Conservation Biology

Conservation Methods

Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity

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Abstract: *Passive acoustic monitoring could be a powerful way to assess biodiversity across large spatial and temporal scales. However, extracting meaningful information from recordings can be prohibitively time consuming. Acoustic indices (i.e., a mathematical summary of acoustic energy) offer a relatively rapid method for processing acoustic data and are increasingly used to characterize biological communities. We examined the relationship between acoustic indices and the diversity and abundance of biological sounds in recordings. We reviewed the acoustic-index literature and found that over 60 indices have been applied to a range of objectives with varying success. We used 36 of the most indicative indices to develop a predictive model of the diversity of animal sounds in recordings. Acoustic data were collected at 43 sites in temperate terrestrial and tropical marine habitats across the continental United States. For terrestrial recordings, random-forest models with a suite of acoustic indices as covariates predicted Shannon diversity, richness, and total number of biological sounds with high accuracy ($R^2 \geq 0.94$, mean squared error [MSE] ≤ 170.2). Among the indices assessed, roughness, acoustic activity, and acoustic richness contributed most to the predictive ability of models. Performance of index models was negatively affected by insect, weather, and anthropogenic sounds. For marine recordings, random-forest models poorly predicted Shannon diversity, richness, and total number of biological sounds ($R^2 \leq 0.40$, MSE ≥ 195). Our results suggest that using a combination of relevant acoustic indices in a flexible model can accurately predict the diversity of biological sounds in temperate terrestrial acoustic recordings. Thus, acoustic approaches could be an important contribution to biodiversity monitoring in some habitats.*

Keywords: acoustic indices, bioacoustics, biodiversity, passive acoustic monitoring, random forest

Eficiencia de la Extracción de Índices a partir de Registros Acústicos a Gran Escala para Monitorear la Biodiversidad

Resumen: *El monitoreo acústico pasivo podría ser una manera poderosa de evaluar la biodiversidad en escalas temporales y espaciales grandes. Sin embargo, la extracción de información significativa a partir de grabaciones puede ser inasequible y requerir de mucho tiempo. Los índices acústicos (es decir, un resumen matemático de la energía acústica) proporcionan un método relativamente rápido para procesar los datos acústicos y cada vez se usan más para caracterizar las comunidades biológicas. Examinamos la relación entre los índices acústicos y la diversidad y abundancia de sonidos biológicos en las grabaciones. Revisamos la bibliografía sobre el índice de acústica y encontramos que más de 60 índices han sido aplicados a una gama de objetivos con éxito variante. Usamos 36 de los índices más indicativos para desarrollar un modelo predictivo de la diversidad de sonidos de animales en las grabaciones. Se recolectaron datos acústicos en 43 sitios en hábitats terrestres templados y marinos tropicales en todos los Estados Unidos continentales. Para*

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las grabaciones terrestres, los modelos de bosques aleatorios junto con un juego de índices acústicos como covariantes predijeron la diversidad de Shannon, la riqueza y el número total de sonidos biológicos con una certeza elevada (R^2 ≥0.94, error medio al cuadrado [MSE] ≤170.2). Entre los índices que se evaluaron, la desigualdad, la actividad acústica y la riqueza acústica fueron los que más contribuyeron a la habilidad predictiva de los modelos. El desempeño de los modelos de índices fue afectado negativamente por sonidos de insectos, del clima y de origen humano. Para las grabaciones marinas, los modelos de bosque aleatorio predijeron pobremente la diversidad de Shannon, la riqueza y el número total de sonidos biológicos (R^2 ≤ 0.40, MSE ≥ 195). Nuestros resultados sugieren que el uso de una combinación de índices acústicos relevantes dentro de un modelo flexible puede predecir con exactitud la diversidad de los sonidos biológicos en un registro acústico de un hábitat terrestre templado. Así, las estrategias acústicas podrían ser una contribución importante para el monitoreo de la biodiversidad en algunos hábitats.

Palabras Clave: bioacústica, biodiversidad, bosque aleatorio, índices acústicos, monitoreo acústico pasivo

摘要: *被动的声音监测可以跨越较大的时空尺度有效地评估生物多样性。然而, 从录音中提取有意义的信息可能会非常耗时。声学指标 (即对声能的数学总结) 提供了一种相对快速地处理声学数据的方法, 正越来越多地被用于描述生物群落的特征。我们检验了声学指标与录音中生物声音的多样性和丰度之间的关系。通过对声学指标文献的综述, 我们找到了超过 60 个用于不同目的的声学指标, 成效不一。我们选用了36 个最具指示性的指标, 以建立录音中动物声音多样性的预测模型。声学数据来自美国大陆的温带陆地和热带海洋生境的 43 个位点。在陆地的录音中, 含有一系列声学指标作为协变量的随机森林模型可以精准地预测香农多样性、丰富度和生物声音的总数 (R^2≥0.94, 平均方差 [MSE] ≤170.2) 。在我们评估的指标中, 声音的粗糙度、活动性和丰富度对模型预测能力贡献最大。指数模型的效果会受到昆虫、天气和人类活动声音的负面影响。对于海洋录音来说, 随机森林模型对香农多样性、丰富度和生物声音总数的预测结果不佳 (R^2 ≤ 0.40, MSE ≥ 195) 。我们的结果表明, 在模型中灵活运用相关声学指标的组合可以准确预测温带陆地生态系统录音的生物声音多样性。因此, 声学方法可以为某些生境的生物多样性监测做出重要贡献。* **【翻译: 胡怡思; 审校: 魏辅文】**

关键词: 声学指标, 生物多样性, 生物声学, 无源声音监测, 随机森林

Introduction

Monitoring trends in biodiversity is essential to assess the effect of accelerating human-caused global change (Tittensor et al. 2014). However, large-scale ecological monitoring is challenging because it often relies on incompatible data collected at limited spatial and temporal scales (Pereira et al. 2012). As a result, consistent and reliable monitoring techniques to rapidly and accurately measure biodiversity change across ecosystems are needed (Stem et al. 2005). Several new technologies have arisen to meet the challenges of monitoring global biodiversity, including metabarcoding (Ji et al. 2013), camera traps (Steenweg et al. 2017), unmanned aerial vehicles (UAVs; Anderson & Gaston 2013), and satellite remote-sensing techniques (Turner 2014). Acoustic surveys are increasingly being applied to questions regarding ecosystem functioning across landscapes and offer a particularly promising approach for long-term, multiscale biodiversity-monitoring programs (Blumstein et al. 2011).

Acoustic monitoring is particularly effective given that, in most ecosystems, a large portion of fauna from many different taxa emit sounds that function in territory defense, mate attraction, predator deterrence, navigation, foraging, and maintenance of social groups (Thomas et al. 2004; Stephens et al. 2007; Bradbury & Vehrencamp 2011). Thus, acoustic monitoring provides a powerful approach to collecting species data noninvasively, continuously, and simultaneously across multiple sites for extended periods. Moreover, because acoustic data provide a permanent record of the survey period, they offer detailed information that can be used to address a variety of objectives, from studying rare species to monitoring behavior (Acevedo & Villanueva-Rivera 2006).

Rapid advances in digital recording technology offer new avenues for acoustic research. Such technology allows standardized surveys that can provide new insights into sound-producing organisms over extended spatiotemporal scales (Merchant et al. 2015). For example, the Alberta Biodiversity Monitoring Institute has collected acoustic recordings at over 600 sites in western Canada (ABMI 2016) and the National Park Service has collected acoustic recordings at 492 sites around the contiguous United States (Mennitt & Fristrup 2016). These efforts have resulted in surveys over entire biomes. This new large-scale sampling approach targets communities, biodiversity, and ecological processes, in addition to particular species or populations (Sueur & Farina 2015). Large-scale acoustic monitoring draws from a new field, soundscape ecology, which examines the collection of anthropogenic, biological, and geological sounds emanating from a landscape that vary over space and time (Pijanowski et al. 2011). By reflecting an ecosystem's biophysical processes, soundscape patterns can be used to diagnose ecosystem health and species diversity (Tucker et al. 2014).

Massive acoustic data sets are accumulating globally, offering the unique opportunity to monitor biodiversity.

In many cases, these large data sets are collected by different research teams with unique protocols, necessitating consistent and reliable analyses. Three main approaches are used to examine acoustic recordings: manually identifying acoustic events by listening to recordings or observing spectrograms (Digby et al. 2013), automatically recognizing species sounds with classification algorithms (Acevedo et al. 2009), and using acoustic indices to summarize variation in acoustic energy (Sueur et al. 2014). Manual processing of acoustic recordings is infeasible for large data sets, and although automated classification algorithms are fast, accounting for accuracy can be challenging and building algorithms for each species is time consuming (Potamitis et al. 2014; Farina et al. 2016). An acoustic index is a mathematical summary of the distribution of acoustic energy and can be used to estimate the diversity of sounds in a recording (Towsey et al. 2014). Many types of acoustic indices have been developed and tested and have been found to reflect vocal species diversity and abundance, community composition, vegetation structure, habitat type, human perception of a soundscape, human activity, and ecological condition in terrestrial and aquatic habitats (Sueur et al. 2014). Acoustic indices offer a potential means for analyzing enormous acoustic data sets given that they are efficient, applicable across locations and habitat types, and can extract multiple types of meaningful information.

Although acoustic indices show great promise for standardizing the analysis of acoustic surveys, the complexity of acoustical conditions necessitates a careful examination of the relationship between an index and the underlying process of interest (e.g., Gasc et al. 2013; Fuller et al. 2015). To facilitate the application of acoustic indices to biodiversity monitoring, we reviewed the acoustic-index literature and summarized the main types of indices and their relationship with biotic and abiotic factors. We used the results of our review to test the efficacy of a subset of indices to characterize biodiversity in large acoustic data sets from terrestrial and aquatic sites in the United States. Specifically, we examined whether acoustic indices can be used to predict the richness, total abundance, and Shannon diversity of biological sounds. Finally, we determined the impact of continuous background sounds on acoustic-index model predictions.

Methods

Acoustic-Index Literature Review

For our literature review, we searched Thompson's ISI Web of Science for articles published from 1900 to April 2017 and applied the following combinations of keywords as topics: *bioacoustic** AND *ind**, *ecoacoustic**, *acoustic** AND *biodiversity*, and *soundscape* AND *ecology*. We discarded papers that counted biological sounds within sound recordings rather than using indices to represent a soundscape or acoustic environment. Of the 1001 results, we found 39 relevant papers. For each relevant paper, we searched the literature cited and the literature that cited the paper to ensure we captured all relevant publications.

We reviewed the resulting publications ($n = 71$) to systematically characterize each study based on 8 attributes (Supporting Information): name and details of the index used; country where recordings were collected; whether recordings were collected in marine, freshwater, or terrestrial habitat; number of recording sites; recording schedule; type of index (see below); research objective (categorized into general types [Supporting Information]); and whether each index was related to anthropogenic (e.g., noise events counted in recordings), biological (e.g., point counts at each site), or spatiotemporal (e.g., time of day) information or more than 1 of these types of information. An index was considered related to anthropogenic, biological, or spatiotemporal information if the study reported a significant correlation or graphically showed a relationship ($R > 0.5$ or $p < 0.05$). Because we identified 69 different acoustic indices, we categorized them into 7 types: difference from background, where a signal was compared to background sound pressure level (SPL) (i.e., logarithmic measure of the effective pressure of a sound relative to a reference value in dB); temporal variation, where variation in SPL over time was summarized; frequency variation, where variation in SPL over frequency was summarized; frequency * temporal variation, where the results of frequency variation and frequency * temporal variation are combined; comparison between the acoustic environment at different locations or times (β indices); channel variation, where variation in SPL between left and right microphones was summarized; and summary of acoustic energy (e.g., average SPL in a frequency range). For the latter category, we reviewed only papers that additionally included another category of index (i.e., we discarded papers that exclusively reported summaries of acoustic energy).

Acoustic Recordings

We obtained terrestrial acoustic recordings from 9 sites in Sequoia and Kings Canyon National Parks (SEKI), California, and 34 sites in the Piceance Basin (PIBA), Colorado, and marine aquatic recordings from 8 sites in Everglades National Park (EVER) (Supporting Information). Recordings were collected for 2 to 155 days at each site from 2014 to 2016 with either Song Meters (Wildlife Acoustics Inc., Concord, Massachusetts), Edirol R-05 (Everglades only; Roland Corporation, Osaka, Japan), or Roland R26 digital audio recorders (Everglades only; Roland Corporation).

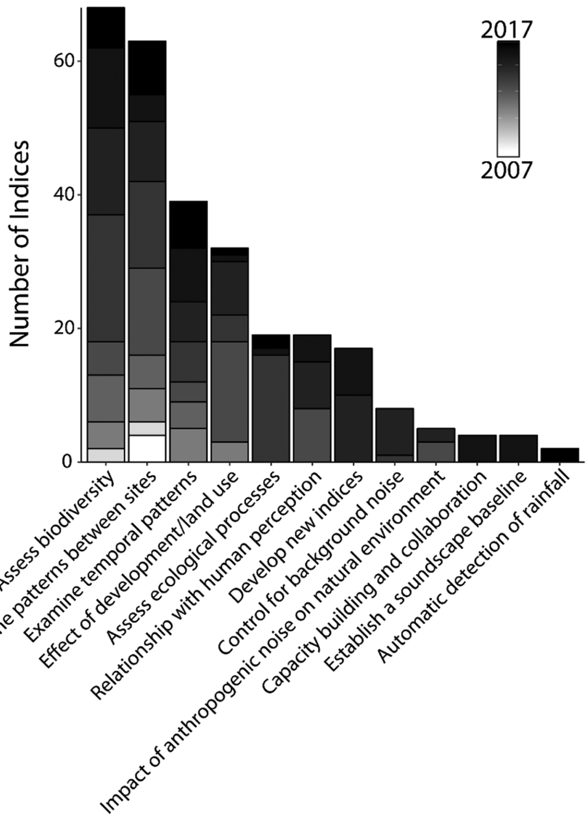

Figure 1. The total number of acoustic indices used to address different research objectives in studies published from 2007 to 2017. The number of indices includes all acoustic indices in each study. Each study used 2–14 indices. See Supporting Information for an explanation of research objective categories and associated studies.

Because acoustic data were initially collected and analyzed for unique objectives at each location, each data set was subsampled into segments of different lengths. For PIBA recordings, we analyzed the first 30 s of each 5 min for 3 randomly selected 2-h dawn recordings at each of 27 sites (972 min). For SEKI recordings, we analyzed 12 randomly selected 10-min clips from 4-h dawn recordings at each of 9 sites (1080 min). For EVER recordings, we analyzed randomly selected 10-minute samples each hour at 7 sites and for a continuous 24 h at 1 site (7980 min).

Acoustic Analyses

We converted audio data to calibrated 1-s one-third octave band SPLs measured as $Leq_{,1s}$ from 12.5 to 8000 Hz because this coarse resolution requires less storage space and shorter computation time than wav files. This conversion works well for large data sets, and data acquired from different recording devices can be calibrated to provide absolute measures of SPL (e.g., different recorders used at EVER) (Merchant et al. 2015). Although one-third octave band resolution is common in noise studies, its usefulness to represent biological sound is just beginning to be explored (Buxton et al. 2016). Moreover, the code to convert recordings is user friendly and freely available (Merchant et al. 2015). We used an end-to-end calibration method, which reverses the transformations made to the audio signal along its path into the data-acquisition system (Merchant et al. 2015).

We calculated 36 acoustic indices (Supporting Information) from our acoustic measurements. We eliminated indices that our literature review indicated were less effective at capturing biological information (i.e., β- and channel-variation indices [see Results and Supporting Information]). We also excluded indices that required processing waveform because all our data were processed into 1-s one-third octave band spectra (McKenna et al. 2016). We calculated indices for each calibrated acoustic sample corresponding to the sample for which we assessed the diversity of biological sounds. For indices intended to capture biological sounds, we used 1.6–8 kHz frequency bands for terrestrial recordings and 200–500 Hz for aquatic recordings. For indices intended to capture background noise (i.e., anthropogenic and weather sounds), we used frequency bands of 0.315–1.25 for terrestrial recordings and 500–8000 Hz for aquatic recordings (Supporting Information).

To assess the diversity of biological sounds for comparison with acoustic indices, trained technicians identified sounds in a subset of recordings. Technicians used the software Raven Pro 1.5 (Cornell University, Ithaca, New York) to visualize spectrograms and listen to audio files. Only 1 technician was responsible for identifying sounds at each location. During the training period, technicians constructed sound libraries with help from acoustic experts. Following the training period, technicians were presented with a test data set of at least 10 randomly selected audio clips with a known number of species to ensure they were able to correctly identify >90% of sounds.

For terrestrial recordings, although all biological sounds were identified, <1% were produced by insects and mammals, of which >80% were from crickets, chipmunks, and squirrels. Thus, only avian sounds were identified to species and biological sounds that were not birds were classified as insect, mammal, or unknown. For avian sounds that acoustic experts were unable to identify to species (approximately 7%), technicians grouped unknown vocalizations with similar structure, saved representative spectrograms, and labeled each group with the same unique classifier (e.g., speciesA, speciesB). Because we were unable to distinguish individual animals based on their sounds, technicians identified and counted the total number of unique biological sounds in a given audio clip. Anthropogenic and geophysical sounds were counted and classified into 9 categories (aircraft, motor vehicle, people, domestic animal, construction,

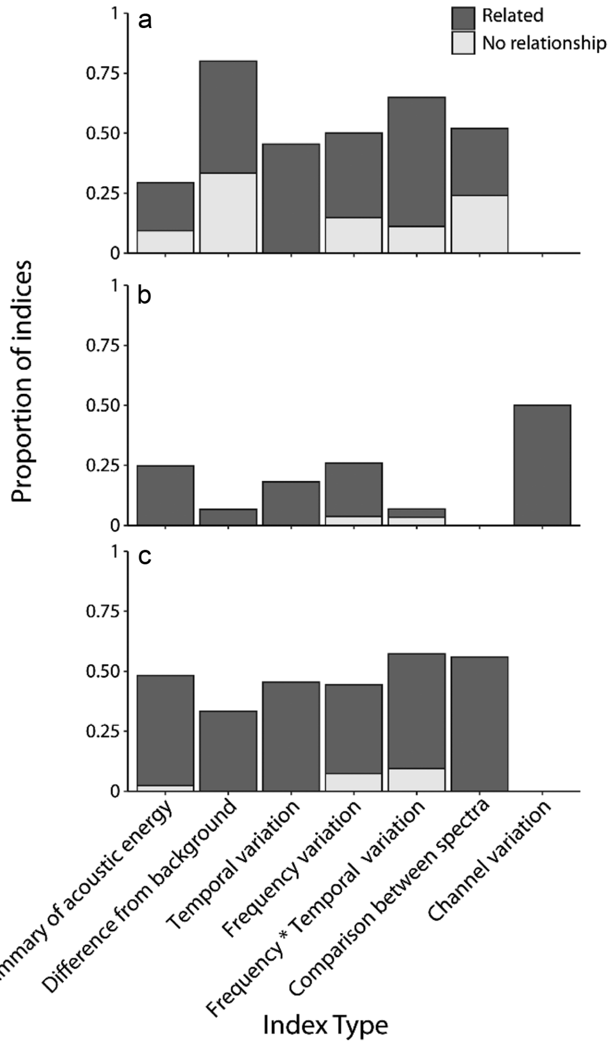

Figure 2. Proportion of acoustic indices in the literature related to or not related to (a) biological information (e.g., counts of species vocalizations in recordings or biodiversity surveys at the recording site), (b) anthropogenic information (e.g., count of anthropogenic noise events in recordings), and (c) spatiotemporal patterns (e.g., examining whether indices vary over time or between sites). Studies reporting only summaries of acoustic energy were not included.

wind, rain, thunder, or unknown). For aquatic recordings, sounds could not be identified to species. Instead, similar to the process for unknown bird species, the technician grouped biological sounds with similar structure, saved representative spectrograms for reference, and labeled each group with the same unique classifier. We did not quantify sounds from snapping shrimp (Alpheidae).

We calculated the total number of biological sounds in each manually analyzed acoustic recording sample and used the Shannon index and richness to estimate the diversity of biological sound types identified by technicians within recordings (vegan package) (Oksanen et al. 2013).

Predicting Biological Sound Diversity and Abundance

All statistical analyses were performed in R version 3.4.1 (R Core Team 2017). To predict the richness, Shannon diversity, and total number of biological sounds in the acoustic recording samples (hereafter bioacoustic activity) from acoustic indices calculated from matching periods, we used a random forest (RF) machine-learning procedure (randomForest package) (Breiman 2001; Liaw & Wiener 2002) because it produced the best performance of the 4 model types explored (random forest, linear model, lasso, and ridge regularized regression [Supporting Information]). Moreover, the RF procedure provides well-supported predictions because it develops multiple classification trees for randomly sampled subsets of data and then combines the trees into a single, best-possible tree given the data (Dwyer et al. 2016). Each global RF model included all 36 indices as predictor variables and one of three response variables for bioacoustic activity (richness, Shannon diversity, and total number of biological sounds) based on either terrestrial or aquatic data. Six models resulted.

Although the RF algorithm accommodates collinearity among predictors, large numbers of covariates may decrease explanatory power (Murphy et al. 2010). Therefore, we tested the predictive ability of models with different combinations of reduced index covariates. To build subsets of indices we removed correlated covariates, used a model-selection procedure, and constructed a priori hypotheses about the importance of different indices derived from the literature review (Supporting Information). To select the final set of covariates (Table 1), we used a bootstrapping cross-validation method and chose the model structure with the lowest median of mean squared error (MSE) and highest R^2 between test data and predicted values (Hastie et al. 2008) (Supporting Information). Because our data were 0inflated to generate the final predictive models, we controlled for imbalance by drawing an equal sample size of data from 0s and non-0s (Breiman 2001).

To measure the importance of each acoustic index, we used the mean percent increase in MSE, which is the loss of predictive accuracy due to the permutation of a variable. The higher the importance and larger the percent increase in MSE, the larger the effect of the variable on the predictive ability of the model (Breiman 2001). We calculated variable importance with the final model structure (Table 1).

Factors Affecting Predictive Ability of Models

Continuous background noise is thought to confound the ability of acoustic indices to detect variation in bioacoustic signals (Parks et al. 2014). To test which background sounds affected the ability of the acoustic index RF model to predict bioacoustic activity, we examined the relationship between model residuals and

Table 1. Mean squared error (MSE) and R^2 of the top models of acoustic indices that predict the richness, Shannon diversity, and total number of biological sounds in acoustic recording samples from multiple sites in terrestrial habitat.

Response variable	*Model type[a]*	*Acoustic index covariates[b]*	*MSE*	R^2
Richness	multicolinear parameters removed (threshold = 0.05), background sound indices removed, model selection approach (Pars = n/a)	acoustic complexity index + median SPL of background (1600–8000 Hz) + average amplitude + spectral entropy + temporal entropy + biophony + soundscape index + acoustic activity + count of acoustic events + duration of acoustic events + roughness + acoustic diversity index + kurtosis + entropy of spectral max + entropy of SPL + spectral persistence + acoustic richness + difference between duration of two main clusters + difference between the Leq of 2 main clusters	1.01	0.86
Shannon diversity	multicolinear parameters removed (threshold = 0.1), model selection approach (Pars = n/a)	acoustic complexity index + count of acoustic events + duration of acoustic events + count of acoustic events (31.5–1250 Hz) + roughness + acoustic diversity index + entropy of spectral max + acoustic richness	0.12	0.78
Total sounds	multicolinear parameters removed (threshold = 0.05), model selection approach (Pars = 0.8)	ratio of biophony to anthrophony + count of acoustic events + count of acoustic events (31.5–1250 Hz) + roughness + L_{10}-L_{90}+ spectral diversity + spectral persistence + acoustic richness	558.7	0.81

[a] *Several methods were used to choose acoustic index covariates, including removing multicolinear indices, using model selection with different thresholds for competing models (Pars), removing acoustic indices calculated in background noise frequency range (31.5–1250 Hz), and creating a priori models informed by the literature review.*
[b] *For definitions of each acoustic index (e.g., soundscape index) see Supporting Information. Abbreviation: SPL, sound pressure level.*

the abundance and presence or absence of different sound types. We used anthropogenic, wind, rain, and all weather (wind, rain, and thunder) sounds. Moreover, we tested the effect of insect sounds because, although they are biological sounds, they are relatively continuous over time and have a wide range of frequencies. We used linear mixed models with absolute values of model residuals as response variables and the abundance (scaled by subtracting the mean and dividing by 1 SD to ensure parameter estimates were comparable [Schielzeth 2010]) and presence or absence of sound types as predictor variables. Because many of the covariates were correlated, we used a model averaging approach in which we constructed a set of models that iteratively excluded correlated covariates (package MuMIn) (Bartoń 2013). We considered sound types with 95% confidence intervals (CIs) excluding 0 to have a strong effect on model residuals.

Results

Acoustic-Index Literature Review

We reviewed 71 papers in which 69 unique acoustic indices captured a variety of biological and anthropogenic components of the soundscape. The majority of studies applying acoustic indices occurred in terrestrial landscapes in the United States; few studies were conducted in equatorial biomes. On average recordings on which indices were calculated were collected at 17 sites (SD 47) for a total of 950 hours (SD 1939). In many studies, the time and frequency resolution for calculating indices were not consistent or details about the methods and initial data-processing steps were not reported.

Many indices were used to address a variety of types of research objectives (Fig. 1). Acoustic indices have been most frequently applied to questions regarding biodiversity, temporal dynamics in acoustic activity, influences of site and habitat structure (Fig. 1), and more recently ecological processes such as phenology (Buxton et al. 2016).

Many indices were positively related to bioacoustic activity in recordings or biological diversity identified in corresponding surveys (Fig. 2a, Supporting Information). However, some types of indices were less consistently related to biological information than others. For example, of the β indices tested, 50% were significantly related to biological information (Fig. 2a). No studies tested relationships between channel-variation indices and biological information. Overall, 66% of studies examined the relationship between indices and biological information (Fig 2a), 30% examined the relationship between indices and anthropogenic information (Fig. 2b), and 84% compared indices over time and space (Fig. 2c). Acoustic indices were not significantly related to biological information 26% of the time ($n = 151$) (Fig. 2a). Although there were fewer instances where acoustic indices were used to examine anthropogenic activity ($n = 48$), most cases (88%) found a relationship (Fig. 2b).

Predicting Biological Sound Diversity and Abundance

We found 52 species or biological sound types in recordings from PIBA, 80 in recordings from SEKI, and 15 from EVER. For terrestrial recordings, the RF models that best predicted bioacoustic activity included 8 and 19 acoustic index covariates (Table 1, Figs. 3 and 4). Included in the final acoustic-index models predicting bioacoustic activity was a range of index types: summary of acoustic information, variation in frequency, measures of how much time sound is above a measure of background levels, and the variation in time and frequency (Fig. 4). In combination, suites of acoustic indices were strongly related to the richness ($R^2 = 0.97$), Shannon diversity ($R^2 = 0.97$), and total number of biological sounds in recordings ($R^2 = 0.94$) (Fig. 3). Predicted values from RF models increased linearly as Shannon diversity of biological sounds increased (Fig. 3b). For richness and total biological sounds in recordings, predicted values were linearly related to actual values until an asymptote was reached at >15 species and 300 sounds, respectively (Fig. 3a, c). Index models predicted low and high bioacoustic activity but less reliably predicted moderate levels of diversity and richness of biological sounds. In the top model predicting richness of biological sounds, indices with the highest variable importance were count of acoustic activity, roughness, and acoustic richness (Fig. 4a). In the top model predicting Shannon diversity of biological sounds, indices with the highest variable importance were roughness, acoustic activity, and acoustic richness (Fig. 4b). In the top model predicting the total number of biological sounds, indices with the highest variable importance were roughness, spectral persistence, and acoustic richness (Fig. 4c). Conversely, individual indices were poor predictors of bioacoustic activity (Supporting Information).

In aquatic recordings, acoustic indices were weakly related to richness ($R^2 = 0.31$), Shannon index ($R^2 = 0.35$), and total number of biological sounds ($R^2 = 0.40$) (Supporting Information). Thus, we excluded aquatic recordings from further analysis.

Influence of Background Sounds on Predictions

In terrestrial recordings, the number of insect sounds drove significantly higher residual values, indicating the model was less likely to predict the richness (95% CI, 0.16–0.21), diversity (95% CI, 0.01–0.02), and total number of biological sounds (95% CI, 1.56–3.46) (Supporting Information) when these sounds were present. The number of sounds from rain and other weather (wind and thunder) in acoustic samples was also related to higher model residuals (Supporting Information). Finally, the number of anthropogenic sounds significantly increased residual values in models predicting diversity and total number of biological sounds (95% CI, 0.14–0.19 and 7.72–9.18) (Supporting Information).

Discussion

Advances in technology, novel analytical methods, and partnerships with other scientific disciplines have allowed more widespread use of acoustic data in biological studies (Blumstein et al. 2011). These data present an opportunity to monitor biodiversity at large scales and to address a myriad of conservation issues. As the scale of research programs using passive acoustic monitoring continues to grow, it is crucial that effective and consistent analytical methods be developed. We demonstrated how a suite of acoustic indices can predict bioacoustic activity in acoustic recordings across a variety of temperate sites.

Review of Acoustic Indices

In our literature review, we found that many different types of acoustic indices have been used to extract biological information from recordings. Papers published in the past decade applied 69 unique indices to a variety of research objectives. In many cases, a variety of indices were applied to the same objective. For example, 35 indices have been used to characterize biodiversity. The use of different methods is likely related to the relative infancy of acoustic indices as a tool for ecological research, which began in the late 2000s. In many cases, acoustic indices have been tested at few locations, making it difficult to assess the scalability and widespread applicability of these methods. Thus, there was a clear need to evaluate existing indices at a variety of sites to understand which are the most reliable for large-scale acoustic monitoring.

Among the studies we reviewed, we found some types of indices less consistently captured biological information in recordings, including β indices and indices that capture variation between channels or microphones. Because β indices compare multiple acoustic communities through pair-wise comparisons (Sueur et al. 2014), they may be less practical for recordings collected

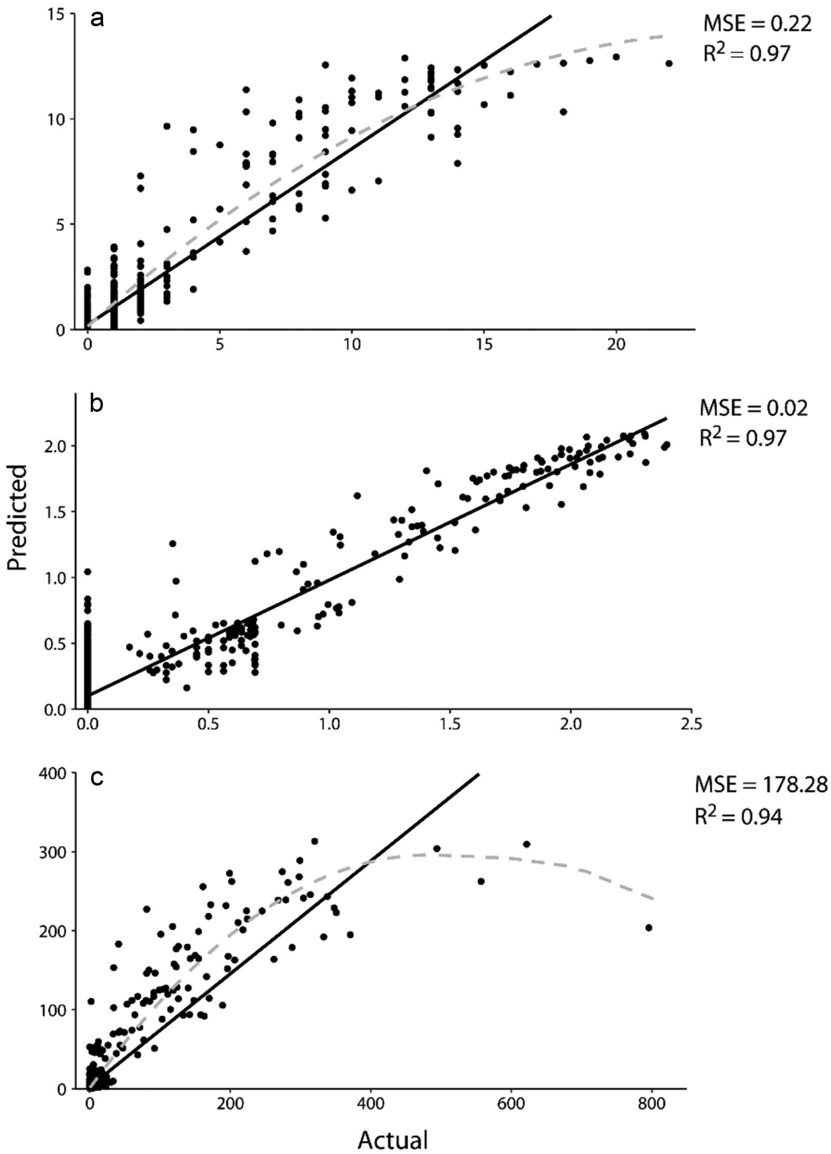

Figure 3. Relationship between actual and predicted values in random-forest models of the relationship between acoustic indices and (a) richness of biological sound types, (b) Shannon diversity of biological sound types, and (c) total number of biological sounds in terrestrial recordings (solid lines, linear relationships between actual and predicted values; dashed lines, polynomial relationships between actual and predicted values; MSE, mean squared error; R^2 calculated from random-forest models).

at dozens of sites over months to years that generate enormous pair-wise matrices. Similarly, channel-variation indices require stereo recordings collected using two microphones, resulting in larger sound files. Although channel-variation indices effectively captured anthropogenic sound information in acoustic recordings and would be useful to classify urban environments (Rychtáriková & Vermeir 2013), they are less practical for large-scale recordings intending to capture bioacoustic activity.

Testing Combinations of Indices

We combined a subset of acoustic indices to examine bioacoustic activity from a large network of passive acoustic-monitoring sites. We calibrated audio data collected with several different types of recorders (Merchant et al. 2015), resulting in a coarser 1-s one-third octave band time and frequency resolution relative to previous studies in which acoustic indices were used. The 1-s resolution is relevant for many avian species in North America that typically have vocalizations that last 0.5–2 s (www.maccaulaylibrary.org). Indices calculated at 1-s intervals may be less effective for recordings at sites with extremely high species diversity, with species vocalizing continuously, with high levels of anthropogenic noise and wind (i.e., saturated acoustic space; Pijanowski et al. 2011), and for biological sounds composed of fast impulses (e.g., marine snapping shrimp and terrestrial insect sounds). Because the energy within one-third octave bands, which widen with increasing frequency, is flattened, acoustic diversity at higher frequencies may be lost using this spectral resolution. Indices calculated using one-third octave bands were highly correlated with bioacoustic activity in our data set. However, future studies could compare the performance of acoustic

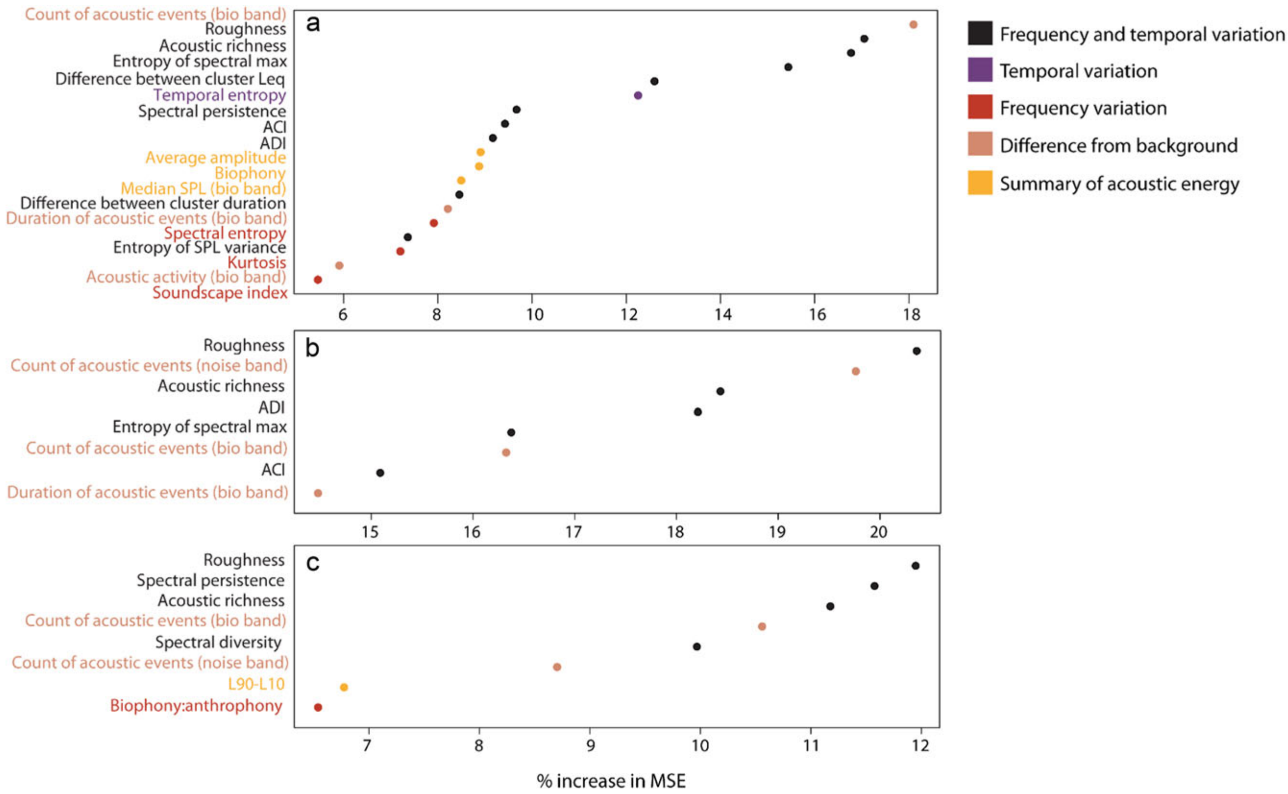

Figure 4. Importance of covariates in random forest models indicated by mean percent increase in mean squared error (MSE): (a) the final model of richness of biological sound types, (b) Shannon diversity of biological sound types, and (c) total number of biological sounds in terrestrial recordings. Greater MSE indicates a larger loss of predictive accuracy when covariates are permuted and thus a larger influence in the model. Results are shown for acoustic index covariates, ordered by MSE. Gray-scale indicates the general type of index. See Supporting Information for a description of the acoustic indices.

indices calculated at different resolutions to determine whether finer resolutions capture significantly more biologically relevant variation in acoustic data.

Many types of indices effectively explained different pieces of information in acoustic recordings, likely because their unique mathematical properties reflect different components of a soundscape (Gasc et al. 2015). However, most researchers used indices individually to describe the acoustic environment. We combined groups of indices to predict bioacoustic activity with a flexible RF modeling approach. In terrestrial recordings, 8–19 indices were included in top models and 5–8 of these indices improved the predictive ability of our models such that their removal increased model error by >10% each. Thus, combinations of acoustic indices are more effective at predicting bioacoustic activity, rather than single indices (Towsey et al. 2014). Moreover, using model selection to reduce redundant indices resulted in better model fit. Indices that had the greatest effect on the predictive ability of models were those that reflected both the temporal and spectral distribution of acoustic energy. For example, the roughness index, calculated by summing the differences in normalized SPL between adjacent 1-s time bins over a time step and taking a median over all frequency bins (Supporting Information), had the largest effect on the predictive ability of the models. However, all five types of indices contributed to the predictive ability of models.

Acoustic index models accurately predicted high and low diversity of biological sounds but less reliably predicted intermediate diversity. The acoustic environment is expected to be more discernable between recordings with low and high diversity because acoustic characteristics will be markedly different. Predictions of richness and total biological sound reached a threshold, likely because of the redundancies in acoustic characteristics of species and overlap between sounds at high rates (Sueur et al. 2008). Thus, acoustic indices may be better proxies of bioacoustic activity below high diversity thresholds, potentially limiting the utility of indices in high biodiversity, equatorial regions, where further research is needed before indices are applied.

Acoustic indices were less reliable at predicting bioacoustic activity in marine environments. Most acoustic indices were originally developed for terrestrial soundscapes, yet there are inherent differences in aquatic sound sources and propagation. First, biological sounds in aquatic environments consistently overlap in frequency with anthropogenic sources, making it difficult to divide the acoustic environment into distinct frequency bands of sounds (Hildebrand 2009). Second, impulsive biological sounds, such as snapping shrimp, potentially make the 1-s resolution we used ineffective. Development of new indices that consider the unique features of the marine environment may be a promising direction for large-scale acoustic monitoring (Parks et al. 2014).

Effects of Background Noise on Index Predictions

Some types of background noise affected the ability of index models to predict bioacoustic activity. Geological sounds, such as wind and rain, anthropogenic sources, such as road or aircraft noise, or constant biotic sounds, such as stridulating insects, can affect background sound conditions and in turn influence the estimation of biological sound diversity. Although some studies suggest that unwanted sounds may be filtered out before analyses, these methods are unrealistic for large-scale acoustic data sets, and background noise can remain even after removing sounds (Gasc et al. 2015). Instead, we included indices of background sound in RF models to control for the presence of unwanted sounds. Model residuals and insect, anthropogenic, and weather sounds were related. This relationship suggests the indices we included may have captured some variability relating to the presence of these sources, but background sounds need further investigation when using indices to evaluate bioacoustic activity. Finally, we did not examine the effect of environment type in our analyses, yet the error introduced by background sounds at different sites would likely affect the efficacy of predictive models.

Applying Acoustic Indices to Large-Scale Data Sets

More research is needed to determine how acoustic indices perform in areas outside the United States, among different types of biomes, in aquatic habitat, and when using different temporal and spectral data resolutions. Combining a large set of different types of indices in flexible models can accurately predict bioacoustic activity, but control for background noise needs to be further considered.

The abundance of research applying acoustic indices demonstrates a promising direction for passive acoustic monitoring in terrestrial environments. One of the trademarks of landscape ecology is the extensive use of landscape metrics. However, understanding the ecological and perceptual significance of indices is key to unraveling the relationship between pattern and ecological process (Li & Wu 2004; Farina & Belgrano 2006). Thus, standardized data-processing methods and ground-truthing with ecological data will facilitate a consistent and reliable acoustic monitoring program that informs conservation across landscapes.

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Supporting Information

Acoustic index literature review (Appendix S1), recording specifications (Appendix S2), manual vocalization identification (Appendix S3), acoustic indices (Appendix S4), and modeling procedure (Appendix S5) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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