

Title: Do soundscape indices predict landscape scale restoration outcomes? A comparative study of restored seabird island soundscapes.

Running Head: Soundscapes of restored seabird islands

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Author Contributions:

AB, RB conceived the idea of a soundscape analysis of existing recordings. RB, HM, IJ, JW designed the 2013 study and coordinated field collection of recordings. AB, RB conducted the analysis. AB wrote the manuscript. RB, HM, IJ, JW, DC, BT revised and edited the manuscript.

Keywords:

Bioacoustics, Soundscape, Ecoacoustics, Monitoring, Restoration outcomes, Seabirds

Implications:

- Analysis of long duration soundscape recordings can provide a rapid, scalable assessment of restoration outcomes measured against reference conditions used for decision making.
- Recording sites should be chosen to minimize differences in non-target noise (eg wind and waves) compared to reference recording sites.
- Soundscape indices are likely to reflect the most conspicuous calling species.
- Soundscape indices should complement rather than replace other approaches, including qualitative listening and call detection.

Abstract

Measuring restoration outcomes is essential, but challenging and expensive, particularly on remote islands. Acoustic recording increases the scale of monitoring inexpensively, however extracting biological information from large volumes of recordings remains challenging. Soundscape approaches, characterizing communities using acoustic indices, rapidly analyze large acoustic datasets and can be used to compare restoration sites against reference conditions. We tested this approach to measure nocturnal

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seabird recovery following invasive predator removal in the Aleutian Islands. We used recordings of nocturnal seabird soundscapes from six islands with varied histories of predators, from never invaded (1 island) to 9 - 34 years post predator removal (4 islands) and currently invaded (1 island). We calculated ten indices of acoustic intensity and complexity, and two pairwise indices of acoustic differences. Three indices reflected patterns of seabird recovery. Acoustic richness (measuring temporal entropy and amplitude) increased with time since predator removal and presence of historical predator refugia ($r^2=0.44$). These factors and moonlight accounted for 30% of variation in cumulative spectral difference from the reference island. Over 10% of acoustic richness and temporal entropy was explained by Leach's Storm-petrel (*Oceanodroma leucorhoa*) calls. However, indices characterized the soundscape of rat-invaded Kiska island like a never invaded island, likely due to high abiotic noise and few seabird calls. Soundscape indices have potential to monitor outcomes of seabird restoration quickly and cheaply, if confounding factors are considered and controlled in experimental design. We suggest soundscape indices become part of the expanding acoustic monitoring toolbox to cost-effectively measure restoration outcomes at scale and in remote areas.

Introduction

Effective environmental restoration relies on rigorous measurement of intervention outcomes, but this can be logistically challenging and costly to achieve. Even at fine geographic scales, outcome metrics are often inconsistent, hampering the ability to evaluate restoration success (Wortley et al. 2013). As restoration interventions are applied at increasingly large scales (Perring et al. 2015), scalable, cost-effective tools are required to monitor patterns of recovery at appropriate landscape scales. Advances in passive acoustic recording technologies offer scalable sampling to measure ecological conditions at high

spatiotemporal resolution (Wrege et al. 2016; Buxton et al. 2018; Hill et al. 2018; Ross et al. 2018).

However, passive acoustic recording has not been widely applied as a monitoring tool largely due to the enormous amount of resulting data and subsequent time consumptive and expensive process of data analysis (e.g., Buxton and Jones 2012).

Large-scale passive recordings, where the entire ambient acoustic environment is recorded for long time periods, serve as a permanent record of ecological conditions for analysis of indicator species, anthropogenic sounds, and other evolving questions. Automated analysis of large acoustic datasets generally falls into two categories: signal detection of particular calls or species (Acevedo et al. 2009) and soundscape approaches that examine patterns and variation in acoustic energy across long duration recordings to index ecological conditions (Sueur, Pavoine, et al. 2008). Signal detection is a powerful approach to measure species activity directly, but effort increases with the number of calls being detected, making the use of automated detectors prohibitively time consuming for large numbers of species. As a complementary approach, characterizing acoustic environments (i.e., soundscapes) using indices of acoustic diversity and intensity can describe ecological patterns without the need for species detection and classification (Pijanowski et al. 2011; Towsey et al. 2013; Sueur et al. 2014). An increasing number of studies suggest that patterns of acoustic energy in soundscapes reflect biodiversity and can be used as a monitoring index (Buxton et al. 2018). By quantifying acoustic diversity, complexity, intensity, and spectral differences between soundscape recordings, acoustic indices have been used to characterize ecological communities (Gasc et al. 2013; Lellouch et al. 2014; Harris et al. 2016), measure the impacts of ecological disturbance (Burivalova et al. 2017; Deichmann et al. 2017), and determine the effectiveness of protected areas (Bertucci et al. 2016). Moreover, using acoustic indices can avoid potential biases of large-scale monitoring programs such as observer and temporal biases.

Much of restoration outcome monitoring focuses on comparing the condition of restoration sites with reference sites (Wortley et al. 2013). Soundscape indices provide a potentially efficient method to compare the acoustic environment of recordings collected at restoration sites to those of reference sites. By directly comparing soundscapes recordings, rather than choosing particular elements, differences may reflect an integrated measure of ecological dissimilarity. Soundscapes contain information about physical and biological processes, as well as species diversity and activity patterns. However, soundscape indices come with potential pitfalls necessitating careful examination of their relationship to ecological conditions before these approaches can be taken to scale. Soundscape analysis does not identify particular species and is not a direct population index, rather, it offers a community acoustic environment appraisal. Understanding biological, geological, and anthropogenic sources driving soundscape indices is essential to link ecological condition to soundscape indices. While numerous studies have examined the potential for soundscape analysis as a monitoring tool, rarely have acoustic indices been applied in a comparative approach with a reference condition (although notably Fuller et al. 2015; Bertucci et al. 2016; Burivalova et al. 2017).

In this paper we utilize a highly successful invasive species removal campaign at the archipelago scale in the Western Aleutian Islands to test the efficacy of soundscape indices to measure restoration outcomes. The removal of invasive Arctic Fox (*Vulpes lagopus*) and Norway Rats (*Rattus norvegicus*) in the Aleutian Islands has been a widely documented ecosystem restoration success, dramatically increasing seabird abundance, and restoring nutrient cycling patterns and plant diversity (Ebbert & Byrd 2000; Croll et al. 2005; Maron et al. 2006; Buxton et al. 2013). Previously we recorded, counted and identified vocalizations of four nocturnal seabirds at replicate sites on six Aleutian islands with varying times since introduced predator eradication (Buxton et al 2013). We found that time since predator

removal and presence of nearby predator refugia (areas that invasive predators could not access, such as talus, cliffs and offshore islets) were the most important positive predictors of seabird acoustic activity (Buxton et al. 2013). Our call detection approach effectively quantified seabird activity in a noisy environment, measuring patterns of recovery that were infeasible by any other method. However, even with automated tools, the analysis required countless hours designing call detectors and evaluating automated detections including 100,953 Leach's and 90,911 Fork-tailed Storm-petrel calls (Buxton et al. 2013). Thus, here we test if soundscape indices can capture similar patterns of seabird recovery, which could assess restoration outcomes at a fraction of the effort. We applied two basic types of acoustic indices (reviewed by Sueur et al 2014): alpha indices, which characterize the acoustic complexity or intensity of a single recording and beta indices, which compare acoustic properties among recordings.

Specifically, we tested if the same factors that influence seabird calling activity predicted soundscape characteristics, particularly the time since invasive predator removal and presence of refugia. We hypothesized that nocturnal soundscapes dominated by seabirds would, with time since predator removal and presence of predator refugia, become increasingly similar to an uninvaded reference island, the restoration target. Furthermore, we expect nocturnal soundscape intensity and complexity would increase with time since predator removal and presence of refugia. We then tested which seabird species calls were important in driving soundscape indices. Finally, we discuss the advantages of a soundscape approach when monitoring restoration outcomes.

Methods

Study Area

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To investigate outcomes of invasive predator removal for seabird island soundscapes, we examined the acoustic environment on six islands in the western Aleutians, Alaska, USA (Buxton et al. 2013). These islands have similar climactic conditions and ecosystems but different histories with two invasive predators, rats and foxes. Arctic foxes were introduced to the archipelago for the fur trade beginning in the mid 1700's (Bailey 1993). All islands have been part of the Alaska Maritime National Wildlife Refuge since 1913, but fox eradication began only in 1949 (Ebbert & Byrd 2000). Waterfowl (e.g., Aleutian Cackling Goose *Branta hutchinsii leucopareia*), ground-nesting Glaucous-winged Gulls (*Larus glaucescens*), and nocturnal seabirds (that we focused on here) including storm-petrels (*Oceanodroma spp.*), Ancient Murrelets (*Synthliboramphus antiquus*) and Cassin's (*Ptychoramphus aleuticus*) and Whiskered (*Aethia pygmaea*) Auklets are believed to have been most negatively affected by introduced foxes (Murie 1959; Ebbert & Byrd 2000; Williams et al. 2003). Arctic Foxes have now been eradicated successfully from over 38 Aleutian Islands (Keitt et al. 2011). Norway Rats were introduced during World War II resulting in many nesting seabird species becoming rare or absent on islands they invaded (Ebbert & Byrd 2000). Norway Rats were successfully removed from one island, Hawadax in 2008 (Croll et al. 2015), but remain on several islands including Kiska. Arctic foxes were eradicated from Kiska in 1986, possibly resulting in an escalation of rat predation on native species (Major et al. 2013).

We collected nighttime acoustic recordings over multiple summers from thirteen sites on four islands with a range of years since fox eradication (Nizki-Alaid, 34 years; Kasatochi, 25 years; Amatignak, 18 years and Little Sitkin Island, 9 years). In total we made 25 acoustic sensor deployments (Table S1, Figure S1). We measured time since fox eradication as the years elapsed between successful eradication and the first acoustic recordings collected for the island, as for four of the seven islands we collected recordings for multiple summers. Foxes were the only invasive predator to have reached these

islands. We also collected acoustic recordings from Buldir Island, which has never been invaded by predators and is the most diverse seabird colony in the northern Hemisphere with dense populations of nocturnal seabirds (Byrd & Day 1986). Thus, we refer to Buldir as the “reference site”. Finally, we collected recordings from five sites on Kiska where foxes were removed (in 1986), but rats are still present and severely limit seabird populations, preventing seabird recovery and thus we refer to this island as “invaded” (Buxton et al. 2013; Major et al. 2013). All these islands are treeless, windswept, uninhabited, experience high surf, and are subject to frequent precipitation in the form of rain, drizzle and mist (i.e., a challenging environment for sound recording). To evaluate factors that would influence the recovery of seabirds after predator eradication, we noted the presence of any historical predator refugia such as talus, cliffs or offshore islets within 100 m of microphones, and calculated the distance to the nearest large predator free source colony using Google Earth (expanded methods in Buxton et al. 2013).

Acoustic Data Collection and Analysis

Recording locations were chosen by identifying suitable burrow nesting seabird breeding habitat 50-150m from shorelines, at elevations under 400m at cardinal locations on each island, or at Kiska Island (<http://www.mun.ca/serg/Kiska-songmeters.html>), in representative areas of suitable habitat >1km from other sensors (Buxton et al. 2013). Suitable habitat for nocturnal seabirds included the following characteristics: well drained (not marshy areas subject to flooding), soft soil suitable for burrowing, vegetated with dense forbs and grasses >25 cm tall to provide cover, and areas with visible natural rock crevices (scree-talus slopes); sheer cliffs, unvegetated areas excepting scree, wetlands, and exposed bedrock areas were avoided (Huntington et al. 1996; Dee Boersma & Silva 2001; Gaston & Shoji 2010; Ainley et al. 2011). Wildlife Acoustics Songmeter SM1 autonomous recorders were deployed in July 2008, 2009 and 2010 attached to a 1m wooden stake. Sensors recorded for 15 minutes of every 30

minutes between 0130 and 0430 (peak nocturnal seabird activity) at a 16kHz sample rate. The number of recording nights per deployment ranged from 13-31 nights (Table S1).

All recordings were processed using packages *seewave* (Sueur, Aubin, et al. 2008), *tuneR* (Ligges et al. 2016), and *soundecology* (Villanueva-Rivera & Pijanowski 2016) in program R version 3.4.3 (R Development Core Team 2011). We analyzed the first ten minutes of each recording after isolating the right channel and applying a 0-200hz band pass filter. For each file we computed a mean frequency spectrum of the time wave (window length=512, overlap=0, Hamming Fourier Transform) and a Hilbert amplitude envelope. These were used to calculate twelve soundscape indices (see below).

Soundscape Indices

We measured ten alpha indices that characterized each night of recordings and two beta indices that measured differences between recordings (Table 1). When calculating beta indices, we measured all pairwise differences between each recording night, and the difference between each night and an averaged spectrum of all Buldir recordings (reference condition). Thus, for each night of recording, we measured the difference from each of the 702 other nights we sampled, as well the difference from the average night on Buldir Island.

Call activity and indices

To examine which aspects of the nocturnal soundscape may be driving patterns in acoustic indices we compared nightly index values with nightly seabird call activity and wind speeds. We measured the rates of nine seabird calls belonging to four nocturnal seabird species (Leach's and Fork-tailed Storm-petrels, Ancient Murrelet, and Cassin's Auklet), and measured call richness (the number of call types present in

an evening). Semi-automated methods for measuring detecting seabird calls were described by Buxton et al. (2013) and Buxton and Jones (2012); briefly, we used automated call-recognizers constructed using SONG SCOPE (version 2.3, Wildlife Acoustics Inc). Automated detections were audited by visually inspecting spectrograms. We measured call rates for all 87% of recordings from restored islands. Daily wind speeds were collected from National Oceanic and Atmospheric Administration weather buoy no. 46071 at 51.16°N, 179.00°E; and no. 46070 at 55.00°N, 175.28°E.

Quantitative methods

Like the soundscape analysis, all statistical modeling and analysis was conducted in program R version 3.4.3 (R Development Core Team 2011). To test if years since fox eradication or presence of refugia predicted any of the ten alpha index values on restored islands we used ten linear mixed effect models fit by maximum likelihood, treating each year within site within island as a nested random factor using package *lmer* (Bates & Sarkar 2007). These models did not include the invaded Kiska Island or uninhabited Buldir Island. Fixed factors included years since fox eradication, presence of predator refugia, distance to source populations and the fraction of the moon illuminated (a known covariate of seabird acoustic activity (Mougeot & Bretagnolle 2000)). We tested all combinations of fixed effects and selected the best fit model by Akaike's Information Criterion (AIC). We scaled and centered continuous predictors to make coefficients comparable within models. Last, we estimated proportion of variance explained by fixed and random effects with marginal and conditional R^2 (Nakagawa & Schielzeth 2013) as implemented in the *MuMIn* package (Barton 2016). For beta index values we used a similar linear mixed effect model procedure to predict the difference from the uninhabited condition (Buldir Island). In addition, we used the beta index pairwise distances among nights at different sites to explore the relative differences between all sites using a principal components analysis.

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Finally, to examine which aspect of the nocturnal soundscape was driving each index we constructed a linear mixed effect model with all recordings (including Kiska and Buldir island) for which we had measured species specific call activity (from Buxton et al. 2013). We included centered and scaled predictors of counts of each seabird call type, call richness and wind speed as fixed effects. We also included a nested random intercept of year within site within island. In all cases, we considered covariates with bootstrapped 95% confidence intervals excluding zero to indicate a significant effect.

Results

We analyzed 4,917 ten-minute samples from 25 sensor deployments at 19 sites on six islands over a total of 703 recording nights (Figure S2, Table S1). The average length of a deployment was 28.6 nights (range=13-31).

The best fit model explaining index values included at least one of the following variables: years since fox eradication, distance to source populations, refugia presence, and moonlight (Table S2). For eight of the twelve indices, years since fox eradication was a significant predictor and the presence of refugia was a significant predictor of five indices. Of all indices, acoustic richness was best predicted by the presence of refugia and years since fox eradication ($\beta_{\text{refugia}} = 1555.06$, $\beta_{\text{years}} = 1757.17$, Marginal $R^2 = 0.44$; Fig. 1). Median amplitude and temporal entropy (which are multiplied to produce acoustic richness) were both also positively related to years since fox eradication, but these factors explained less of the model variability. Other alpha indices were positively related to years since fox eradication and presence of refugia but explained considerably less variation (maximum signal to noise ratio, number of spectral peaks, and number of acoustic events). Total entropy, the percent of acoustic activity, the acoustic

complexity index (ACI), and spectral entropy were not meaningfully explained by years since fox eradication or presence of refugia (Marginal $R^2 < 0.1$).

Soundscapes were more similar to the reference condition of Buldir Island with increasing years since predator removal (spectral difference D_f and cumulative spectral difference D_{cf} from never invaded Buldir Island decreased with increasing years since predator removal; Fig. 2, Figure S3). Years since predator removal, distance from source populations and moonlight explained 30% of the variation in cumulative spectral difference from Buldir, the reference condition ($\beta_{\text{years}} = -0.02$, $\beta_{\text{distance}} = -0.0073$, $\beta_{\text{moonlight}} = 0.019$, Marginal $R^2 = 0.30$; Table S2).

We measured 494,209 pairwise differences from 703 recording nights on all islands. To visualize the differences between all recordings, the first principal components captured 81.3% of the variation in the cumulative spectral difference matrix and 57.9% of the variation in the spectral difference matrix (Fig. 3). Among restored islands, the first principal component of each beta index was correlated with the number of years since fox eradication, (Cumulative spectral dissimilarity $r = -0.15$, $p_{df=499} < 0.05$, Spectral dissimilarity $r = 0.32$, $p_{df=499} < 0.05$) indicating that as years pass after predator removal the soundscape becomes increasingly like a never invaded island.

In models testing the relationship between soundscape components and each index we found that for all but one index, Leach's Storm-petrel calls and/or call richness were the only significant factors predicting indices (Table S3, Figure S4). These factors described a low proportion of variance in indices (Marginal R^2 values ranged from 0.01 to 0.15), with the highest variance explained for temporal entropy, ACI, and acoustic richness (Marginal $R^2 > 0.1$). Leach's Storm-petrel chuckle calls had a significant effect on nine of twelve indices (negative on ACI, AR and D_{cf} from Buldir, positive on H, H_f , H_t , NP.001 and

PercAcoAct). Call richness had a significant effect on six of twelve indices (negative on ACI, AR, NumEvents and log median amplitude; positive on H_t and NP.001). The only other significant predictor of indices from call rates was a small positive effect of Ancient Murrelet chick calls on the cumulative spectral difference from Buldir Island. Wind speed was not included in any of the final best fit models.

Discussion

We tested the effectiveness of acoustic indices as a technique to compare soundscapes of restored Aleutian Islands with increasing time since predator removal against a never invaded reference site. We used a chronosequence approach (space-for-time substitution), where a series of islands representing a chronological sequence of increasing time since eradication were used to draw inference on patterns in seabird recovery. We expected indices to vary with time since predator removal, reflecting the recovery of seabirds, whose calls dominate the nocturnal soundscape. Of the twelve indices we tested that have been previously used to describe biological patterns in soundscape recordings, we found acoustic richness performed best in indicating seabird recovery on islands. Almost half of the variation in acoustic richness on restored islands was explained by seabird recovery factors such as years since fox eradication and the presence of historical predator refugia. Moreover, acoustic richness was related to Leach's Storm petrel calls, a prominent element of nocturnal seabird soundscapes, as well as seabird call richness. This suggests that some indices can provide an initial rapid analysis of the difference between soundscapes of restored and a reference uninvaded site by identifying coarse differences in the amount of seabird acoustic activity, and different emergent patterns of acoustic environments. This can inform more detailed acoustic analysis by manual listening or semi-automated detection of specific species.

Comparing the efficacy of the ten alpha indices that describe individual recordings, those that characterized amplitude (e.g., median amplitude, temporal entropy, acoustic richness and number of events) increased with time since fox eradication, and some with other predictors of seabird recovery such as distance to source populations, and the presence of refugia. However, indices that characterized spectral complexity (e.g., spectral entropy, acoustic complexity index and the number of spectral peaks) were generally not well predicted by recovery variables. This may be related to a pattern of recovery in which increased seabird activity rather than diversity is the most dramatic result of invasive species removal. While soundscape intensity or amplitude is a simplistic way to gauge seabird call activity, intensity based indices are consistent with the idea that many seabirds use broad band, repetitive signals to communicate effectively in a noisy environment (Bretagnolle 1996). The emphasis in other soundscape studies on complexity indices may reflect the need to monitor passerine birds, which generally have more complex and discrete calls. Contrastingly, our results suggest that in soundscapes dominated by repetitive, broadband seabird calls with lower overall acoustic diversity than many bird choruses, complexity indices may be less useful.

The two beta indices, that characterized soundscape differences between restored islands and the reference, uninvaded island (Buldir), both captured increasing soundscape similarity to Buldir with increased time since predator removal. Whereas spectral difference only measures overlap between frequency spectra, cumulative spectral difference is also sensitive to the distances in frequency between spectral peaks. The cumulative spectral difference performed best, with 30% of variance explained by years since fox eradication, distance to source populations, and moonlight. Principal component analysis of the large pairwise spectral difference matrices allowed visualization of soundscape differences in two dimensions and for both indices, the first principle component was correlated with years of recovery. This

could be a good starting point for data exploration of acoustic datasets and comparing sites of varied restoration treatments.

While acoustic indices showed great promise characterizing soundscapes on restored islands, many index values from invaded Kiska Island (where introduced rats are still present) were similar to uninvaded Buldir Island, despite far fewer seabird calls (Buldir has millions of nesting storm-petrels, Kiska has almost none, Buxton et al. 2013). Few seabird calls, and noise from wind, rain, and waves apparently inflated acoustic indices. This is an issue for entropy based indices, and a reason why acoustic richness is calculated by weighting temporal entropy with a ranked measure of amplitude (Depraetere et al. 2012). In this study, weighting by amplitude may have been less effective because even in the absence of seabird calls, the sound of wind, waves, and rain generated significant signal amplitude. Our recordings on invaded Kiska island were made in 2010, a notably windy and rainy year that was likely to add abiotic noise. For beta indices based on differences between relative energy spectra, a call saturated spectrum from uninvaded Buldir Island appeared similar to a spectrum from invaded Kiska Island containing broadband wind and wave noise. This remains an issue in extending acoustic indices to noisy environments, emphasizing the importance of relating soundscape indices to relevant biological information in recordings. One index characterized invaded Kiska Island as strongly different from uninvaded Buldir Island: the number of acoustic events. This event-based index measuring amplitude in half second frames and relative to background noise was resilient to the longer duration wind and wave noises and sensitive to seabird call syllables. However only 11% of the variation in the number of acoustic events was explained by recovery variables. Index values from Kiska serve as a cautionary case that in the absence of at least some qualitative analysis, fully automated analysis can produce spurious results, and that researchers should be wary of temporal biases when recordings are not conducted

simultaneously across all sites. Given that our recordings were collected opportunistically over multiple years, and in some cases over non-overlapping time spans, it is possible that wind and weather patterns are driving some of the results. Ideally these could be accounted for by measuring environmental factors as co-variables.

Seabird acoustic activity and soundscape characteristics, while potentially being correlated with changes in nocturnal seabird relative abundance (Buxton et al. 2013), also reflect behavioral changes such as inherently variable colony attendance and vocal activity (e.g., Ancient Murrelet, Jones et al. 1990), or activity patterns unlinked to nest density (e.g., Manx Shearwater *Puffinus puffinus*, Arneill et al. 2019). Changing prey availability related to oceanographic conditions, weather (especially wind and cloud cover) and other factors across years, or even weeks are likely to affect activity levels. In our study, recordings were always during the month of July, but across different years leaving room for temporal bias in relative activity levels. Ideally all recordings should be collected simultaneously, or covariates of activity closely measured for all recordings. With respect to Ancient Murrelet (one of the nocturnal seabird species considered here), Gaston et al. (1988) and Jones et al. (1990) explicitly concluded that extreme night to night variation and inconsistent seasonal variation in counts of arrivals and calls “preclude their usefulness for population indexing”. Colonies with more unpaired individuals and courting behaviors, caused by colony growth, divorce rates, higher predation or loss of nesting habitat may be more acoustically active per individual than older colonies consisting of more breeders (Storey 1984; James 1985; Sheffield et al. 2006; Major & Jones 2011). While this may make it easier for acoustic indices to detect seabird restoration progress due to higher call rates per individual compared to an established colony, it may confound using any acoustic monitoring method to directly compare relative abundance to reference sites. It is important to remember that soundscape analysis is acoustic activity

related, not a direct population index or measure of relative abundance of any particular species. Even so, we believe acoustic activity provides a powerful, low-cost and scalable approach to evaluating nocturnal seabirds' response to island conservation efforts.

Despite its limitations, acoustic monitoring is particularly important for monitoring seabirds on remote islands, as other approaches can be cost prohibitive, dangerous, or logistically infeasible (Borker et al. 2014). In the case of seabird islands, invasive species removal could benefit 73% of threatened seabird species (Spatz et al. 2017), and having additional tools to measure patterns of recovery is important to evaluate outcomes. Acoustic recordings have already proven valuable in indicating trends in seabird relative abundance indirectly by measuring call activity (e.g., Buxton et al. 2013), and our acoustic index analysis strengthens the case for recording seabird colony soundscapes to monitor restoration outcomes. More studies that connect seabird behavior, abundance, phenology, and call activity with soundscape indices would strengthen passive acoustic recording as a seabird assessment approach.

Based on this study, we suggest that pairwise soundscape indices that compare restored areas against restoration target reference sites are a broad and rapid approach to measure patterns of recovery. Some alpha indices based on individual recordings effectively indexed restoration outcomes; however, a comparative approach (i.e., beta indices) allows a direct comparison to desired ecological conditions. In the absence of a reference condition, changes in single alpha indices should be used with caution. Indices should be considered as features of soundscape recordings to be analyzed in a multi index comparative framework against controls or reference condition, rather than as a direct index of ecological condition (Buxton et al. 2018; Phillips et al. 2018).

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While perhaps not as precise as direct measurements of call activity, soundscape indices identified similar patterns of recovery across restored islands, for comparatively little effort. This approach can be more easily scaled to include increased sampling, both in the number of sites and recording duration. At the archipelago scale, for multiple species, species detection approaches in many cases are not feasible given the time and effort required to design multiple detectors and audit detections. We suggest that a comparative soundscape approach does not replace but complements the acoustic monitoring toolbox for measuring the outcomes of seabird restoration activities. As a first pass, it can guide the identification of activity-rich time periods, identify the most acoustically diverse recordings, and broadly describe biological community patterns compared to a reference condition. Recording at sites with equivalent levels of non-target noise (and including year effects in sampling designs) will be particularly important for comparing soundscape indices, more than for comparing detected call activity, although extreme levels of wind and wave noise also decrease the effectiveness of call detection (Buxton & Jones 2012). Given decreasing costs and increasing capabilities of acoustic sensors, increased temporal and spatial sampling effort is one method of addressing variability driven by other sources of noise.

To measure progress in restoration of a wide array of degraded ecosystems, scalable approaches are required to measure outcomes. Acoustic recordings, collected at scale for low cost, and analyzed without laborious call detectors could be a complement to remote sensing of landscape variables when comparing restoration outcomes to reference sites.

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Table 1. Indices used in this study to describe nocturnal Aleutian Island soundscapes in July of 2008, 2009, 2010 and 2011.

| Index Name | Abbreviation | Description | Source |
|--------------------------------------|---------------------|--|------------------------|
| Temporal Entropy | H_t | Temporal Entropy (Sueur et al. 2008b) | Seuer et. al. 2008 |
| Spectral Entropy | H_f | Entropy of the normalized mean frequency spectrum | Seuer et. al. 2008 |
| Number of Spectral Peaks | NP | Number of spectral peaks (slope >.001) in the normalized mean frequency spectrum | Gasc et al. 2013 |
| Total Entropy | H | Product of Spectral and Temporal Entropy | Seuer et. al. 2008 |
| Median Amplitude | M | Median of the amplitude envelope | Depraetere et al. 2012 |
| Acoustic Richness | AR | Spectral Entropy x Ranked Median Amplitude | Depraetere et al. 2012 |
| Maximum Signal-to-noise Ratio | MaxSNR | Maximum Amplitude:Background Noise Level (25% Quartile Amplitude) | Towsey et al. 2013 |

| | | | |
|--|------------|--|----------------------|
| Acoustic Activity Fraction | PercAcoAct | The proportion of .5s Frames with amplitude about the 25% quartile | Towsey et al. 2013 |
| Number of Acoustic Events | NumEvents | The number of continuous sets of .5s frames where amplitude was above the 25% quartile | Towsey et al. 2013 |
| Acoustic Complexity Index | ACI | A measure of amplitude variability | Pieretti et al. 2011 |
| Spectral Dissimilarity | D_f | Difference between normalized mean frequency spectra | Seuer et. al. 2008 |
| Cumulative Spectral Dissimilarity | D_{cf} | Difference between normalized cumulative mean frequency spectra | Lellouch et al. 2014 |

Figure 1. Acoustic richness on six islands in the Western Aleutian Islands with varied history of invasive species. Acoustic richness increased on restored islands with time since predator removal. Points are mean values of acoustic richness for each acoustic sensor deployment, with $\pm 95\%$ confidence intervals around the mean. Points nudged to show overlapping confidence intervals. Dashed line is the best fit line from a linear mixed model that explained 44% of the variation in acoustic richness.

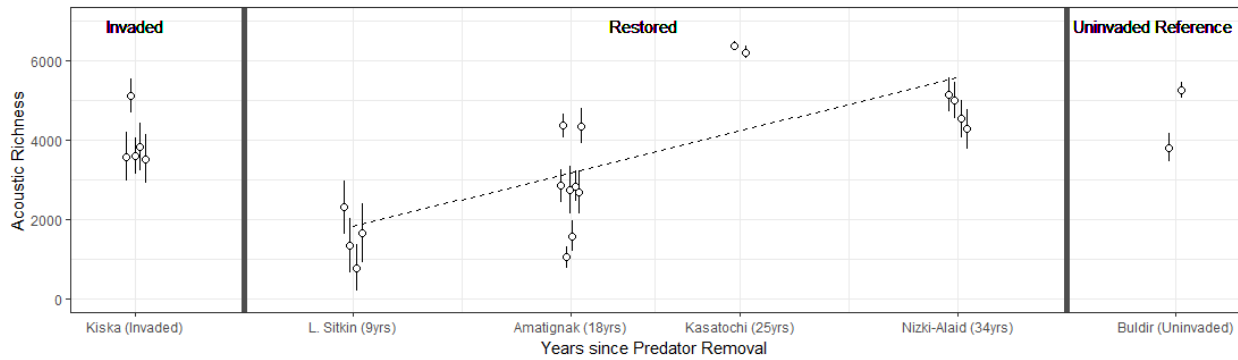


Figure 2. Soundscape difference of Western Aleutian Islands from restoration target, uninhabited Buldir Island as measured by Spectral Difference (above) and Cumulative Spectral Difference (below). On restored islands, soundscape differences from Buldir Island decreased with years of recovery from invasive predators. Points display the mean value for each deployment with $\pm 95\%$ Confidence Intervals. Points nudged to show overlapping CIs. Dashed line represents a fit line from a single fixed term linear mixed model treating deployments as a nested random effect.

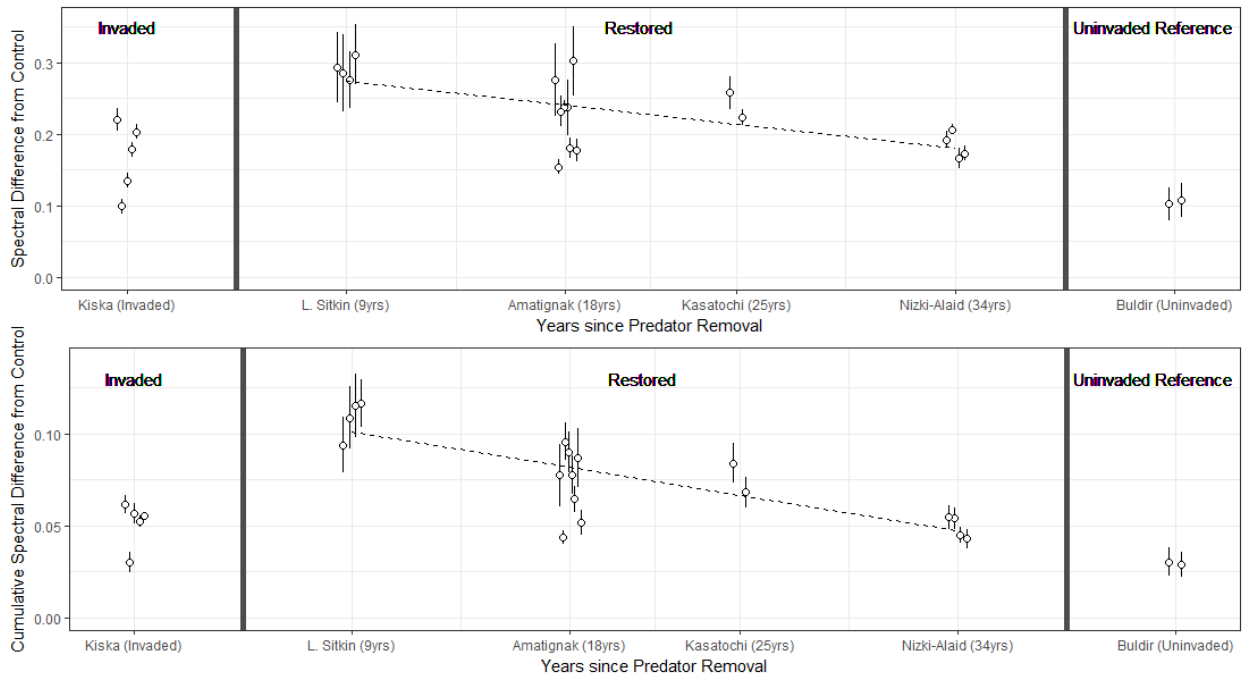


Figure 3. Principle components of a difference matrix of nightly spectral averages of recordings from six Western Aleutian Islands during the month of July. Error bars are $\pm 95\%$ confidence intervals of mean spectral differences (above) and mean cumulative spectral differences (below). Labels are abbreviations for site names and islands (Table S1) and are shaded by invasion history from purple (invaded), blue-green (increasing years since predator removal) to yellow (pristine, never invaded). Dashed error bars indicate a site had predator refugia present within 500m.

