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Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal

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Noise pollution is a novel, widespread environmental force that has recently been shown to alter the behaviour and distribution of birds and other vertebrates, yet whether noise has cumulative, community-level consequences by changing critical ecological services is unknown. Herein, we examined the effects of noise pollution on pollination and seed dispersal and seedling establishment within a study system that isolated the effects of noise from confounding stimuli common to human-altered landscapes. Using observations, vegetation surveys and pollen transfer and seed removal experiments, we found that effects of noise pollution can reverberate through communities by disrupting or enhancing these ecological services. Specifically, noise pollution indirectly increased artificial flower pollination by hummingbirds, but altered the community of animals that prey upon and disperse *Pinus edulis* seeds, potentially explaining reduced *P. edulis* seedling recruitment in noisy areas. Despite evidence that some ecological services, such as pollination, may benefit indirectly owing to noise, declines in seedling recruitment for key-dominant species such as *P. edulis* may have dramatic long-term effects on ecosystem structure and diversity. Because the extent of noise pollution is growing, this study emphasizes that investigators should evaluate the ecological consequences of noise alongside other human-induced environmental changes that are reshaping human-altered landscapes worldwide.

Keywords: anthropogenic noise; birds; ecological service; human disturbance; pollination; seed dispersal

1. INTRODUCTION

Human activities have altered over 75 per cent of the Earth's land surface [1,2]. Concomitant with these surface changes is a pervasive increase in anthropogenic noise, or noise pollution, caused by expanding dendritic transportation networks, urban centres and industrial activities [3]. The geographical extent of noise exposure varies by region and scale, but estimates suggest that one-fifth of the United States' land area is impacted by traffic noise directly [4] and over 80 per cent of some rural landscapes are exposed to increased noise levels owing to energy extraction activities [5]. Despite the potentially substantial scale of noise exposure across the globe, surprisingly little is known about how these ecologically novel acoustic conditions affect natural populations and communities.

We are beginning to understand the impacts of increased noise exposure on the behaviours of individuals and the distributions of species [6–10], and several recent reviews outline potential and some known effects of noise [3,11–13]. Despite this recent attention given to the effects of noise, we still have limited knowledge of how these impacts scale to community and ecosystem-level processes. A few studies have shown that predators avoid noisy areas [7,14–16], presumably because noise impairs predators' abilities to locate prey. These studies provide us with insights on how noise may directly affect predator–prey interactions, but do not provide information on whether noise may have cumulative, indirect consequences for other interactions and organisms that are not impacted by noise directly.

Our goal was to investigate whether noise pollution can reverberate through ecological communities by affecting species that provide functionally unique ecological services. We focused our efforts on ecological services provided primarily by birds because they are considered to be especially sensitive to noise pollution owing to their reliance on acoustic communication [11]. However, because not all species respond uniformly to noise exposure [6,7,10,17], we can evaluate how different responses by functionally unique species impact other organisms indirectly and trigger further changes to community structure. We studied ecological services provided by *Archilochus alexandri* (black-chinned hummingbird) and *Aphelocoma californica* (western scrub-jay), which serve as mobile links for pollination and *Pinus edulis* (piñon) seed dispersal services, respectively [18–20]. Because *A. alexandri* preferentially nests in noisy environments and *A. californica* avoids noisy areas [5,7], we proposed that their noise-dependent distributions could result in a higher rate of pollination

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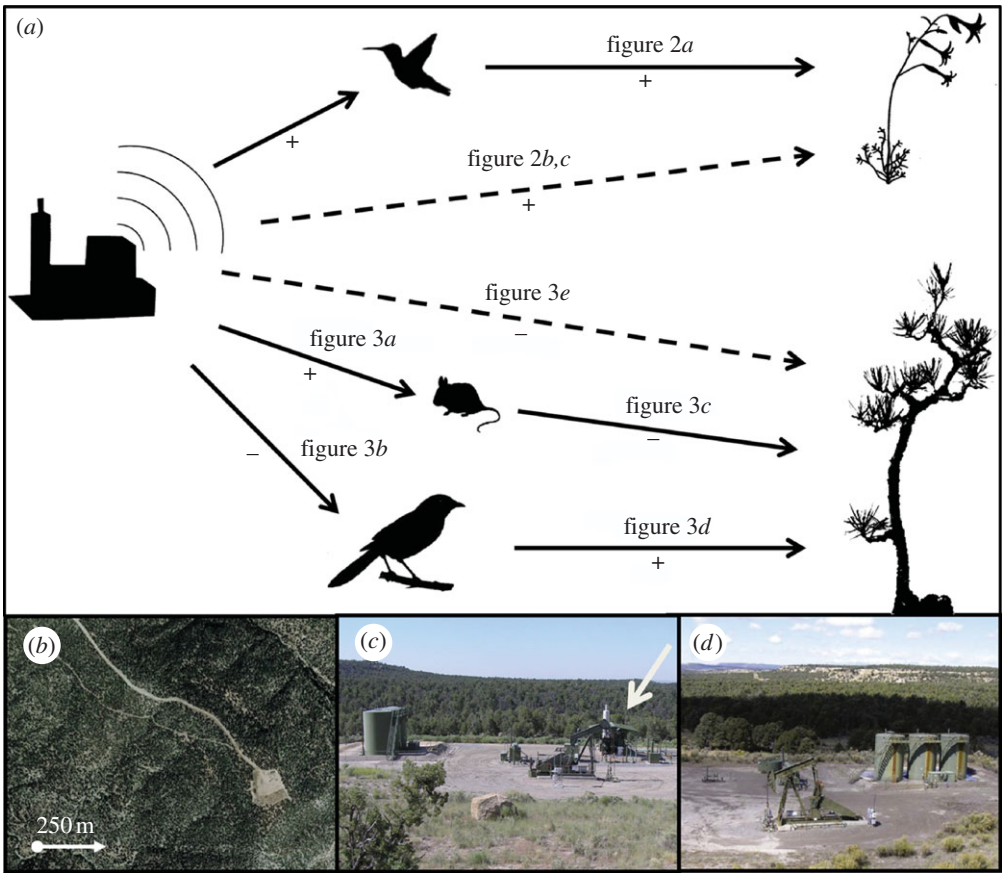

Figure 1. (*a*) Pathway by which noise alters pollination and seed dispersal services. Solid and dashed arrows denote direct and indirect interactions, respectively. Signs refer to effect direction, and support for each effect is indicated by figure number. See main text for results and citations supporting the dependence of *I. aggregata* on *A. alexandri* (arrow labelled figure 2*a*) and for the functional quality of *Peromyscus* mice and *A. californica* as *P. edulis* seed dispersers (arrows labelled figure 3*c*,*d*). (*b*) Active gas wells located at the end of access roads served as (*c*) noisy treatment sites owing to the presence of noise-generating gas well compressors (white arrow) or (*d*) quiet control sites.

for hummingbird-pollinated plants and disrupt *P. edulis* seed dispersal services in noisy areas and potentially affect seedling recruitment (figure 1*a*).

To test these predictions, we used a unique study system that isolates the influence of noise exposure from many confounding factors common to noisy areas, such as vegetation heterogeneity, edge effects and the presence of humans and moving vehicles (see below). We used observations, vegetation surveys and pollen transfer and seed-removal experiments on pairs of treatment and control sites to determine how ecological interactions differ in noisy and quiet areas and whether noise indirectly affects plants that depend on functionally unique avian mobile links.

2. MATERIAL AND METHODS

Our study took place in the Rattlesnake Canyon Habitat Management Area (RCHMA), located in northwestern New Mexico. Study area and site details can be found elsewhere [5–7]. Briefly, RCHMA is dominated by woodland consisting of *P. edulis* and *Juniperus osteosperma* (juniper) and has a high density of natural gas wells (figure 1*b*). Many wells are coupled with compressors that run continuously and generate noise at high amplitudes (greater than 95 dB(A) at a distance of 1 m), and, like most anthropogenic noise, compressor noise has substantial energy at low frequencies and diminishes towards higher frequencies (electronic supplementary material, figure S1) [5–7]. Additionally, human activity at wells and major vegetation features in the woodlands surrounding wells do not differ between wells with (noisy treatment sites) and without noise-generating compressors (quiet control sites, figure 1*c*,*d*)[7], providing an opportunity to evaluate the indirect effect of noise on supporting ecological services in the absence of many confounding stimuli common to most human-altered landscapes.

(a) *Pollination experiment*

To determine whether hummingbird-pollinated flowers indirectly benefit from noise, we used a field experiment controlling for the density and the spatial arrangement of hummingbird nectar resources with patches of artificial flowers that mimicked a self-incompatible, hummingbird-pollinated plant common to our study area: *Ipomopsis aggregata* (electronic supplementary material, figures S2 and S3*a*). In May 2010, we established seven pairs of treatment and control sites within RCHMA for the pollination experiments. Sites were paired geographically to minimize potential differences in vegetation features within each pair; however, to ensure that background noise levels were significantly different between paired sites, sites were greater than or equal to 500 m apart and resulted in relatively quiet conditions at control sites. The resulting distance between treatment-control pairs was 767 m ($\pm$57 s.e.m., minimum = 520 m, maximum = 954 m).

Artificial flower patches were established 125 m from either the wellhead or compressor on control and treatment sites,

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respectively (electronic supplementary material, figure S2*a*). The direction of the first patch relative to the wellhead or compressor was determined randomly and the second patch was established 40 m from the first and also at 125 m from the wellhead or compressor. Prior to the experiment, at each patch, we measured background noise amplitude as A-weighted decibels (dB(A)) for 1 min to confirm that noise levels were significantly higher at treatment patches relative to control patches. In all cases, measurements on paired treatment and control sites were completed on the same day and at approximately the same time. We measured amplitude as the equivalent continuous noise level (L_{eq}, *fast* response time) with Casella convertible sound dosimeter/sound pressure metres (model CEL 320 and CEL 1002 converter). We used 95 mm acoustical windscreens, and we did not take measurements when wind conditions were categorized three or above on the Beaufort Wind Scale (approx. 13–18 km h^{-1}), or when sounds other than compressor noise (i.e. bird vocalizations and aircraft noise) could bias measurements.

Artificial flowers are frequently used in pollination studies [21,22] and those used in our experiment were constructed from 0.6 ml microcentrifuge tubes. This microcentrifuge tube size had been used previously in pollination experiments with *A. alexandri* [23]. To mimic the appearance of *I. aggregata*, we wrapped each microcentrifuge tube with red electrical tape (electronic supplementary material, figure S3). Additionally, we attached three small pieces of yellow yarn to provide a substrate for marking flowers with fluorescent dye and subsequent transfer and deposition on other flowers by pollinators. Each artificial plant consisted of three flowers attached to a 53 cm long metal rod with green electrical tape (electronic supplementary material, figure S3*b*). Patches of plants were arranged in a 3 m^2 area with four plants marking each corner and one at the centre (electronic supplementary material, figure S2*a*).

Plant patches were established simultaneously or one immediately after another (less than or equal to 30 min) on paired sites. Because *I. aggregata* nectar is 20–25% sucrose [24,25], we filled each flower with a reward of 0.4 ml 25 per cent sucrose solution with pipettes and calibrated plastic droppers, returning each day at approximately the same time to refill the flower with the sucrose reward so that pollinators learned to use the flowers as a foraging resource. Only rarely did we encounter a single artificial flower completely depleted of the reward between visits to replenish the reward, but never all three flowers on the same plant.

We conducted observations to determine pollinator visitation rates at 11 (79%) of 14 pairs of treatment and control patches. Because the establishment of our patches took several days, prior to our observations, four pairs of patches were refilled for 4 days, two patches were refilled for 3 days and five patches were refilled for 2 days and all observed patches had been established for greater than 38 h prior to observation. We then conducted observations at patches on pairs of control and treatment sites simultaneously or one immediately after the other. We watched flowers at focal patches for 15 min and tallied the number of visits to each plant from a distance of 5 m, using binoculars when necessary to identify arthropods visiting the flowers. All non-hummingbird pollinators were separated into their orders (Hymenoptera, Diptera and Lepidoptera) and we used Poisson generalized linear-mixed models (GLMM) within the lme4 package in R [26] to examine whether patch visitations by *A. alexandri* or other pollinators differed between treatment and control sites. Individual sites and geographically paired sites were treated as random effects.

Following focal observations, on 28 May 2010, we returned to all patches between 07.00 and 12.00 to refill all artificial flowers with the sucrose reward and uniquely marked one plant per patch with either yellow or red fluorescent powder (Day-Glo Color Corporation, Cleveland, Ohio, USA) such that plants within the same site but at different patches received a unique coloured powder. Use of fluorescent powder as a proxy for pollen transfer is a technique widely used in pollination studies because the transfer of powder is strongly correlated with the transfer of pollen [27,28]. Each patch was permitted 24 h of exposure for pollinator visits before we collected each plant for subsequent examination for powder transfer in the laboratory.

In the laboratory, we used an ultraviolet lamp under dark conditions to record the presence or absence of powder on each inflorescence, noting whether the powder was from the marked plant within the same patch or the patch located at 40 m. We then used Poisson GLMMs to examine within-patch and between-patch pollen transfer with number of individual flowers per patch with transferred pollen as response variables. We treated each site and geographically paired treatment and control site as random effects in all models.

(b) *Pinus edulis seed-removal experiment*

We conducted *P. edulis* seed-removal experiments throughout RCHMA to determine whether and how seed-removal rates and the community of seed predators and dispersers respond to noise exposure. *Pinus edulis* trees within a region typically synchronize production of large-cone crops every 5–7 years [20]. As cones gradually dry and open in September, seeds not harvested by corvids from cones in the canopy fall to the ground where rodents, corvids and other bird species consume and harvest seeds for several months [20]. Monitoring rates of autumn seed removal from the ground can be problematic as seeds continue to fall from trees; therefore, we conducted our experiments in June–July when no other *P. edulis* seeds were available, similar to other studies that have examined *P. edulis* seed removal and dispersal during summer months [29].

We used six pairs of treatment and control sites that were geographically coupled. Sites met those same criteria described for the pollination experiment. The mean distance between treatment-control pairs was 821 m ($\pm$51 s.e.m., minimum = 642 m, maximum = 1029 m). At each site, we established seed stations at 10 locations within 150 m of each well or compressor (electronic supplementary material, figure S2*b*). Locations were selected randomly provided that the distance between each station was greater than or equal to 40 m, and each station was located on the ground under a reproductively mature *P. edulis* tree.

Seed-removal experiments lasted for 72 h with visits to each station every 24 h to quantify the daily rate of seed removal. At the beginning of each 24 h period, we simulated natural seed fall by scattering 20 *P. edulis* seeds on the ground in a 0.125 m^2 area. We then returned 24 h later to document the number of removed seeds, determine whether there was evidence for *in situ* seed predation by carefully searching the immediate area (approx. 2 m^2) for newly opened *P. edulis* seeds (usually conspicuous as a clumped collection of seed-coat fragments from several seeds) and to again scatter 20 seeds at the station. Evidence of seed predation

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at a station was defined as whether recently opened (and empty) seed coats were detected during any of the three visits used to quantify seed-removal rate. All seeds were collected locally within RCHMA and were handled with latex gloves so that human scent was not transferred to the seeds. During one of the four visits to each station, we measured background noise amplitude following the methods described above for the pollination experiment.

To document the identity of animals removing seeds, we paired each station with a motion-triggered digital camera (Wildview Xtreme II). Cameras were mounted on a trunk or a branch of an adjacent tree within 1–3 m from the seed station for a clear view, yet positioned in a relatively inconspicuous location to avoid drawing additional attention to the station. Cameras remained on each station for the entire 72 h period and documented both diurnal and nocturnal seed removal. A positive detection of a species removing seeds was recorded only when an individual was documented removing or consuming seeds.

The number of seeds removed per 24 h period was used to calculate a daily mean proportion of seeds removed, which we arcsine square-root transformed to meet assumptions of normality and homogeneity of variance. We used linear-mixed models (LMMs) to examine whether the proportion of seeds removed differed between treatment and control seed stations or owing to the presence or absence of individual species. We used binomial GLMMs to determine how the presence of individual species explained *in situ* seed predation, evidenced by the presence of newly opened *P. edulis* seed coats. For the models in which we examined the influence of individual species on seed removal or predation, we started with models containing all documented species as predictor variables and proceeded to remove each non-significant variable one at a time based on the highest p-value until only significant effects remained. We used Poisson and binomial GLMMs to examine whether species richness of the seed removing community and detections of individual species differed at treatment and control seed stations, respectively. For all models, we treated each site and geographically paired treatment and control sites as random effects. Some models evaluating detections of individual species on treatment and control sites would not converge; therefore, for these cases, we used χ^2-tests to determine whether there was a difference between the total number of detections on control and treatment sites.

(c) *Seedling recruitment surveys*

In 2007, we completed 129 random vegetation surveys on 25 m diameter vegetation plots (approx. 490 m^2) located on nine treatment and eight control sites, some of which were not the same sites used in the seed-removal experiments, which included only six pairs of sites (12 total). Ten treatment sites were surveyed in 2007, but we excluded vegetation plots from one site from this analysis because the compressor was installed in 2006, thus confounding the acoustic conditions during which many seedlings may have been established (see below). Compressors on all other treatment sites had been in place for at least 6 years, but over 10 years for several sites.

Because our fieldwork in previous years had documented an avoidance of noise by *A. californica* [7], in 2007, we counted all *P. edulis* seedlings per vegetation plot. We restricted counts of seedlings to those less than or equal to 20 cm to make sure that they had been dispersed and established relatively recently and under the same acoustic conditions that were present in 2007. We assumed seedlings less than or equal to 20 cm had been dispersed and established within the previous 6 years because 1 year-old *P. edulis* seedlings were measured to have an average height of 5.3 cm [30] and because the closely related *Pinus cembroides* reaches a height of 1 m at around 5 years old [31]. Thus, our assumptions should be considered conservative. We analysed seedling recruitment with the number of seedlings per plot as the response variable using Poisson GLMMs. Predictor variables included plot location on either a treatment or control site, but also plot-level features that may influence seedling establishment and recruitment, such as the number of shrubs, *P. edulis* and *J. osteosperma* trees, the amount of canopy cover, leaf litter depth and the proportion of ground cover classified as living material, dead matter or bare ground. Site identity was treated as a random effect. We followed the same model selection procedure described above for seed removal and seed predation. Data for seedling recruitment, plus data from the seed removal and pollination experiments have been deposited at Dryad (www.datadryad.org; doi:10.5061/dryad.6d2ps7s7).

3. RESULTS

(a) *Pollination*

Noise amplitude values were significantly higher (approx. 12 dB(A)) at treatment patches relative to control patches (LMM: $\chi^2_1 = 25.550$, $p < 0.001$, electronic supplementary material, figure S2*c*) and similar to those experienced approximately 500 m from motorways [32,33]. Focal observations at a subset of patches revealed that several taxa visited artificial flowers supplied with a nectar reward (electronic supplementary material, table S1), yet only *A. alexandri* visits differed between treatment and control sites. *Archilochus alexandri* visits were five times more common at treatment patches than control patches (Poisson GLMM: $\chi^2_1 = 6.859$, $p = 0.009$, figure 2*a*).

Consistent with more *A. alexandri* visits to plants in noisy areas, within-patch pollen transfer occurred for 5 per cent of control site flowers, but 18 per cent of treatment site flowers (Poisson GLMM: $\chi^2_1 = 15.518$, $p < 0.001$, figure 2*b*) and between-patch pollen transfer occurred for 1 per cent of control site flowers and 5 per cent of treatment site flowers (Poisson GLMM: $\chi^2_1 = 6.120$, $p = 0.013$, figure 2*c*). Analyses using the presence or absence of transferred pollen at the patch level revealed the same pattern (within-patch binomial GLMM: $\chi^2_1 = 8.800$, $p = 0.003$; between-patch binomial GLMM: $\chi^2_1 = 5.608$, $p = 0.018$).

(b) *Pinus edulis seed removal*

Noise amplitude values were consistently higher (approx. 14 dB(A)) at treatment seed stations relative to control seed stations (LMM: $\chi^2_1 = 19.084$, $p < 0.001$, electronic supplementary material, figure S2*d*), yet neither seed-removal rate (LMM: $\chi^2_1 = 2.209$, $p = 0.137$), nor documented species richness per seed station differed between sites with and without noise (Poisson GLMM: $\chi^2_1 = 0.461$, $p = 0.497$).

The majority of animals detected with motion-triggered cameras removing seeds from stations were easily identified to species; however, for two groups, *Peromyscus* mice and *Sylvilagus* rabbits, we were not always able to identify individuals to species; therefore, they were assigned to their

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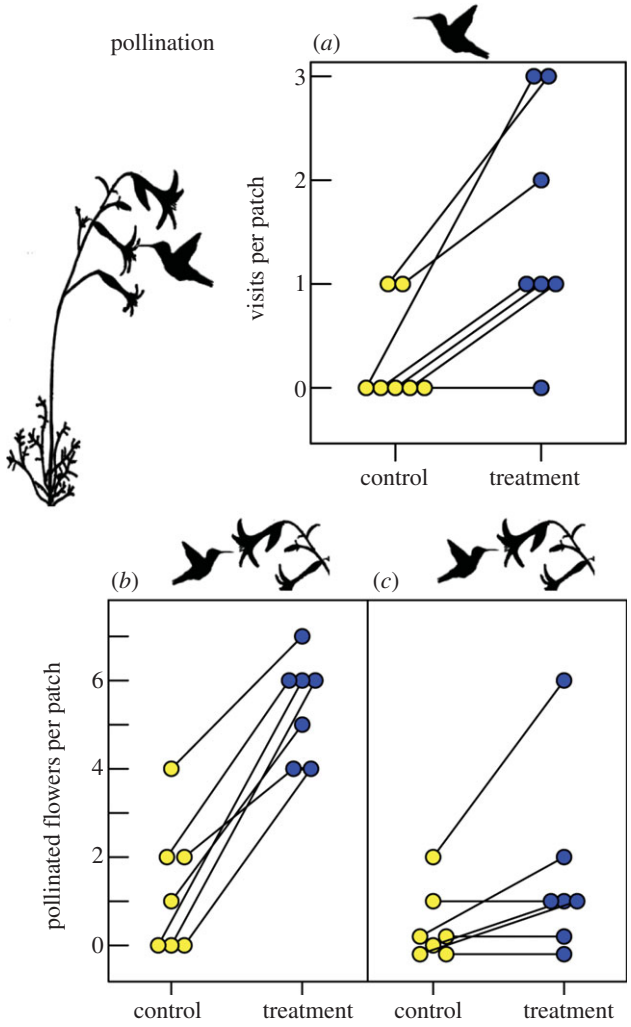

Figure 2. Evidence from pollination experiment. (*a*) *Archilochus alexandri* visited artificial flowers on noisy treatment patches more than quiet control site patches. The values displayed reflect the sum of visits per site (14 sites total with two patches per site, five plants per patch and three flower per plant). (*b*,*c*) Pollination of individual flowers was higher on treatment sites relative to control sites both (*b*) within and (*c*) between patches. Values displayed reflect the sum of pollinated flowers in both patches per site. (*a*-*c*) Lines link geographically paired sites.

respective genera. In total, we document 11 taxa removing seeds, nine of which were considered seed predators (electronic supplementary material, table S2). Cameras failed to detect the identity of animals that removed seeds at approximately one station per site, primarily owing to battery failure. However, there was no difference in the number of camera failures between treatment and control sites that would suggest our detections were biased towards one site type over the other (binomial GLMM: $\chi^2_1 = 0.240$, $p = 0.624$); therefore, any relative differences in detections between treatment and control sites should reflect actual differences between noisy and quiet areas.

Of the nine seed predators documented removing seeds, only one, *Pipilo maculatus*, was detected more frequently on control sites relative to treatment sites (binomial GLMM: $\chi^2_1 = 4.133$, $p = 0.042$); a pattern consistent with previous findings that *P. maculatus* avoids noise in its nest placement [7]. We also documented seed removal by *Peromyscus* mice and *A. californica*, considered to be primarily seed predators and important seed dispersers, respectively [20]. Mice were detected at 63 per cent of treatment seed stations and only 45 per cent of control stations (binomial GLMM: $\chi^2_1 = 4.023$, $p = 0.045$; figure 3*a*). By contrast, *A. californica* was detected removing seeds exclusively at control stations ($\chi^2_1 = 5.486$, $p = 0.019$; figure 3*b*). *Peromyscus* mice and *A. californica* were also the only taxa with strong effects on seed removal and, along with *Tamias minimus*, were taxa with strong influences on patterns of seed predation at the seed station (i.e. presence of opened seed coats). Seed removal rates were approximately 30 per cent higher at stations where *Peromyscus* mice or *A. californica* were documented removing seeds compared with stations where they were not detected (LMM: $\chi^2_2 = 35.775$, $p < 0.001$; figure 3*c*,*d*). Seed predation was positively affected by the presence of *Peromyscus* mice ($\beta_{\text{mouse}} = 0.841 \pm 0.412$ s.e.) and *T. minimus* ($\beta_{\text{chipmunk}} = 1.199 \pm 0.544$ s.e.), both typically considered seed predators [20], but negatively affected by the presence of *A. calilfornia* ($\beta_{\text{scrub-jay}} = -2.031 \pm 1.005$ s.e.; binomial GLMM: $\chi^2_3 = 13.748$, $p = 0.003$). Indeed, most stations where *Peromyscus* mice (74%) and *T. minimus* (81%) were detected also had evidence of seed predation, but only 33 per cent of stations where *A. california* was detected were there signs of seed predation.

(c) Pinus edulis *seedling recruitment*

Consistent with the difference in animals removing seeds in noisy and quiet areas, *P. edulis* seedlings were four times more abundant on control sites relative to treatment sites ($\beta_{\text{Treatment}} = -1.543 \pm 0.240$ s.e.; figure 3*e*), but number of *J. osteosperma* trees ($\beta_{\text{Juniper}} = 0.036 \pm 0.016$ s.e.) and the proportion of dead organic ground cover ($\beta_{\text{Dead}} = 0.023 \pm 0.008$ s.e.) had small, positive effects on seedling abundance (Poisson GLMM: $\chi^2_3 = 38.583$, $p < 0.001$). However, neither of these variables, nor number of *P. edulis* trees, differed between treatment and control sites (juniper LMM: $\chi^2_1 = 0.726$, $p = 0.394$; dead ground cover LMM: $\chi^2_1 = 0$, $p = 1.0$; *P. edulis* LMM: $\chi^2_1 = 2.560$, $p = 0.110$), suggesting that other habitat features can be excluded as alternative explanations for *P. edulis* seedling recruitment on treatment and control sites.

4. DISCUSSION

Elevated noise levels affected pollination rates by hummingbirds and *P. edulis* seed dispersal and seedling recruitment, but the direction of each effect was different. Noise exposure had an indirect positive effect on pollination by hummingbirds, but an indirect negative effect on *P. edulis* seedling establishment by altering the composition of animals preying upon or dispersing seeds. These results extend our knowledge of the consequences of noise exposure, which has primarily focused on vocal responses to noise [8,34,35], somewhat on species distributions and reproductive success [7,10,32,36] and very little on species interactions [7,14–16]. In an example of the latter, traffic noise negatively affects bat (*Myotis myotis*) foraging efficiency by impairing its ability to locate prey by listening to sounds generated from prey movement [14]. Here, our data demonstrate that the frequency of species interactions can change without a direct effect of noise on the interaction itself, suggesting that noise exposure may trigger changes to numerous ecological interactions and reverberate through communities.

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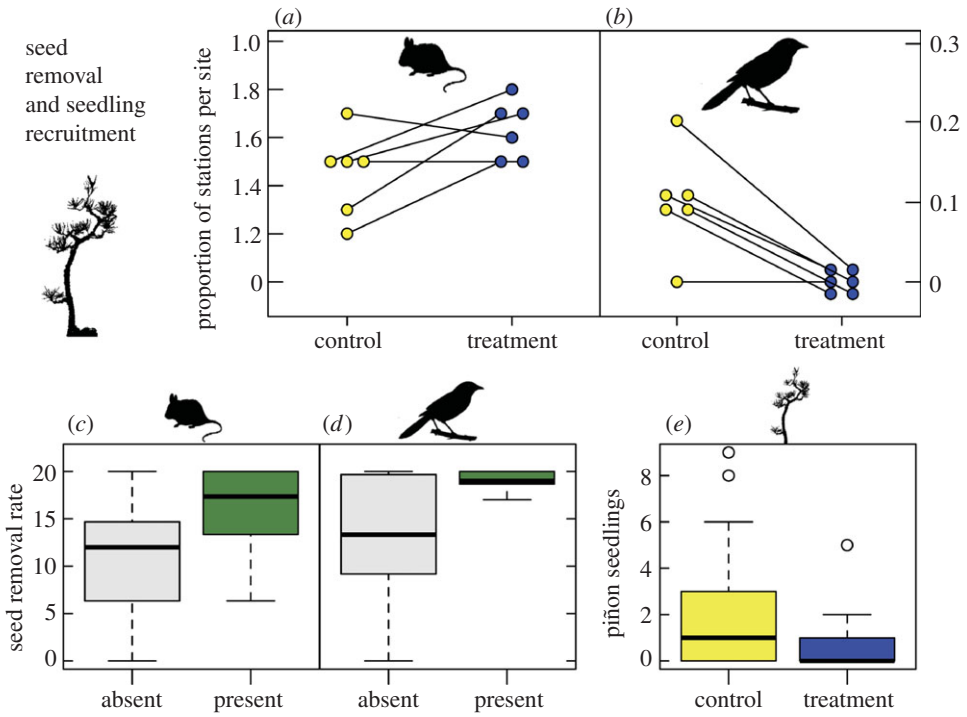

Figure 3. (*a*) *Peromyscus* mice were detected more frequently at treatment seed stations relative to control stations. (*b*) *A. californica* removed seeds exclusively on control sites. Values displayed in (*a*) and (*b*) reflect the proportion of seed stations per site where mice or jays were detected. (*c*,*d*) Seed removal rates (per 24 h) were higher when (*c*) *Peromyscus* mice or (*d*) *A. californica* were detected at a seed station. (*e*) *Pinus edulis* seedling recruitment was significantly higher on control sites relative to treatment sites. Box plots indicate the median value (solid black line), 25th and 75th percentiles (box), and whiskers denote 1.5 the interquartile range. Outliers are denoted by open circles.

Increases in pollination rates were in line with our prediction based on the positive responses to noise by *A. alexandri*, both in terms of nest-site selection [7] and abundances determined from surveys [17]. Our experimental design and use of artificial flowers were advantageous because we could control for variation in density and the spatial arrangement of nectar resources that can influence pollination patterns [37]. However, this approach precluded us from determining whether increases in pollination in noisy areas results in greater seed and fruit production. This is probable for *I. aggregata* because it can be pollen limited throughout its range [38–40] and fruit set is strongly correlated with pollinator (e.g. hummingbird) abundance [18]. Therefore, noise-dependent increases in *A. alexandri* abundances [7,17] coupled with increases in visits to artificial flowers in this study is suggestive that *I. aggregata* plants exposed to elevated noise levels may have greater reproductive output relative to individuals in quiet areas.

Seed removal, seed predation and seedling recruitment data were consistent with one another and our expectations, suggesting that noise has the potential to indirectly affect woodland structure. It is plausible that the suite of species removing seeds may differ in June and July when we conducted our study from that found in the autumn when seeds are typically available. Yet, all species documented removing seeds are year-round residents and their relative abundances are unlikely to fluctuate between treatment and control sites throughout the year. Instead, it is more likely that we underestimated the magnitude of the difference in seed dispersal quality between noisy and quiet areas for two main reasons. First, because *A. californica* typically provision young with protein-rich animal prey [41], individuals at our study area may have been foraging primarily on animal prey rather than *P. edulis* seeds during our experiments. Second, our use of seed stations on the ground did not account for seed removal from cones in the canopy by other important seed dispersers, such as *Gymnorhinus cyanocephalus* (piñon jay); a species that occurs in RCHMA, but also avoids noisy areas [7,42]. The degree to which these factors contribute to reduced seedling recruitment in noisy areas is unknown, but provides an interesting avenue of research for future study.

Although, *A. californica* and *Peromyscus* mice had the greatest influence on seed-removal rates, we were unable to track the fate of individual seeds. Nevertheless, these species influenced patterns of seed predation in a manner consistent with knowledge of how these species differ as mobile links for *P. edulis* seed dispersal and seedling establishment. Evidence of seed predation was less common at seed stations visited by *A. californica*, potentially reflecting its role as an important disperser of *P. edulis* seeds. For example, one *A. californica* individual may cache up to 6000 *P. edulis* seeds in locations favourable for germination during a single autumn [43]. Many seeds are relocated and consumed, but many go unrecovered and germinate [20]. By contrast, although *Peromyscus* mice might function as conditional dispersers under some circumstances [44,45], here their presence at a seed station was a strong predictor of seed predation, reflecting their primary role as seed predators [20]. Previous research using experimental enclosures to study caching behaviour in the field supports our findings [29,44]. *Peromyscus* mice consume a large proportion (approx. 40%) of encountered seeds and typically cache

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many encountered seeds that are not immediately consumed [44]. Yet, cached seeds are often recovered and eaten (greater than 80%) along with seeds cached by other individuals or species [29]. Thus, the reduced density of seedlings in noisy areas could be explained not only by fewer seeds entering the seed bank as a result of reduced densities of important avian seed dispersers that cache many thousands of seeds, but because seeds present within the seed bank experience elevated rates of predation via cache pilfering associated with noise-dependent increases in *Peromyscus* mice.

Despite the concordance between our findings and the literature regarding the roles of *A. californica* and *Peromyscus* mice on *P. edulis* seed dispersal and predation, seedling mortality caused by key seedling predators, such as *Odocoileus hemionus* (mule deer) and *Cervus canadensis* (elk), could potentially explain the higher density of seedlings in quiet relative to noisy areas. However, ungulates such as *C. canadensis* appear to avoid areas exposed to noise from high traffic volume [46], suggesting that seedling mortality owing to browsing ungulates should be greater in areas with less noise and leading to a pattern opposite from that which we observed. Still needed are confirmatory studies that track the fate of cached seeds and document patterns of seedling predation within noisy and quiet areas.

Despite the downstream consequences of species-specific response to noise exposure, the mechanistic reasons for species-specific responses are still not clear. *Aphelocoma californica* may avoid noisy areas because noise can mask their vocal communication. Larger birds with lower frequency vocalizations are more sensitive to noise than smaller species with higher frequency vocalizations because their vocalizations overlap low-frequencies where noise has more acoustic energy [17]. *Aphelocoma californica* is also the main nest predator in the study area [7,16] and it is possible that noise masks acoustic cues used to locate prey at nests (e.g. nestling and parent calls). It is also possible that these forms of acoustic interference may lead to elevated stress levels that could influence patterns of habitat use [13], but research on this potential link is currently lacking.

In contrast to the direct effect noise may have on *A. californica* communication and foraging, positive responses to noise by *A. alexandri* and *Peromyscus* mice probably reflect indirect responses to noise. Noisy areas may represent refugia from predators and key competitors that typically avoid noisy areas, including jays. For example, *A. alexandri* may preferentially settle in noisy areas in response to cues indicative of lower nest predation pressure from *A. californica*. Similarly, *Peromyscus* mice populations may increase in noisy areas not only because of reduced competition with *A. californica* and other jays for key-foraging resources, but also in response to reduced predation by nocturnal acoustic predators that may avoid noise [14], such as owls.

That noise may alter patterns of seedling recruitment adds important insights to our earlier work where we found neither *P. edulis* tree density, nor 12 other habitat features differed between treatment and control sites [7]. This, however, may be slowly changing. Reduced *P. edulis* seedling recruitment in noisy areas may eventually translate into fewer mature trees, yet because *P. edulis* is slow growing and has long generation times [47], these initial changes in stand structure could have gone undetected for decades. Such long-term changes may have important implications for the woodland community as a whole by prolonging the negative consequences of noise exposure. That is, noise may not only result in large declines in diversity during exposure by causing site abandonment or reduced densities by many species [7,10], but diversity may suffer long after noise sources are gone because fewer *P. edulis* trees will provide less critical habitat for the many hundreds of species that depend on them for survival [48].

These separate experiments highlight that noise pollution is a strong environmental force that may alter key ecological processes and services. Over a decade ago, Forman [4] estimated that approximately one-fifth of the land area in the United States is affected by traffic noise, yet the actual geographical extent of noise exposure is undoubtedly greater when other sources are considered. Additionally, this spatial footprint of noise, the anthropogenic soundscape, will only increase because sources of noise pollution are growing at a faster rate than the human population [3]. These data suggest that anthropogenic soundscapes have or will encompass nearly all terrestrial habitat types, potentially impacting innumerable species interactions both directly and indirectly. It is critical that we identify which other functionally unique species abandon or preferentially settle in other noisy areas around the world. Early detection of altered species distributions and the resulting disrupted or enhanced ecological services will be key to understanding the trajectory of the many populations and communities that outwardly appear to persist despite our industrial rumble.

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