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UNIVERSITY OF CALIFORNIA SANTA CRUZ

APPLYING ECOACOUSTICS TO BIRD CONSERVATION AND MONITORING

A dissertation submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ECOLOGY AND EVOLUTIONARY BIOLOGY

by

Abraham L. Borker

December 2018

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Lori Kletzer, Vice Provost and Dean of Graduate Studies Copyright © by

Abraham L. Borker

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Abstract

Applying ecoacoustics to bird conservation and monitoring

by

Abraham L. Borker

Passive acoustic monitoring is a transformative tool for increasing the scale of ecological monitoring. The biggest challenges remain in analyzing large volumes of recordings to produce ecological information useful for decision making. Ecoacoustics, a holistic, quantitative analysis of soundscapes and their emergent properties is an appealing way to distill information from many recordings, but new tools require rigorous studies to measure their efficacy tracking ecological patterns. This thesis contains three studies testing the efficacy of ecoacoustic approaches to monitoring species and communities. The first study uses simulations to test if a variety of indices of soundscape complexity, intensity and differences can measure realistic bird community changes in simulated dawn choruses. In addition, I explore combining indices to increase predictive power, and how the addition of anthropogenic noise and changes in bird behavior impact the usefulness of acoustic indices. The second study examines the acoustic monitoring of Cassin's Auklets (*Ptychoramphus aleuticus*), a chorusing colonial seabird that is notoriously challenging to monitor. I test how a traditional automated call detection compares to a novel approach based on energy spectrums of the entire soundscape to index auklet activity. I discuss how for some species, this approach may be more effective in indexing activity, and in this case is a reliable predictor or relative burrow density, and could be applicable for other nocturnal, vociferous seabirds. In the third study I move from single seabird species to seabird communities. I apply acoustic indices of soundscape differences, complexity and intensity to measure seabird restoration outcomes in the Western Aleutian Islands. I find that acoustic richness, and the spectral differences from a pristine reference island are predicted by years of seabird recovery and other factors that promote seabird recovery. Acoustic indices provided similar information to traditional and more laborious approaches. In summation, ecoacoustic approaches are a valuable part of the acoustic monitoring toolbox. Across all three studies, acoustic indices reflected meaningful ecological patterns, at a fraction of the time and effort needed for other approaches. This can greatly improve the scale and speed at which monitoring programs can inform management decisions and iteratively improve conservation outcomes.

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1. Introduction

Passive acoustic monitoring is a transformative tool in wildlife monitoring. Soundscapes, the ambient sonic environment, contain vast amounts of ecological information that many animals use to find food, shelter and mates (Farina et al. 2011). Applied biologists can inexpensively eavesdrop on this information to measure species distributions, abundance, and ecological patterns at wide spatial and temporal scales. These large acoustic datasets necessitate scalable analysis tools. Current approaches include spectrogram assisted listening (Swiston & Mennill 2009), semiautomated signal detection and classification algorithms (Mellinger & Clark 2000), and data driven indices that characterize entire recordings (Sueur, Pavoine, et al. 2008; Eldridge et al. 2015). The coupling of autonomous sensors and semiautomated analysis has greatly increased the scale and feasibility of acoustic wildlife monitoring (Van Parijs et al. 2009; Newson et al. 2015; Thompson et al. 2010).

Robust, scalable, cost-effective monitoring tools are urgently needed in the face of a global extinction crisis to measure the outcomes of conservation actions (Sutherland et al. 2004; Kapos et al. 2008, 2009; Ferraro & Pattanayak 2006). The adaptive management paradigm is widely advocated by academics, agencies and funders, however without scalable and cost-effective ways to measure ecological outcomes it is rarely fully realized in conservation or management (Keith et al. 2011; Walters 2007). Optimizing resources for monitoring is important to assure that resources that could have been used for conservation action are not wasted

(McDonald-Madden et al. 2010) and at the same time sufficient statistical power is retained in the evaluation of conservation outcomes (Legg & Nagy 2006).

An emerging approach to analyzing passive acoustic recordings considers the entire acoustic environment as an integrated reflection of biological communities (Pijanowski, Farina, et al. 2011; Sueur & Farina 2015). Soundscape indices (also referred to as "ecoacoustic" and "global acoustic" indices) characterize an entire recording and measure emergent properties such as spectro-temporal complexity and spectral differences (Sueur et al. 2014). The link between these acoustic features and community properties rests on behavioral theory regarding signal optimization (Marler 1955) and partitioning (Krause 1987), suggesting that patterns of soundscapes manifest patterns in biological communities. These emergent properties of soundscapes have attracted the attention of applied biologists who believe these emergent properties are a potentially powerful biodiversity monitoring tool (Sueur et al. 2012; Sueur, Pavoine, et al. 2008; Gasc et al. 2015; Depraetere et al. 2012; Gasc, Sueur, Jiguet, et al. 2013; Lellouch et al. 2014; Deichmann et al. 2017; Towsey et al. 2013; Buxton et al. 2016).

Index based approaches for biodiversity monitoring require rigorous testing and illustrative case studies if they are going to advance conservation outcome monitoring. In this spirit, this dissertation includes three studies that test the efficacy of soundscape-based indices to measure bird communities, and index patterns relevant to management and conservation outcomes.

The first chapter harnesses uses simulations and call libraries to test if soundscape indices can detect realistic changes in bird communities under idealized conditions. By controlling the simulation process, I test how common sources of heterogeneity, like alarm calling behavior and the addition of road noise impact the efficacy of these indices. The results indicate that indices do capture realistic change in the composition of the bird community represented in the simulated chorus. Spectral dissimilarity among choruses was highly correlated with bird community dissimilarity. In addition, many complexity indices had strong linear relationships with species richness. These relationships were robust to changing the proportion of alarm calls to songs, and the addition of moderate traffic noise. This study advances the application of soundscape index based approaches to monitoring forest bird communities by directly addressing concerns of changes in background noise and animal behavior on the efficacy of these indices, while simulating realistic levels of bird community changes.

The second chapter applies a soundscape approach to a familiar challenge of measuring the relative abundance of a focal species. Cassin's auklets (*Ptychoramphus aleuticus*) are a highly colonial seabird whose raucous colonies are filled with overlapping calls in conspecific choruses. Because of chorusing behavior and overlapping calls, traditional call detection approaches fail to accurately measure acoustic activity as a predictive index of relative abundance. We found that emergent spectral properties of colony recordings, specifically the amount of acoustic energy within frequency bands of auklet calls, was a powerful index of relative abundance

and compared this directly to an ineffective call detection approach. These results suggest that for other chorusing and highly vocal species, soundscape characteristics, rather than call counts, may be a better index of abundance.

The third chapter considers if automated soundscape indices can be used to measure restoration outcomes by comparing the soundscapes of restored seabird islands to a pristine reference site. We found that the strongest predictors of restored island soundscapes were years since invasive predator removal, and the presence of predator refugia. These findings echo a previous study that used call rates to identify patterns of seabird recovery, suggesting soundscape indices are a low-cost, scalable alternative to relatively laborious call detection and classification approaches for multiple species. This study provides a framework and case study for evaluating restoration outcomes against a reference condition using soundscape indices and suggests that soundscape indices are a powerful tool to measure other restoration outcomes. 2. Evaluating automated acoustic indices as a long-term avian community monitoring tool with simulations of dawn choruses, alarm calls and road noise.

Abstract

Inexpensive scalable tools are needed for biodiversity monitoring. Passive acoustic monitoring is a promising approach to measuring biodiversity at large scales, and emerging ecoacoustic indices are designed to measure community level patterns in biodiversity. To test the principles of these indices, we simulated environmental recordings based on realistic changes in a forest breeding bird community from a long-term monitoring program. Simulations contained songs and alarm calls belonging to 36 species in an agent-based model to produce three-minute simulated soundscapes. We added two experimental treatments to these simulated recordings, an addition of moderate road noise, and increased proportions of alarm calls. We tested the efficacy of twenty alpha indices to measure patterns in species richness, and the efficacy of nine beta indices to measure community dissimilarity under each experimental treatment. Most alpha indices were linearly related to species richness, many predicted species richness to within ten species. Experimental treatments often influenced the intercept, but not the slope of this relationship. Indices may work in the presence of road noise and alarm calling, but they are sensitive to changes in these conditions over time and could signal false changes in bird communities if used in isolation. Matrices generated from pairwise soundscape difference indices were highly correlated with a matrix of community dissimilarity, and this correlation was

robust to road noise and moderate levels of alarm calls. Simulations are far from empirical recordings, but our study suggests that ecoacoustic indices may be useful for monitoring realistic changes in bird communities. Empirical studies of soundscape indices in well monitored bird communities could help advance the emerging field to a scalable, powerful biodiversity monitoring tool.

Introduction

Low cost, high power tools to monitor biodiversity are necessary to meet global targets for biodiversity conservation and to improve the efficacy of the billions of dollars spent on conservation actions (Waldron et al. 2013). One such tool is passive acoustic monitoring which can be used to monitor hierarchical nested levels of biodiversity (Noss 1990) from trait diversity (Laiolo & Tella 2006), to populations (Mellinger & Clark 2000), and potentially scaling to community-ecosystems and the regional landscape scale (Lomolino et al. 2015; Gasc, Sueur, Pavoine, et al. 2013). A passive acoustic approach to monitoring biodiversity has three advantages over traditional approaches. First, sound recordings may be used to monitor everything from phenotypic diversity in song within a species, to population indices, up to beta diversity across the landscape. Second, data collection is automated, low cost (and decreasing), and scalable over space and time, lending itself to broad scale, long term monitoring programs. Finally, a permanent record of ecological conditions is preserved in a multi-faceted, information rich acoustic recording.

The last ten years have seen a proliferation of acoustic indices that characterize entire soundscapes, agnostic to the identity of callers (Pijanowski, Villanueva-Rivera, et al. 2011; Gasc et al. 2015; Sueur, Pavoine, et al. 2008; Sueur & Farina 2015; Burivalova et al. 2017; Fuller et al. 2015; Villanueva-Rivera et al. 2011). Building on theory, simulations and observational studies, indices are linked to community structure by mechanisms of signal optimization, partitioning and competition (Ey & Fischer 2009; Villanueva-Rivera 2014; Pijanowski, Villanueva-Rivera, et al. 2011; Krause 1987). These indices have the potential to transform acoustic monitoring from a species centric tool to a community-level monitoring tool. When combined with improvements in the quality and decreases in the costs of acoustic sensors, they may enable monitoring of biodiversity at scales needed to routinely assess the outcomes of management actions (Krause & Farina 2016; Sueur, Pavoine, et al. 2008). In this paper we use simulations to evaluate the potential of 29 published and proposed acoustic indices to measure patterns of communities and diversity from ambient sound recordings.

Acoustic indices come in two types: those that characterize an individual recording (e.g. Spectral Entropy and Acoustic Diversity) known as alpha indices, and those that characterize the distance between a set of recordings (eg Spectral Distance) known as beta indices (Sueur et al. 2014). Beta indices are theoretically well suited to measuring changes in community composition across time and variation between management units and controls. Consequently, they could enable conservation biologists to measure the positive and negative impact of human activities; providing

a comprehensive, integrated measure of ecological changes that reflects diversity, behavior and even abiotic conditions.

Unlike signal specific passive acoustic monitoring programs, acoustic indices are being adopted slowly by managers and practitioners. This may be due to 1) a lack of proof of concept studies that explicitly look at the predictive power of acoustic indices to measure changes in communities that are meaningful to managers 2) an indirect approach to tracking ecological changes 3) a lack of application to solving real world problems, and 4) a lack of clear understanding of how global acoustic indices relate to more traditional ecological metrics. In order to help managers evaluate if these approaches can be taken to scale, there is a need to develop theory, simulations, and empirical studies that link community dynamics to soundscape characteristics.

Previous studies have used simulations to test acoustic indices. Sueur et al. (2008b) described acoustic entropy and dissimilarity with randomly organized acoustic communities drawn from 45 Western Palearctic soniferous birds, insects and amphibians. A later analysis of 19,000 French breeding bird communities found that among empirical bird communities, spectral dissimilarity matrices of avian songs were correlated with phylogenetic distances, and the temporal acoustic dissimilarities with correlated with functional diversity distances (Gasc, Sueur, Jiguet, et al. 2013). Lellouch et al. (2014) used a combination of simulations and field recordings to test the utility of beta indices. Measuring dissimilarity matrices based on a) a binary

species community derived from a field recording, b) simulated recordings of bird choruses using referenced calls and c) the field recording. They found acoustic distances from simulations were correlated with community distance, however, this did not extend to the empirical recordings. They identified the relative abundance of species songs composing the acoustic community as the most striking difference in simulated vs empirical recordings and concluded that dissimilarity methods don't yet provide detailed information on changes in the species composition of bird communities. Gase et al. (2015) used one hundred of these same binary bird communities to test the sensitivity of alpha indices to a five sources of heterogeneity; song amplitude, song overlap, background amplitude, species identity and recording duration. An emphasis on binary species communities in previous literature has ignored an important benefit of acoustic sensors to conservation biologists who are interested in changes to community composition rather than species lists.

Here I use simulated choruses based on realistic bird communities. With these simulated choruses, I test two major hypothesis (1) Indices of acoustic complexity are positively correlated with species diversity among simulated choruses and (2) Indices of acoustic distance between simulated choruses are positively correlated with community dissimilarity. I test published alpha and beta soundscape indices to detect changes in species richness and community structure (Table 2.1). I also evaluate the efficacy of higher order and multivariate indices to predict richness and community change. To address skepticism in the extension of theory and simulations to empirical recordings, I test for the impact of alarm calls, and road noise

on the efficacy of acoustic indices, as both are widespread in real world conditions. I hypothesize that both alarm calls and road noise will decrease the predictive power of acoustic indices compared to a control as they increase the complexity and variation of simulated choruses independent of changes in species composition.

Materials and Methods

I simulated choruses based on 42 years of breeding bird abundance data from Hubbard Brook Experimental Forest (HBEF)'s 10ha study plot in New Hampshire (Holmes 2012; Holmes et al. 1986). During this period species richness varied between 12 and 25 species. Choruses were synthesized using an agent-based model of birds and simple calling behaviors for each of the 42 years, drawing on a library of species and behavior referenced bird recordings.

Signal Library

I built a library of 45 songs and 75 calls for the 36 species present at HBEF from the Cornell Guide to Bird Sounds Master Set for North America (Macauley Library 2014) and Xeno-canto (http://www.xeno-canto.org/), an online avian recording repository. For each species I selected short repeated phrases and classified them as songs, alarms or ambiguous calls. Clips ranged from <1s to 10s. All clips were then normalized to control for variable source amplitudes.

I used background noise recordings from Glacier National Park that contained no biological noise. These were captured using an Edirol R09 recorder in mp3 format at 128kbps. The microphone was 15m from the center of Going to the Sun road, 1.5m above the plane of the pavement at coordinates 48°40'15.3"N 113°49'34.8"W.

Simulation Process

Birds were randomly placed in a 200 row by 200 column matrix representing 4ha of forest (Figure 2.1). Bird abundance per 10ha was scaled down to per 4ha and rounded up to the nearest whole number. Each individual bird was programmed to call randomly at four discrete times in each 180s chorus. I used R (R Development Core Team 2011) and Sound eXchange (Bagwell 2016) to layer calls and individual birds onto a 180s audio sample. For species that had multiple vocalizations for a given type (e.g. alarm, song or call) I randomly chose a recording for each calling event. I attenuated each signal for distance to the sensor with a spherical attenuation model and constant signal source volume (44db / 1m). Output files were comprised of single channel 44100hz uncompressed audio files (*.wav) for each year.

Simulated Experimental Treatments

In total, 252 simulated choruses were produced for a crossed design of six treatments manipulating three levels of alarm call frequency and two levels of background noise. (Figure 2.2). The three treatments of calling behavior contained and increasing proportion of non-song vocalizations from no non-song vocalizations (0:1 Alarms:Songs), to a moderate treatment included three songs and a single alarm or call (1:3 Alarms:Songs), and an extreme treatment included an equal number of

songs and non-songs per individual bird (1:1 Alarms:Songs). I crossed these treatments with two levels of background noise, one with and one without road noise. For the null treatment, I selected a five second clip of background audio from Glacier National Park with no audible road noise or bird song, cross faded and repeated for 180s. For the road noise treatment (moderate traffic, twelve cars/minute), I randomly sampled with replacement twenty three 25s recordings of passenger car passes, so that a total of 36 randomly spaced car passes were in each 180s recording (similar to Mcclure et al. 2013).

Soundscape Analyses

For each file, I calculated twenty indices that describe a simulated chorus (alpha indices), and nine indices that describe the pairwise acoustic distance between simulated choruses (beta indices) (Table 2.1). Nearly all indices are reviewed by Sueur et al 2014. For event based indices described in Towsey et. al. 2013 I used a .05s window size to detect events above background levels. All recordings were pre-processed with a 300hz high-pass filter, and no additional processing (e.g. noise reduction). All analysis was performed in R (R Development Core Team 2011) using packages seewave (Sueur, Aubin, et al. 2008) and soundecology (Villanueva-Rivera & Pijanowski 2016). For alpha indices I also conducted principal component analysis, using the first principal component of variation as a multivariate index (Alpha PC1).

Evaluating Alpha Indices

I evaluated each index against the known species richness for the given simulation year. I performed an ANCOVA on each index to determine how the slope and intercept of the linear relationship were influenced by each experimental treatment (richness~index+alarmratio+alarmratio:index+road+road:index). I also used linear regression on a reduced single term model (richness~index) within each treatment to understand the effect of treatment on the 95% predictive interval for species richness.

I also tested for a combination of indices that best predicts species richness. I screened predictors by testing correlations between indices. For pairs of indices that were highly correlated (Pearson's r>0.8), I removed the index that had a higher mean correlation value across all indices. (Supplemental Figure 2.8). I also removed multivariate and second-order indices (eg. H (product of H_f and H_t), AR (product of ranked H and ranked M) as they are already combinations of indices (similiar to Towsey et al. 2013)) I used the package leaps (Lumley 2017) in R to test what combination of remaining indices (maximum of five) could best predict species richness within each experimental treatment, and used BIC for model selection, reporting the top five linear models for predicting species richness within each treatment. **Evaluating Beta Indices**

I compared a Bray-Curtis community dissimilarity matrix of the breeding bird community across years with distance matrices based on six published acoustic dissimilarity indices (Gasc, Sueur, Jiguet, et al. 2013; Sueur, Pavoine, et al. 2008), a Euclidean distance based on relative energy in 1khz frequency bins, a Euclidean distance based on alpha index measurements, and a Euclidean distance based on the first two principal components of alpha indices. I calculated the correlation between each distance matrix and the actual community distance matrix using Mantel's r statistic, and conducted permutations to measure significance (Legendre & Legendre 2012).

Results

Alpha Indices

Almost all univariate alpha indices showed significant linear relationships with species richness (Figure 2.3, Supplemental Figure 2.7, Table 2.2). In most of these, the intercept was influenced by the proportion of alarm calls or adding road noise (p_{index}), and for about half the indices, the slope of the relationship was changed by interactions of the index and either road or alarm treatment ($p_{alarm}, p_{traffic}$). Mean 95% prediction intervals for reduced models of species richness ranged from ±7.0 species to ±3.7 species.

Multiple regression models had smaller 95% prediction intervals than single term models (Table 2.3). Of the top models for each simulation treatment, prediction intervals ranged from ± 3.2 to ± 3.6 species. Multivariate indices better predicted species richness. The first principal component of the fifteen alpha indices described 32.5% of variation (Figure 2.4) and when regressed against species richness, had a predictive interval between ± 3.6 to ± 4.3 species depending on alarm call and traffic treatment.

Beta Indices

Acoustic distance matrices generated from beta indices were correlated with the Bray-Curtis distance matrix of the bird community, in nearly all cases (Figure 2.5, 2.6). The highest alarm call treatment (1:1 Alarms:Songs) dramatically decreased the matrix correlation of most indices and the community distance. The average Mantel's r was 0.32 across all treatments and indices. The highest performing index across all treatments was Spectral Dissimilarity (mean Adj $r^2=0.56$)

Discussion

This analysis of simulated avian choruses supports expanding evidence that acoustic indices can be used to measure community level diversity and are robust to sources of heterogeneity such as non-song calls and traffic noise. Many indices predicted the richness of a given chorus within 10 species, out of a gamma species pool of 36 species. Furthermore, in most cases over 40% of the variation in acoustic distance indices could be explained by community dissimilarity. These findings suggests that indices can detect realistic long-term changes in bird communities and are consistent with previous literature with simulated choruses (Sueur, Pavoine, et al. 2008; Gasc, Sueur, Jiguet, et al. 2013) based on old world bird communities, adding to a body of evidence that soundscape indices are useful community monitoring tools.

Many alpha indices were correlated with species richness, some being more robust to alarm calls and road noise than others, and a combination of alpha indices can significantly decrease predictive intervals around species richness. The best performing single order indices considered entropy (e.g. Temporal Entropy, Entropy of Spectral Maxima and Acoustic Richness) or a diversity measure (e.g. Acoustic Diversity). Indices that had weaker predictive relationships with species richness were still valuable in composite and higher order indices. For example, alpha indices that focused on events (e.g. the percentage of acoustic activity or the number of acoustic events) did not perform well in predicting richness but were heavily loaded in principle components that predicted community distance. A few intensity based indices performed well (Average Event Amplitude, Median Amplitude and Max Signal:Noise Ratio), but this may be confounded by a positive relationship between total bird abundance and richness in the HBEF bird community.

Complex non-acoustic phenomena, such as oceanic patterns (Wolter & Timlin 1993), behavior of soils (Dawes & Goonetilleke 2006), and water quality (Cao et al. 1996; Primpas et al. 2010) are often better predicted by multivariate indices than by univariate indices. In previous literature, higher order acoustic indices such as Total Entropy (Sueur et. al. 2008b) and Acoustic Richness (Depraetere et al. 2012) are a multivariate approach, as is weighting multiple indices (Towsey et al. 2013). In this study we took two approaches, exploring a principal component based index, maximizing the variability captured in a single index, as well as a multiple regression approach to test combinations of first order indices by resampling. The principal component index performed well (second lowest species richness predictive intervals across treatments), suggesting that this approach could have promise for analysis of empirical recordings. A potential weakness is this type of index could be influenced by highly sensitive or variable component indices in less controlled environments. Using resampling, we found the best performing multivariate linear regression models included both intensity related and spectral complexity related indices, supporting the theory behind second order indices like Acoustic Richness.

Most of the highest performing multiple regression models included at least one variable representing intensity (Median Amplitude, Maximum Signal:Noise, Average Event Amplitude), and paired this with a measure of complexity such as the Acoustic Diversity Index, Spectral Entropy, Number of Spectral Peaks or Avian Complexity Index. Some indices such as the Bioacoustic Index were found in all the top models for a given treatment but absent in nearly all others. The Acoustic Complexity Index was found in nearly all models predicting species richness with high levels of alarm callings, but conspicuously absent in other treatments. In sum these results suggest that when calibration studies can be done on a known community or training recordings, it's important to calculate multiple, orthogonal indices and build a multivariate index. It seems unlikely that there is a one size fits all multi-variate index to apply to different communities and soundscapes and effectively predict species richness. The selection of indices appears highly dependent on the soundscape of that area, including the anthropogenic noises and species signals (in this case relative rates of alarm calling).

Additional predictive power decreased after using three to four indices in combination (Supplemental Figure 2.9), likely due to limitation in the number of methodologically non-orthogonal indices. This suggests that future research should focus on expanding the toolbox of soundscape indices rather than refining complexity, or intensity indices. Multi label transition indices (Zhang et al. 2016) and machine learning (Eldridge et al. 2015) approaches could add new non-correlated measurements to increase the power of a multivariate approach to characterizing recordings. Perhaps as importantly, they need to be presented in accessible, transparent ways to managers and conservation practitioners such as R packages like seewave and soundecology.

Beta indices are particularly important in conservation and restoration, allowing managers to compare acoustic recordings to control sites, or past recordings when evaluating management outcomes. Consistent with the findings of Lellouch et al. (2014), we found that beta indices based on spectral distances reflected differences in community composition in simulated choruses. Of these previously published beta indices, our highest performing beta index was perhaps the most straight forward, spectral dissimilarity. The two new approaches to beta indices based on comparing alpha indices between recordings performed equally well and were more resilient to alarm calls and road noise. This suggests that characterizing recordings with nonpairwise approaches, and then using these metrics to estimate pairwise distances between recordings may be useful when dealing with noisy or variable recordings and should be tested with empirical recordings.

Contrary to expectations, the addition of alarm calls more often improved or had little effect on the predictive power of alpha and beta indices, suggesting that at moderate levels (1:3 Alarms : Songs), non-song vocalizations, often enhance rather than reduce the predictive power of alpha indices (Supplemental Figure 2.11). Only at a 1:1 ratio of alarm and calls to songs did predictive power of alpha indices begin to deteriorate, and the correlation between beta indices and community dissimilarity decreased (Figure 2.5).

An assumption of our analysis approach was a constant treatment effect over the 40 years of simulated choruses, however managers should concern themselves if alarm calling behavior increased significantly during a long-term monitoring program, or road noise changed background conditions. Either of these events could create false increases in predicted species diversity or reduce the correlation between community dissimilarity and acoustic distance, and potentially over-estimate community changes. Road noise generally decreased the predictive power of alpha indices (Table 2.2) and had a larger impact on index values than call types.
Importantly, indices responded differently, suggesting that it's important to consider distance to roads and traffic noise when deciding appropriate alpha indices and interpreting results. An advantage of long term acoustic monitoring approaches is the permanent nature of recordings that lend themselves to re-analysis and choosing the most appropriate indices at the time of analysis, rather than data collection; so while this is a concern, it can be addressed post-hoc. The effect of road noise was minimal and inconsistent on the predictive power of beta indices. Additionally, there was little evidence of an interaction effect of alarm calling and road noise on predicting community dissimilarity (Figure 2.5).

In general, we found that soundscape indices could be strong predictors of the community composition of simulated choruses, particularly when assembled into composite indices. These composite indices varied though, suggesting that calibration and training sets are needed to monitor new communities. Background noise and non-song call types had limited impact on the sensitivity of the indices we tested. However, while simulation approaches can always be refined and improved they will never mimic the complexity of empirical recordings. Thus, the important next step is testing these tools against natural recordings with associated community information. Studies that attempt to "calibrate" indices are few, (but notably Gasc et al. 2013*a*, Lellouch et al. 2014), and managers may want to see a suite of proof of concepts before determining if this is an effective approach for bird community monitoring. Ultimately, annotated empirical recordings to showcase and validate the utility of community level acoustic indices and rich case studies are needed. The most

detailed analysis of sound recordings will always involve human listening, but these indices provide a powerful first pass analysis, identifying broad changes and patterns. As with all passive acoustic monitoring programs, a significant benefit is an archived, permanent record of ecological conditions that can be re-analyzed as tools, as well as ecological insight from acoustic patterns improve.

The expansion of bioacoustics from focal recordings and species detection to analysis of communities and entire ambient soundscapes is challenging, but eventually fruitful for conservation. The benefits of this approach are enormous, acoustic indices are highly scalable: a home computer can characterize many thousands of hours of recordings without human input. Thus, as the spatial and temporal scales of monitoring projects increase, human hours stay relatively low. If we can link soundscape characteristics to the ecosystem characteristics of interest (eg. animal communities, phenology), we can measure ecological processes from micro to landscape scales, and how they respond to management, conservation, and human disturbance. Figures

Figure 2.1. Diagram of agent based model for simulating choruses. Birds (X's) were randomly placed in a 201x201 cell matrix. For each sound sample, volume was attenuated based on its distance (1 cell = 1 meter) from the center cell of the matrix.



Figure 2.2. Spectrograms of six 60s portions of simulated choruses, one from each experimental treatment of vocalization types and road noise based on the 2010 avian breeding community at Hubbard Brook Experimental Forest.



Figure 2.3. The relationship between six alpha indices and species richness over 42 years of simulated avian choruses, the full suite of indices is in Supplemental Figure 2.7. Purple, teal, and yellow lines represent treatments with increasing proportions of alarm calls to songs (0:1,1:3,1:1). Solid lines and circles denote treatments with moderate traffic noise compared to dashed lines and triangles without. Both traffic noise and alarm calls can change the slope and intercept of the relationship.



Figure 2.4. A) The relationship between multivariate first principle component of eighteen alpha indices (Table 1, Supplemental Figure 2.7) and species richness over 42 years of simulated choruses. Purple, teal, and yellow lines represent treatments with increasing proportions of alarm calls to songs (0:1,1:3,1:1). Solid lines denote moderate traffic noise compared to dashed lines without. B) Variable loading plot for principal component analysis of twenty alpha indices.



Figure 2.5. Mantel r values for matrix correlations between the Bray-Curtis community distances and pairwise beta indices. Solid lines denote treatments without road noise, and dashed lines denote treatments with no added road noise. Triangles represent significant (p<.05 via resampling) correlations, circles were non-significant.



Figure 2.6. Relationship between beta index acoustic distances from simulated choruses without road noise and Bray Curtis dissimilarity measurement of the bird community for 42 years of simulated choruses at Hubbard Brook Experimental Forest. Purple, teal, and yellow lines represent treatments with increasing proportions of alarm calls to songs (0:1,1:3,1:1).



Tables

Table 2.1. Descriptions, names and sources for the indices used to characterize

 simulated choruses and their acoustic distances (Modified from Sueur et al. 2014).

Index Type	Abbreviation	Index Name and Description
		Median of the amplitude envelope
Alpha - Intensity	М	(Depraetere et al. 2012)
		Background amplitude level (25%
Alpha - Intensity	Amp1Q	Quartile) (Towsey et al. 2013)
		Maximum Amplitude:Background
		Noise Level (25% Quartile Amplitude)
Alpha - Intensity	MaxSNR	(Towsey et al. 2013)
		Acoustic Activity Fraction (.5s Frames
		with events above background level)
Alpha - Intensity	PercAcoAct	(Towsey et al. 2013)
		Count of acoustic events (Towsey et al.
Alpha - Intensity	NumEvents	2013)
		Average duration of events (Towsey et
Alpha - Intensity	AvgEventDur	al. 2013)
		Average Event Amplitude (Towsey et
Alpha - Intensity	AvgEventAmp	al. 2013)
Alpha - Complexity	H _t	Temporal Entropy (Sueur et al. 2008b)

Alpha - Complexity	H _f	Spectral Entropy (Sueur et al. 2008 <i>b</i>)
		Entropy of spectral maxima (Towsey et
Alpha - Complexity	H _m	al. 2013)
		Entropy of spectral variance (Towsey et
Alpha - Complexity	H _v	al. 2013)
		Acoustic Complexity Index (Pieretti et
Alpha - Complexity	ACI	al. 2011)
		Number of peaks (slope >.01) (Gasc et
Alpha - Complexity	NP.01	al. 2013 <i>b</i>)
		Number of peaks (slope >.005) (Gasc et
Alpha - Complexity	NP.005	al. 2013 <i>b</i>)
		Number of peaks (slope >.001) (Gasc et
Alpha - Complexity	NP.001	al. 2013 <i>b</i>)
		Acoustic Diversity (H) (Spectral x
Alpha - Complexity	Н	Temporal Entropy) (Sueur et al. 2008b)
		Shannon's Index (db threshold -100)
Alpha - Complexity	ADI _{db100}	(Villanueva-Rivera et al. 2011)
		Shannon's Index (db threshold -50)
Alpha - Complexity	ADI _{db50}	(Villanueva-Rivera et al. 2011)
		Acoustic Richness (Ht * Ranked(M))
Alpha - Complexity	AR	(Depraetere et al. 2012)

		Bioacoustic Index / Area under the
Alpha - Complexity	BI	spectral curve (Boelman et al. 2007)
Beta	D _f	Spectral Dissimilarity (Sueur 2008b)
		Kolmogorov-Smirnov distance (Gasc et
Beta	K-S Distance	al. 2013b)
		Kullback-Leibler distance (Gasc et al.
Beta	K-L Distance	2013b)
		Itakuro-Saito distance (Gasc et al.
Beta	I-S Distance	2013b)
		Cumulative Dissimilarity (Lellouch et
Beta	\mathbf{D}_{cf}	al. 2014)
		Euclidean distance based on energy
Beta	1 Khz Bins	within 1khz frequency bins (this paper)
		Euclidean distance of first two Principal
	РСОА	Components of Alpha index variation
Beta	Distance	(this paper)

Table 2.2. P-values of ANCOVA results testing alarm call treatments as covariates (p_{model} term) in predicting species richness alongside 95% predictive intervals for linear models based on single indices predicting species richness per treatment (Background noise and Alarm:Song ratio). Indices (full descriptions in Table 2.1) are ordered by increasing mean prediction interval across all treatments.

						Range of 95% Predictive Interval of Species								
							Richness							
	P value from ANCOVA							t Backgro	ound	Traffic Background				
Index Name	pindex	palarm	ptraffic	pindex:alarm	pindex:traffic	palarm:traffic	0:01	1:3	1:1	0:01	1:3	1:1		
Ht	<.01	<.01	<.01	<.01	<.01	0.92	7.58	6.98	7.47	7.71	7.38	7.20		
Alpha PC1	<.01	0.04	<.01	0.64	0.67	0.90	7.47	7.24	8.59	8.60	8.21	7.81		
ADI _{db100}	<.01	0.82	<.01	0.66	<.01	0.13	8.21	7.85	10.50	8.84	7.67	8.78		
H _m	<.01	<.01	<.01	0.02	0.50	0.65	9.68	8.21	8.80	9.89	8.31	8.79		
AR	<.01	<.01	<.01	<.01	0.47	0.37	8.94	8.61	10.28	10.22	7.78	8.01		
ADI _{db50}	<.01	0.12	0.55	0.04	<.01	<.01	8.27	7.83	9.66	10.72	8.49	10.23		
AvgEventAmp	<.01	<.01	<.01	0.05	0.34	0.52	8.94	10.60	9.94	8.67	10.06	9.36		
Amp1Q	<.01	0.15	<.01	<.01	0.80	0.01	10.09	9.64	9.45	10.29	9.24	9.74		
H _v	<.01	0.89	<.01	0.74	0.21	0.96	8.23	8.04	9.33	10.71	12.20	12.11		
М	<.01	<.01	<.01	0.04	<.01	0.50	13.14	8.82	8.67	13.79	10.05	9.43		
MaxSNR	<.01	<.01	<.01	<.01	0.32	0.72	10.43	11.22	10.77	10.19	11.18	10.58		
Н	<.01	0.02	<.01	0.04	0.54	0.49	10.24	7.93	10.76	12.61	10.18	12.99		
BI	<.01	0.54	<.01	0.30	<.01	0.77	13.01	13.32	13.69	9.54	10.39	10.11		
NumEvents	<.01	0.98	0.86	<.01	<.01	0.01	10.05	14.27	14.25	11.14	10.99	10.91		
AvgEventDur	<.01	0.44	0.78	<.01	<.01	0.03	10.68	14.15	13.58	11.83	11.81	11.58		
PercAcoAct	0.10	0.99	0.17	<.01	0.03	<.01	8.36	13.27	13.73	12.76	14.15	14.28		
H _f	<.01	0.27	<.01	0.04	0.04	0.10	12.83	11.04	13.71	14.21	13.24	14.28		
ACI	0.01	0.02	0.01	0.17	0.44	0.63	14.16	13.65	12.71	14.12	13.62	12.87		
NP.005	<.01	0.16	0.04	0.21	0.90	0.26	14.18	14.11	13.29	14.15	13.86	12.03		
NP.01	0.66	0.98	0.84	0.02	0.23	0.38	14.23	13.16	14.25	14.09	13.85	13.95		
NP.001	0.03	0.88	0.29	0.34	0.56	0.61	14.11	14.22	13.82	14.13	14.24	13.46		

Table 2.3. The top five multiple regression models predicting species richness using multiple alpha soundscape indices within each crossed treatment of alarm calling and road noise. Models were limited to five terms and did not consider interaction terms. Models were ranked on BIC and report the Adjusted R² and mean 95% Prediction Interval (PI). Abbreviations in predictor variables from Table 2.1.

	Predictors	BIC	Adj. r ²	PI	Rank	Alarm Ratio	Noise
	BI+MaxSNR+Ht+M	-50.491771	0.7865796	6.7512447	1	0:1	Quiet
	$BI+MaxSNR+NumEvents+H_t+M$	-50.029589	0.7971078	6.6586216	2	0:1	Quiet
	BI+AvgEventAmp+MaxSNR+Ht	-49.848367	0.7832851	6.8030961	3	0:1	Quiet
	BI+AvgEventAmp+Ht	-49.380632	0.7667657	6.9770517	4	0:1	Quiet
	BI+H _t +M	-49.220098	0.7658726	6.9903312	5	0:1	Quiet
	ADI _{db50} +H _m	-54.425372	0.7797095	6.7011158	1	1:3	Quiet
34	ADI _{db50} +H _t	-54.419513	0.7796788	6.7011355	2	1:3	Quiet
	BI+H _t	-53.836034	0.7765966	6.7487177	3	1:3	Quiet
	ACI+ADI _{db50} +Ht	-53.831642	0.7902184	6.6167493	4	1:3	Quiet
	ADI _{db50} +BI+H _t	-53.657887	0.7893488	6.6297234	5	1:3	Quiet
	ACI+AvgEventAmp+H _t	-50.582504	0.7733454	6.8783597	1	2:2	Quiet
	$ACI+BI+AvgEventAmp+H_t$	-50.424673	0.7862384	6.7573901	2	2:2	Quiet
	ACI+AvgEventAmp+MaxSNR+Ht	-50.372383	0.7859721	6.761874	3	2:2	Quiet

	$ACI+BI+AvgEventAmp+MaxSNR+H_t$	-49.853045	0.7962531	6.6731638	4	2:2	Quiet
	H _f +BI+AvgEventAmp+M	-48.958164	0.7786427	6.8763421	5	2:2	Quiet
	NP.001+BI+AvgEventAmp+H _m	-46.055809	0.7628052	7.1180511	1	0:1	Road
	$BI+AvgEventAmp+H_m$	-44.968459	0.7409308	7.3532117	2	0:1	Road
	$BI + H_t$	-44.682498	0.7221948	7.524907	3	0:1	Road
	AvgEventAmp+M	-44.629456	0.7218437	7.5306527	4	0:1	Road
35	AvgEventAmp+H _m	-44.497667	0.7209695	7.543109	5	0:1	Road
	NP.001+Ht	-49.603289	0.7529085	7.0982001	1	1:3	Road
	$H_f + H_t$	-49.558972	0.7526477	7.1018101	2	1:3	Road
	$H_f + AvgEventAmp + H_m$	-49.036663	0.7648478	7.0069407	3	1:3	Road
	NP.001+ACI+Ht	-48.626186	0.7625383	7.041054	4	1:3	Road
	$H_f + ACI + H_t$	-48.246362	0.7603811	7.0730882	5	1:3	Road
	ACI+Ht+Amp1Q	-55.53086	0.7985363	6.4852751	1	2:2	Road
	ACI+H _t	-54.267329	0.778879	6.7151226	2	2:2	Road

ACI+MaxSNR+Ht+Amp1Q	-53.576409	0.8016923	6.5091009	3	2:2	Road
ACI+AvgEventDur+Ht+Amp1Q	-52.800889	0.7979966	6.5689505	4	2:2	Road
ACI+BI+H _t +Amp1Q	-52.490337	0.7964974	6.5937969	5	2:2	Road

Appendix

Supplemental Figure 2.7. The relationship between twenty alpha soundscape indices and species richness over 42 years of simulated avian choruses. Purple, teal, and yellow lines represent treatments with increasing proportions of alarm calls to songs (0:1,1:3,1:1). Solid lines and circles denote moderate traffic noise compared to dashed lines and triangles without. Shaded areas represent a 95% confidence interval around the slope.



Supplemental Figure 2.8. Correlation matrix of all alpha indices (left) and those in the final multivariate models, after removing those with correlations to other indices >.8 (right)



Supplemental Figure 2.9. Adjusted R² values for the highest performing multivariate models of alpha indices predicting species richness with one to five predictor variables





Supplemental Figure 2.10. Variable selection for top 10 ranked models predicting species richness within each treatment. Black boxes represented selected variables.

Supplemental Figure 2.11. Adjusted R² values alpha indices predicting species richness across alarm call and traffic treatments.



Supplemental Figure 2.12. Heuristic of experimental treatments for each of the 252

simulated choruses



3. Band limited acoustic energy, not call rate, predicts relative burrow density of Cassin's Auklets (*Ptychoramphus aleuticus*): implications for passive acoustic monitoring of chorusing species.

Abstract

Colonial seabirds that attend cryptic nest sites at night are often highly threatened, ecologically important and notoriously challenging to monitor. Cassin's Auklets (Ptychoramphus aleuticus) are one such colonial seabird with raucous nighttime nest site calls suited for passive acoustic monitoring. Unfortunately, the efficacy of acoustic detection tools can be limited by masked and overlapping signals in dense nighttime choruses. We propose a novel approach using a frequency band limited energy index of auklet activity levels and relative abundance. We tested this approach by comparing it with a conventional call detection approach using nighttime recordings from a well-studied auklet colony in central California. Moonlight, burrow abundance, and hour of the night explained 38% of variation in auklet activity measured by a band limited energy index. These factors explained only 11% of variation in detected auklet calls per minute using conventional call detection measures. Conventional call detection was a less robust index of Cassin's Auklet vocal activity and abundance compared to the band limited energy index due to call saturation, particularly during choruses. At the seasonal scale, band limited energy explained 63% of the variation in breeding densities across sites and predicted burrow density to within +/-0.13burrows/ m^2 . In contrast, the number of auklet calls detected per minute could not be used to predict burrow density. Our results expand the toolbox for monitoring the relative abundance of colonial seabirds with passive acoustic recording. The emergent patterns of acoustic

energy across frequencies was a powerful predictor of relative abundance. In addition to mitigating problems associated with call saturation, this approach also required significantly less human effort. This study and others suggest that acoustic monitoring, including band limited energy indices, can be important tools for seabird monitoring programs. If widely applied, this approach could fill a problematic knowledge gap in monitoring population trends for elusive burrow nesting seabirds.

Introduction

Monitoring seabird breeding populations on islands is critical to establishing baselines, detecting population trends, and measuring the efficacy of conservation actions; particularly for the 30% of extant seabirds at risk of extinction (Croxall, Stuart H M Butchart, et al. 2012). A review of global trends in seabird populations found that most monitored populations have declined dramatically since 1950, and there is a relative lack of monitoring data for nocturnal and elusive (i.e. burrow and crevice nesting) seabirds, for which declines are also likely (Paleczny et al. 2015). Even when crevice and burrow nesting seabirds are locally abundant in colonies, abundance is notoriously difficult to monitor due to cryptic nest sites, nocturnal attendance, and fragile habitat.

For seabirds that attend their colonies at night, monitoring is increasingly relying on acoustic activity rather than visual counts (Dufour et al. 2016; Croll et al. 2015; Raine et al. 2017; Harvey et al. 2016). Seabird calling activity has been found to be a reliable index of relative abundance for a growing number of species (Borker et al., 2014; Oppel et al., 2014), enabling seabird biologists and managers to monitor relative abundance of more species (particularly nocturnal and elusive nesters) at wider scales and lower cost. This approach has been transformative, particularly for seabird populations where traditional monitoring was infeasible due to cost, remoteness or fragile habitats.

While the adoption of passive acoustic monitoring has improved the scale of seabird monitoring efforts, significant challenges remain. The high temporal resolution and information density of autonomous passive acoustic recordings presents an enormous amount of data to interpret, requiring sub sampling or semiautomated approaches to detect and classify sounds of interest. Semi-automated tools rarely exist as turn-key solutions and methodological approaches are diverse with unique biases. In addition, manual human review of automated detections can be laborious and expensive. For the most vociferous seabirds, acoustic monitoring may paradoxically be the most challenging as overlapping calls may decrease the effectiveness of detectors (Buxton & Jones 2012). For many seabird species, acoustic communication is accomplished amongst high levels of both external and conspecific noise (Bretagnolle 1996; Aubin & Jouventin 1998). Many colonial birds have sharply modulated, wide spectra, repetitive calls that may increase signal detection and help receivers locate senders (Wiley & Richards 1982). These densely packed and overlapping calls can create a chorus of overlapping or masked signals, which can lead to calls being easily missed by most semi-automated detection tools. As a result, the use of call-based acoustic activity for highly vocal or densely nesting seabirds as an index of abundance may not yield meaningful information or risk

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misidentifying activity trends. An alternative to measuring individual calls is to measure the emergent pattern of relative acoustic energy across frequencies. This approach has been useful in measuring the activity of a chorusing aquatic insect (Desjonquères et al. 2018) and another colonial seabird, the Leach's Storm-petrel (R. Orben *pers. comm. 8/2018*), suggesting that it may have wide applications for monitoring chorusing species.

We investigated acoustic monitoring in a large colony of Cassin's Auklets (*Ptychoramphus aleuticus*), a densely burrow breeding, nocturnally chorusing, colonial seabird. This nighttime chorus has been described similarly to a frog chorus that ebbs and flows in intensity (Thoreson 1964). Or, as William Leon Dawson (1923) wrote, "A thousand dolorous voices take up the chorus. The uproar gets upon the nerves. Is this a bird lunatic asylum?". We chose this challenging environment to compare the efficacy of an index of acoustic energy within frequency bounds (henceforth, a band limited energy index) compared to a conventional call-based approach at a well-studied seabird colony. Given the raucous, overlapping nature of auklet choruses we hypothesized that band limited spectral energy would be a stronger predictor of burrow density than detectable call activity.

Materials and methods

Study Area and Species

Southeast Farallon Island, part of the Farallon Islands National Wildlife Refuge, is a 44ha granitic island 43km from San Francisco, California in the Central California Current. It is the largest seabird colony in the contiguous United States and has been the focus of a long-term monitoring program since 1971 (Sydeman et al. 2001; Ainley & Boekelheide 1990).

Southeast Farallon Island has a rich and varied acoustic landscape. Nighttime biological sounds include the barking of California sea lions (*Zalophus californianus*), the roar of Steller sea lions (*Eumatopias jubatus*), and vocalizations of four seabird species that are primarily nocturnal in their activity: Ashy Storm-petrel (*Oceanodroma homochroa*), Leach's Storm-petrel (*Oceanodroma leucorhoa*), Rhinoceros Auklet (*Cerorhinca monocerata*), and Cassin's Auklet. In addition, diurnal species often call during nighttime hours, so recordings include calls of the Western Gull (*Larus occidentalis*), Black Oystercatcher (*Haematopus bachmani*) and Pigeon Guillemot (*Cepphus columba*). The island is heavily exposed to the elements and both wind and wave noise are ubiquitous in recordings. Where Cassin's Auklets are abundant on the island, they are the most common biological element of the nighttime soundscape.

Cassin's Auklets were the most common seabird species on Southeast Farallon Island for over a century (Dawson 1911). However,populations have dramatically declined from over 100,000 in the 1970's (David A Manuwal 1974a) to an estimated 25,000 during this study (Warzybok et al. 2011; Carter et al. 1992). Cassin's Auklets were listed as near threatened in 2015 by the IUCN following significant population declines over the last forty years (Birdlife International, 2015) and are a California Species of Special Concern (Shuford & Gardali 2008). Breeding success and timing is predicted by regional ocean conditions, but generally auklets begin laying eggs in early March to late April (Wolf et al. 2009; Ainley et al. 2011). During this study 27.5% of auklets attempted a second brood, but this can be highly variable between years (Johns et al. 2017). Adult Cassin's Auklet have three types of calls; *Kut-I-er* (the most common ground call used for courting, advertisement and contact/alarm), *Kreerr-er* (a contact call occasionally used in flight), and *Kut-reeah* (an uncommon advertisement call) (Seneviratne et al. 2009).

Acoustic Data Collection

We deployed acoustic sensors at seven sites (Supplemental Figure 3.7 and Supplemental Table 3.1) on Southeast Farallon Island: three at existing Cassin's Auklet monitoring plots, and four more at sites chosen to represent a wide range of Cassin's Auklet burrow densities. We deployed sensors during two consecutive summers from May 29th through August 1st in 2010 and 2011, coinciding with the post-laying to fledging period of Cassin's Auklets.

We used Song Meter 2 devices (Wildlife Acoustics, <u>www.wildlifeacoustics.com</u>) outfitted with a single SMX-II omni-directional microphone connected through the left channel of each sensor and oriented vertically. The sensor was kept upright with rocks and protected from gulls with a wire cage. We used a 20kHz sampling rate to capture the frequency range of seabird vocalizations and a +36db setting gain was used to avoid clipping from loud acoustic sources (e.g. wind gusts). Sensors were programmed to make one-minute recordings every nine minutes (for a total of 6 minutes of sound per hour) between 10pm and 5am.

Auklet burrow counts

We counted all likely Cassin's Auklet burrows within 10m of recording sites after the breeding season in 2013 to determine auklet density within the effective range of the acoustic sensors. It is unlikely that relative burrow density between sites dramatically changed between 2010 and 2013. In ten separate long-term monitoring plots of varying burrow density, despite an overall increase in burrow density, there was no significant change in the proportions of burrows in each plot from 2010 to 2011 and from 2011 to 2013 (Supplementary Table 3.2).

Moonlight

Nocturnal activity patterns are known to decrease in periods around the full moon (Manuwal 1974, Ainley and Boekelheide 1990). Therefore, we calculated the moon azimuth and fraction illuminated during each recording using package *suncalc* (Agafonkin & Thieurmel 2017) in R. We calculated a moonlight index that ranged from zero to one from the fraction of the moon illuminated while above the horizon.

Spectrogram cross-correlation

We used spectrogram cross-correlation (Mellinger & Clark 2000), implemented in XBAT (Figueroa 2007) to detect the "Kut-I-er" call used in courting, advertisement, contact and alarm calling (Supplemental Figure 1). Specifically, we chose a clear recording of the ascending note II or "kut" syllable as described by Seniviratne et al. (2009) as our detection template. We tested this template against 70 minutes of randomly sampled recordings to measure accuracy and sensitivity of call detection. We chose a detection threshold (spectrogram cross correlation threshold=0.4) with moderate sensitivity, but high accuracy to measure patterns of relative activity, minimizing the effect of type I (false positive) errors on relative call rates. We reported the average rate of "kut" detections per minute for each hour of the night as an index of acoustic activity.

Spectral Analysis

We measured the mean relative amplitude across the frequency distribution of the time wave for the six minutes of acoustic data collected each hour using packages *seewave* (Sueur, Aubin, et al. 2008) and *tuneR* (Ligges et al. 2016). We used a fast fourier transform with hanning window length of 512 samples to measure relative energy in 256 frequency bins from 0-10kHz. We were interested in the amount of relative energy within the range of dominant frequencies of Cassins's Auklet "*kut*" syllables (Seneviratne et al. 2009), 2.3kHz +/- 0.25kHz (StdDev). Thus, we measured the ratio of mean relative energy within 2.05kHz-2.55kHz to mean relative energy outside this limited frequency window as an index of auklet acoustic activity (Figure 3.2). We refer to this metric as a band limited energy ratio (BLER).

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Comparing Acoustic Indices

We modeled the relationship between "kut" syllables per minute and the band limited energy ratio using a nested linear mixed model using package *nlme* (Pinheiro et al. 2017), and a corAR1 correlation structure. We modeled site within year as a nested effect with a random coefficient and intercept. We included a quadratic predictor to account for a possible curvilinear nature of the relationship between the band limited energy ratio and "kut" syllables per minute. We selected the final model by AIC score and report delta AIC below the next best model when reporting the top model. We reported 95% confidence intervals around model estimates to assess significance. Finally, we estimated the proportion of variance explained by fixed and random effects (pseudo R²) using conditional and marginal coefficients of determination (R_GLMM²) (Nakagawa & Schielzeth 2013) as implemented in the MuMIn (Barton 2017) package for R.

Modeling Patterns of Activity

To measure differences in both "kut" syllables per minute and the band limited energy ratio across hours of the night we fit nested linear mixed effect models using *lme* with a categorical fixed factor of hour, and a random nested effect of year within site. We fit each model using a corAR1 correlation structure that reduced temporal autocorrelation. We tested for differences across hours using an ANOVA.

To measure the factors that influenced acoustic activity we used a linear mixed model to test if burrow density, moonlight, and hour of the night predicted acoustic activity (with the band limited energy ratio or "kut" syllables per minute) at the hourly scale. We fit these models with a nested structure (of site and year) with random intercepts and a corAR1 correlation structure (night within year within site). We centered and scaled parameter estimates so that we could directly compare the effects of moon illumination and burrow density.

Seasonal Scale Acoustic Indices of Abundance

We took a simplified modeling approach as an example of how managers might use an acoustic activity index at the site level; calculating the mean acoustic index value for sites in each year and used this to predict burrow density, treating year as a categorical random factor. Because we no longer needed a temporal correlation structure we fit the model using package *lme4* (Bates & Sarkar 2007). By switching the dependent and independent variable we calculated 80% prediction intervals for burrow density given a future observation of the band limited energy ratio (via bootstrap (n=100,000) implemented in package *merTools* (Knowles & Frederick 2016)).

Results

We collected 36,974 one-minute recordings from May 29th through Aug 1st over two years (Figure 3.1). The spectrogram-cross correlation "kut" detector identified 69,680 likely Cassin's Auklet calls at an average rate of 1.89 calls per minute (range=0-4.5). The detector's accuracy was 92% based on reviewing a random sample of one hundred detections. The band limited energy ratio averaged 3.588 (range=0.36-10.61) (Figures 3.2, 3.3). Auklet burrow density within 10m from each acoustic sensor ranged from $0.04/m^2$ to $0.37/m^2$ (mean= $0.18/m^2$).

Comparison of Call Activity and Band Limited Energy Ratio

There was a positive relationship between the rate of "kut" syllables detected per minute and the band limited energy ratio (Figure 3.4). The best model predicting "kut" syllables detected per minute included the band limited energy ratio (Coefficient=0.69, 95% CI 0.56,0.82), a quadratic term for the band limited energy ratio (Estimate=-0.059, 95% CI(-0.066, -0.052)), the categorical variable year (Coefficient=0.73, 95% CI (0.48,0.99), and the interaction of the band limited energy ratio quadratic term and year (Estimate=-0.022, 95% CI (-0.026,-0.018)) as well as a random slope and intercept for year nested within site. This model performed better than a model without a quadratic term (dAIC=300.2). This quadratic term also increased the amount of variation in calls per minute explained by fixed effects (Marginal R_GLMM²= 0.35 versus Marginal R_GLMM2=0.33 without a quadratic term).

Acoustic Activity Patterns

The band limited energy ratio varied between hours (Nested ANOVA, $F_{df=6}=812.01$, p<.001) and 19 of 21 pairwise Tukey comparisons were significant (p<.05). "Kut" syllables detected by minute also varied by hour ($F_{df=6}=153.20$, p<.001), however post-hoc comparisons detected fewer pairwise differences (15 of 21 comparisons had a p<.05). Regardless of method used, pre-midnight hours had lower activity than after midnight hours (Figure 3.5).

The best fit model for predicting band limited energy ratio values at the hourly scale included hour, burrow density and moonlight as fixed factors in a random intercept model with a nested random factor of year within site and temporal correlation structure AR1 (name/year/day). By scaling and centering fixed factors we estimated the positive effect of burrow density on the band limited energy ratio (Coefficient=0.61, 95%CI= (0.28, 0.95) as twice the negative effect of moonlight (Coefficient=-0.13, 95%CI= (-0.18, -.086). These fixed predictors, along with a categorical fixed effect of hour explained 38% of variability in the band limited energy ratio (Marginal R_GLMM²= 0.38, Conditional R_GLMM²=0.46).

A similarly structured model was used to predict "kut" syllables detected per hour. However, we found no significant effect of burrow density on call rates (Coefficient=0.07, 95%CI (-0.23, 0.38), and a weaker effect of moonlight (Coefficient=0.07, 95%CI (-0.098, -0.046)). These predictors, along with categorical fixed effect of hour only explained 11% of variability in calls per minute (Marginal R_GLMM^2 = 0.11, Conditional R_GLMM^2 =0.35).

We also fit a model at the seasonal scale, to determine if burrow density at each site could be predicted by the seasonal mean of acoustic activity (measured by the band limited energy ratio or "Kut" syllables per minute). This is a realistic way in which the tool would be applied by managers, measuring acoustic activity across a season rather than a single hour or night. This model contained only 14 data points and a random intercept for each year. The mean band limited energy ratio was strongly predicted by burrow density within 10m (Coefficient=0.017, 95%CI= (0.010, 0.024)) explaining 63% of variation in the band limited energy ratio (Marginal $R_GLMM^2=0.63$). The random intercept for year only explained an additional 9% of band limited energy ratio variance (Conditional $R_GLMM^2=0.72$), and this model had lower AIC than one that allowed the slope to change between years (dAIC = 3.22). Bootstrapped 80% prediction intervals for future measurements of the band limited energy ratio averaged +/- 0.13 burrows/m². By contrast, the mean rate of "kut" syllables per minute over the season was not predicted by burrow density (Coefficient=0.0022, 95%CI (-0.0028, 0.0072)), and this model failed to explain meaningful variance in "kut" notes per minute (Marginal $R_GLMM^2=0.033$, Conditional $R_GLMM^2=0.55$) (Figure 3.6).

Discussion

We found strong evidence that emergent spectral properties of long-term environmental recordings can be used as a powerful index of abundance for a chorusing colonial seabird at the seasonal scale. Specifically, the ratio of acoustic energy within the frequencies of Cassin's Auklet vocalizations to background acoustic energy can be used as an index of relative abundance. Prediction intervals for burrow density based on a seasonal average of band limited energy ratio were +/-0.13 burrows per m². This tool can be used by managers to estimate auklet burrow
abundance where burrow counting may be logistically or cost prohibitive and expand monitoring programs for minimal cost and effort.

Multiple lines of evidence suggested that the band limited energy ratio accurately captured patterns of Cassin's Auklet vocal activity. First, at the hourly scale we saw a negative effect of moonlight on the band limited energy ratio, corroborating patterns of auklets restricting activity on moonlit nights due to predation risk (David A Manuwal 1974b; Nelson 1989; Ainley & Boekelheide 1990). Second, there was greater auklet acoustic activity in early morning hours as previously documented (Ainley & Boekelheide 1990; David A Manuwal 1974b). Finally, and most importantly, there was a strongly predictive relationship (Marginal $R_GLMM^2=.63$) between BLER and burrow density in both years at the seasonal scale (Figure 3.6).

Our study provides evidence that under some conditions, automated call detection rates can be a poor way to measure acoustic activity or predict the relative abundance of a colonial seabird. We propose that the spectral patterns are a powerful alternative when calls are densely packed and overlapping, making them difficult to detect. In comparing the two approaches directly, we found that detectable "kut" syllables peaked below the highest amounts of activity as measured by the band limited energy ratio (Figure 3.4). The automated detector failed to detect many overlapping and masked calls, while the band limited energy ratio approach was able

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to capture the effect of the increased acoustic energy during these intense choruses of overlapping calls.

Measuring mean frequency spectra of recordings is relatively straightforward, and while computationally expensive, does not require significant human supervision unlike designing and evaluating call detection algorithms. The efficacy of a band limited energy ratio to index acoustic activity is most applicable to chorusing, highly vocal, or densely nesting species that make up the dominant element of the soundscape, particularly within their respective frequency range. There are potential pitfalls of a strictly band limited approach that should be considered before being applied to other species and soundscapes. Energy measures are very sensitive to non-target signals influencing the index of acoustic activity. This is especially true if the activity of interest is low, as it doesn't discriminate between calls of the species of interest and other sounds in that frequency range. Non-target signals within the frequency band obscure the relationship of acoustic energy and calls, and signals outside the band may diminish the response of the ratio to increases in calls. In the range of approaches to analyzing acoustic data these energy approaches are crude but may be effective when coupled with inspecting recordings and a greater holistic understanding of the soundscape under analysis, including sources of biological and non-biological noise such as waves crashing and the effect of wind. We chose to calculate a ratio to account for common wide spectrum noise (both from wind and biological sources) present in oceanic seabird island soundscapes, but in quieter soundscapes, band restricted energy may also be a

useful index. At the hourly scale, only 38% of variation in our band limited energy ratio acoustic activity index was explained by burrow density, hour and moonlight, leaving a large portion of acoustic activity unexplained. Wave noise, the impacts of wind, and the activity of non-target species all had large impact on recordings and the index. This low portion of variation explained at the hourly scale illustrates the importance of long duration recordings to deal with high variability in acoustic indices.

Two weakness of this study are that we did not measure burrow occupancy and that burrow counts were not conducted until two years after acoustic data collection. On Southeast Farallon Island most burrows are occupied annually, however because they persist between years, burrow density does not translate directly into breeding abundance. However, burrow occupancy is exceedingly difficult to measure, so counting burrow entrances is often a de-facto measure of breeding density, particularly for measuring relative abundance at large scales. In fact, acoustic indices may be more likely to directly index the number of breeding individuals rather than available nesting sites. Secondly, it would have been ideal to conduct independent burrow counts after the 2010 and 2011 breeding seasons. However, when we examined burrow density trends in ten monitored study plots around the island, we found there was no change in the proportions of burrows in each plot from 2010 to 2011 and then to 2013 (Supplemental Table 3.2). That is, a plot with high burrow density remained a high-density plot, even if the absolute number of burrows changed between years. In fact, burrow counts were 37% higher

in 2011 versus 2010 (Warzybok et al. 2011). This may explain the higher intercept in the fitted relationship between band limited energy and burrow density in 2011 compared to 2010 (Figure 3.6).

This study has opened up future directions for Cassin's Auklet monitoring, and the potential of designing a scalable range-wide monitoring program for this sentinel of ecosystem change (Wolf et al. 2010). Even though we sampled over two months of the summer breeding season, auklet breeding can begin as early as March in some years. Considering auklets breeding flexibility, earlier season recordings may have been able to capture seasonal patterns and begin to estimate phenology. Based on our findings, deployments could be made longer by reducing sampling effort to early morning hours when auklets are more vocally active. It's also important to test these methods across the broader range of Cassin's auklet breeding colonies in the Northeast Pacific where soundscapes, and the efficacy of analyses approaches may differ.

Monitoring acoustic activity through spectral properties may also have applications for other colonial seabirds, particularly those that nest in dense, loud colonies where calls are frequent and overlapping. Comparison studies of approaches to measuring acoustic activity would be helpful, particularly with problematic taxa for which few scalable abundance monitoring approaches exist. Even for species where call activity measured by call detectors has been effective, band limited energy approaches may be more efficient, requiring less time and effort in data analysis. This approach may also be useful in measuring other chorusing animals such as cicadas, frogs, and others producing overlapping signals in discrete frequencies.

The recent advances in both acoustic recorders and automated acoustic analysis suggest that acoustic monitoring programs hold great promise for monitoring seabird populations. Recording hardware has continued to come down in cost as the market for these devices expands (Hill et al. 2018). Powerful detection algorithms (Katz et al. 2016), ecoacoustic indices (Villanueva-Rivera & Pijanowski 2016) and analyses toolboxes (Towsey et al. 2012) are increasingly available in freely accessible open source software. The archival and information-rich nature of sound recordings lends them to re-analysis as tools and questions evolve. To advance the passive acoustic monitoring of colonial seabirds, researchers should consider utilizing sites of known or closely monitored abundance to calibrate acoustic indices that can be used to estimate abundance in inaccessible or remote sites. Relatively inexpensive data collection and management makes acoustic data collection a low risk endeavor, and at best a transformative tool to increase the temporal and spatial scale of monitoring effort. Ultimately acoustic monitoring could go a long way in estimating population trends for nocturnal and burrow nesting seabirds and understanding how their populations respond to threats and conservation actions.

Figures

Figure 3.1. Long Term Spectral Averages of Relative Energy during nighttime hours at six sites on Southeast Farallon Island during June and July, in 2010 and 2011. Each column represents an averaged spectrum of relative energy for a single night based on 42 one-minute samples. Sites are presented from top to bottom in order of decreasing ranked abundance of Cassin's Auklet (*Ptychoramphus aleuticus*) acoustic activity.



Figure 3.2. Five second spectrograms, and respective mean spectral energy distributions, of nocturnal soundscapes at Southeast Farallon Island. From top to bottom, these illustrative short clips are from recordings that scored within the lowest, middle and highest quintiles of Cassin's auklet acoustic activity as measured by a frequency band limited energy ratio. The right column of plots shows the mean distribution of acoustic energy across the frequency spectrum. The range of frequencies associated with Cassin's Auklet "kut" syllables and used to calculate the energy ratio is indicated by dashed lines.



Figure 3.3. Cassin's Auklet (*Ptychoramphus aleuticus*) acoustic activity patterns measured by band limited energy ratio (BLER; 2.05kHz-2.55kHz) during June and July, 2010 and 2011 on Southeast Farallon Island. Sites are presented from top to bottom in order of decreasing ranked abundance of Cassin's Auklet acoustic activity.



Figure 3.4. Relationship between detected "kut" syllables per minute and a band limited energy ratio (2.05kHz-2.55kHz) as indices of Cassin's Auklet acoustic activity on Southeast Farallon Island during 2010 and 2011. Curves represent predicted fits of a linear mixed model nested by site within year.



Figure 3.5. Hourly patterns of Cassin's Auklet acoustic activity at three sites on Southeast Farallon Island collected over two years using a band limited energy ratio (2.05kHz-2.55kHz) (purple) and calls per minute (green). From left to right sites contain high, medium and low auklet burrow abundance. Notched boxplots hinges represent 25th and 75th percentiles, and whiskers are the range up to 1.5 times the IQR from the hinge, outliers beyond that range are indicated by points.



Figure 3.6. Relationship between Cassin's Auklet burrow density and mean acoustic activity measured by a band limited energy ratio and "kut" syllables detected per minute on Southeast Farallon Island in 2010 (purple) and 2011 (green). Solid lines are predicted linear mixed model fits for each year. Dashed lines represent 80% prediction intervals around the model fit.



Appendix

<image>

Supplemental Figure 3.7. Map of sampling sites on Southeast Farallon Island.

Latitude	Longitude	Location Name	Burrow Density within 10m				
			(burrows/m ²)				
37.70016	123.00314	Northeast corner of Egger's Building	0.366				
37.69900	123.00224	Lighthouse Trail	0.089				
37.69780	123.00042	Carp Shop (E. Landing)	0.051				
37.69916	123.00463	Nest Boxes	0.045				
37.70027	123.00358	The Gap (L9)	0.331				
37.69778	123.00154	Generator Shed (E4)	0.051				
37.69641	123.00180	Road to Nowhere (F1)	0.178				

Supplemental Table 3.1. Locations of acoustic sensors and associated burrow densities.

Supplemental Table 3.2. Cassin's auklet burrow abundance in 12 long term monitoring plots (A-L) in the years of this study. Despite an increasing population, pearson's χ^2 statistic showed no change in the relative proportion of burrows in each site (2010v2011 $\chi^2_{df=11}=7.60$, p=0.765; 2010v2013 $\chi^2_{df=11}=16.95$, p=0.11; 2011v2013 $\chi^2_{df=11}=18.59$, p=0.07)

Year	A	В	С	D	E	F	G	Η	I	J	K	L	Total
2010	14	9	16	10	9	3	11	9	73	29	0	18	201
2011	17	14	27	12	9	4	17	9	90	54	1	23	277
2012	31	25	33	15	11	4	14	-	91	48	6	26	304
2013	31	31	26	17	15	4	16	11	98	60	7	34	350

Supplemental Figure 3.8. A spectrogram of a single Cassin's Auklet "*Kut-I-eer*" vocalization with the introductory "kut" syllables denoted with yellow dashed lines (described in Seneviratne et. al. 2009) from a field recording used in the study.



Supplemental Figure 3.9. Time series of indices of Cassin's Auklet acoustic activity and moonlight on Southeast Farallon Island. Faded color lines are decomposed seasonal trend of sites from low ranked auklet abundance (purple) to high ranked auklet abundance (yellow). Thin lines are a LOESS smoother line (span=0.2) with a shaded standard error interval. Black lines are hourly levels of moonlight (fraction of the moon illuminated when above the horizon).



4. Does seabird recovery predict soundscape indices? A comparative study in the Western Aleutian Islands

Abstract

Measuring restoration outcomes is essential, but challenging and expensive, particularly on remote islands. Acoustic recording increases the potential scale of ecological 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. We evaluated soundscape indices as measures of seabird recovery following invasive predator removal in the Aleutian Islands. We used recordings of nocturnal seabird soundscapes from six islands with varied histories of predator removal, ranging 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 levels of

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 will be 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 (Buxton et al. 2018; Hill et al. 2018; Wrege et al. 2016; Ross et al. 2018). However, passive acoustic recording 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 (Sueur et al. 2014; Pijanowski, Villanueva-Rivera, et al. 2011; Towsey et al. 2013). 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 (Lellouch et al. 2014; Gasc, Sueur, Jiguet, et al. 2013; Harris et al. 2016), measure the impacts of ecological disturbance (Deichmann et al. 2017; Burivalova 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. However, soundscape indices come with potential pitfalls necessitating careful examination of their relationship to ecological conditions before these approaches can be taken to scale. Namely, characterizing biological, geological, and anthropogenic sources driving soundscape indices is essential to link ecological condition to soundscape indies. 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 (Bertucci et al. 2016; Burivalova et al. 2017; Fuller et al. 2015)).

Invasive predator removal as a restoration technique on islands has created substantial conservation gains (Jones et al. 2016). In some cases, outcomes have been varied, where ecosystem responses range from rapid (Whitworth et al. 2013), to prolonged (Beltran et al. 2014), complex (Donlan et al. 2002), and unanticipated (Bergstrom et al. 2009). Because of their role as ecosystem engineers (Lorrain et al. 2017) and threatened status (Croxall, Stuart H. M. Butchart, et al. 2012), seabirds are often the target beneficiaries of invasive species removal (Brooke et al. 2018) . However, seabird characteristics such as cryptic nesting, sensitivity to disturbance, and nocturnal nesting activity make some seabird populations a challenge to monitor using traditional methods. Passive acoustic monitoring has been applied as an efficient means of monitoring seabird populations (Buxton & Jones 2012; Borker et al. 2014; Oppel et al. 2014; Croll et al. 2015).

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 (Croll et al. 2005; Maron et al. 2006; Buxton et al. 2013; Ebbert & Byrd 2000). Buxton et al. (2013) investigated Aleutian nocturnal soundscapes using seabird call detectors and found that time since predator removal and presence of nearby predator refugia (areas that invasive predators could not access when they were present, such as talus, cliffs and offshore islets) were the most important positive predictors of seabird acoustic activity. A 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 these automated tools, this analysis required a great deal of hours designing call detectors and evaluating automated detections. Thus, here we test if soundscape indices can capture similar patterns of seabird recovery, which could measure 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 pristine reference islands. Furthermore, 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

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 and

have made many nesting seabird species rare or absent (Ebbert & Byrd 2000) on islands they invaded. Rodents 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 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). 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. 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" (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).

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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). 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 (detailed in Buxton et. al. 2013).

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 4.1). 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.

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Quantitative methods

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, site and islands as a nested random factor using package *lmer* (Bates & Sarkar 2007). 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 R² (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 reference 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.

Finally, to examine which aspect of the nocturnal soundscape was driving each index we constructed a linear mixed effect model. 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 0 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 recording 703 nights (Supplemental Figure 4.4, Supplemental Table 4.4). 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 years since fox eradication, distance to source populations, refugia presence, and moonlight (Table 4.1). 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 (Marginal $R^2 = 0.44$; Figure 4.1). Median amplitude and temporal entropy (which are multiplied to produce acoustic richness) were both also positively related to years since fox eradication and presence of refugia but had considerably less variation explained (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 $R^2 < .1$).

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The two beta indices, spectral difference (D_f) and cumulative spectral difference (D_{cf}) from never invaded Buldir Island decreased with increasing years since predator removal (Figure 4.2). Years since predator removal, distance from source populations and moonlight explained 30% of the variation in cumulative spectral difference from Buldir, the reference condition (Table 4.2).

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 (Figure 4.3). 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, $p_{df=499} < .05$, Spectral dissimilarity r = 0.32, $p_{df=499} < .05$) 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 4.2). These factors described a low proportion of variance in indices (Marginal R² values ranged from 0.01 to 0.15), with the highest variance explained for temporal entropy, ACI, and acoustic richness (Marginal R² > 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 models.

Discussion

We tested the effectiveness of acoustic indices as a technique to compare soundscapes of Aleutian Islands with increasing time since predator removal against a never invaded reference sites. 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 indexing 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, the most 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 reference sites 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 the 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 island, Buldir, both captured patterns of recovery.

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 Kiska Island (where introduced rats are still present) were similar to the pristine 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 and waves likely 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 waves generated significant signal amplitude. Kiska Island is larger than the other islands in this study, and topographic complexity possibly resulted in two problematic recording sites: one site (KIS_C), on a very steep cliff clearly captured the sound of oceanic waves, and another picked up small wavelets from an intermittent stream (KIS_P).

For beta indices based on differences between relative energy spectra, a seabird call saturated spectrum from Buldir Island appeared similar to a spectrum from Kiska Island containing broadband wind and wave noise (Supplemental Figure 4.5). 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 Kiska Island as strongly different from Buldir Island, the number of acoustic events (Figure 4.3). 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 soundscape monitoring sites should have comparable levels of non-target noise.

Based on this study, we suggest that pairwise soundscape indices that compare restored islands with a pristine reference sites are a coarse and rapid approach to measure patterns of recovery. Some alpha indices based on individual recordings effectively indexed seabird restoration outcomes; however, a comparative approach (i.e., beta indices) allows a direct comparison to desired ecological conditions is important. 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).

While perhaps not as effective as measuring seabird call activity directly as an index of recovery, 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 index approach doesn't 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 is 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.
Seabird acoustic activity and soundscape characteristics, while indicative of seabird relative abundance, also reflect behavioral changes in individuals. Growing colonies with more unpaired individuals and courting behaviors may be more acoustically active per individual than older colonies consisting of more breeders (Storey 1984; James 1985). 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 introduce error when using any acoustic monitoring method to compare relative abundance to reference sites.

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 tools to measure patterns of recovery is important to evaluate outcomes. Acoustic recordings have already proven valuable in indexing seabird abundance through call activity, 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, call activity with soundscape indices would strengthen passive acoustic recording as a seabird monitoring approach. 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.

Figures

Figure 4.1. 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 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 4.2. Soundscape difference of Western Aleutian Islands from pristine 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 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 4.3. 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 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.





Tables

Table 4.1. Indices used in this study to describe nocturnal Aleutian Islandsoundscapes in July of 2008, 2009, 2010 and 2011.

Index Name	Abbreviation	Description	Source
Temporal Entropy	H _t	Temporal Entropy (Sueur	Seuer et. al.
		et al. 2008 <i>b</i>)	2008
Spectral Entropy	H _f	Entropy of the	Seuer et. al.
		normalized mean	2008
		frequency spectrum	
Number of	NP	Number of spectral peaks	Gasc et al. 2013
Spectral Peaks		(slope >.001) in the	
		normalized mean	
		frequency spectrum	
Total Entropy	Н	Product of Spectral and	Seuer et. al.
		Temporal Entropy	2008
Median Amplitude	М	Median of the amplitude	Depraetere et al.
		envelope	2012
Acoustic Richness	AR	Spectral Entropy x	Depraetere et al.
		Ranked Median	2012
		Amplitude	

Maximum Signal-	MaxSNR	Maximum	Towsey et al.
to-noise Ratio		Amplitude:Background	2013
		Noise Level (25%	
		Quartile Amplitude)	
Acoustic Activity	PercAcoAct	The proportion of .5s	Towsey et al.
Fraction		Frames with amplitude	2013
		about the 25% quartile	
Number of	NumEvents	The number of	Towsey et al.
Acoustic Events		continuous sets of .5s	2013
		frames where amplitude	
		was above the 25%	
		quartile	
Acoustic	ACI	A measure of amplitude	Pieretti et al.
Complexity Index		variaibility	2011
Spectral	D _f	Difference between	Seuer et. al.
Dissimilarity		normalized mean	2008
		frequency spectra	
Cumulative	D _{cf}	Difference between	Lellouch et al.
Spectral		normalized cumulative	2014
Dissimilarity		mean frequency spectra	

Table 4.2. Best fit models and scaled predictor coefficients predicting soundscape index values from predictors of seabird recovery and moonlight on four restored islands in the Western Aleutians. Models were fit with a random intercept and nested by year, within site, within island. Best fit models were selected by AIC, coefficients estimated by maximum likelihood and 95% confidence intervals were generated by model bootstrapping. Proportion of variance explained by fixed and random effects was estimated using conditional and marginal coefficient of determination. Indices are sorted in decreasing order of proportion of variance explained by recovery factors.

Index	Best fit model predictors	Intercept	Years since Predators	Distance to Source	Refugia presence	Moonlight	Marginal GLMM_R ²	Conditional GLMM_R ²
Acoustic Richness (H _t x Ranked MedianAmp)	years+refugia	2340.51 (1460.76, 3276.11)	1757.17 (1179.45, 2307.64)	-	1555.06 (141.16, 2821.57)	-	0.443	0.622
Log Median Amplitude	years+refugia	-12.03 (-12.91, - 11.1)	0.97 (0.3,1.61)	-	0.6 (-0.22, 1.33)	-	0.337	0.659
Cumulative Spectral Difference (D _{cf}) from Buldir	years+distance+ moon	0.074 (0.067, 0.081)	-0.02 (-0.027, -0.013)	-0.0073 (-0.014, -0.00086)	-	0.0019 (-0.00063, 0.0044)	0.304	0.436
Maximum Signal:Noise Ratio	years+refugia+d istance+moon	136.82 (101.11, 169.84)	-29.3 (-53.51, -6.04)	39.59 (23.79, 56.38)	-69.12 (-120.94, -11.06)	5.58 (-1.7, 13.03)	0.234	0.304
Temporal Entropy (H _t)	years+distance	0.97 (0.97, 0.97)	0.0045 (0.0014, 0.0077)	-0.0064 (-0.0096, -0.0033)	-	-	0.156	0.209
Spectral Difference (D _f) from Buldir	years+distance	0.23 (0.21, 0.25)	-0.034 (-0.051, -0.017)	-0.014 (-0.03, 0.0042)	-	-	0.15	0.295
Number of Spectral Peaks (NP) (>.001)	distance	10.26 (8.76, 11.97)	-	-2.17 (-3.71, -0.62)	-	-	0.127	0.323

Number of Events	years+refugia	74.1 (62.33, 85.25)	14.77 (7.05, 22.72)	-	20.61 (2.75, 38.07)	-	0.113	0.194
Total Entropy (H _f x H _t)	years+distance	0.88 (0.87, 0.9)	0.0096 (-0.0034, 0.023)	-0.011 (-0.023, 0.0014)	-	-	0.058	0.170
Percent Acoustic Activity	years+distance	0.64 (0.63, 0.66)	-0.02 (-0.036, -0.0061)	-0.022 (-0.04, - 0.0058)	-	-	0.048	0.091
Acoustic Complexity Index (ACI)	moon	20148.27 (18105.72, 22223.14)	-	-	-	238.24 (18.93, 449.71)	0.007	0.471
Spectral Entropy (H _f)	none	0.91 (0.89, 0.93)	-	-	-	-	0.000	0.209

Table 4.3. Significant predictors of nightly soundscape index values from seabird call activity on four restored islands in the Western Aleutians. Models were fit with a random intercept and nested by year, within site, within island. Scaled predictor coefficients were estimated by restricted maximum likelihood and significance determined with bootstrapped 95% confidence intervals.

Index	Intercept	Leach's Storm-petrel Chuckles	Leach's Storm-petrel Chuckles Call Richness		Conditional GLMM_R ²
Temporal Entropy (H _t)	0.97 (0.96,0.98)	0.0084 (0.0059,0.011)	0.0048 (0.0013,0.0083)	0.15	0.47
Acoustic Complexity Index (ACI)	19689.5 (18586.98,20811.30)	-375.65 (-658.86,-58.32)	-966.29 (-1378.99,-558.68)	0.13	0.37
Acoustic Richness (Ht x Ranked MedianAmp)	3428.4 (2025.68,4855.92)	-318.75 (-474.18,-168.92)	-577.97 (-782.06,-375.51)	0.11	0.72
Total Entropy (H _f x H _t)	0.89 (0.86,0.92)	0.02 (0.012,0.027)	0.01 (0.0013,0.02)	0.10	0.41
Number of Events	81.85 (70.67,94.11)	-	-10.5 (-14.84,-5.54)	0.085	0.29
Number of Spectral Peaks (NP) (>.001)	11 (7.9,14.07)	1.03 (0.34,1.59)	1.31 (0.47,2.11)	0.081	0.53
Log Median Amplitude	-11.62 (-12.62,-10.54)	-0.18 (-0.28,-0.083)	-0.36 (-0.50,-0.22)	0.078	0.75
Percent Acoustic Activity	0.66 (0.62,0.71)	0.032 (0.018,0.045)	-	0.075	0.34
Spectral Entropy (H _f)	0.92 (0.90,0.94)	0.013 (0.0073,0.019)	-	0.060	0.36
Spectral Difference (D _f) from Buldir	0.21 (0.16,0.26)	-0.043 (-0.063,-0.023)	-	0.052	0.54
Cumulative Spectral Difference (D _{cf}) from Buldir	0.072 (0.046,0.1)	-	-	0.010	0.58

Maximum	96.39			0.0081	0.24
Signal:Noise Ratio	(52.98,144.42)	-	-	0.0081	0.24

Appendix

Supplemental Figure 4.4. Nightly spectral averages from 25 sites on six Western Aleutian nocturnal soundscapes during the month of July.



Supplemental Figure 4.5. Mean relative energy spectrums of nighttime recordings from six Western Aleutian Islands during July (above); and spectral difference from the never-invaded Buldir Island (below). Shaded areas are a 95% confidence interval around the mean. Colors/shades represent a continuum of ecological recovery from invasive predators from degraded Kiska Island (KIS) currently invaded with rats, Little Sitkin Island (LSI) with foxes removed nine years earlier, Amatignak Island (AMA) with foxes removed 18 years earlier, Kasatochi Island (KAS) with foxes removed 25 years earlier, Nizki-Alaid Islands (NIZ) with foxes removed 34 years earlier, to Buldir Island (BUL) that has never been invaded by predators.



			Position		Recording
Island	Site	Abbreviation	(WGS 84)	Year	Nights
			51.264°N		
Amatignak	East	AMA_E	179.074°W	2008	26
				2009	31
			51.293°N,		
	North	AMA_N	179.090°W	2008	31
				2009	31
			51.230°N,		
	South	AMA_S	179.010°W	2008	31
				2009	31
			51.262°N,		
	West	AMA_W	179.134°W	2008	22
				2009	31
			52.372°N,		
Buldir	North Bight	BUL_O	175.894°E	2008	27
				2009	30
			52.169°N,		
Kasatochi	Troll Talus	KAS_O	175.524°W	2009	31
				2011	29

Supplemental Table 4.4. Locations and number of nights recorded on six western Aleutian Islands

			51.919°N,		
Kiska	Bukhti Point	KIS_B	177.461°E	2009	25
	Christine		52.087°N,		
	Cliff	KIS_C	177.552°E	2010	31
			51.007°N,		
	Pond Midden	KIS_P	177.580°E	2010	31
	Raynard		52.018°N,		
	Cove	KIS_R	177.587°E	2010	30
			51.940°N,		
	West	KIS_W	177.430°E	2009	29
			51.975°N,		
Little Sitkin	North	LSI_N	178.457°E	2008	31
			51.904°N,		
	South	LSI_S	178.538°E	2008	22
			51.932°N,		
	West	LSI_W	178.453°E	2008	13
			51.955°N,		
	Northwest	LSI_X	178.452°E	2008	30
			52.748°N,		
Nizki-Alaid	West	NIZ_A	173.950°E	2009	31
			52.750°N,		
	North	NIZ_B	173.898°E	2009	31

		52.750°N,		
South	NIZ_C	173.928°E	2009	31
		52.733°N,		
East	NIZ_D	173.967°E	2009	30

5. Conclusion

Preventing biodiversity loss may be the defining environmental challenge of the 21st century. Fortunately, there exists a large toolbox of innovative conservation actions to safeguard biodiversity and restore damaged ecosystems. Monitoring wildlife and evaluating the outcomes of these conservation actions is critical to spending conservation dollars wisely and assessing progress towards conservation targets. To meet the challenge of assessing biodiversity outcomes at scale, managers and policymakers need low-cost, robust, replicable tools to measure animal populations and communities.

Soundscapes contain a vast amount of ecological information and can be inexpensively sampled using autonomous passive acoustic recorders. These large acoustic datasets require scalable analysis, ranging from time intensive manual listening to semi-automated signal detection and classification algorithms, and now automated soundscape indices characterizing the emergent properties of recordings without a priori decision making. Depending on the scale of monitoring questions, from individuals to communities, different approaches may be best suited and are not exclusive.

Despite analytic simplicity, automated soundscape indices that characterize entire recordings by measuring complexity, intensity or spectral differences, reflect meaningful biological patterns in species communities. These indices characterize entire recordings without discrimination of signals but can be more rapidly applied than signal detection and classification approaches. This data-driven, fully automated approach to acoustic analysis is relatively new and likely to advance considerably with the application of more sophisticated machine learning and unsupervised feature extraction-based approaches.

In this dissertation, I examined how soundscape indices and analysis can play an informative role in wildlife monitoring, with an attention to measuring conservation outcomes. Each chapter tackled a different piece of a wider challenge of applying new analysis techniques to existing acoustic monitoring challenges. The common thread between these chapters is an emphasis on low-cost and scalable approaches to capture sufficiently reliable information to be used in conservation planning.

In the first chapter I used simulations of forest bird dawn choruses to assess the underlying efficacy of soundscape indices to measure realistic community changes. By using simulated choruses, I was able to directly test how changes to calling behavior, and anthropogenic noise influenced the efficacy of these indices. The main result is that soundscape indices are surprisingly robust to these sources of heterogeneity. Furthermore, by testing combinations of over a dozen published indices we found that orthogonal indices in combination were most effective at measuring species richness, and when used in a multi-variate distance framework, these distances were correlated with bird community dissimilarity. This suggests that future research should be put into finding more orthogonal indices to characterize recordings, perhaps more than refining complexity and entropy-based indices that are becoming widespread. The next step is taking these conclusions to empirical studies using field recordings of known forest bird communities.

In the second chapter I used a soundscape approach to measure the relative abundance of a vocally conspicuous, however cryptically nesting seabird, the Cassin's Auklet. Traditional call detection methods did not accurately measure auklet acoustic activity in the presence of heavily overlapping calls and chorusing behavior. By understanding the entire soundscape of Southeast Farallon Island, we clearly showed how a non-discriminating spectral approach to recordings contained a more accurate index of auklet activity. This band limited acoustic energy index was highly predictive of relative auklet abundance and could be used to measure cryptic and remote auklet breeding abundance at broad scales. This approach is highly relevant to other vocally conspicuous, and chorusing species that dominate their respective soundscapes.

In the final chapter I apply soundscape indices to measure patterns of seabird recovery across restored seabird islands. This application could have widespread impact, as we directly apply soundscapes to measure the outcomes of invasive predator removal on seabird communities. Invasive species removal to benefit island breeding seabirds is a widespread, potent conservation action where outcomes are complex and monitoring approaches are inconsistent. We found that soundscape differences from a reference condition where a powerful index to measure seabird activity, and the pattern of seabird recovery on restored islands.

Together, these three studies further the case to promote soundscape indices in an expanded toolbox of standard analysis tools used in passive acoustic monitoring. These types of low-cost, scalable approaches are needed if passive acoustic monitoring is to measure conservation outcomes at scale.

Soundscape approaches greatly expand the power of acoustic monitoring programs. A soundscape approach can unveil patterns of seabird abundance, phenology and recovery in a fraction of the time of other approaches. Original recordings remain for manual listening or automated call detection and classification for asking further questions, or to confirm initial findings. The last two chapters of my dissertation directly apply to real world seabird monitoring needs. Passive acoustic recordings are often the only feasible tool to monitor seabirds nesting cryptically in habitats that are remote, fragile and extremely sensitive to human disturbance. A soundscape approach to analyzing these large acoustic datasets doesn't exclude follow-up analysis and they have a much lower technical barrier to entry than other approaches, meaning soundscape indices may be more likely to be adopted by newcomers to acoustic monitoring.

The narrative of conservation is all too often one of doom and gloom and documenting declines. It is true that the planet is rapidly losing biodiversity, and the human footprint has extended to every corner of the globe. However, there has also never been a greater number of people with 21st century tools and innovation working to protect biodiversity and restore ecosystems. This gives me hope that future generations will continue to reap the benefits of biodiversity and functioning ecosystems. Monitoring and evaluation will be the guide we use to find the most effective solutions and bring them to the same scale as environmental problems. Technology is rapidly transforming our ability to collect and analyze monitoring data at scale, and conservationists would be wise to embrace it.

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