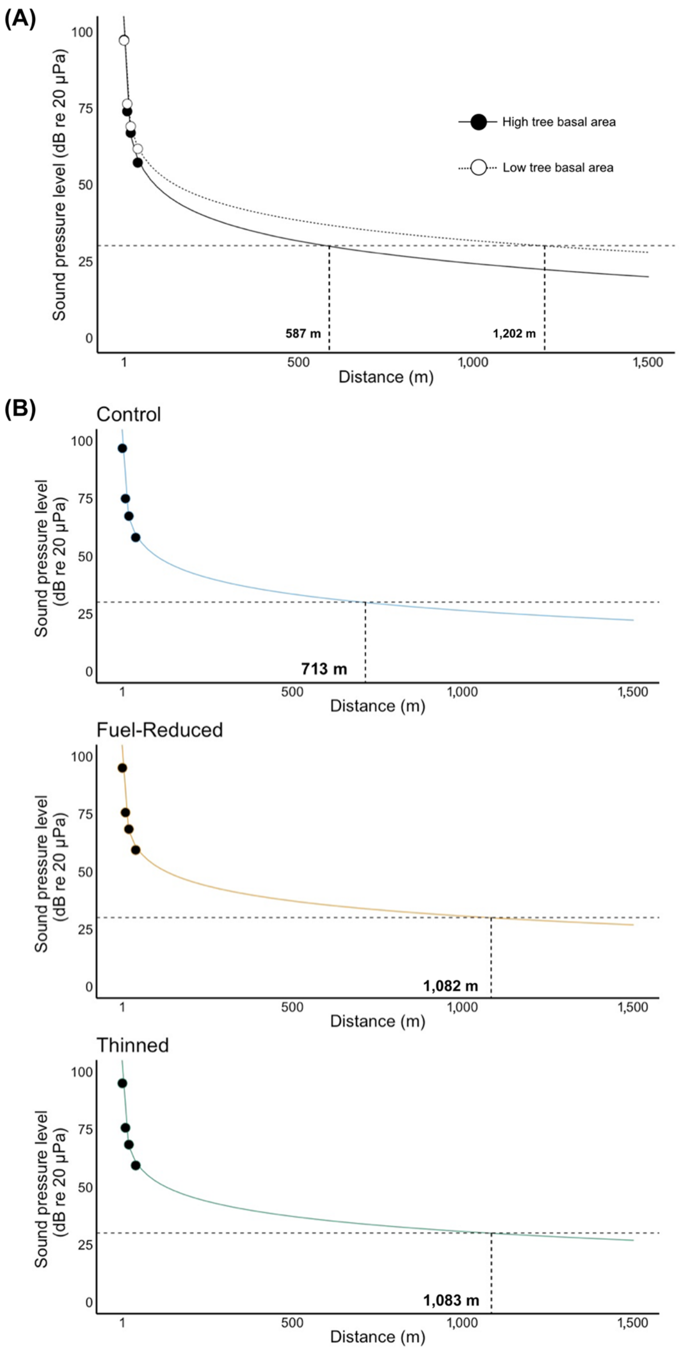

FIGURE 4 Attenuation curves displaying the average loss of amplitude of standardized Mount Graham red squirrel rattles over distance in the Pinaleño Mountains in Arizona, USA, 2023. Communication distance (vertical dashed line) represents the distance at which the amplitude drops below a conservative hearing threshold estimate (horizontal dashed line) of red squirrels (~30 dB), and the communication distance values are given in bold. Dots represent measured attenuation values. A) Average communication distance estimation for the lowest and highest living tree basal area (m^2/ha). B) Average communication distance estimation for each Pinaleño Ecosystem Restoration Project (PERP) forest treatment.

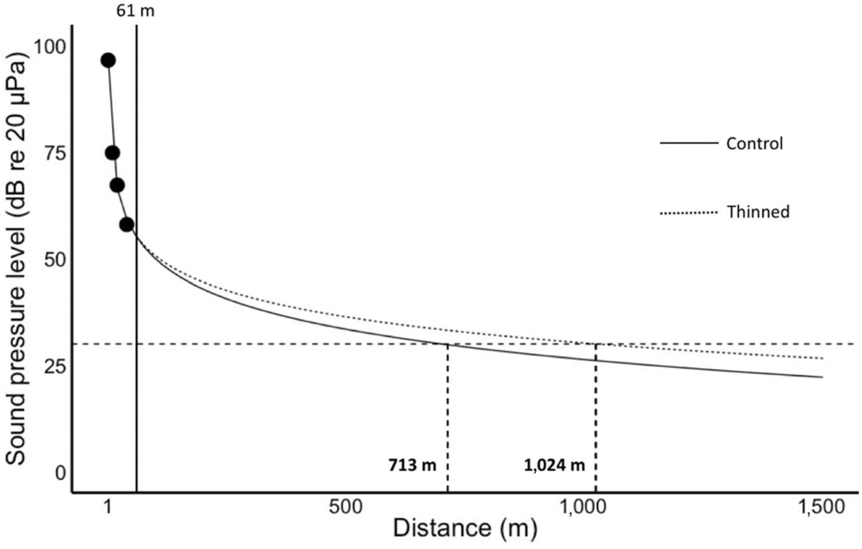

FIGURE 5 Pinaleño Ecosystem Restoration Project (PERP) treatments specify a maximum treatment buffer radius of 61 m around Mount Graham red squirrel middens to reduce disturbance, potentially creating complex and heterogenous acoustic environments. Attenuation curves, displaying the loss of amplitude over distance, of Mount Graham red squirrel rattles were produced from playback experiments in the Pinaleño Mountains in Arizona, USA, 2023. The solid curve represents the rattle attenuation within PERP untreated (control) plots. The dotted curve represents attenuation of a rattle traveling through a midden buffer (61 m) and then into a thinned area outside the treatment buffer. The horizontal dashed line represents a conservative hearing threshold estimate for red squirrels and the vertical dashed line represents the communication distance of a rattle. Beyond the vertical dashed line, rattles are too quiet to be heard by a receiver. Rattles theoretically produced in buffers that then propagate through treated (thinned) plots travel approximately 300 m farther.

acoustically isolated, and therefore less familiar with neighbors, than squirrels in treated, thinner forest where rattles are heard at greater distances. Assessment of how thinning influences neighborhood familiarity awaits formal study. However, we caution that the same structural factors that benefit rattle propagation may affect raptor predation (responsible for 65-75% of Mount Graham red squirrel deaths; Goldstein et al. 2018) through increased visibility or acoustic eavesdropping (Vargas-Castro et al. 2017, Legett et al. 2020). Thus, future studies that evaluate the role of rattles in neighborhood dynamics will need to consider the cumulative impact of forest restoration.

Habitat loss from insect invasions and high-intensity fire are the most pressing and severe threat to persistence of Mount Graham red squirrels (Koprowski et al. 2006, Blount and Koprowski 2012). PERP aims to reduce the frequency and severity of severe disturbances with forest restoration and management (U.S. Forest Service 2010). While action to reduce the threat of habitat loss is necessary for the long-term persistence of Mount Graham red squirrels, PERP forest treatments may negatively impact squirrels, specifically by reducing ease of movement through interconnected canopies and other changes in habitat quality (Merrick et al. 2007, Wood et al. 2007). For example, Mount Graham red squirrels prefer dense forest patches with high canopy cover when choosing nest and midden sites (Merrick et al. 2007, Wood et al. 2007). The PERP specifies maintaining higher stand densities, basal tree areas, and canopy closure around (23–61 m) current Mount Graham red squirrel middens to preserve patches of optimal habitat while still reducing fire severity (U.S. Forest Service 2010). Thus, in the short-term, PERP forest treatments may facilitate development of acoustic social neighborhoods that increase squirrel fitness while concomitantly limiting dispersal and reducing the available area for midden and nest selection (Merrick et al. 2007). The mosaic of forest conditions resulting from management will have complex, non-uniform effects on habitat use and rattle attenuation that will require further study.

Our inferences come with minor caveats. First, while using synthesized rattles permitted strong standardization and within-site replication of attenuation patterns, rattles vary in numerous acoustic properties, including frequency, rate, and duration (Smith 1978, Digweed et al. 2012). Our analyses indicated a minor effect of playback file on attenuation patterns, suggesting squirrel-specific rattle properties may contribute to variation in sound propagation. Therefore, future studies that assess attenuation would benefit from quantifying if particular rattle properties (such as duration and properties potentially related to age or sex) are more sensitive to forest treatments. Additionally, our communication distance values should be interpreted as an estimate of the maximum distance senders can be detected but not necessarily discriminated. Red squirrels use a combination of acoustic properties to discriminate neighbors and kin (Digweed et al. 2012, Wilson et al. 2015) and we have not yet tested if squirrels can distinguish between familiar and unfamiliar rattles. Finally, our estimates of communication distance are conservative because electrophysiological methods of hearing sensitivity (e.g., auditory brainstem response) are typically higher (10–30 dB) than behavioral measures (Heffner and Heffner 2003, Dent et al. 2018), translating into much farther communication distances (e.g., 0 dB hearing thresholds = 13.3 km). Future studies that quantify inter-individual variation of Mount Graham red squirrel rattles, refine estimates of hearing sensitivity, and assess responses to playback experiments will collectively help reveal the spatial extent of acoustic interactions and importance of the social environment.

The ability to quantify the 3-dimensional structure of forested ecosystems can improve habitat assessments (Davies and Asner 2014, Li et al. 2019). Lidar metrics are often integrated into studies of habitat selection, distribution modeling, and biodiversity assessments (Rachlow et al. 2014, Simonson et al. 2014, McLean et al. 2016, Smith et al. 2022). More recently, integration of lidar and bioacoustic data has been used to estimate and model forest biodiversity (Pekin et al. 2012, Rappaport et al. 2020) and to study bat flight behavior in relation to vegetation structure (Hermans et al. 2023). The similarities in attenuation estimates found between on-the-ground and lidar-derived measures indicate that remote sensing can be a powerful tool to model acoustic environments across broader spatial scales. Such tools have great potential to benefit wildlife conservation and management, especially when integrated with information on sensory ecology.

CONSERVATION IMPLICATIONS

Our results highlight the importance of considering how management that alters forest structure may affect the acoustic signaling and the sensory ecology of threatened and endangered species that rely on acoustic communication. The forest treatments of PERP are necessary and designed to benefit long-term persistence of Mount Graham red squirrels by reducing fire frequency and intensity, as habitat loss to fire has been identified as the greatest threat to the population. Although these treatments may have some negative impacts on the squirrels, such as avoidance of thinned areas when choosing nest and midden sites (Merrick et al. 2007, Wood et al. 2007), we show that PERP treatments increase the communication distance of Mount Graham red squirrel territorial vocalizations, which may affect fitness through facilitating greater familiarity with neighbors and reducing costs of territoriality. However, lower density forests may negatively affect squirrels by increasing visual detection and acoustic eavesdropping by predators, so further investigation is necessary to evaluate the full impact of a changing acoustic environment on Mount Graham red squirrels and to evaluate the complex impacts of PERP treatments. Integration of signaling and sensory ecology will be critical to understanding wildlife responses to forest management and can be enhanced using remote sensing techniques.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ETHICS STATEMENT

All procedures were approved by The University of Arizona's Institutional Animal Care and Use Committee (2022-0864). All research followed the guidelines for ethical treatment of animals established by the American Society of Mammalogists (Sikes 2016).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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