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Artificial light at night and anthropogenic noise alter the foraging activity and structure of vertebrate communities

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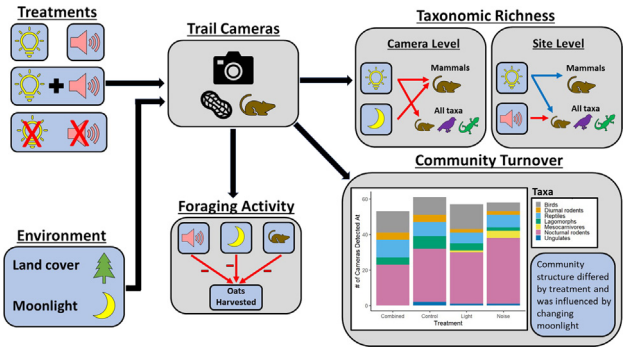
HIGHLIGHTS

- Artificial night-lighting had a scale-dependent effect on species richness.
- Noise negatively influenced richness but the addition of light mitigated this effect.
- Artificial light and moonlight most strongly influenced community structure.
- Noise and moonlight, but not artificial light, decreased the amount of oats removed.

GRAPHICAL ABSTRACT



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ABSTRACT

Light and noise pollution from human activity are increasing at a dramatic rate. These sensory stimuli can have a wide range of effects on animal behavior, reproductive success, and physiology. However, less is known about the functional and community-level consequences of these sensory pollutants, especially when they co-occur. Using camera traps in a manipulative field experiment, we studied the effects of anthropogenic light and noise, singularly and in tandem, on richness and community turnover at both the taxa and functional group level as well as foraging activity. We showed that both light and noise pollution did alter taxonomic richness and that these effects can differ depending on the scale of observation. Increases in light levels had a negative effect on richness at the camera-level scale, but light-treated sites had the highest pooled (i.e., cumulative) richness of all treatment types. In contrast, noise was found to have a negative effect on cumulative richness; however, when both stimuli were present, the addition of night-lighting mitigated the effects of noise. Artificial light and moonlight had the strongest influence on community turnover, and results remained consistent at both the taxa and functional group level. Additionally, increases in ambient noise and moonlight, but not artificial light, reduced foraging activity. Our study provides evidence that alterations to the sensory environment can alter the richness and composition of communities and that effects can be scale-dependent and also alter foraging behavior. Unexpectedly, the addition of artificial light may have mitigated the negative effects of noise on cumulative taxonomic richness. This highlights the importance of researching the consequences of co-exposure to these globally common pollutants.

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1. Introduction

Urbanization threatens biodiversity around the world (McKinney, 2008; Seto et al., 2012). In addition to loss and fragmentation of natural land cover, urbanization fundamentally alters the sensory environment via artificial night-lighting, anthropogenic noise, and other pollutants (Halfwerk and Slabbekoorn, 2015; Swaddle et al., 2015). Although the weight of evidence suggests that noise and light pollution have negative consequences for wildlife and their supporting ecological communities, substantial variation exists in species-specific responses to altered sensory environments (Dominoni et al., 2020b; Francis and Barber, 2013). For example, research involving ecological consequences of energy-sector noise found that Woodhouse's scrub-jays (*Aphelocoma woodhouseii*) strongly avoided noisy sites while both black-chinned hummingbirds (*Archilochus alexandri*) and house finches (*Carpodacus mexicanus*) nested almost exclusively in noisy areas (Francis et al., 2009). A recent meta-analysis revealed similar divergent responses among mammals to natural photoperiod regimes (reviewed in Prugh and Golden, 2014). Given species-specific variation in responses to these stimuli, at the community level noise and light pollution could act as environmental filters by excluding less tolerant species, reducing overall species richness and resulting in community homogenization. It is also possible that some species are able to exploit areas experiencing sensory disturbance through predator shielding, thus increasing overall species richness in these areas (Berger, 2007).

Previous research involving effects of light and noise on wildlife have focused primarily on behavioral responses, but changes to reproductive success and physiology have also received some attention, although most studies only investigated the effects of one of these stimuli (Du et al., 2010; Habib et al., 2007; Halfwerk et al., 2011; Kleist et al., 2018; Senzaki et al., 2020; Shannon et al., 2014). A number of studies have also examined how interactions among species change with alterations to light and noise regimes, how communities are structured, and whether light or noise influences patterns of species richness (e.g., Davies et al., 2012; Francis et al., 2009; Jung et al., 2020; Proppe et al., 2013; Schoeman, 2016). Most of these examples have focused on responses of a limited number of species. More importantly, however, the community-level consequences of co-exposure to noise and light have received almost no attention despite often co-occurring (Dominoni et al., 2020b). Community turnover, or beta diversity, is an index for the change in community composition of the community or the dissimilarity between communities. The effects of sensory pollutants on community turnover remain largely unexplored and, to our knowledge, the only study to evaluate community turnover resulting from the combined effects of light and noise evaluated winter bird community assemblages along urban gradients where many other human stressors that can influence bird distributions co-occur (Ciach and Fröhlich, 2017). As such, further research into the combined effects of light and noise pollution at the community-level is needed, especially through manipulative field experiments that eliminate or otherwise minimize the influence of confounding human stressors.

Studies investigating whether light and noise pollution influence patterns of species distribution or abundance provide valuable information about the effects of these stimuli, but may not capture the full range of responses. Past work has found that alterations to the sensory environment can result in reduced foraging activity, which, if persistent, could result in alterations to richness patterns and community structure (Bird et al., 2004; Farnworth et al., 2016; Le et al., 2019; Rabin et al., 2006). Thus, how independent and interactive exposure to light and noise pollution may affect foraging activity, and whether those effects can result in community-wide changes, remains an important area of research.

Here, we investigated if and how artificial night-lighting, anthropogenic noise pollution, and the combination of the two influenced species richness, community turnover, and resource harvesting among vertebrates in a mixed pinyon pine (*Pinus edulis*) - juniper (*Juniperus osteosperma*) woodland. We isolated the effects of light and noise in a unique study system in northwest New Mexico where we excluded or controlled for confounding factors often associated with these stimuli along urban gradients such as roads, human structures, and human presence, which were consistent across all of our sites. Previous work in this system took advantage of the presence of natural gas wells with and without noise-generating compressors to isolate the effects of noise (Francis et al., 2009, 2012; Kleist et al., 2018). We leveraged this unique system to explore exposure to noise and light by adding lights to both noisy and quiet sites to study the singular and combined effects of these stressors.

Our objectives were to use camera traps to investigate the effects of light and noise on 1) patterns of species richness, 2) alterations to community turnover, and 3) changes in foraging, measured as oat harvesting activity by granivorous mammals and birds. Because past studies found numerous negative effects of exposure to increased levels of either light or noise, species richness should decrease with experimental exposure to these stimuli when present alone (e.g., Bird et al., 2004; Ciach and Fröhlich, 2017; Clarke, 1983; Proppe et al., 2013). Additionally, potential additive or synergistic effects of co-exposure to light and noise may result in larger declines in species richness than either stimulus alone. Thus, we predicted that species richness measured at individual camera traps would decline with increases in noise and light levels and that species richness would be lowest with co-exposure to high noise and light levels. This pattern should also be apparent in terms of cumulative richness across treatment types, where quiet and dark sites would have the highest cumulative richness, sites exposed to noise and light together would have the lowest cumulative richness, and those exposed to noise or light alone would have intermediate levels of cumulative richness. For community turnover, because past work found a negative effect of both light and noise on richness, communities on sites where both stimuli are present should differ most strongly from communities on dark, quiet sites due to more sensitive species being excluded and species compositions becoming more homogeneous (Ciach and Fröhlich, 2017; Meyer and Sullivan, 2013; Proppe et al., 2013). Because some species are more sensitive to one stimulus than the other or even benefit from some amount of sensory disturbance, sites treated with only light or noise should have intermediate levels of community dissimilarity compared to control sites and those with both noise and light (Francis et al., 2011a; González-Bernal et al., 2016; Minnaar et al., 2015). For oat harvesting activity, because past work has found a negative effect of both elevated light and noise on foraging activity, locations exposed to increased amounts of light and noise should have fewer oats removed than control sites and, due to possible synergistic effects, sites exposed to both stimuli should have the fewest oats removed (Bird et al., 2004; Farnworth et al., 2016; Le et al., 2019; Ware et al., 2015).

2. Materials and methods

The study took place within the Rattlesnake Canyon Habitat Management Area (RCHMA) in northwestern New Mexico, an area consisting of mixed pinyon pine (*Pinus edulis*) - juniper (*Juniperus osteosperma*) woodland and great basin sagebrush (*Artemisia tridentata*) shrublands. Briefly, our sites were located at gas wells with and without noise-generating compressors. To some sites we added lights, creating a full-factorial study design with four treatments: light alone, noise alone, light and noise combined, and a dark, quiet control. Sites were grouped into six geographically distinct "clusters" to control for landscape-level variation in environmental variables. Each cluster contained one site of each treatment resulting in 24 sites total (Fig. 1a). Sites were a minimum of 375 m apart. [See Willems et al., 2021 for a thorough site description].

2.1. Artificial night lighting

We illuminated light-treated sites from March until August of 2018 and 2019. In March of each year, a total of five light towers were placed

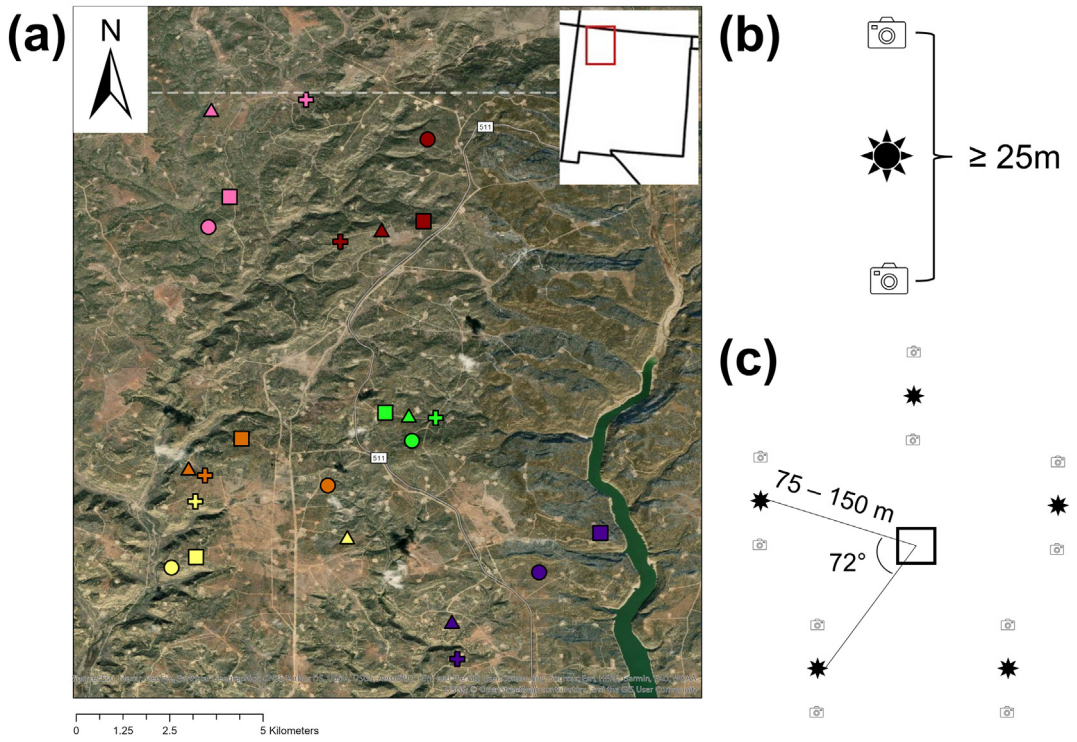

Fig. 1. (a) Overview of study area in the Rattlesnake Canyon Habitat Management Area (RCHMA). Inset shows location of the RCHMA in northwestern New Mexico. Each color indicates one of six separate clusters. Circles denote control treatment sites, squares denote noise treatment sites, triangles denote light treatment sites, and crosses denote combined treatment sites. (b) Camera trap array design at each sampling location (5 per site). At lit sites, the center point was established at pre-existing light tower locations (star). (c) Layout of trapping arrays at each site surrounding well pad (square). Distances not to scale.

at randomly assigned directions and distances spanning 75-150 m from the center of the sites' well pad for each of the six light-treated sites (30 towers total) and six sites exposed to noise and light (30 towers total). The well pad center was defined as the compressor location on noisy sites and the pump jack or wellhead location on quiet sites. Each light tower was constructed by attaching two 400-lm, white, 54 LED floodlights with 6 V/6 W solar panels to a 3 m metal pole. Lights were on during all nighttime hours (i.e., sunset to sunrise) for the duration of the study.

2.2. Camera deployment

Between 27 May and 25 June of the 2019 field season, Bushnell Trophy cameras (20-megapixel, no-glow infrared) were deployed at each cluster for 72 consecutive hours per camera. Once cameras were collected from one cluster, they were moved to the next until all clusters had been sampled. Ten cameras were deployed at each site (40/cluster) for a total of 720 camera trap days (i.e., 24 h) across the duration of the study. We set cameras to be triggered by motion and to take three images per trigger. At lit sites, cameras were placed ≥25 m apart near light towers (Fig. 1b). Mean distance from cameras to the closest light tower was 11.4 m (range = 1.3-25.8 m). At dark sites, the method of camera placement was replicated at locations 72 degrees from one another and located at random distances between 75 and 150 m from the center of the well pad, matching placement on lit sites (Fig. 1c).

We followed established protocols of using oats to gauge foraging activity (e.g., Leaver and Daly, 2003; Yunger et al., 2002). We initially baited cameras with ~20 g of rolled oats provided at the time of deployment. Cameras were checked 48 h after deployment and any remaining seed was collected and replaced with 8 g of oats. Cameras and any remaining oats were collected the morning after the third night as close to sunrise as possible. We analyzed all images manually and for each detection, the species of the animal, time of detection, and number of images per detection was recorded. This overall approach was designed to detect animals that consume grains, such as many small mammals and birds. However, it also provided detections for other animals, such as reptiles and insectivorous birds, which we included in subsequent analyses. Additionally, we were not able to reliably identify mice in the genus *Peromyscus*, woodrats in the genus *Neotoma*, or bluebirds in the genus *Sialia* to species, thus they were grouped by genus. Physical trapping conducted the same season suggests that the majority of *Peromyscus* mice present were pinyon mice (*Peromyscus truei*; 90% of captures) with some deer mice (*Peromyscus maniculatus*; 9% of captures) and brush mice (*Peromyscus boylii*; 1% of captures) present as well. Mexican woodrats (*Neotoma mexicana*) were the only species captured, although both bushy-tailed woodrats (*Neotoma cinerea*) and Stephen's woodrats (*Neotoma stephensi*) were also potentially present (Willems et al., 2021). Bluebirds were either Western bluebirds (*Sialia mexicana*) or mountain bluebirds (*Sialia currucoides*). We excluded from subsequent analyses detections where we were not able to identify an individual to species or the above-listed genera.

2.3. Oat harvesting

To quantify the amount of oats removed, we collected all the remaining oats upon camera collection after the third night of camera deployment (see above). The amount of oats harvested was calculated as the amount of oats remaining subtracted from the original weight that was deployed (8 g).

2.4. Noise and light measurements

We measured noise levels at each camera location using a Larson Davis 831 Type 1 Sound Level Meter. Care was taken to ensure the ambient noise level during measurements was representative of the overall noise environment and did not include atypical noise sources, such as airplane flyovers or high winds, that could increase measured noise levels. At each camera, we measured the sound level for one minute at

0.5 m above the ground as the A-weighted (LAeq) and *Z*-weighted (LZeq) equivalent noise level (L_{eq}, fast response, re. 20 μPa; Table A.1). Although longer or additional measurements would be ideal to characterize noise levels at each location, previous work suggests that short measurements adequately capture general ambient noise conditions in this system because they are highly repeatable (Kleist et al., 2018).

We measured light levels in lux at each light-treated camera location using a Konica-Minolta T-10A Illuminance Meter (Table A.1). Measurements were not taken at dark camera locations because light levels on moonless nights were below the unit's response minimum (i.e., 0.01 lx). As such, light levels of cameras at dark sites were assigned zero lux. All light measurements were taken at least one hour after sunset. For each measurement, the light meter was placed flat on the ground facing up. A three-second acclimation period was used before recording the lux value.

2.5. Land cover data

To account for the potential influence of land cover on species' presence and abundance, we obtained land cover classifications for each camera location from the 2016 U.S. National Land Cover Database (30 m resolutions) using the *extract* function in the 'raster' R package (Hijmans et al., 2019; Homer et al., 2015). All cameras were located in either mixed evergreen forest or shrubland land cover classifications.

2.6. Moon phase data

To account for potential effects of natural ambient light regimes on camera trap detections, we obtained continuous data on moon phase for each night that cameras were deployed using the 'lunar' package in *R* (Lazaridis, 2014). For each night, the moon phase was represented as the percent face of the moon. We used the 'suncalc' package in *R* to obtain daily sun and moon rise/set times (Thieurmel and Elmarhraoui, 2019). We then created a moonlight index as the proportion of night that the moon was above the horizon multiplied by the percent of the moon face visible each night. This moonlight index ranged from zero, which could represent either a new moon or moon below the horizon at night, to one, which represented a full moon in the sky for the entire night.

2.7. Data analysis

2.7.1. Taxonomic richness

We compared taxonomic richness using two approaches. First, we compared apparent camera-level richness (i.e., number of species observed at each camera) using generalized linear mixed-effect models. We initially constructed models to evaluate support for individual variables not directly pertaining to our main hypothesis (moon index, overnight temperature, date, land cover classification). We included parameters with apparent effects on the response in subsequent modelling. We then created two competing global models, one using our categorical treatment variable and one using our continuous, measured light and noise values, to determine which approach best fit the data. The treatment global model also included the interaction between treatment and moon index while the numerical global model included the interaction between light and noise as well as the interaction between light and moon index. We then used the *dredge* function from the package 'MuMIn' version 1.43.15 in R to select the best fitting models (Barton, 2019). These steps were repeated separately for total taxonomic richness and mammal richness.

Second, we used the *specaccum* function from the R package 'vegan' to create site-level and treatment-level (i.e., pooling all sites per treatment) rarefaction curves, which were not asymptotic (see below), suggesting undetected species remained (Oksanen et al., 2019). Because of the problems comparing richness across locations with incomplete sampling or different sampling effort, we also calculated cumulative richness estimates for each treatment (i.e., estimated number of species present across all pooled sites for each treatment) using first order jackknife and bootstrap estimators using the *specpool* function in the package 'vegan' (Gotelli and Colwell, 2001; Oksanen et al., 2019). For apparent differences in cumulative richness estimates among treatments, we used the degree to which the SE bars did or did not overlap to reflect the relative confidence in whether estimated cumulative richness was different between the treatments. These analyses were performed for all taxa combined and separately for all mammalian taxa. Camera-level models of total taxonomic richness and mammalian richness were under-dispersed; therefore, we used Conway-Maxwell Poisson error with the *glmmTMB* function from the 'glmmTMB' package in R for all camera-level analyses (Magnusson et al., 2020). We initially used control treatments as the reference for the treatment factor, but for well-supported models changed the reference state to other treatments to obtain all contrasts.

2.7.2. Community structure

We analyzed community turnover at the camera level in two ways: 1) by presence/absence of each taxa because individuals were unmarked and 2) by presence/absence of taxa pooled into broader functional groups (nocturnal rodents, diurnal rodents, birds, lagomorphs, reptiles, ungulates, and mesocarnivores). We quantified the extent of change in community composition between all possible pairwise comparisons with beta-diversity/dissimilarity indices (Anderson et al., 2011). Because analyses of beta diversity require communities of at least 1 species, 77 of 240 camera-trap locations, which had no detections, were removed from the analysis ($n = 163$). For each approach we ranked the binary versions of several dissimilarity indices (i.e., euclidean, manhattan, gower, altGower, canberra, clark, kulczynski, horn, binomial, jaccard, and bray) with the *rankindex* function from the 'vegan' R package to determine which index best captured the dissimilarities among treatments (Oksanen et al., 2019). We then used the *adonis2* function in vegan to perform PERMANOVA on the best-ranked index (Oksanen et al., 2019). For each of the two analyses (taxa level and functional group level) we created three models: 1) using the categorical treatment variable, 2) using the measured light and noise values with no interactions, and 3) using the measured light and noise values with an interaction between them. Each model also contained the land cover classification of the camera, average Julian date, and average moon index during camera deployment. We also included the cluster in which the camera was located as a random effect. Finally, we also performed an indicator species analysis using the *multipatt* function from the 'indicspecies' R package to characterize any associations among taxa or functional groups with specific treatments (Cáceres et al., 2020).

2.7.3. Oat harvesting

We used linear mixed-effects models to evaluate foraging activity as measured by the amount of oats harvested at each camera. We initially constructed models to assess the influence of variables not directly related to our main hypotheses (moonlight, overnight temperature, landcover classification) with the amount of oats removed as the response variable. As with richness mixed-effect models, parameters with apparent effects were included in the global models, which included one using the categorical treatment variable and one using the measured light and noise values. The treatment global model also included the interaction between treatment and moon index while the numerical global model included the interactions between moon index and light level as well as between light and noise levels. Oats harvested data were square-root transformed to meet normality assumptions. To investigate species-specific influences on oat harvesting, we also included the number of *Peromyscus* mice (which are primarily nocturnal) detections during the last night of deployment as an explanatory variable in each global model, as it was the only taxa with enough

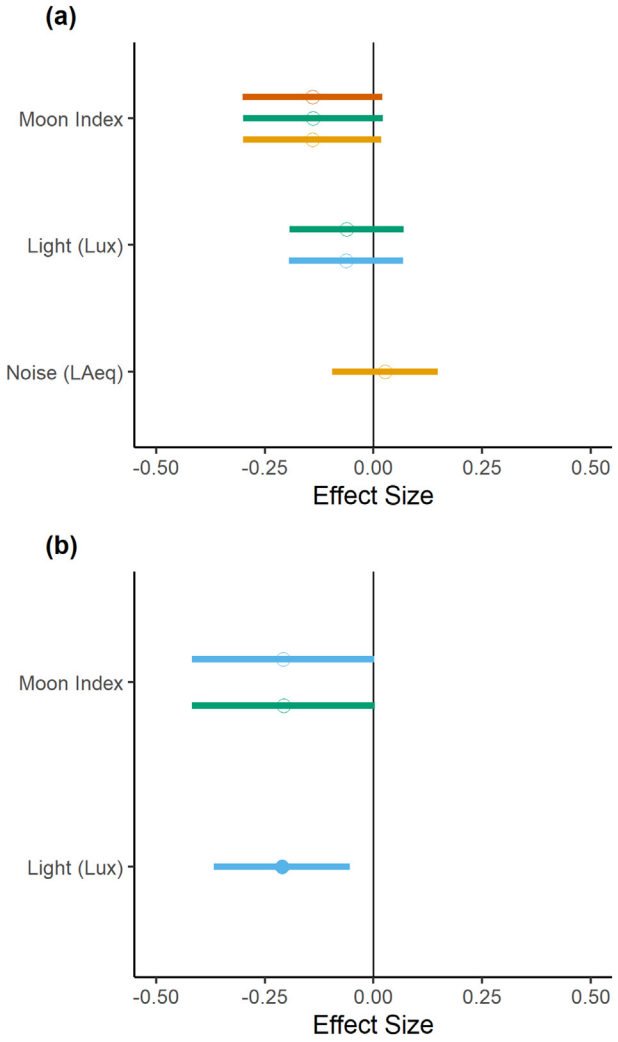

Fig. 2. Results of all top-ranked models (ΔAICc≤2) for apparent camera-level taxonomic richness for (a) total taxonomic richness and (b) mammal richness. Each color indicates a different model from Table A.3. For panel a, red = top-ranked model for total richness, green = second-ranked model, blue = third-ranked model, and yellow = fourth-ranked model. For panel b, blue = top-ranked model for mammal richness and green = second-ranked model. For all parameters, estimates and 95% CIs are shown. Solid circles indicate effects where 95% CI does not cross zero. See table A.3 for complete model ranking details.

detections during the resource harvest phase of deployment for formal analysis. We then used the *dredge* function from the package 'MuMIn' version 1.43.15 in R to select the best fitting models (Barton, 2019).

All analyses were performed using *R* (R Core Team, 2019). For all analyses, we use a more nuanced approach to reporting the strength and confidence of effects than the use of arbitrary thresholds with significance testing (Ferraro et al., 2020; Senzaki et al., 2020; Hurlbert et al., 2019). Specifically, we report all apparent trends with continuous variables and differences for categorical variables. Given their conventional use, we report 95% confidence intervals (95% CIs). Generally, we consider CIs that do not overlap zero to provide greater precision in the effect estimates. Similarly, the degree to which CIs overlap or are far from overlapping zero also reflects the precision of the estimated effect. For the PERMANOVA models, because 95% CIs are not reported, we adopt a similar nuanced approach in the interpretation of the p, R^2 and pseudo-F values. In the results, for models involving model selection, we report parameter estimates and confidence intervals from the top-ranked model in which that parameter appeared but also report other highly competitive models (i.e. ΔAICc≤2).

3. Results

Due to technical issues with some cameras (i.e. battery failure, memory card errors, etc), our final sample size was 685 camera trap days across 233 camera locations. In total, 5583 detections of 24 taxa were made across all cameras (Fig. A.1; Table A.2).

3.1. Species richness

For apparent camera-level total taxonomic richness, the top-ranked model contained only the moon index variable which had a negative effect on total richness, though the precision of the effect was low (β = -0.14, 95% CI = -0.30, 0.02; Table A.3; Fig. 2a). The null model including only random effects was also in the set of highly competitive models and no other variables had an effect on total taxonomic richness (Table A.3; Fig. 2a). For apparent camera-level mammal richness, increases in artificial light and moonlight caused comparable decreases in richness, but the precision of the effect was lower for artificial light than moonlight (artificial light; β = -0.21, 95% CI = -0.42, 0.003; moonlight, β = -0.21, 95% CI = -0.37, -0.05; Table A.3; Figs. 2b, 3).

Individual-based rarefaction and richness estimators both suggest that cumulative estimated richness was higher on light-treated sites than all other sites, with cumulative estimated richness on light sites nearly double that of noisy sites (Fig. 4a,b, Table A.4). Although noise-treated sites appear to have lower cumulative estimated richness than all other treatment types based on rarefaction and bootstrapped richness estimator,

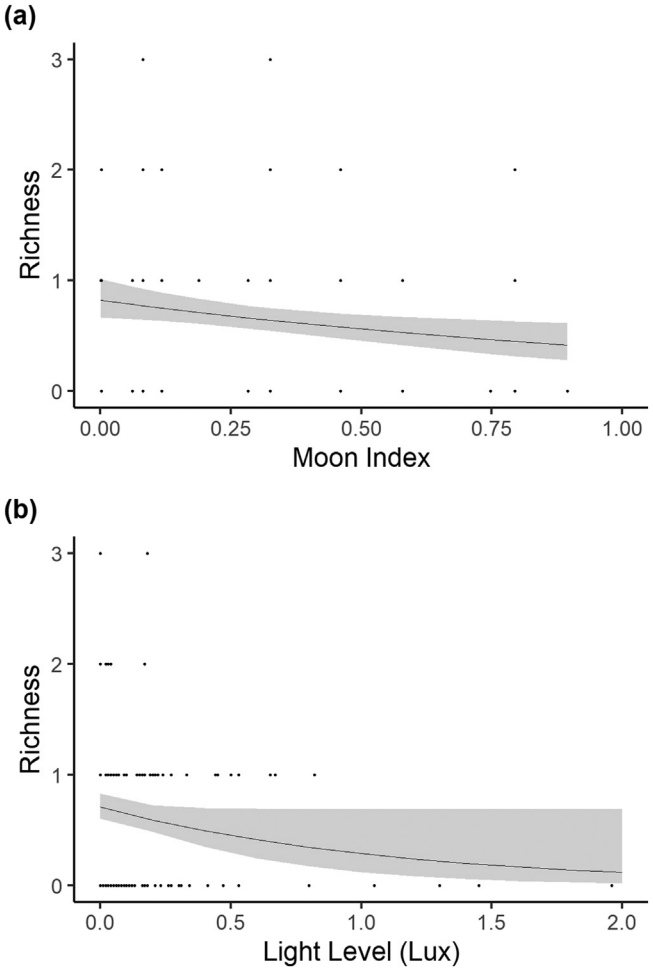

Fig. 3. Apparent camera-level mammal taxonomic richness decreases with (a) percent moon face, which reflects more natural ambient light and (b) artificial light level.

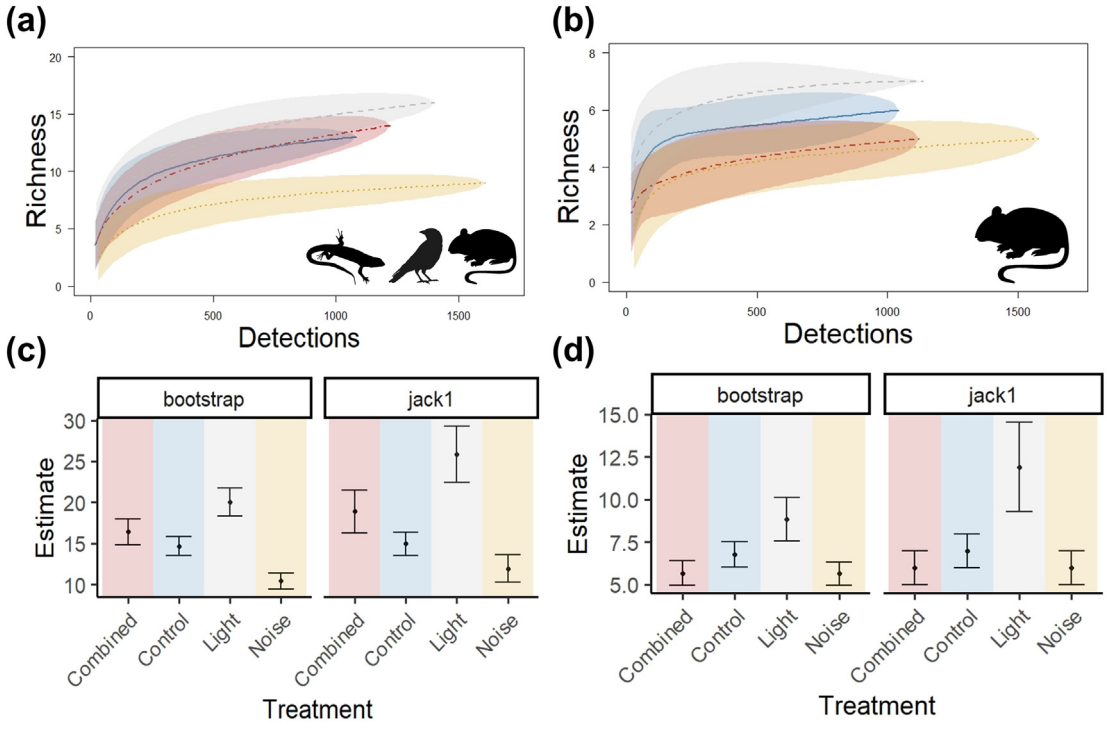

Fig. 4. Rarefaction curves and taxonomic richness estimates by treatment for all taxa (a,c) and mammals (b,d). For all panels, red is combined treatment, blue is control, grey is light, and orange is noise. In panel a long dashed grey line is light, solid blue line is control, dotted orange line is noise and the dot-dashed red line is combined. 95% confidence bands shown in panels a and b, standard error bars shown in panels c and d.

there was no difference between cumulative estimated richness on control and noise-treated sites using the jackknife estimator (Fig. 4a,b, Table A.4). Rarefaction and richness estimators also suggest that there were no differences in cumulative estimated richness between combined and control sites for either estimator (Fig. 4a,b, Table A.4).

For mammals, rarefaction curves and richness estimators suggest that light-treated sites had the highest cumulative estimated richness with all other treatments not differing from one another, with cumulative estimated richness on light-treated sites about 1.5 times higher than on noisy sites (Fig. 4c,d, Table A.5).

3.2. Community turnover

Community turnover analyses based on taxa-level and functional group level were highly consistent with one another. Specifically, treatment and moon index strongly influenced turnover in both analyses (Tables 1, 2; Fig. 5c). In the taxa analysis, there was some, but weaker, evidence for an influence of light or the interaction between light and noise on turnover. However, variation in light strongly influenced functional group turnover (Table 2). In both analyses, artificial light, moon index, and treatment influenced turnover, as did the interaction between light and noise for the taxa-level analysis, though there was no influence of noise for either analysis (Tables 1, 2, Fig. 5). There was also an effect of land cover on the functional group turnover, although the estimate of the effect was less precise (Table 2). For pairwise treatment comparisons for the taxa-level analysis, community composition was dissimilar between light and combined treatments

Table 1
Results of PERMANOVA for taxa analysis. Bolded variables denote those that warrant consideration for inference. The diversity metric for each model is listed as are the degrees of freedom, sum of squares, mean squares, F-statistic, partial R^2, and *p*-value for each variable.

Model	Diversity Metric	Variable	df	Sums of Squares	F Model	R^2	p
Light * Noise	altGower	**Light * Noise**	**1**	**0.435**	**1.672**	**0.010**	**0.131**
		Moon Index	**1**	**1.022**	**3.923**	**0.024**	**0.005**
		Landcover	1	0.263	1.010	0.006	0.365
		Date	1	0.235	0.901	0.005	0.484
Light + Noise	Gower	**Light**	**1**	**0.446**	**1.706**	**0.010**	**0.116**
		Noise	1	0.174	0.665	0.004	0.716
		Moon Index	**1**	**1.045**	**3.995**	**0.024**	**0.004**
		Landcover	1	0.248	0.946	0.006	0.410
		Date	1	0.234	0.896	0.005	0.501
Treatment	Gower	**Treatment**	**3**	**0.023**	**1.905**	**0.034**	**0.050**
		Moon Index	**1**	**0.021**	**5.183**	**0.031**	**0.001**
		Landcover	1	0.002	0.378	0.002	0.771
		Date	**1**	**0.011**	**2.654**	**0.016**	**0.039**

Table 2
Results of PERMANOVA for the functional group analysis. Bolded variables denote those that warrant consideration for inference. The diversity metric for each model is listed as are the degrees of freedom, sum of squares, mean squares, F-statistic, partial R^2, and *p*-value for each variable.

Model	Diversity Metric	Variable	df	Sums of Squares	F Model	R^2	p
Light * Noise	Jaccard	Light * Noise	1	0.110	0.448	0.003	0.749
		Moon Index	**1**	**1.027**	**4.159**	**0.025**	**0.011**
		Landcover	1	0.073	0.294	0.002	0.880
		Date	1	0.141	0.570	0.003	0.653
Light + Noise	Jaccard	**Light**	**1**	**1.119**	**4.547**	**0.027**	**0.006**
		Noise	1	0.051	0.207	0.001	0.939
		Moon Index	**1**	**1.049**	**4.263**	**0.025**	**0.010**
		Landcover	1	0.063	0.356	0.002	0.913
		Date	1	0.141	0.572	0.003	0.669
Treatment	Gower	**Treatment**	**3**	**0.245**	**2.438**	**0.043**	**0.029**
		Moon Index	**1**	**0.162**	**4.829**	**0.028**	**0.011**
		Landcover	**1**	**0.068**	**2.029**	**0.012**	**0.140**
		Date	1	0.061	1.825	0.011	0.167

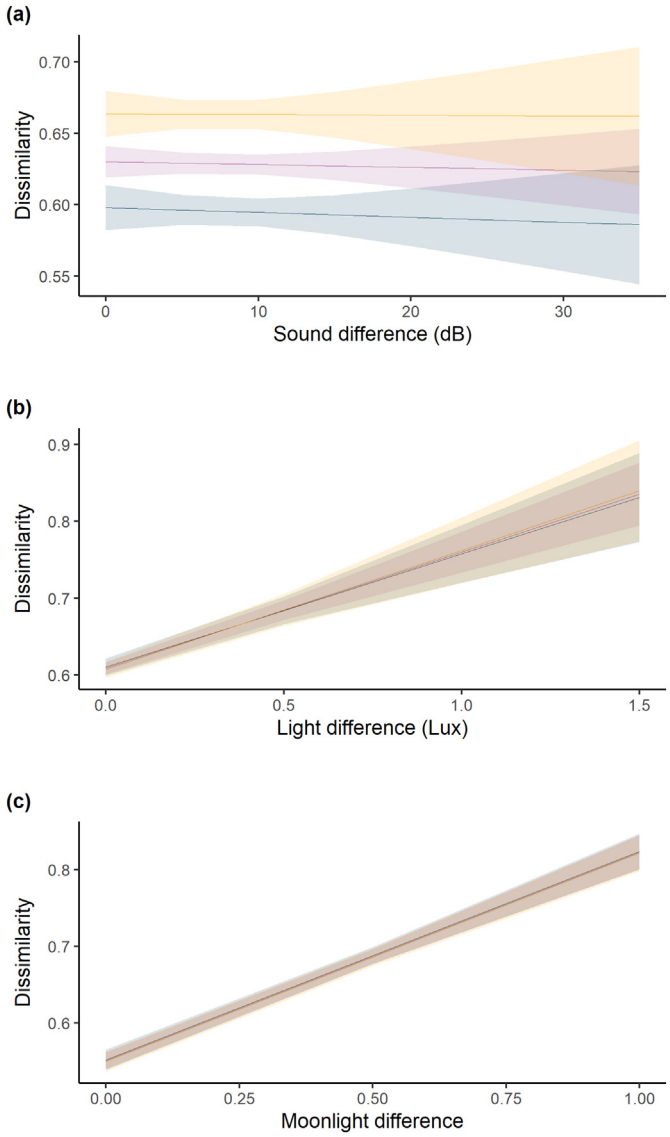

Fig. 5. Plots of environmental and community dissimilarity to help visualize results from PERMANOVA taxa-level analyses. X-axes reflect pairwise differences at individual cameras in sound level (a), light level (b) and average moonlight (c). Difference in sound had no effect in community dissimilarity (a) while increasing differences in both artificial light (b) and moonlight (c) resulted in increased community dissimilarity. For panel a, different color bands represent different levels of artificial light dissimilarity (blue, 0.00; pink, 0.13; yellow, 0.36). For panels b and c, different color bands represent different levels of noise dissimilarity (blue, 1.98; pink, 8.16, yellow, 14.33). For all panels, the altGower dissimilarity index was used. Trends for functional group dissimilarity analyses were nearly identical.

and control and noise treatments. Weaker evidence suggested that composition was also different between light and noise treatments. For the functional group analysis, only the communities on noise and combined treatments were dissimilar (Table 3).

For the taxa-level indicator species analysis, Woodhouse's scrub-jays (*A. woodhouseii*) were associated with light treatments (IV = 0.33, p = 0.011), wild turkeys (*Meleagris gallopavo*) were associated with combined treatments (IV = 0.38, p = 0.043), and grey foxes (*Urocyon cinereoargenteus*) were associated with noise treatments (IV = 0.27, p = 0.043). For the functional group analysis, birds were associated with control, light, and combined treatments (IV = 0.52, p = 0.035) and mesocarnivores were associated with noise treatments (IV = 0.27, p = 0.032).

Table 3
Pairwise comparisons of treatments from PERMANOVA analyses. Bolded variables denote those that warrant consideration for inference. The diversity metric for each analysis is listed as are the F-statistic, partial R^2, and p-value for each variable.

Analysis	Diversity Metric	Comparison	F Model	R^2	p
Taxa Pres/Abs	Gower	Control – Light	1.295	0.016	0.297
		Control – Noise	**2.763**	**0.032**	**0.051**
		Control – Combined	1.441	0.018	0.255
		Light – Noise	**1.902**	**0.024**	**0.123**
		Light – Combined	**2.871**	**0.039**	**0.031**
		Noise – Combined	1.685	0.022	0.174
Functional Group Pres/Abs	Gower	Control – Light	0.603	0.007	0.596
		Control – Noise	1.699	0.020	0.228
		Control – Combined	0.924	0.012	0.434
		Light – Noise	1.724	0.021	0.192
		Light – Combined	1.193	0.016	0.368
		Noise – Combined	**3.790**	**0.046**	**0.022**

3.3. Oat harvesting

The top-ranked model explaining the quantity of oats removed contained the measured noise level, moon index, and number of *Peromyscus* mice detections (Table A.6). Both noise (β = -0.02, 95% CI = -0.04, -0.01; Table A.6; Fig. 6a) and moon index (β = -0.99, 95% CI = -1.55, -0.43; Table A.6; Fig. 6b) had negative effects on the amount of oats removed even while accounting for the number of visits by the taxa responsible for most of the oat removal (*Peromyscus* β = 0.03, 95% CI = 0.03, 0.04; Table A.6; Fig. 6c). The measured light level was also included in the top-ranked model set but did not have any apparent influence on resource removal (β = -0.02, 95% CI = -0.47, 0.31; Table A.6). To verify that the relationships between oat removal and moon and noise levels were not the result of changes in the number of visits by *Peromyscus*, we created a post-hoc model with the number of *Peromyscus* detected as the response variable and measured noise value and moon index as predictor variables. From this model, increasing moon index had a negative effect on the number of *Peromyscus* detected though the precision of the estimate was lower (β = -8.51, 95% CI = -17.07, 0.04; Fig. 6d) while the measured noise level had no effect (β = -0.08, 95% CI = -0.36, 0.21), thus oat removal appears to decline with noise independent of *Peromyscus* foraging visits.

4. Discussion

Evidence for the effects of noise and light pollution are growing (Dominoni et al., 2020b; Swaddle et al., 2015), but to our knowledge, no study has examined the combined effect of both on vertebrate community turnover in an experimental context. Results from our manipulative field experiment demonstrate that both artificial night-lighting and anthropogenic noise can alter taxonomic richness and community turnover. They also show that these effects can differ depending on the scale of observation and that their combined influence can result in unexpected patterns. Our results partially matched our predictions that both light and noise would negatively affect taxonomic richness, such that noise had a negative effect on richness for some taxa whereas light had a positive effect for others. Increased light levels had a negative effect on richness at the camera level, but light-treated sites had the highest estimated cumulative richness. For community turnover, artificial light and moonlight most strongly influenced community composition at both the taxa and functional group level. Increased artificial noise and moonlight, but not artificial light, were found to decrease oat harvesting, partially matching our predictions. Despite this evidence of the effects of sensory pollution, some of the specific details of our study area and design should be kept in mind when interpreting our results.

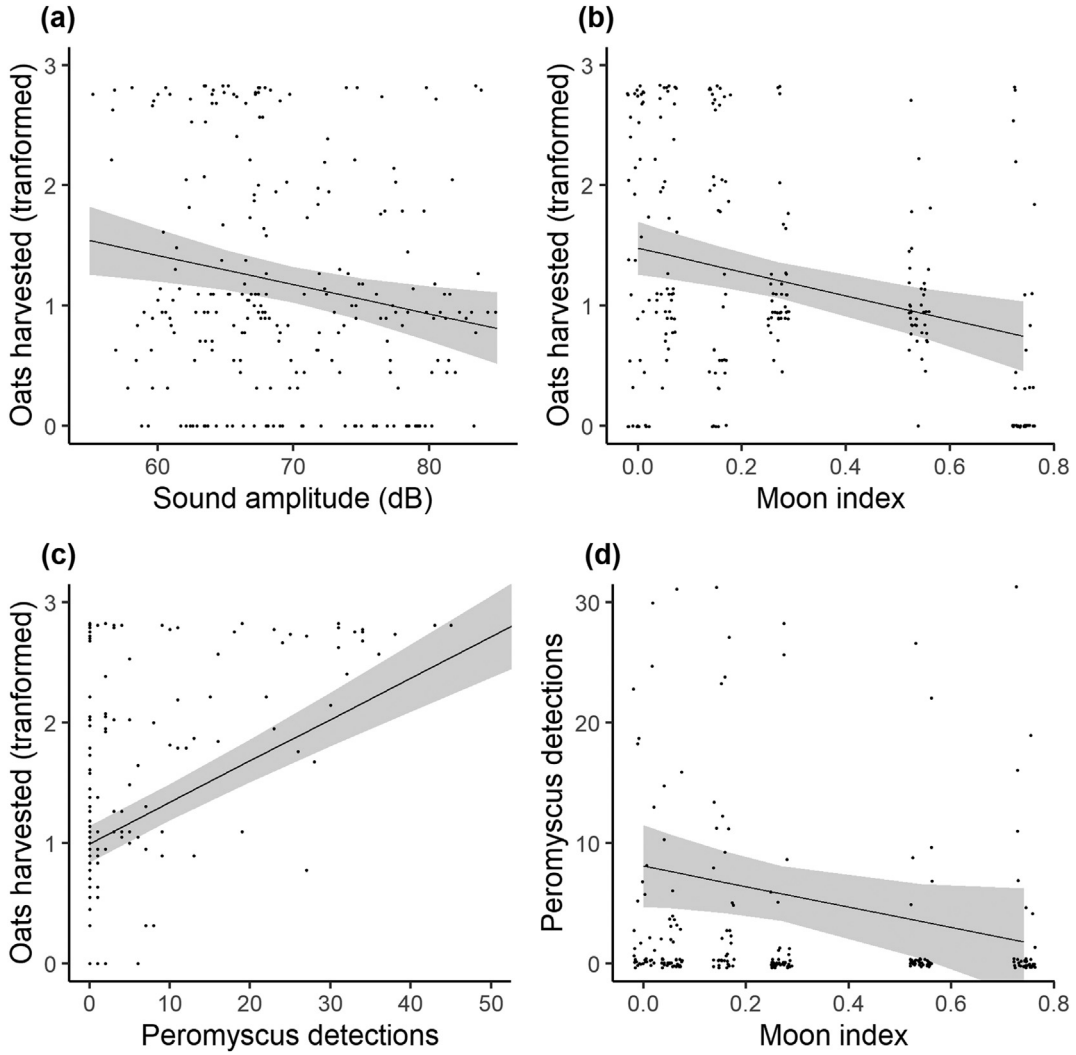

Fig. 6. Effect of a) artificial noise, b) moonlight, and c) Peromyscus detections on oat harvesting and d) effect of moonlight on Peromyscus detections from the post-hoc model. Oats harvested data (panels a-c) have been square-root transformed.

In RCHMA, artificial noise had been present for a long period of time whereas artificial light had only been present for two months and during the previous spring and summer. Therefore, it is possible that we measured responses to these two stimuli at different points along the response/habituation gradient if responses do indeed change over time with exposure to these stimuli. For noise, recent research in our system documents a persistent, and long term, reduction in the recruitment of pinyon pine trees with noise exposure (Phillips et al., 2021). This pattern suggests that animals that disperse pinyon pine seeds do not eventually habituate to noise exposure over the long term (i.e., decade scale). Of course, it is also possible that longer term exposure is needed to document the full consequences to animal communities where reductions in abundance could play out via demographic processes rather than behavioral responses. Longer term studies of how animal responses to sensory pollution change over time will provide insights on potential habituation, but also provide key data that may help separate behavioral and population-level responses. It is also important to note that by using oats as bait, we were targeting small, granivorous species, such as small mammals and some birds. As such, there will be some bias in the data against species that would not be attracted to oats, such as carnivores and insectivorous birds – although there is no reason to believe such biases would systematically vary with sensory conditions. Future camera trapping studies are needed to gather data that more accurately represents the entire community.

4.1. Community richness

For both total and mammalian richness, we found a negative effect of light on apparent richness at the camera level, which matched our prediction. Increases in artificial night lighting can have a wide range of negative effects including increased predation risk and reduced foraging behavior, which could cause animals to avoid areas that are most brightly lit (Bird et al., 2004; Blubaugh et al., 2017; Clarke, 1983). Despite potential negative effects of increased night-lighting, comparisons of observed and estimated cumulative taxonomic richness across treatments revealed higher taxonomic richness on light-treated sites for both mammals and all taxa combined.

There are no simple explanations for the difference in camera-level apparent richness and cumulative estimated richness, but they could potentially result from a combination of responses, such as avoidance of the brightest conditions and attraction to low light areas for foraging. Increased levels of artificial night lighting have been shown to attract insects (reviewed in Owens and Lewis, 2018; Stewart, 2021) and insects were observed in high densities surrounding our lights at night (J.

Willems, personal observation). Additionally, a number of insectivorous taxa take advantage of this phenomenon, including bats, spiders, and toads, although foraging in brightly lit areas does not always increase foraging efficiency (González-Bernal et al., 2016; Heiling, 1999; Jung et al., 2020; Minnaar et al., 2015; Yuen and Bonebrake, 2017). There is also evidence that increased night lighting can lead to temporal niche expansion among diurnal species, allowing them to forage under lit conditions during nighttime hours (Amichai and Kronfeld-Schor, 2019; Leveau, 2020). This combination of increased prey abundance and/or density along with the potential for increased foraging time per day under dim lighting conditions could lead to greater foraging success and/or efficiency for species occurring in areas experiencing increased levels of light at night. Thus, it is possible that a tradeoff between the negative effects of increased light, such as increased predation risk and sleep disruption, and the positive effects of increased food resources or extended activity time in dim light could explain why we found lower richness at the cameras under the brightest artificial light conditions but the highest cumulative richness at light treatment sites (Clarke, 1983; Raap et al., 2015). These results highlight the importance of not only considering scale of observation when investigating the effects of sensory pollutants, but also of weighing both positive and negative outcomes of exposure to these stimuli.

Although we found evidence for a negative effect of noise on cumulative richness, the addition of light seems to act as a rescue effect because cumulative estimated richness at combined sites was greater than that of noise alone sites for both richness estimators. It is possible that the addition of light could serve to offset some negative effects of increased levels of noise. As discussed above, the presence of increased invertebrate food resources and/or increased foraging opportunities due to an increased effective daylength at lit sites could offset the negative effects of increased background noise for many species. Supporting this possibility, there is some evidence that alterations to the natural light-dark cycle dominate or override behavioral alterations to acoustic regimes. A recent lab-based study with great tits (*Parus major*) found that individuals exhibited similar behavior patterns when exposed to both light and noise as individuals who were exposed to only light (Dominoni et al., 2020a). Finally, the lack of a scale-dependent response to noise such as that observed for light could be due to the fact that, in our study system, light levels attenuated at much shorter distances than did compressor noise. This resulted in considerable heterogeneity in light levels at sites treated with light. Sites surrounding compressors experience a gradient in sound levels, but levels remain well above ambient levels until at least 350 m from compressors (Francis et al., 2011b). Future research should focus on the relative role of spatial heterogeneity in noise and light exposure that may permit individuals to exploit benefits provided by these stimuli, such as increased prey densities and extended foraging time, but still avoid deleterious effects, such as sleep disruption and hormone dysregulation (Amichai and Kronfeld-Schor, 2019; González-Bernal et al., 2016; Jung and Kalko, 2010; Kleist et al., 2018; Raap et al., 2015).

4.2. Community turnover

In addition to changes in richness, we found that alterations to the sensory environment changed community composition. Analyses of both approaches we used to quantify beta-diversity (i.e., turnover in taxa presence/absence, functional group presence/absence) revealed community dissimilarity. For both analyses, we found differences in artificial light levels and moonlight to explain community turnover. Altered communities due to illumination is supported by past studies that found divergent responses of nocturnal species to changing levels of illumination from moonlight and from our own finding of community turnover with moon index (Kronfeld-Schor et al., 2013; Prugh and Golden, 2014). Many organisms are strongly influenced by both daily and seasonal light-dark cycles and high levels of artificial light at night could serve to override or mask these natural cues (Kronfeld-Schor et al., 2013). Species are known to respond differently to changing levels of moonlight with some reducing activity during the brightest phases and others increasing activity (reviewed in Prugh and Golden, 2014). As such, any disturbance of natural moonlight cues by light pollution could have significant effects on activity patterns, species interactions and, ultimately, community structure. Our results also indicate that animals living in habitats experiencing increased levels of both anthropogenic noise and light could experience some benefits from these sensory disturbances, which could help to, at least temporarily, offset the negative effects of increased noise levels. Clearly, more work is needed to understand whether such offsets are widespread where noise and light exposure co-occur.

Noise treatment sites tended to have the lowest cumulative estimated richness and were most dissimilar from all other treatments in terms of community composition based on the taxa analysis. This is in contrast to our prediction that control and combined sites would be most dissimilar. Species are known to show differing sensitivities to noise pollution, which could allow certain species to be more resilient to acoustic disturbances than others. One such example is that bird species with lower frequency vocalizations have been found to be more sensitive to anthropogenic noise pollution, likely due to masking of important intraspecific cues (Francis et al., 2011a). Alterations to the acoustic environment have also been shown to alter the ways in which species interact, which could lead to the reduction or exclusion of some species from areas with high amounts of sensory disturbance. For example, previous work in this system found that the avoidance of noise by Woodhouse's scrub-jays (*A. woodhouseii*), an important nest predator, led to increased nest success of songbirds in noisier areas (Francis et al., 2009). However, the authors also found that both black-chinned hummingbirds (*A. alexandri*) and house finches (*Carpodacus mexicanus*) were strongly associated with noisy sites (Francis et al., 2009). These sorts of species-specific responses to alterations of the acoustic environment could explain why we found that noise treatment sites differed in community composition from other treatment sites. The differences among noise-treated sites could also reflect that noise has been part of these landscapes for many years, but our light treatments had been in place for only two years. However, the addition of light to noisy sites appears to lead to different patterns of richness and community composition suggests that animal communities may change relatively quickly with changes in sensory conditions.

4.3. Oat harvesting activity

Our results not only reveal an influence of noise and light on the composition of animal communities, but that the sensory environment also alters food harvesting rates within taxa, implying a change in foraging behavior by the primary taxa responsible for oat removal. Even after accounting for the number of detections of *Peromyscus* at each camera, increased noise resulted in fewer oats removed, as did increases in moonlight, thus the response cannot be attributed to changes in the frequency of visits by this taxa and appear to represent a functional response to these stimuli rather than a numerical response. Ambient noise has repeatedly been shown to increase visual vigilance at the expense of foraging, presumably in response to elevated perceived risk with compromised surveillance through passive listening (Le et al., 2019; Rabin et al., 2006; Shannon et al., 2014; Ware et al., 2015). Thus, rather than reducing the number of visits to resource patches in response to elevated noise, individuals spent less time foraging per visit, reducing the overall amount of oats removed during the exposure period. If this pattern reflects broader *Peromyscus* foraging activity, it could explain the negative relationship between noise exposure and body condition for this species earlier in the season (Willems et al., 2021).

Past studies have found a reduction in small mammal activity in response to increased ambient light levels, which is likely due to increased foraging success of visually-oriented predators under bright conditions

(Bird et al., 2004; Clarke, 1983; Sone, 2002). A reduction in activity due to a greater level of perceived risk on nights with more moonlight could explain why less oats were removed on more brightly lit nights. However, we did not observe the same response to increased levels of artificial light. We previously found that pinyon mice reduced their activity in response to elevated levels of artificial light (Willems et al., 2021). Therefore, we expected to find a reduction in oat harvesting in more brightly lit areas, which was not the case. There is no clear explanation for these differing responses. Perhaps changes in community structure in response to increased artificial light altered species interactions in a way that resulted in no net change in oat harvesting with increasing levels of artificial light. For example, we found that Woodhouse's scrub-jays, a species we observed harvesting oats, were associated with lit sites. If Woodhouse's scrub-jays, or other less light-sensitive species, did in fact harvest more oats on brightly lit sites this could explain why we observed no effect of artificial light on overall oat harvesting despite previously finding a reduction in *Peromyscus* activity under brightly lit conditions. Future work is needed to investigate how sensory pollution potentially alters species interactions.

4.4. Conclusion

Our results provide evidence that alterations to the sensory environment from artificial night-lighting and anthropogenic noise pollution can have effects on taxonomic richness, community structure, and foraging activity. Our results documenting oat removal suggest that the functional influence of a species within the community can change in response to sensory conditions via behavioral changes, but we also documented influences of both noise and light on community structure. Counter to our expectations, multiple lines of evidence also suggest light exposure may offset the negative effects of noise on community richness and structure. We also found that the effect of light pollution on richness was scale-dependent, with increased light levels having a negative effect on apparent richness measured at the camera level but a positive effect in terms of cumulative estimated richness across all light-exposed sites. These results highlight both the need to continue research into the combined effects of light and noise pollution at the community level and the importance of considering scale when investigating sensory disturbances. Because the intensity and spatial extent of sensory disturbances from human activities will continue to increase, understanding how natural systems respond to the singular and combined influence of these novel stressors will be critical to ongoing management and conservation efforts.

Credit authorship contribution statement

JSW, JNP and CDF conceived the ideas and designed methodology; JSW and JNP completed fieldwork; JSW and CDF analyzed the data; JSW and CDF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

Data supporting this paper is available as supplementary files.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150223.

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