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Direct and indirect effects of noise pollution alter biological communities in and near noise-exposed environments

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Noise pollution is pervasive across every ecosystem on Earth. Although decades of research have documented a variety of negative impacts of noise to organisms, key gaps remain, such as how noise affects different taxa within a biological community and how effects of noise propagate across space. We experimentally applied traffic noise pollution to multiple roadless areas and quantified the impacts of noise on birds, grasshoppers and odonates. We show that acoustically oriented birds have reduced species richness and abundance and different community compositions in experimentally noise-exposed areas relative to comparable quiet locations. We also found both acoustically oriented grasshoppers and odonates without acoustic receptors to have reduced species richness and/or abundance in relatively quiet areas that abut noise-exposed areas. These results suggest that noise pollution not only affects acoustically oriented animals, but that noise may reverberate through biological communities through indirect effects to those with no clear links to the acoustic realm, even in adjacent quiet environments.

1. Introduction

Expansion of transportation networks, urbanized areas and industry have created evolutionarily novel acoustic conditions across every ecosystem on Earth. As such, a burgeoning research focus seeks to understand how altered acoustics owing to anthropogenic noise affects wildlife [1–5]. Substantial evidence suggests that noise alters a variety of behaviours in animals such as acoustic communication, foraging, vigilance and movement [6–9] and a smaller body of evidence has documented noise-induced changes to animal physiology, fitness, population dynamics and ecosystem functioning [10–15]. Despite this progress, key questions remain poorly understood, especially how noise alters components of biological diversity such as species richness, abundance and composition [5] and how community-level responses to noise manifest with increasing distance from noise sources.

A few previous studies have demonstrated that noise alters species richness, abundance and community composition in several taxa including birds [16–20], fishes [15] and frogs [21]. However, because these studies focus only on a specific taxon, and species within a taxon tend to interact with their environment through similar sensory modalities, our understanding of how a broader suite of organisms within a community respond to noise is limited. Differences in primary sensory modalities and other biological traits probably influence how and why particular taxa respond to noise [5]. For example, avoidance responses to noise may be more rapid in taxa capable of higher mobility, such as birds, than in those with lower mobility, such as many ground-dwelling insects. Furthermore, because noise can directly affect organisms via several mechanisms, such as acoustic masking, distraction and aversive effects [22–24], noise should have
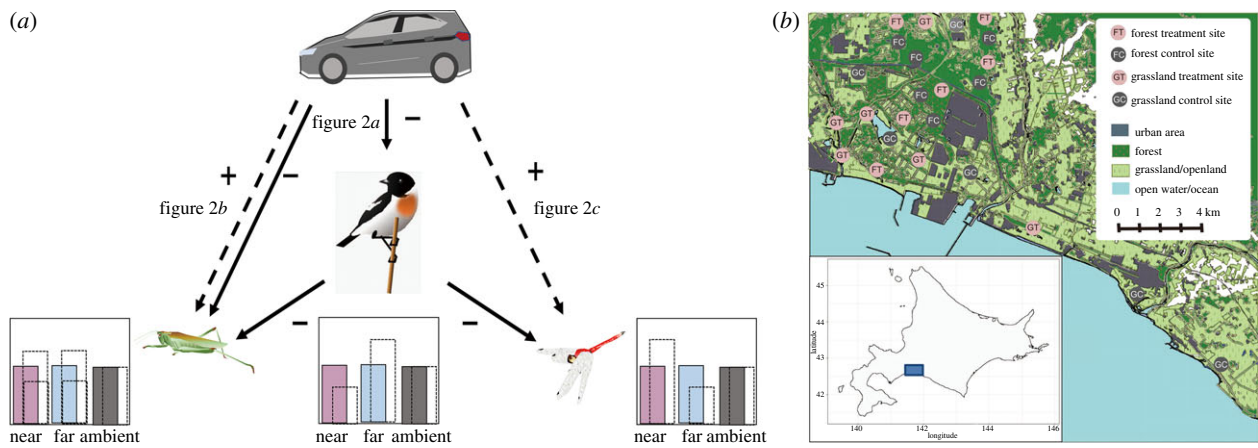
Figure 1. (a) Study design and expectations at near- and far ranges to phantom road and at ambient condition. Solid and dashed arrows indicate expected direct and indirect effects of noise, respectively. The plus and minus signs also indicate positive and negative effects of noise, respectively. These arrows and signs represent hypothesized responses in areas with the greatest noise exposure (near range). Unfilled dashed bars show hypothetical responses of each taxon during noise playback, while filled bars show theoretical conditions before playback. Observed direct and indirect effects of noise in figure 3 are also indicated on the corresponding lines. (b) Study region and sampling sites. (Online version in colour.)

stronger direct impacts on animals with, as opposed to without, auditory receptors. However, non-auditory animals may also be directly affected by substrate-borne vibrations caused by noise [25]. Thus, examining how different taxa with varied biological traits and links to the acoustic environment respond to noise within a single study system is critical to better understand the community-level influences of noise pollution.

Direct effects of noise on acoustically oriented taxa are typically negative and well documented in the literature [9,10,17]. However, biological communities in natural systems may show more complex responses to noise than expected from direct effects on acoustically oriented taxa through indirect effects that cascade through communities [12,16]. For example, well-documented avoidance of noise by mobile animals such as birds [17,18] could increase their distributions and abundances in nearby, quieter less-disturbed areas. These distribution changes may not only change interactions, such as predation on arthropods, in noise-exposed areas, but also in less-disturbed areas with higher bird abundance. Importantly, these indirect effects may affect organisms without auditory receptors (e.g. some arthropods, plants). Therefore, the indirect consequences of noise exposure may not only affect organisms exposed to altered acoustic regimes, but also organisms with no clear link to the acoustic environment in quiet areas abutting noise-exposed areas.

Here, we experimentally applied a field-placed noise playback manipulation and quantified the influence of noise exposure on three taxonomic groups (birds, grasshoppers and odonates) from different trophic levels and varying mobility and dependence on the acoustic realm. Birds generally rely on the acoustic environment throughout their life for communication, foraging and habitat selection [26–28]. Grasshoppers also rely upon acoustic signals and cues for mating and predator detection [29,30]. Odonates have no auditory receptors [31,32]. Among these, birds have a higher trophic position and mobility than the other two taxa. Grasshoppers and odonates are preyed upon by many birds and other predators such as small mammals, and their behaviour can change with predation risk [33,34]. Because animal movement speed is generally higher in birds than arthropods and in flying animals than non-volant, ground-dwelling animals [35], we assumed mobility of our focal taxa declines from birds to

odonates to grasshoppers. Thus based on their relationships to the acoustic environment, we might expect noise to have direct negative effects on bird and grasshopper distributions and abundance by interfering with their ability to interact with their environments acoustically, but odonates would be unaffected. Furthermore, we would expect that grasshoppers would respond less strongly than birds owing to their lower mobility and potential release from predation from birds owing to noise exposure (figure 1). Thus, with both direct and indirect pathways by which noise can influence grasshoppers, we could potentially determine which pathway is stronger. Odonates might also increase in noise-exposed areas avoided by birds and other predators owing to benefit from predation release and movement of individuals from areas with higher predation risk (figure 1). Such responses in odonates, if detected, would provide strong evidence of indirect effects of noise. Furthermore, if noise displaces acoustically oriented taxa, such as birds, to nearby areas with lower noise exposure, we might expect that grasshopper and odonate abundance decrease relative to comparable quiet areas owing to heightened predation (figure 1).

In a large natural landscape of forests and grasslands in northern Japan, we established a 'phantom road' experiment at 12 treatment sites with an 80 m 'phantom road' and 12 control sites (figure 1). The phantom road approach experimentally creates traffic noise, which is the most ubiquitous source of anthropogenic noise [1], and thereby enables us to separate the effects of traffic noise from those of other confounding factors associated with roads, such as altered vegetation structure, moving vehicles and emitted light [17]. In each study site, we sampled the focal taxa intensively both before and during playback in two distinct areas. For noise treated sites, we sampled those near the phantom road with high noise levels and those far from the phantom road that experienced relatively low noise levels (henceforth, near and far range, respectively). For control sites, we applied the same sampling procedure and sampled near and far from equipment deployed to control for the presence of novel objects (figure 1). In doing so, we were able to quantify the impact of noise exposure on each taxon in a modified before-after-control-impact design, permitting not only comparisons to untreated control sites, but also potential shifts in abundance in noise treated near
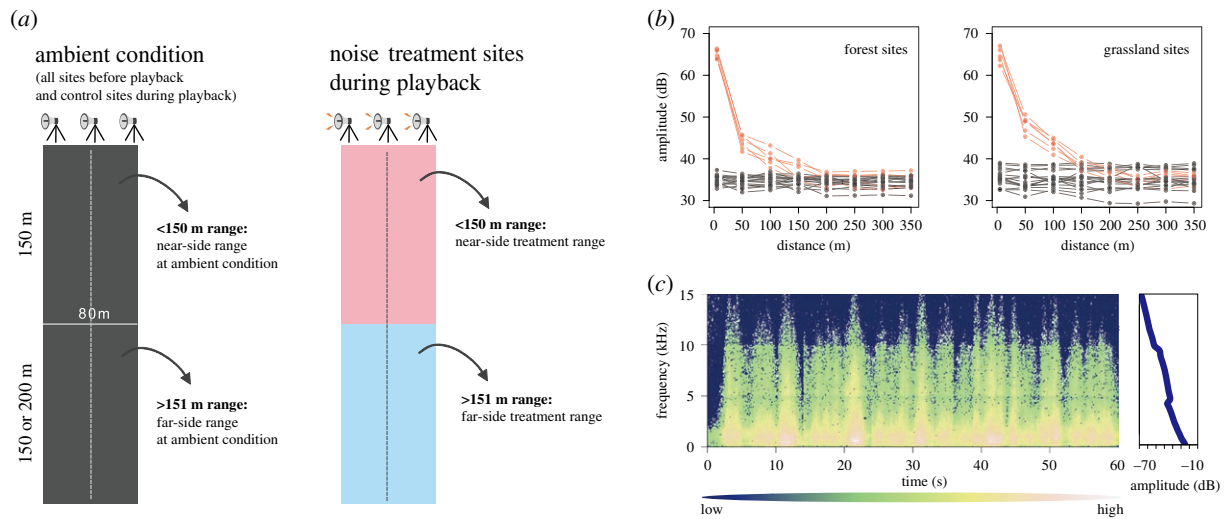
Figure 2. (a) Sampling procedures of our playback systems. Dashed lines indicate survey routes. (b) Relationship between noise amplitude and distance from the speakers broadcasting traffic noise. Squares represent noise attenuation at treatment sites during playback and circles at control sites plus treatment sites before playback. (c) An example of a traffic noise file used in the playback experiment. (Online version in colour.)

and far sites owing to movements away from the phantom road or changes in the intensity of predation. In this study, we specifically tested the following two hypotheses that are expected from both direct and indirect effects of noise on our focal taxa (figure 1).

   (i) *Direct effects*. Noise would negatively affect bird and grasshopper distributions and abundance at noise-exposed areas, but not those of odonates.
   (ii) *Indirect effects*. Noise would positively affect grasshopper and odonate distribution and abundance at noise-exposed areas but negatively affect those at quiet areas that abut noise-exposed areas.

2. Material and methods

(a) Study area and experimental sites

This study was conducted in grassland and forest patches in the Yufutsu plain, central Hokkaido, northern Japan (figure 1). The grasslands are dominated by species from the family Poaceae, such as the common reed *Phragmites australis*. Forests are dominated by species from Fagaceae, such as the daimyo oak *Quercus dentata*. Among our 24 sites (12 grassland and 12 forest) we changed the size and dimension of each site depending on focal taxon: 80 m × 300 m for birds and 80 m × 350 m for grasshoppers and odonates (see below for the detail, figure 2). We visually ensured that both near and far ranges of each site were dominated by a similar vegetation cover and similar vegetation height and density. To avoid spatial autocorrelation and pseudo-replication, we spaced all experimental sites greater than 1 km apart. We also avoided selecting areas where nationally endangered bird and grass species have been recorded in our previous studies [36,37]. Half of the grassland and forest sites were randomly assigned as phantom road treatment sites and the remaining were left as control sites.

(b) Noise recording and file arrangement for playback

We recorded vehicle noise at a roadway in our study area. Details of the noise recording and sound generation procedures are available elsewhere [23]. Briefly, we created 1 min-long traffic noise files consisting of 28 vehicle pass-by events (23 passenger vehicles and five trucks), which corresponded to the average diurnal traffic level of major roads in our study region [8,23].

To compensate for the lower frequency response among our playback speakers (see below) below 10 kHz, we amplified all files at frequencies between 5 and 10 kHz by 6 dB until broadcasted noise had similar spectral characters to the original recording files [23].

(c) Noise playback system

Ideally, we would have treated and sampled all focal taxa during the same period for logistical reasons and to better explore potential indirect effects. However, because the focal taxa differ in the timing of their peak abundance, to ensure reliable detection of each taxon, our treatments and surveys were conducted in two different periods. Specifically, we broadcasted traffic noise from late June to mid-July for birds in forest and grassland sites and late-August to mid-September for the other two taxa in the grassland sites. For the treatment sites, we set three waterproof speakers (JBL Charge3; JBL, CA, USA; frequency response = 65 Hz–20 kHz) spaced at 40 m each. Each speaker was placed at 1.5 m height using a tripod and was connected to a player (Walkman NW-E080; Sony Corporation, Tokyo, Japan) and a 12 V, 75 amp-hour battery (ACDelco Voyager M24MF; ACDelco, MI, USA) in a plastic box. Each battery was assisted by a solar panel (Sunyooo solar limited SY-M12 W-12; Sunyooo Solar, Jiangsu, China). We adjusted the amplitude of broadcasted traffic noise to represent noise attenuation of a moving vehicle at 60 km h^{-1} [9] (see below). We also turned noise off during 23.00 to 04.00 to mimic realistic traffic patterns of a major highway in our study region. We used different traffic noise files for each site to avoid pseudo-replication in playback [38]. To control for the potential influence of novel objects or potential predatory bird perches, we also placed similar objects (plastic box, tripod and dummy speaker) on control sites.

To assess acoustic conditions at all sites, on days with mild weather we measured the equivalent continuous sound pressure level in A-weighted decibels for 5 min (LAeq (5 min); fast sampling rate, re. 20 µPa) at 5, 50, 100, 150, 200, 250, 300, 350 m distance from the central speaker/speaker-like object before and during playback using a sound level metre (ACO Co., Ltd, Type 6236, Miyazaki, Japan). As a result, broadcasted noise attenuated to background sound levels by approximately 150 m distance from the speakers during playback (figure 2), which well represented noise attenuation of a moving vehicle at 60 km h^{-1} [9]. Thus, we defined areas less than or equal to 150 m from the speaker/speaker-like array as the near noise-exposed range and

areas greater than 150 m as the far range. We averaged measured sound pressure levels within each range (i.e. measurements at 5, 50, 100, 150 m were averaged for the near range and those at 200, 250, 300, 350 m for the far range). For the grassland sites, the average sound pressure levels (±s.d.) were 48.85 ± 1.07 dBA for the near ranges during playback ($n = 6$, hereafter 'near treatment range'), 36.56 ± 0.95 dBA for the far ranges during playback ($n = 6$, hereafter 'far treatment range') and 34.17 ± 2.09 dBA for ambient condition (i.e. both ranges of the control sites before and during playback plus both ranges of the treatment sites before playback; $n = 18$). For the forest sites, the average sound pressure levels were 46.58 ± 6.15 dBA for the near treatment ranges ($n = 6$), 35.76 ± 1.02 dBA for the far treatment ranges ($n = 6$) and 34.66 ± 3.96 dBA for ambient condition ($n = 18$).

(d) Field sampling

We surveyed birds in both grassland and forest sites and grasshoppers and odonates in the grassland sites. We did not survey grasshoppers and odonates in the forest sites owing to the low abundance of these taxa. For birds, to sample individuals from the near to far ranges consecutively, we established a 300 m survey route that ran in a straight line from the central speaker/speaker-like object (figure 2). A single surveyor walked slowly (1 km h^{-1}) on the survey route between sunrise and 08.00 and counted abundance of seen or heard individuals within 40 m width from the survey route. We assumed that this sampling range (less than 40 m from the observer) ensured high detection probabilities of birds across forests and grassland sites [39–41]. Flying individuals were not recorded. We assigned birds recorded in the first 1–150 m areas of the survey route into the near range and those in the 151–300 m areas into the far range. In rare occasions when a bird was detected in one range and subsequently moved to the other, it was assigned to the range in which it was detected first. The transect surveys were conducted four times before initiation of playback (early to mid-June) and six times during playback (from late-June to mid-July). For both before and during playback periods, we surveyed each site once before conducting the next round of surveys at each site. All sites were surveyed every 2–4 days. For grasshoppers and odonates, we established a total of eight 2 × 2 m quadrats at intervals of 50 m from the central speaker/speaker-like object to 350 m distance (figure 2) [31,42]. A single surveyor counted abundances of seen or heard grasshoppers and seen odonates in each quadrat [31,42]. We assigned individuals recorded in quadrats at 0, 50, 100 and 150 m from the speaker/speaker-like object into the near range and those at 200, 250, 300 and 350 m into the far range. To remove potential residual effects of an earlier playback for the bird surveys, the surveys for these taxa were initiated from 33 to 35 days after the final dates of the earlier playback. Specifically, the surveys were conducted four times before playback (mid- to late-August) and four times during playback (late-August and mid-September). Half of the surveys during each period (i.e. before or during playback) were conducted during daytime (10.00–16.00) and the remaining were during night-time (18.00–23.00) to investigate both diurnal and nocturnal grasshoppers. As with bird surveys, all sites were surveyed every 2–4 days for grasshoppers and odonates. Importantly, because noise is known to influence animal detections [43], we turned noise playbacks off during surveys.

(e) Statistical analysis

Because of large differences in species compositions, we analysed bird responses in the grassland and forest sites separately. We also conducted separate analyses of grasshopper responses from the daytime and night-time surveys because active species differed between day and night. Analyses of odonate distributions were restricted to daytime surveys. To elucidate more specific variations in responses to noise within taxa, we also analysed responses of individual species with greater than 50 unique observations throughout the surveys at all sites (i.e. cumulative abundance). We decided to use this threshold value (50 unique observations) because preliminary analyses suggested that models of species with less than 50 unique observations did not converge in many cases. The number of species that met this criterion were 13 forest bird species, eight grassland bird species and two odonate species, plus 11 grasshopper species during daytime surveys and 10 grasshopper species during night-time surveys. We calculated abundance and species richness of each focal group and abundance of each focal species in the near and far ranges of noise treated and quiet control sites.

We first analysed species richness and abundance using generalized linear mixed models (GLMMs). For each focal group/species, we used abundance and species richness (for each focal group only) in each range in each sampling occasion as response variables. We used noise treatment representing three categorical levels as a primary explanatory variable: 'ambient condition' (i.e. both ranges of the control sites before and during playback plus both ranges of the treatment sites before playback), 'near range' (i.e. the near ranges during playback) and 'far range' (i.e. the far ranges during playback). This approach enabled comparisons not only between near/far ranges and ambient conditions but also between near and far ranges. However, we confirmed that the results of simpler approaches using only near or far ranges were qualitatively unchanged. We also included sampling time (e.g. 5.00 = 500) and sampling date (1 June = 1) as additional predictors to control for potential effects of daytime and season on detectability. The site was used as a single random intercept. We initially constructed these models with a Poisson error. We then evaluated over- and under-dispersion and model fitting using multiple diagnostics: a scale parameter, a dispersion test and a Kolmogorov–Smirnov K-test. In the former test, we concluded that there was no over- or under-dispersion problem if the scale parameter was between 0.75 and 1.4 (electronic supplementary material, table S1) [44]. In the latter two tests, we assessed significance at 5% (electronic supplementary material, table S1). For models that violated at least one of these criteria or failed to converge (electronic supplementary material, table S1), we alternatively constructed models with a Conway Maxwell Poisson error, which can account for over/under dispersions. For each model, we finally conducted pairwise comparisons across treatment types using Tukey's HSD tests. We interpreted statistical significance at 5% levels for these pairwise comparisons. These analyses were conducted in program R with the packages 'lme4' [45], 'glmmTMB' [46] and 'lsmeans' [47].

To determine whether treatment explained community turnover, i.e. β diversity among near, far and control sites during playback, we used PERMANOVA using the *adonis* function available in the *vegan* 2.3 package in R [48]. When differences were detected, we used a modified version of the *adonis* function to make pairwise comparisons. As response variables, we used average abundance across surveys at the site under the 'during' acoustic conditions. To test the effects of noise, we only used 'during' surveys because *adonis* does not incorporate random effects. We repeated the analysis with 'before' surveys to make sure community differences attributed to acoustic conditions among control, near and far treatment sites did not differ for latent reasons. Prior to analyses, for each group (i.e. forest birds, grassland birds, day grasshopper surveys, night grasshopper surveys and odonate surveys) we first used the *rankindex* function in the *vegan* package to determine which β diversity index best-separated samples across treatments. We also used nonmetric multidimensional scaling to ordinate the dissimilarity indices and visualize species composition among the treatments. To assess ordination fit we examined stress values and convergence to determine the appropriate number of dimensions.
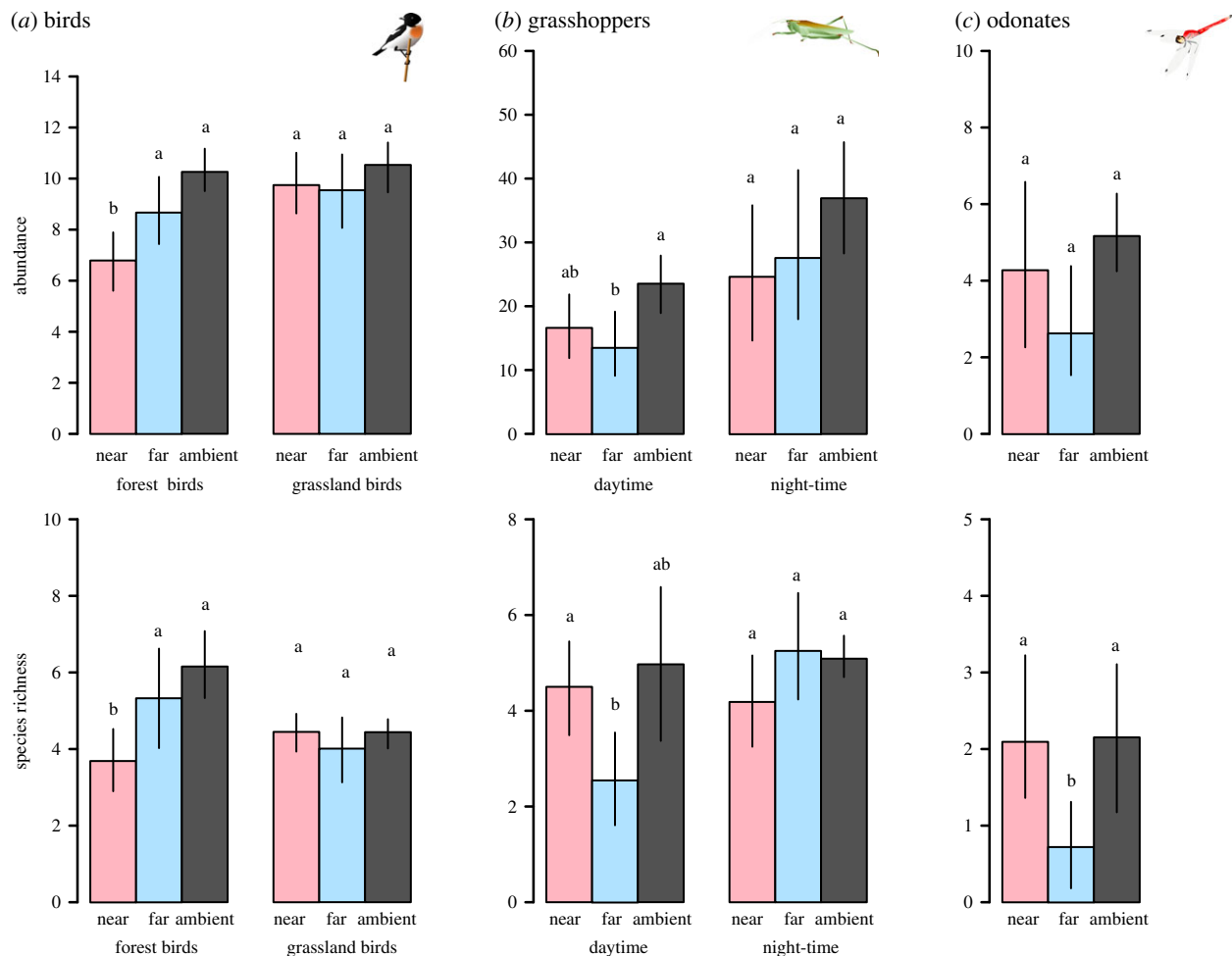
Figure 3. Results of multiple comparisons for species richness and total abundance of three focal taxa: (*a*) birds, (*b*) grasshoppers and (*c*) odonates. Forest and grassland birds are shown separately in (*a*) and grasshoppers at day and night are shown separately in (*b*). Predicted values in GLMMs are shown, Bars denote standard errors. Different letters indicate statistical significance ($p < 0.05$). (Online version in colour.)

3. Results

We recorded a total of 2270 unique observations of 39 bird species in the forest sites, 2475 unique observations of 40 bird species in the grassland sites, 2577 unique observations of 21 grasshopper species during the daytime surveys, 4278 unique observations of 17 grasshopper species during the night-time surveys and 553 unique observations of 14 odonate species.

(a) Species richness and abundance

For birds in the forest sites, the total abundance and species richness in the near range during playback were approximately 38% and 31% lower than those in ambient condition (i.e. the data that were pooled from both ranges of the control sites before and during playback and both ranges of the treatment sites before playback), respectively, and were also approximately 27% and 23% lower than those in the far range during playback, respectively (figure 3; electronic supplementary material, tables S2 and S7). Several individual species showed similar responses; four species had significantly lower abundance in at least one of the near and far ranges relative to ambient condition (electronic supplementary material, figure S1 and tables S2 and S7). One species (*Anthus hodgsoni*) had significantly higher abundance in the near range than in the far treatment range during playback. Another (*Ficedula narcissina*) had significantly lower abundance in the near

range relative to the far range during treatment (electronic supplementary material, figure S1 and tables S2 and S7).

By contrast to the clear responses to noise among forest birds, those in grassland sites did not differ in total abundance or species richness across the treatments (figure 3; electronic supplementary material, tables S3 and S8). Species-specific models showed that one species (*Saxicola stejnegeri*) had significantly higher abundance in the near range compared to the far range during playback or compared to sites during ambient sound conditions. Another species (*Emberiza fucata*) had significantly lower abundance in the near range than in the far range during playback (electronic supplementary material, figure S1, tables S3 and S8).

Although we did not detect major differences among treatment types for grassland birds, the total abundance of daytime-surveyed grasshoppers in the far range during playback was approximately 34% lower than abundance for ambient conditions (figure 3, tables S4 and S9). During playback species, richness in the far range were also approximately 41% lower than those in the near range. Contrary to these responses, the abundance of three species (*Kuwayamaea sapporensis, Conocephalus chinensis, Dianemobius nigrofascatus*) was significantly lower in the near range than in ambient conditions and the far range (electronic supplementary material, figure S1, tables S4 and S9). By contrast, both total abundance and species richness of grasshoppers at night did not differ across the treatments (figure 3; electronic supplementary material, tables S5

Table 1. PERMANOVA and pairwise PERMANOVA results for turnover in community species composition across treatments. (β diversity index used for each test are denoted in parentheses. Significant contrasts in community composition are denoted in italics.)

	species turnover		
variables	**F**	**R^2**	**p**
during			
forest birds (Bray–Curtis)	*2.552*	*0.196*	*0.036*
ambient versus *near*	*1.889*	*0.106*	*0.047*
ambient versus *far*	*1.700*	*0.096*	*0.044*
near versus far	1.410	0.123	0.173
grassland birds (Gower)	1.155	0.099	0.259
grasshoppers, day (Manhattan)	0.381	0.035	0.982
grasshoppers, night (Kulczynski)	0.678	0.061	0.786
odonates (Euclidian)	0.767	0.068	0.580
before			
forest birds (Manhattan)	1.216	0.104	0.243

and S10). Only one species (*Eobiana engelhardti subtropica*) had significantly lower abundance in the near range relative to ambient conditions and far range (electronic supplementary material, figure S1, tables S5 and S10).

During playback, total species richness of odonates in the far range was approximately 57% lower than that in the near range and approximately 57% lower than that in ambient condition, respectively (figure 3; electronic supplementary material, tables S6 and S11). No other significant effects of treatments were detected for this taxon (electronic supplementary material, tables S6 and S11).

(b) Community turnover

PERMANOVA analyses suggest that forest bird communities, but not grassland bird, grasshopper or odonate communities were significantly dissimilar across treatments (table 1). Specifically, forest bird communities in ambient conditions at control sites during playback were significantly dissimilar to those at the near and far ranges, but near and far range communities were not significantly dissimilar (electronic supplementary material, figure S2; table 1). Importantly, forest bird communities in near, far and control sites were not significantly dissimilar before traffic noise playback (table 1).

4. Discussion

Despite the current pervasive distribution of anthropogenic noise across our planet, how noise affects various dimensions of diversity within biological communities remains poorly understood [5]. Here, we experimentally created traffic noise in a roadless landscape and tested hypotheses involving the direct and indirect effects of noise on each taxa based on their dispersal ability, reliance on acoustics and trophic position. Although responses to noise differed within each taxon

(see the electronic supplementary material, supplementary discussion in appendix S14), we found that noise exposure resulted in lower species richness and abundance and different community composition in forest birds, especially at the near range compared to ambient conditions, which is consistent with our prediction that noise would interfere with birds' use of the acoustic environment. We also found that noise exposure altered grasshopper abundance and richness, plus richness of odonates. These findings were consistent with our indirect effect hypothesis whereby top-down control from predation may alter grasshopper and odonate abundance and richness. For both taxa, counts were lower in the far range noise treated areas relative to near range noise treated areas or sites during ambient conditions. Collectively, these results suggest that distributional changes owing to noise may occur not only through direct responses, but also indirectly via biotic interactions that extend beyond areas where noise levels are raised above ambient conditions.

As we expected, noise exposure resulted in the reduced abundance and/or species richness of forest birds and a few grasshopper species in the near range. These results are probably explained by direct effects of noise that manifest as avoidance of areas where acoustic communication and passive acoustic surveillance is difficult. Indeed, previous studies have demonstrated avoidance responses or behavioural alterations owing to noise in birds [49–53] and in grasshoppers [29,54]. Forest bird communities in the near and far ranges were also significantly dissimilar from communities located in ambient conditions on control sites during playback, but not before playback, providing strong evidence that altered acoustic regimes are responsible for the observed differences and matching previous findings that avian communities in areas exposed to noise are significantly dissimilar from those in relatively quiet areas [16].

Despite the clear evidence for direct effects of noise exposure for forest birds, we found no such responses for grassland birds. Two possibilities exist that could explain this discrepancy. First, differences in the breeding schedule between forest and grassland birds might be responsible. Birds breed earlier in forests than in grasslands in our study region and our noise treatment period corresponded with the fledgling to dispersing stages for forest birds but with nestling to fledgling periods for grassland birds (M Senzaki 2014–2017, personal data). Therefore, it is possible that grassland birds, which established nests under pre-treatment ambient sound conditions, were constrained by their reproductive effort around their nests or recently fledged young and thus did not avoid near ranges where noise exposure was most intense. Had they not been restricted by their nests, they might have avoided noise exposure just as was observed for forest birds. The apparent failure to avoid could be interpreted as a lack of sensitivity to noise; however, several studies have found declines in reproductive success owing to noise exposure [10,52,55], as well as indirect benefits owing to relaxed predation risk [16]. We do not know the fate of nests in this experiment, but future work should strive to understand how reproductive success changes with acoustic conditions that change drastically across the nesting period. Additionally, future work could aim to understand how different stages of the breeding process, e.g. territorial settlement, mate attraction, nest building, incubation, chick rearing and fledgling stage, may be susceptible to the negative effects of noise and result in either avoidance or reproductive failure.

Alternatively, the discrepancy in responses between forest and grassland birds might simply reflect higher tolerance to noise exposure among grassland species. Grassland species tend to vocalize at higher frequencies than forest species and hence may not experience as much masking from low-frequency human-made noise [56]. If avian responses are primarily owing to energetic masking and not other mechanisms (reviewed in [23]), grassland birds with higher-pitched songs may respond to noise less severely or not at all. Outwardly, this possibility seems supported from two studies involving grassland birds in the mixed-grass prairie of Alberta, Canada [57,58]. However, both studies failed to properly quantify sound levels and, because they included 'noisy' and 'quiet' sites that appear to have similar acoustic conditions, the design does not permit proper comparisons of bird abundances or reproductive success across sites with different noise treatments. Thus, whether grassland birds are less sensitive in general remains an open question.

Direct effects of noise on birds appear likely and are supported by a vast literature involving noise and vocal communication [59]. We also found grasshoppers and odonates to have lower species richness and/or abundance in the far treatment range relative to ambient condition or the near range; this pattern is opposite of predicted differences if noise directly affects grasshoppers by interfering with communication. Instead, the indirect effects of noise may be responsible for these results. Our results for grasshoppers, in particular, suggest that the indirect effects of noise may predominate over direct effects. If direct effects had been more prominent, reductions in grasshopper abundance should have been most severe at the near noise-exposed range because noise can affect grasshoppers via auditory effects, such as acoustic masking, but also non-auditory effects, such as ground vibrations caused by noise propagation. However, we did not observe this pattern. Thus, our results suggest similar community-level reverberations are likely for taxa of similar mobility and trophic levels and our findings add to the few studies that have documented indirect effects of noise exposure, which include altered patterns of pollination and seed dispersal [12] and, via noise-induced relaxed predation of lady beetles on aphids, which subsequently suppresses plant biomass [60].

That indirect effects are responsible for the patterns observed among grasshoppers and odonates is supported by evidence that birds prey upon both groups and that birds are known to exert strong top-down control on grasshoppers [61,62]. This possibility could also explain why diurnal grasshoppers responded to noise more strongly than those at night because most birds are diurnal species in the study area. Yet grassland birds, the predators that would be responsible for top-down control of odonates and grasshoppers, showed no clear negative responses to noise during our playback period. The temporal asynchrony among our measurements of grassland bird responses to noise and those for grasshoppers and odonates could explain these conflicting patterns and limits our ability to link responses to top-down control via predation by birds. Thus, the mechanisms underlying the observed responses among these invertebrate taxa need to be elucidated in future work, including explicit consideration of other possible predators that may change their distributions owing to noise. Nevertheless, if grassland birds avoid noise during the fledgling and dispersal stage, as documented for forest birds, lower abundance or richness of grasshoppers and odonates in the far range relative to near range is consistent with an increase in top-down control exerted from higher densities of birds in far ranges following avoidance of noise playback.

5. Conclusion

Using a field-placed manipulative 'phantom road' experiment that controlled for other confounding factors such as moving vehicles and light emission from noise itself, we show that road noise not only negatively impacts acoustically oriented animals, but can influence distributions of organisms with no clear links to the acoustic realm and affect distributions in relatively quiet areas adjacent to noise-exposed environments. The latter suggests that the ecological impacts of noise may extend well beyond areas where sound levels are elevated owing to anthropogenic sources. Thus, even though elevated noise levels owing to human activity are already pervasive [63], the ecological 'footprint' of noise may be even larger. Given the breadth of biological responses to this stimulus [1,5], policy makers and land managers should consider noise reduction or removal opportunities [64,65] and prioritize the protection of existing quiet areas [66,67]. Finally, because the indirect consequences of noise and other sensory stimuli have received such scant attention, future work will inevitably reveal surprising responses that complicate the ecology of an increasingly loud world.

References

1. Barber JR, Crooks KR, Fristrup KM. 2010 The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25, 180–189. (doi:10.1016/j.tree.2009.08.002)

2. Francis CD, Barber JR. 2013 A framework for understanding noise impacts on wildlife:

an urgent conservation priority. Front. Ecol. Environ. 11, 305–313. (doi:10.1890/120183)

3. Kunc HP, McLaughlin KE, Schmidt R. 2016 Aquatic noise pollution: implications for individuals, populations, and ecosystems.

Proc. R. Soc. B 283, 20160839. (doi:10.1098/rspb.2016.0839)

4. Slabbekoorn H, Bouton N, van Opzeeland I, Coers A, ten Cate C, Popper AN. 2010 A noisy spring: the impact of globally rising underwater sound levels

on fish. *Trends Ecol. Evol.* **25**, 419–427. (doi:10.1016/j.tree.2010.04.005)

5. Shannon G *et al.* 2016 A synthesis of two decades of research documenting the effects of noise on wildlife. *Biol. Rev.* **91**, 982–1005. (doi:10.1111/brv.12207)

6. Slabbekoorn H, Peet M. 2003 Birds sing at a higher pitch in urban noise. *Nature* **424**, 267. (doi:10.1038/424267a)

7. Kern JM, Radford AN. 2016 Anthropogenic noise disrupts use of vocal information about predation risk. *Environ. Pollut.* **218**, 988–995. (doi:10.1016/j.envpol.2016.08.049)

8. Nakano Y, Senzaki M, Ishiyama N, Yamanaka S, Miura K, Nakamura F. 2018 Noise pollution alters matrix permeability for dispersing anurans: differential effects among land covers. *Glob. Ecol. Conserv.* **16**, e00484. (doi:10.1016/j.gecco.2018.e00484)

9. Senzaki M, Yamaura Y, Francis CD, Nakamura F. 2016 Traffic noise reduces foraging efficiency in wild owls. *Sci. Rep.* **6**, 30602. (doi:10.1038/srep30602)

10. Kleist NJ, Guralnick RP, Cruz A, Lowry CA, Francis CD. 2018 Chronic anthropogenic noise disrupts glucocorticoid signaling and has multiple effects on fitness in an avian community. *Proc. Natl Acad. Sci. USA* **115**, E648–E657. (doi:10.1073/pnas.1709200115)

11. Simpson SD, Radford AN, Nedelec SL, Ferrari MCO, Chivers DP, McCormick MI, Meekan MG. 2016 Anthropogenic noise increases fish mortality by predation. *Nat. Commun.* **7**, 10544. (doi:10.1038/ncomms10544)

12. Francis CD, Kleist NJ, Ortega CP, Cruz A. 2012 Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal. *Proc. R. Soc. B* **279**, 2727–2735. (doi:10.1098/rspb.2012.0230)

13. Cox K, Brennan LP, Gerwing TG, Dudas SE, Juanes F. 2018 Sound the alarm: a meta-analysis on the effect of aquatic noise on fish behavior and physiology. *Glob. Change. Biol.* **24**, 3105–3116. (doi:10.1111/gcb.14106)

14. Phillips JN, Gentry K, Derryberry E, Luther D. 2018 Surviving in the city: higher apparent survivial for urban birds but worse condition on noisy territories. *Am. Ornithol. Soc.* **9**, 1–12. (doi:10.1002/ecs2.2440)

15. Herbert-Read JE, Kremer L, Bruintjes R, Radford AN, Ioannou CC. 2017 Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. *Proc. R. Soc. B* **284**, 20171627. (doi:10.1098/rspb.2017.1627)

16. Francis CD, Ortega CP, Cruz A. 2009 Noise pollution changes avian communities and species interactions. *Curr. Biol.* **19**, 1415–1419. (doi:10.1016/j.cub.2009.06.052)

17. Mcclure CJW, Ware HE, Carlisle J, Kaltenecker G, Barber JR. 2013 An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proc. R. Soc. B* **280**, 20132290. (doi:10.1098/rspb.2013.2290)

18. Ware HE, McClure CJW, Carlisle JD, Barber JR. 2015 A phantom road experiment reveals traffic noise is

an invisible source of habitat degradation. *Proc. Natl Acad. Sci. USA* **112**, 12 105–12 105. (doi:10.1073/pnas.1504710112)

19. McClure CJW, Ware HE, Carlisle JD, Barber JR. 2017 Noise from a phantom road experiment alters the age structure of a community of migrating birds. *Anim. Conserv.* **20**, 164–172. (doi:10.1111/acv.12302)

20. Francis CD, Ortega CP, Cruz A. 2011 Noise pollution filters bird communities based on vocal frequency. *PLoS ONE* **6**, e27052. (doi:10.1371/journal.pone.0027052)

21. Grace MK, Noss RF. 2018 Evidence for selective avoidance of traffic noise by anuran amphibians. *Anim. Conserv.* **21**, 343–351. (doi:10.1111/acv.12400)

22. Luo J, Siemers BM, Koselj K. 2015 How anthropogenic noise affects foraging. *Glob. Chang. Biol.* **21**, 3278–3289. (doi:10.1111/gcb.12997)

23. Senzaki M, Kadoya T, Francis CD, Ishiyama N, Nakamura F. 2018 Suffering in receivers: negative effects of noise persist regardless of experience in female anurans. *Funct. Ecol.* **32**, 2054–2064. (doi:10.1111/1365-2435.13130)

24. Dominoni D *et al.* In press. Why and how conservation biology should benefit from sensory ecology. *Nat. Ecol. Evol.* (doi:10.1038/s41559-020-1135-4)

25. Bunkley JP, McClure CJW, Kawahara AY, Francis CD, Barber JR. 2017 Anthropogenic noise changes arthropod abundances. *Ecol. Evol.* **7**, 2977–2985. (doi:10.1002/ece3.2698)

26. DeJong LN, Cowell SD, Nguyen TNN, Proppe DS. 2015 Attracting songbirds with conspecific playback: a community approach. *Behav. Ecol.* **26**, 1379–1388. (doi:10.1093/beheco/arv094)

27. Suzuki TN. 2018 Alarm calls evoke a visual search image of a predator in birds. *Proc. Natl Acad. Sci. USA* **115**, 1541–1545. (doi:10.1073/pnas.1718884115)

28. Konishi M. 1973 How the owl tracks its prey: experiments with trained barn owls reveal how their acute sense of hearing enables them to catch prey in the dark. *Am. Sci.* **61**, 414–424.

29. Lampe U, Reinhold K, Schmoll T. 2014 How grasshoppers respond to road noise: developmental plasticity and population differentiation in acoustic signalling. *Funct. Ecol.* **28**, 660–668. (doi:10.1111/1365-2435.12215)

30. Stumpner A, Von Helversen D. 2001 Evolution and function of auditory systems in insects. *Naturwissenschaften* **88**, 159–170. (doi:10.1007/s001140100223)

31. Kadoya T, Suda SI, Tsubaki Y, Washitani I. 2008 The sensitivity of dragonflies to landscape structure differs between life-history groups. *Landsc. Ecol.* **23**, 149–158. (doi:10.1007/s10980-007-9151-1)

32. Futahashi R, Kawahara-Miki R, Kinoshita M, Yoshitake K, Yajima S, Arikawa K, Fukatsu T. 2015 Extraordinary diversity of visual opsin genes in dragonflies. *Proc. Natl Acad. Sci. USA* **112**, E1247–E1256. (doi:10.1002/qua.24176)

33. Lack D. 1946 Competition for food by birds of prey. *J. Anim. Ecol.* **15**, 123–129. (doi:10.2307/1552)

34. Fowler AC, Knight RL, George TL, McEwen LC. 1991 Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology* **72**, 1775–1781. (doi:10.2307/1940976)

35. Hirt MR, Jetz W, Rall BC, Brose U. 2017 A general scaling law reveals why the largest animals are not the fastest. *Nat. Ecol. Evol.* **1**, 1116–1122. (doi:10.1038/s41559-017-0241-4)

36. Senzaki M, Yamaura Y, Nakamura F. 2015 The usefulness of top predators as biodiversity surrogates indicated by the relationship between the reproductive outputs of raptors and other bird species. *Biol. Conserv.* **191**, 460–468. (doi:10.1016/j.biocon.2015.07.027)

37. Senzaki M, Yamaura Y. 2016 Surrogate species versus landscape metric: does presence of a raptor species explains diversity of multiple taxa more than patch area? *Wetl. Ecol. Manag.* **24**, 427–441. (doi:10.1007/s11273-015-9469-4)

38. Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu W-C. 2001 Pseudoreplication in playback experiments, revisited a decade later. *Anim. Behav.* **61**, 1029–1033. (doi:10.1006/anbe.2000.1676)

39. Yoshii C, Yamaura Y, Soga M, Shibuya M, Nakamura F. 2015 Comparable benefits of land sparing and sharing indicated by bird responses to stand-level plantation intensity in Hokkaido, northern Japan. *J. For. Res.* **20**, 167–174. (doi:10.1007/s10310-014-0453-2)

40. Hanioka M, Yamaura Y, Senzaki M, Yamanaka S, Kawamura K, Nakamura F. 2018 Assessing the landscape-dependent restoration potential of abandoned farmland using a hierarchical model of bird communities. *Agric. Ecosyst. Environ.* **265**, 217–225. (doi:10.1016/j.agee.2018.06.014)

41. Hanioka M, Yamaura Y, Yamanaka S, Senzaki M, Kawamura K, Terui A, Nakamura F. 2018 How much abandoned farmland is required to harbor comparable species richness and abundance of bird communities in wetland? Hierarchical community model suggests the importance of habitat structure and landscape context. *Biodivers. Conserv.* **27**, 1831–1848. (doi:10.1007/s10531-018-1510-5)

42. Gardiner T, Hassall M. 2009 Does microclimate affect grasshopper populations after cutting of hay in improved grassland? *J. Insect Conserv.* **13**, 97–102. (doi:10.1007/s10841-007-9129-y)

43. Ortega CP, Francis CD. 2012 Effects of gas-well-compressor noise on the ability to detect birds during surveys in northwest New Mexico. *Ornithol. Mono.* **74**, 78–90.

44. Korner-Nievergelt F, Roth T, von Felten S, Guelat J, Almasi B, Korner-Nievergelt P. 2015 *Bayesian data analysis in ecology using R, BUGS and Stan.* Cambridge, MA: Academic Press.

45. Bate D *et al.* 2019 Package 'lme4.' See https://cran.r-project.org/web/packages/lme4.

46. Magnusson A *et al.* 2019 Package 'glmmTMB.' See https://cran.r-project.org/web/packages/glmmTMB.

47. Russell L, Love J. 2018 Package 'lsmeans.' (doi:10.18637/jss.v069.i01). See https://cran.r-project.org/web/packages/lsmeans.

48. Oksanen AJ et al. 2017 Package 'vegan.' See https://cran.r-project.org/web/packages/vegan.

49. Strasser EH, Heath JA. 2013 Reproductive failure of a human-tolerant species, the American kestrel, is associated with stress and human disturbance. J. Appl. Ecol. 50, 912–919. (doi:10.1111/1365-2664.12103)

50. Forman RTT, Reineking B, Hersperger AM. 2002 Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environ. Manage. 29, 782–800. (doi:10.1007/s00267-001-0065-4)

51. Nemeth E, Pieretti N, Zollinger SA, Geberzahn N, Partecke J, Brumm H, Miranda AC. 2013 Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. Proc. R. Soc. B 280, 20122798. (doi:10.1098/rspb.2012.2798)

52. Halfwerk W, Holleman LJM, Lessells CM, Slabbekoorn H. 2011 Negative impact of traffic noise on avian reproductive success. J. Appl. Ecol. 48, 210–219. (doi:10.1111/j.1365-2664.2010.01914.x)

53. Grade AM, Sieving KE. 2016 When the birds go unheard: highway noise disrupts information transfer between bird species. Biol. Lett. 12, 20160113. (doi:10.1098/rsbl.2016.0113)

54. Lampe U, Schmoll T, Franzke A, Reinhold K. 2012 Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. Funct. Ecol. 26, 1348–1354. (doi:10.1111/1365-2435.12000)

55. Injaian AS, Poon LY, Patricelli GL. 2018 Effects of experimental anthropogenic noise on avian settlement patterns and reproductive success. Behav. Ecol. 29, 97. (doi:10.1093/beheco/ary097)

56. Bertelli S, Tubaro PL. 2002 Body mass and habitat correlates of song structure in a primitive group of birds. Biol. J. Linn. Soc. 77, 423–430. (doi:10.1046/j.1095-8312.2002.00112.x)

57. Nenninger HR, Koper N. 2018 Effects of conventional oil wells on grassland songbird abundance are caused by presence of infrastructure, not noise. Biol. Conserv. 218, 124–133. (doi:10.1016/j.biocon.2017.11.014)

58. Bernath-Plaisted J, Koper N. 2016 Physical footprint of oil and gas infrastructure, not anthropogenic noise, reduces nesting success of some grassland songbirds. Biol. Conserv. 204, 434–441. (doi:10.1016/j.biocon.2016.11.002)

59. Slabbekoorn H. 2013 Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. Anim. Behav. 85, 1089–1099. (doi:10.1016/j.anbehav.2013.01.021)

60. Barton BT, Hodge ME, Speights CJ, Autrey AM, Lashley MA, Klink VP. 2018 Testing the AC/DC hypothesis: rock and roll is noise pollution and weakens a trophic cascade. Ecol. Evol. 8, 7649–7656. (doi:10.1002/ece3.4273)

61. Belovsky GE, Slade JB. 1993 The role of vertebrate and invertebrate predators in a grasshopper community. Oikos 68, 193–201. (doi:10.2307/3544830)

62. Bock CE, Bock JH, Grant MC. 1992 Effects of bird predation on grasshopper densities in an Arizonan grassland. Ecology 73, 1706–1717. (doi:10.2307/1940022)

63. Buxton RT, Mckenna MF, Mennitt D, Fristrup K, Crooks K, Angeloni L, Wittemyer G. 2017 Noise pollution is pervasive in U.S. protected areas. Science 533, 531–533. (doi:10.1126/science.aah4783)

64. Dumyahn SL, Pijanowski BC. 2011 Beyond noise mitigation: managing soundscapes as common-pool resources. Landsc. Ecol. 26, 1311–1326. (doi:10.1007/s10980-011-9637-8)

65. Gentry KE, McKenna MF, Luther DA. 2018 Evidence of suboscine song plasticity in response to traffic noise fluctuations and temporary road closures. Bioacoustics 27, 165–181. (doi:10.1080/09524622.2017.1303645)

66. De Meester L, Vanoverbeke J, Kilsdonk LJ, Urban MC. 2016 Evolving perspectives on monopolization and priority effects. Trends Ecol. Evol. 31, 136–146. (doi:10.1016/j.tree.2015.12.009)

67. Grman E, Suding KN. 2010 Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. Restor. Ecol. 18, 664–670. (doi:10.1111/j.1526-100X.2008.00497.x)

68. Senzaki M, Kadoya T, Francis CD. 2020 Data from: Direct and indirect effects of noise pollution alter biological communities in and near noise-exposed environments. Dryad Digital Repository. (https://doi.org/10.5061/dryad.qz612jmb1)