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Long-term noise pollution affects seedling recruitment and community composition, with negative effects persisting after removal

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Noise pollution can affect species' behaviours and distributions and may hold significant consequences for natural communities. While several studies have researched short-term effects of noise, no long-term research has examined whether observed patterns persist or if community recovery can occur. We used a long-term study system in New Mexico to examine the effects of continuous natural gas well noise exposure on seedling recruitment of foundational tree species (*Pinus edulis*, *Juniperus osteosperma*) and vegetation diversity. First, we examined seedling recruitment and vegetation diversity at plots where current noise levels have persisted for greater than 15 years. We then examined recruitment and diversity on plots where noise sources were recently removed or added. We found support for long-term negative effects of noise on tree seedling recruitment, evenness of woody plants and increasingly dissimilar vegetation communities with differences in noise levels. Furthermore, seedling recruitment and plant community composition did not recover following noise removal, possibly due in part to a lag in recovery among animals that disperse and pollinate plants. Our results add to the limited evidence that noise has cascading ecological effects. Moreover, these effects may be long lasting and noise removal may not lead to immediate recovery.

1. Introduction

Global population growth, urbanization and the continued development of resource extraction have all contributed to dramatically increased levels of anthropogenic noise over recent decades [1]. Anthropogenic noise (herein referred to as noise) is gaining the attention of biologists, resource managers and policymakers as a growing body of evidence suggests that it may have detrimental impacts on natural ecosystems [2]. Research in the past 10 years has set the groundwork for the effects of increased noise exposure on the behaviour of individuals [3,4] and, to a lesser extent, the distributions or abundances of species [5–7]. Yet, we still have a limited understanding as to how noise may be impacting processes on an ecosystem and community level.

A handful of short-term studies have shown noise to lower species richness and composition, which causes a fundamental restructuring of communities [5–7]. Fewer studies have evaluated how noise-dependent restructuring may have cascading consequences on the ecological community through altered species interactions. Playback of noise disrupts host–parasitoid interactions, with lower parasite (*Corethrella* sp. and *Ormia ochracea*) abundance observed with increased noise levels [8,9]. Similarly, experimentally applied traffic noise reduced bird species abundance and richness with apparent community composition differences between quiet and noisy areas [7]. Although these documented short-term responses have important implications for how ecological processes and communities may respond in the long term to noise, no prior research has

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investigated whether short-term responses to noise persist over longer time periods or whether the consequences of noise exposure remain once the noise source is removed.

Previous research has used noise generated by oil and natural gas compressors in large-scale systems to assess ecological impacts [6,10]. These unique study systems are capable of minimizing confounding factors typical of noisy areas including vegetation heterogeneity, edge effects and the presence of humans, while simultaneously providing the valuable opportunity to address questions related to long-term persistent noise exposure on ecosystems. Reporting on fieldwork conducted from over a decade ago in the natural gas fields of NW New Mexico, Francis *et al*. [6,11] documented avoidance of energy-sector noise by Woodhouse's scrub-jay (*woodhouseii*), which is an important seed disperser of pinyon pine (*Pinus edulis*, hereafter called pinyon) [12], and found that pinyon seedlings were four times more abundant on quieter control plots (hereafter Control) relative to noisy treatment plots (hereafter Noise) [13]. Additional work in this system documented noise-dependent changes in pollinator abundances and pollination activity, suggesting additional pathways by which effects of noise may indirectly affect vegetation communities [5,13,14]. Despite these earlier findings suggestive of indirect effect of noise on plants, to our knowledge, whether noise pollution has cumulative cascading effects on plant community composition remains unexplored.

Here, building on prior research in our long-term research sites in NW New Mexico (area detailed in [6,15]), we investigated how noise may affect pinyon (*P. edulis*)–juniper (*Juniperus osteosperma*) woodland plant communities on longer timescales and shifts in acoustic regimes. We resurveyed 115 plots 12 years following initial data collection to determine whether the previously reported patterns for pinyon seedlings hold over a longer time frame [13], but also included analyses of an additional foundational tree species (Utah juniper, henceforth 'juniper') and several metrics that describe plant communities. We then examined how changes in noise regimes influenced tree seedling recruitment and plant communities. For the long-term analyses, we used plots that have not changed treatment since at least 2005 (long-term Noise, $n = 31$, and Control, $n = 20$). To investigate how seedling densities and plant communities respond to changes in noise conditions, we used long-term noise and control plots, plus those that changed from Noise to Control and vice versa (previously noisy, 'prevNoise', $n = 39$, previously quiet, 'prevControl', $n = 25$).

First, we hypothesized that pinyon seedling recruitment and sapling abundance would decline with increases in background sound levels among plots that have remained noisy or quiet since at least 2004 (total long-term plots $n = 51$). We expected similar patterns in seedling recruitment rates of juniper and juniper sapling abundance (total long-term plots $n = 42$, see Methods for sample size difference), given its reliance on vertebrate seed dispersers documented to avoid noise, such as mountain bluebird (*Sialia currucoides*) [16]. Furthermore, based on noise-dependent changes to the distribution of animals that disperse, pollinate and browse on plants in this system [5,13,14], we expected species richness and woody plant community (trees and shrubs) evenness to decline with increasing noise. Coupled with these differences, we also expected plant community turnover (i.e. β-diversity) to be explained by variation in sound level.

To determine whether seedling recruitment and forest composition recovers from prior exposure to noise and whether the recent introduction of noise to formally quiet areas reduces seedling recruitment and degrades forest composition, we took advantage of the addition or removal of noise-producing infrastructure since the previous study in 2007 [13]. We expected categorical Control plots to have more seedling recruitment than Noise plots. We hypothesized that sites that transitioned from noisy to quiet (prevNoise) over the 12 years should show recovery in pinyon and juniper seedling recruitment, because Woodhouse's scrub jays and other potential dispersers would no longer avoid those areas. Next, we hypothesized that sites that have changed from quiet to noisy (prevControl) may experience lower seedling recruitment resulting from short-term noise deterrence of seed dispersers into these areas. Lastly, because noise affects the broader ecological community in this system, including many animals with direct or indirect links to plants, such as pollinators including hummingbirds [13], bats [14] and insects [5], we also hypothesized that overall plant species richness and turnover may be affected by altered acoustic regimes. We predicted that (i) overall species richness would be lower in prevNoise and prevControl plots when compared with long-term Control plots, but higher in richness when compared with long-term Noise plots; (ii) overall β-diversity would vary between treatments; (iii) β-diversity for animal-pollinated plants would differ between plots due to disrupted pollination; and (iv) functional groups of pollinators would vary between treatments. For example, hummingbird-pollinated species are expected to be higher in noisy sites [13], while species pollinated by insects including bees, beetles and moths may be lower [5].

2. Methods

We conducted our study in NW New Mexico, USA, within the Bureau of Land Management's Rattlesnake Canyon Habitat Management Area (RCHMA) [15]. Briefly, RCHMA is dominated by pinyon–juniper woodland with intermittent areas of *Artemisia tridentata* (sagebrush) shrubland and contains a high density of natural gas wells. Some wells are coupled with compressors that run continuously and generate chronic noise at high amplitudes (95 dB(A) at a distance of 1 m) [13]. Other wells lack a compressor and generate much lower amplitude noise or no chronic noise at all. Overall, major vegetation features and human activity levels do not differ surrounding well pads that contain compressors and those lacking compressors [6], providing the opportunity to evaluate the indirect effect of noise on supporting ecological services.

Vegetation plots were selected randomly in 2007 [13] and resurveyed in 2019. Vegetation surveys were conducted on 25 m diameter vegetation plots (approx. 490 m^2) located on nine treatment and eight control sites (totalling 17 well pads). Long-term Noise and Control sites have had the same treatment since at least 2004. Out of 25 sites that changed from Control to Noise (prevControl), 84% changed between 2010 and 2013 and the remaining 16% changed between 2013 and 2016. Of 39 plots that changed from Noise treatment to Control (prevNoise), 100% appear to have changed between 2015 and 2017 as recorded by site visits and/or aerial imagery.

Surveys were conducted between 6 May and 22 August 2019 and followed the protocol used in 2007 [13]. Briefly, a team of two to three people identified to species and counted all individual shrubs (greater than 50 cm), trees, tree saplings and seedlings. Saplings were defined as individuals greater than 20 cm and less than 2 m in height and with less than 8 cm diameter at breast height (DBH). Seedlings were defined as less than or equal to 20 cm in height to ensure they had been dispersed and established relatively recently. Pinyon seedlings were counted on all 115 plots and sampling was expanded to quantify juniper seedlings on the 98 plots surveyed after 14 May 2019. Therefore, the juniper seedling analyses has a smaller sample size (Control = 20, Noise = 22, prevNoise = 31, prevControl = 25). Point intercept 1 m sampling was used to collect plot-level features, where two transect tapes each measuring 25 m were laid perpendicular running N–S and E–W. One surveyor (S.E.T.) conducted point intercept sampling at 1 m intervals for a total of 52 sampling points per plot. At each sampling point, ground cover was classified as living vegetative material, dead vegetative material or bare ground. Canopy cover, qualified by the presence of a tree or shrub directly overhead measuring greater than 1 m in height, was also collected at each sampling point. Canopy was considered above 1 m owing to the dwarf nature of the woodland and to match that used in previous work [6,13]. We then calculated the percentage of each ground cover type as well as canopy cover for each plot.

In addition to the 2007 protocol, we completed presence/absence floristic inventories on each vegetation plot to quantify species diversity. Functional pollinator groups were assigned to flowering non-grass species based on the most likely pollinator, although it is likely that some species have multiple pollinators. For example, *Mirabilis longiflora* is pollinated by both bees and hawkmoths, but nectar tubes flow mostly at night, thus we categorized it as moth pollinated [17]. Generally, plants with white or pale coloured flowers were categorized as moth pollinated, red flowers were categorized as hummingbird pollinated and other colourful flowering plants (e.g. purple, yellow, blue) were categorized as diurnal insect pollinated [18]. Wind-pollinated, autogamous or plants with unknown pollinator species were dropped from the animal-pollinated subset.

(a) Background noise measurements

Ambient background noise levels were measured on all plots as an A-weighted equivalent continuous sound level (LAeq) using a calibrated sound-level meter (SLM; Larson Davis model 831, firmware 2.206, A-weighting, fast response, 0.0 dB gain, re: 20 µPa) for 1 min at the centre of each vegetation plot in 2019 with the microphone held horizontally in a random direction. Previous studies suggest that the repeatability of short-term sound levels in this system are highly repeatable [13,19]. We used A-weighting, which approximates human hearing range, because it is the most appropriate weighting for birds [20]. All measurements were taken opportunistically at the time of the survey or during subsequent visits in order to avoid wind noise or other ephemeral environmental noise such as cicada chorus.

(b) Statistical analysis

(i) Long-term noise exposure

First, we tested whether long-term noise affects seedling recruitment in both pinyon ($n = 51$) and juniper ($n = 42$). To model pinyon seedling and juniper seedling counts, we used generalized linear mixed-effect models (GLMM) with Poisson error in the *glmer* function in R package lme4 1.1-23 [21]. In a global model, for fixed effects, we included sound level (LAeq) and several other plot-level features that were previously shown to influence seedling recruitment [13] or hypothesized to influence establishment and recruitment: number of shrubs, number of pinyon and juniper trees, per cent canopy cover, and the per cent of ground cover classified as living material, dead matter or bare ground. We used variance inflation factors (VIFs) to evaluate collinearity and retained all variables with VIF < 5 [22]. We used the scale function in base R to centre and standardize all continuous variables (i.e. centring by subtracting the mean from all values and then dividing by the standard deviation) for comparisons of effects within models. Well pad ID was treated as a random effect to account for clustering of surveyed plots. We used packages AICcModavg [23] and MuMIn [24] to compare candidate models consisting of all potential subsets of variables in the global model with the dredge function. We calculated model-averaged effects from strongly supported models ($\Delta\text{AICc} \leq 2$) and report the model-averaged conditional effects in the main text and report model selection results in the electronic supplementary material. We used *QQ* plots using the *simulateResiduals* function in DHARMa R package [25] to evaluate model performance. We repeated these analyses for saplings of both species.

Next, we assessed long-term species diversity (richness, evenness, $n = 51$ for both). Species richness was quantified as the observed number of species per plot. We analysed the full richness dataset (117 species possible), and a subset of only animal-pollinated species (58 species possible). We defined evenness using the inverse Simpson's diversity index. Evenness was calculated from abundances of predominantly tree and shrub species (13 species total, electronic supplementary material, table S1). Being that most of these species are long lived and slow growing, their densities are unlikely to be altered as a result of recent changes to acoustic conditions; therefore, we restricted our analyses to long-term sites only. Evenness was log-transformed to meet linear model assumptions. We used AICcModavg to examine linear mixed-effect candidate models that included all potential additive effects for sound level, Julian date and canopy cover as fixed effects and well pad ID as a random effect. Canopy cover was included because it is known to influence the understory conditions such as soil nutrients and light availability [26]. Julian date was included because detectable floral diversity may vary seasonally. We initially use GLMMs with Poisson error for richness, but model diagnostics and AICc suggested that a model with Gaussian error better fit the data. Additionally, when the random effect of well pad ID had an estimated variance near zero (i.e. less than 0.0001), it was dropped and we report results from linear models [27]. We examined AICc values and report estimates from the model with the lowest AICc value or the averaged model if multiple models fall within 2 AICc, as described above.

To determine how long-term sound regimes influence floristic β-diversity, we used the PERMANOVA *adonis* function using the binary Bray–Curtis dissimilarity index with 999 permutations in R package vegan [28]. Models included effects of Julian date and sound level. To test hypotheses about whether noise may affect plant occurrences based on potential pollinators, we repeated this process for subsets of the data that (i) included all animal-pollinated plants and (ii) plants pooled to animal-pollinated functional group (i.e. pollinated by diurnal insect, moth or hummingbird; non-binary Bray–Curtis dissimilarity).

(ii) Treatment groups

To test for differences in seedling recruitment among treatments (Control, Noise, prevNoise, prevControl), we used the same GLMM models and model selection procedure described above but replaced sound level with treatment as a fixed factor to account for changes in sound regime over the 12-year period using the expanded dataset (pinyon $n = 115$; juniper $n = 98$). We used the *glht* function in the R package multcomp [29] for Tukey's pairwise comparisons of seedling recruitment between treatments for the highest ranked model.

To determine how current and past sound regimes (treatment) influence floristic richness and β-diversity, we used PERMANOVA with treatment replacing sound level as above. As in the long-term dataset, we repeated this process for subsets of the data that (i) included all animal-pollinated plants and (ii) animal-pollinated functional groups. We used package pairwiseAdonis 0.3 [30] to compare differences between treatments. In package vegan, we used non-metric multidimensional scaling function *metaMDS* to visualize community differences between treatments.

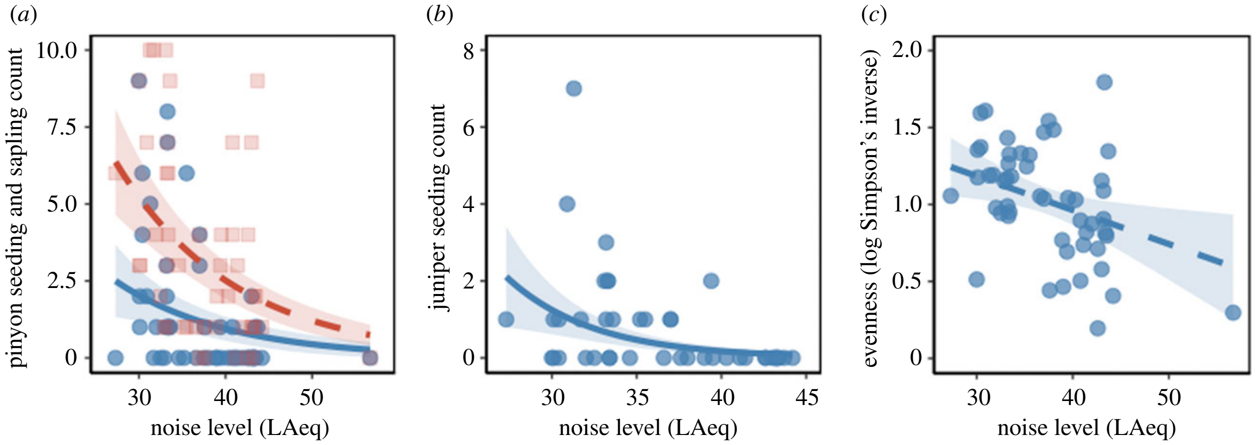

Figure 1. As noise increases (LAeq) across all long-term sites (Control and Noise), the number of (*a*) pinyon seedlings (blue circles) and sapling (red squares) decreases; (*b*) the number of juniper seedlings recruited decreases. *Y*-axis is per plot (490 m^2). (*c*) Evenness of 13 mostly woody species is negatively affected by sound level. Displayed are estimates (lines) and s.e. (shaded bands) from top-ranked models, which closely match model-averaged estimates. (Online version in colour.)

Table 1. *p*-Values for (*a*) PERMANOVA models for community turnover, as measured by dissimilarity (i.e. β-diversity) on long-term Noise and Control sites, where β-Diversity∼LAeq + Julian Date for all species, animal-pollinated species and animal-pollinated functional groups; and (*b*) *Adonis* pairwise comparisons for β-diversity∼treatment for all species, animal-pollinated species, animal-pollinated functional groups. Italics indicate a significant effect. See electronic supplementary material, table S10*a–c* for full results.

variable	all species	animal-pollinated species	functional groups
(*a*) long-term noise and control sites			
sound level (LAeq)	*0.004*	0.094	*0.021*
Julian date	*0.002*	*0.021*	*0.002*
(*b*) contrasts among all site types			
Control versus Noise	*0.008*	0.179	0.064
Control versus prevControl	0.182	0.192	0.614
Control versus prevNoise	*0.004*	*0.025*	*0.047*
Noise versus prevControl	*0.001*	*0.001*	*0.002*
Noise versus prevNoise	*0.001*	*0.034*	0.277
prevControl versus prevNoise	*0.001*	*0.001*	*0.002*

3. Results

(a) Effects of long-term noise exposure

For pinyon seedling recruitment on long-term plots, 13 models were strongly supported (ΔAICc ≤ 2, electronic supplementary material, table S2*a*). The model average indicates a significant negative effect of sound level and a positive effect of bare ground and dead matter on pinyon seedling recruitment (Poisson GLMM; electronic supplementary material, table S2*b*). Model estimated pinyon seedling per plot declined from approximately 2.5 seedlings per plot (approx. 51 ha^{-1}) at 30 dB(A) to zero at 60 dB(A) ($\beta = -0.429$, s.e. = 0.211, $z = -1.976$, $p = 0.048$; figure 1*a*). For juniper seedling recruitment on long-term plots, only a single model was strongly supported (ΔAICc ≤ 2) and contained sound level and total pinyon as fixed effects (Poisson GLMM: AICc = 90.62, $w_i = 0.96$, ER = 32, electronic supplementary material, table S3). Similar to the trend with pinyon seedlings, juniper seedlings declined from 1.75 seedlings per plot (approx. 35 ha^{-1}) in the quietest locations to zero in the loudest ($\beta = -0.967$, s.e. = 0.326, $Z = -2.935$, $p = 0.003$; figure 1*b*). The influence of sound levels on pinyon saplings (i.e. 20 < 200 cm) matched those of seedlings on the long-term plots ($\beta = -0.399$, s.e. = 0.112, $Z = 3.481$, $p = 0.001$, electronic supplementary material, table S4; figure 1*a*) but did not for juniper saplings (electronic supplementary material, table S5).

Top models (ΔAICc ≤ 2) for overall plant species richness and that of animal-pollinated plants at our long-term sites did not include sound level or canopy cover (electronic supplementary material, table S6*a–d*). However, for evenness of woody species, two strongly supported models (ΔAICc ≤ 2) included sound level as a fixed effect (electronic supplementary material, table S6*f*). Evenness strongly declined with sound level ($\beta = -0.135$, s.e. = 0.048, $z = -2.766$, $p = 0.005$; figure 1*c*) and increased with canopy cover ($\beta = 0.111$, s.e. = 0.045, $z = 2.424$, $p = 0.015$), while the effect of Julian date was not significant ($\beta = 0.075$, s.e. = 0.046, $z = 1.595$, $p = 0.111$). Finally, community turnover (i.e. β-diversity) among long-term sites for all plant species, those pollinated by animals and functional groups was explained by sound

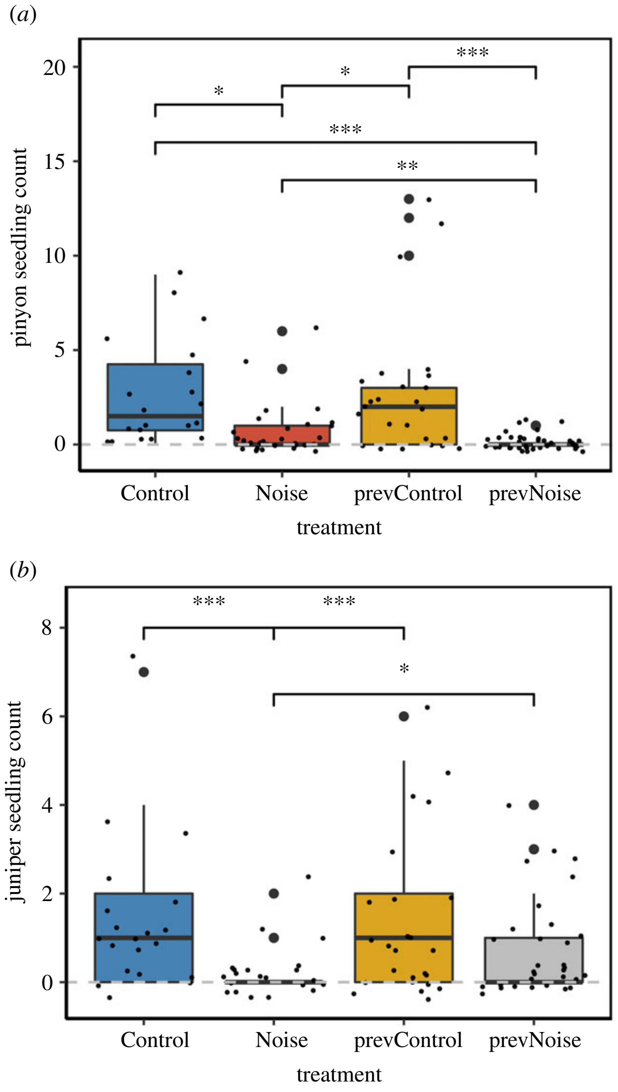

Figure 2. Boxplots with jittered raw data for (*a*) treatment effects on pinyon seedling recruitment and (*b*) treatment effects on juniper seedling recruitment. $*p = 0.05–0.01$; $**0.009–0.001$; $***p < 0.0001$. *Y*-axis is per plot (490 m^2). (Online version in colour.)

level and Julian date (table 1*a*; electronic supplementary material, table S6*h*).

(b) Effects of changing noise treatments

In our analysis of how changes in acoustic conditions affect pinyon seedling recruitment, 11 models were strongly supported (ΔAICc ≤ 2) and all included treatment as a significant effect (Poisson GLMMs: electronic supplementary material, table S7*a*). Previously noisy sites (prevNoise) have not recovered and have lower pinyon seedling recruitment compared to Control (electronic supplementary material, table S7*b*; figure 2*a*). Sites that changed to noise (prevControl) did not differ from Control sites, but had more pinyon recruitment than prevNoise or Noise sites, suggesting that they have not been exposed to noise long enough to have lower rates of seedling recruitment (electronic supplementary material, table S7*b*,*c*; figure 2*a*). Finally, consistent with the decline in pinyon seedling recruitment with sound level on long-term sites, Noise treatment sites had lower pinyon seedling recruitment than Control sites (electronic supplementary material, table S7*b*,*c*; figure 2*a*).

Juniper seedling recruitment was related to treatment in seven of eight strongly supported models (ΔAICc ≤ 2) (electronic supplementary material, table S8*a*) with a strong model-averaged effect of Noise treatment on juniper seedling recruitment (Poisson GLMM: $\beta = -2.089$, s.e. $= 0.709$, $z = 2.910$, $p = 0.004$; electronic supplementary material, table S8*b*). Juniper recruitment on formerly noisy (prevNoise) sites has recovered to some extent when compared with Noise sites, and have statistically similar juniper seedling recruitment relative to Control sites (electronic supplementary material, table S8*b*; figure 2*c*). Formerly quiet sites (prevControl) likely have not been loud for long enough to have lower rates of seedling recruitment, as they also are not significantly different in juniper seedling recruitment compared to Control sites (figure 2*c*). Consistent with the negative influence of sound level on long-term juniper seedling recruitment, Noise treatment sites have lower juniper seedling recruitment than Control sites (electronic supplementary material, table S8*c*; figure 2*b*).

Observed species richness for all species and animal-pollinated species were not related to treatments (electronic supplementary material, table S9). Community turnover was significantly explained by treatment and Julian date for all species (electronic supplementary material, table S10*a*; table 1*b* and figure 3*a*) and animal-pollinated plants (electronic supplementary material, table S10*b*; table 1*a* and figure 3*b*), although pairwise differences were weaker for communities on noisy sites versus recently noisy sites for animal-pollinated species (electronic supplementary material, table S10*b*). Functional groups of animal pollinators show similar trends of treatment and Julian date (electronic supplementary material, table S10*c*; table 1*b* and figure 3*c*), with the largest differences between treatments between Noise and prevControl and prevControl to prevNoise (table 1*b*).

4. Discussion

Our results indicate that elevated sound level was negatively associated with seedling recruitment rates for both pinyon and juniper. Noise likely directly alters the community of seed-dispersing fauna for both of these trees, resulting in an observable decline in these foundational species. We also found that the differences in recruitment persist past the vulnerable seedling stage, at least for the seed masting pinyon. When reviewing the long-term history of treatment sites, formerly noisy sites that are now quiet (prevNoise) show significantly less pinyon recruitment compared to long-term quiet (Control) sites, while juniper seedlings appear to show some recovery. This suggests that there is a potential lag in re-establishment of formerly noisy areas by pinyon seed-dispersing fauna, but less of a lag for juniper dispersing fauna. Additionally, noise may have longer lasting effects on pinyon recruitment, as it is a masting species that produces seeds roughly only every 2–7 years [31], while juniper is not. Sites where acoustic conditions had changed from quiet to noisy (prevControl) did not show significantly lower rates of seedling recruitment, but it is possible these sites had not been subjected to noise long enough to show an effect. Additionally, we find differences in community composition across sound levels and among treatment types, suggesting that noise likely affects pollinator clades, with ecological cascades to the plants that depend upon them. A limitation of our study is that our results provide insights from two

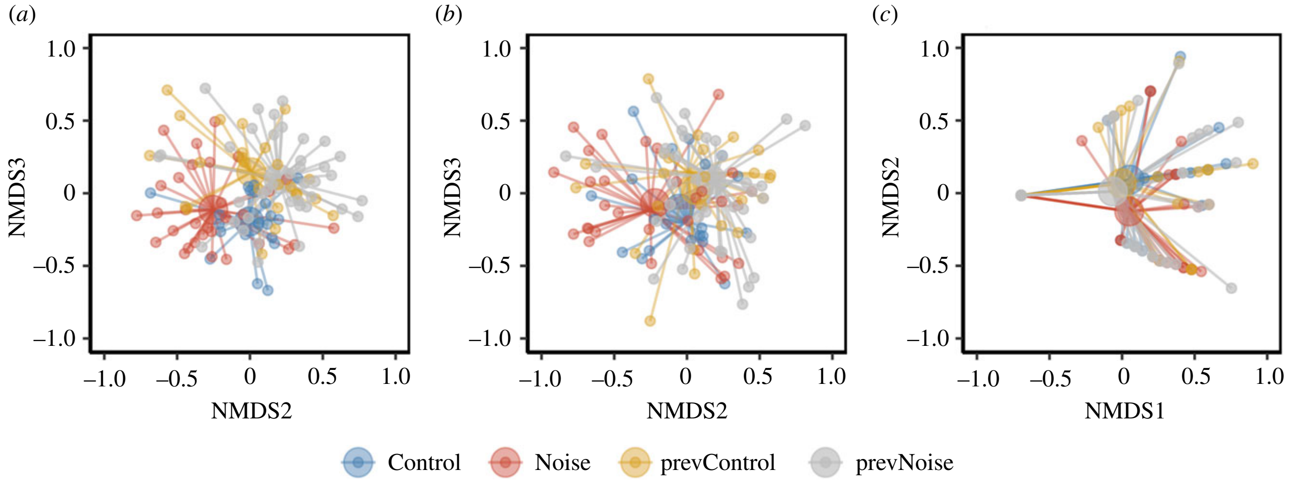

Figure 3. Ordispider plots in non-metric multidimensional scaling (NMDS) for the Bray–Curtis β-diversity provide an illustration of the dissimilarity in plant community composition among plots with different acoustic conditions: (*a*) all plant species ($k = 5$, stress = 0.117), (*b*) animal-pollinated species ($k = 5$, stress = 0.116) and (*c*) functional pollinator groups ($k = 5$, stress = 0.010). Only two of five axes shown for illustrative purposes. Each point represents a single plot and is joined with a line to ordination centroids for each acoustic condition. (Online version in colour.)

snapshots in time. A more nuanced understanding of the forces shaping changes in seedling recruitment and vegetation studies would come from long-term studies that can sample communities yearly. Annual sampling would also track the fate of individual seeds from source trees to establishment. Despite these caveats, our findings add to a limited pool of research regarding the consequences of noise exposure on species interactions [6–9,13] and suggest that noise influences long-term processes on an ecosystem and community level.

Our findings show pinyon and juniper seedling recruitment is negatively affected by long-term noise and changing noise regimes, which both confirms and extends patterns from short-term work conducted 12 years earlier on pinyon recruitment [13]. Based on our plot-level means, pinyon recruiting to noisy sites is only 24% of those recruiting to control sites. In more real-world terms, this translates into approximately 55 pinyon seedlings per hectare on control sites and only 13 on noisy sites. An equally stark difference was apparent for juniper seedling recruitment (29 and four seedlings per hectare on quiet and noisy sites, respectively). Both juniper and pinyon seeds are dispersed by animals, where seeds are often cached and survive to later germinate [32]. Pinyon seeds are adapted for dispersal by birds, including corvids such as jays [32], while juniper seeds are dispersed by frugivorous birds like Townsend's solitaire (*Myadestes townsendi*) [33] and mountain bluebird [34], as well as grey fox (*Urocyon cinereoargenteus*) and other mammals [32,35]. Previous research within this system has shown that mountain bluebirds avoid noise [16], as do Woodhouse's scrub jays [6], suggesting that reduced densities of these animal dispersers in noisy areas likely contribute to declines in pinyon and juniper recruitment. Although no research has investigated whether grey foxes avoid areas with noise, an aversion to noise by this key seed disperser could also help to explain the observed lower rates of juniper seedling recruitment. Ultimately, persistent lack of recruitment will result in far fewer mature individuals of these two foundational species in the long-term and produce notable consequences for the many species that depend on each within these woodlands [36].

Our examination of changing noise regimes supports the long-term patterns of noise affecting seedling recruitment. For both pinyon and juniper, Control plots had higher recruitment than Noise plots. Interestingly, for both species, previously quiet (prevControl) plots still show similar recruitment rates as Control, opposite to our predictions, which suggests that longer-term exposure to noise may be necessary to cause lower recruitment rates. In addition to avoidance by seed-dispersing animals, pinyon is a masting species [32] and juniper seed germination requires temperature stratification [37,38] likely contributing to a lag in the reduction of seedling recruitment. Pinyon masting events occurred in the region in 2015 [31] and winter 2018–2019, indicating that at least one masting event has occurred since possible noise removal between 2015 and 2017. Similarly, the winter of 2018–2019 was a wet, cold year after many years of drought and high temperatures in this region [31], likely resulting in ideal germination conditions to bring juniper seeds out of dormancy [38]. Contrasting our hypothesis that sites would recover from noise once it is removed because seed dispersers would return to previously noisy areas, we found that formerly noisy sites (prevNoise) show very low rates of seedling recruitment for pinyon. This suggests that effects of noise may persist and impede restoration of ecological function even after removal. The same apparent trend applies to juniper seedling recruitment, but the difference was not statistically significant. Given that pinyon is a masting species [32], our results could be affected by timing of masting events, where junipers yearly production of cones allows for faster recovery from noise pollution when compared with pinyon. Continued monitoring of these dynamic treatments will help to refine the timescales and spatial patterns needed for noise to affect seedling recruitment.

We expected pinyon seedling recovery to rebound after noise removal because Woodhouse's scrub jays have territories of 2 ha [39] and female dispersal distances of up to 5 km [40], which would allow for movement into formerly noisy areas. However, our results suggest a lack of seedling recruitment recovery. There are a number of reasons seed dispersers like jays may continue to avoid noise once it is removed. The lack of social cues for settlement or philopatry could slow movement back into previously noisy areas. Additionally, episodic memory may also keep older individuals from going back to an area they previously explored and encountered unfavourable conditions like high sound levels. The closely related California scrub-jay (*Aphelocoma californica*) have been shown to be capable of episodic-like memory in their ability to recall the spatial location, time of placement and the specific contents of their caches [41]. Furthermore, California scrub-jay's food caching behaviour exhibits sensitivity to conditions of cache-retrieval, with individuals quickly learning to avoid areas where their caches had been stolen [42]. In our study system, *Peromyscus* mice are known to remove seeds at higher rates on noisy sites [13], which may also discourage scrub jays from caching seeds near noisy wellpads. Additionally, episodic memory of the inability to communicate with conspecifics [1,43,44], inability to eavesdrop and prey upon nests of other species [6], or altered glucocorticoid levels [19,45] due to elevated perceived risk that is associated with hampered acoustic surveillance for threats [46–49] could increase the long-term avoidance of noise. Understanding to what degree episodic-like memory may contribute to patterns of habitat use and ecological interactions is an intriguing avenue for future research.

While there was no strong relationship between overall apparent species richness and sound levels or differences in overall apparent species richness among treatments for presence–absence richness data, for the 13 species where abundance data were collected, we found that plant communities become less even with increased noise exposure. One potential reason for an effect of noise on evenness, but not richness, can be explained by use of abundance data and presence–absence, respectively. The significant effect on noise on evenness, which contains abundance data in the diversity index, emphasizes the need for full botanical inventories rather than just presence–absence data to understand the broader ecological consequences of noise exposure. Several non-mutually exclusive explanations could explain patterns in evenness. The effects of seed dispersers avoiding noise and changing seedling recruitment of juniper and pinyon would contribute to the evenness of these species and could be occurring for other woody species. Additionally, more seed predation by *Peromyscus* mice in noise might reduce seed set in long-term noise sites [13]. Woody shrubs like mountain mahogany (*Cercocarpus montanus*), Utah serviceberry (*Amelanchier utahensis*) and bitterbrush (*Purshia tridentata*) may have less seed production in noise because of increased browsing by ungulates [50]. Furthermore, the whitish to yellow flowers of some of these shrubs are pollinated by insects, which are likely to be negatively affected by noise [5]. Future research is needed to parse out the complex mechanisms—direct or indirect—that cause long-term changes in species evenness across soundscapes.

Our study is the first to show that plant community composition (β-diversity) is affected by long-term and changing noise regimes. These patterns are strongest in the full dataset, which includes species with unknown pollinators and wind-pollinated species. There is also some evidence to suggest that pollinator type may influence patterns of β-diversity. Previously in our system, abundance of five different arthropod families decreased with noise level, as assessed by pitfall traps [5]. Wolf spiders (Lycosdiae) and grasshoppers (Acrididae) are two notable families that are negatively affected by noise that are known acoustic communicators [51,52]. However, arthropods that are typically thought of as pollinators—butterflies, moths, bees and flies—are not well captured by pitfall traps. We suggest that noise may discourage insect pollinators such as bees, beetles and flies because they communicate acoustically [53]. Although more research is needed to explicitly test this possibility [54], findings from other studies highlight how noise can negatively influence members of these groups: parasitoid flies are less able to acoustically orient towards their hosts in noise [8,9], and female crickets are unable to locate males in noisy conditions [55]. Thus, it is likely that many pollinators that communicate acoustically avoid noisy areas, causing broader ecological cascades through altered patterns of pollination. Noise-induced changes in pinyon–juniper woodland could similarly change insect abundances and community composition. Black-chinned hummingbirds (*Archilochus alexandri*), which tend to nest close to noise [13], likely as a predator shield from scrub jays [11], may also change abundances of the plants they pollinate, although larger survey samples are needed to determine whether this hypothesis is supported in this system. Our results show how community composition is beginning to separate after 3–15 years, and future surveys are needed to see if community dissimilarity strengthens with more time, and if pollinators are one of the driving forces behind changes in community composition.

5. Conclusion

A slow yet pervasive shift caused by noise in the basic vegetation community and stand structure of pinyon–juniper woodlands can have far-reaching impacts on numerous species that rely on this unique habitat. We provide initial evidence suggesting that seedling recruitment of foundational tree species is affected by long-term noise, which may have multiple cascading effects into the general community. Species such as pinyon have dispersers and/or a life-history strategy through seed masting that render them more sensitive to noise disturbance such that they may continue to experience negative consequences of noise even after it is gone. Juniper, while sensitive to noise, has a life-history strategy and/or dispersers that makes it more responsive to changes in acoustic conditions. Keystone avian seed dispersers and potentially pollinators appear to be directly affected by long-term noise and changing noise treatments, which indirectly changes both α and β-diversity of the pinyon–juniper community. Our study highlights the need for long-term research across taxa to fully comprehend the complex interactions between vegetative habitat, birds, insects and mammals, which can inform long-term management and conservation of diverse ecosystems.

Data accessibility. The data are currently submitted as electronic supplementary material.

Authors' contributions. J.N.P., S.E.T. and C.D.F. conceived the project. Fieldwork was conducted by S.E.T. and J.N.P. J.N.P. conducted the analyses. The manuscript was written by S.E.T., J.N.P. and C.D.F.

Competing interests. We declare we have no competing interests.

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