

Using ecoacoustics metrics to track grassland bird richness across landscape gradients



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ABSTRACT

Ecoacoustics is an emerging field that allows inferences about biodiversity trends and ecosystem health. Several acoustic indices have been developed for fast, automated assessments of ecosystem condition and are often used to assess changes in species richness/diversity across space or time. However, studies have reported inconclusive relationships between acoustic indices and species richness/diversity and the conclusions regarding “best” performing index differ between ecosystems. Here we assess the use of acoustic indices, using birds as a proxy for ecosystem health in a Northern Great Plains grassland system. We recorded soundscapes during bird morning chorus at 47 sites for 12–14 consecutive days and used these data to assess the accuracy of four acoustic indices (i.e. Bioacoustic Index; Acoustic Evenness Index; Acoustic Diversity Index; and Acoustic Complexity Index). We compared indices to bird richness derived from a trained ornithologist listening to sound recordings. The Bioacoustic Index (BI) and Acoustic Complexity Index (ACI) had the absolute highest correlation with bird richness in Northern Great Plains systems. Where Bioacoustic Index had a positive correlation and Acoustic Complexity Index had a negative correlation with grassland birds. The latter had the opposite direction from the ‘theoretical’ prediction. We further explored the relationship between indices and landscape gradients with known influences on bird diversity to further validate each index. We also discuss implications of acoustic indices as a tool for monitoring grassland birds. We found BI model outcomes align with known relationships between grassland birds and spatial covariates, whereas ACI did not concur these trends. We discuss these outcomes in relation to habitat-specific bird biophonic characteristics and provide possible explanations for differences between studies.

1. Introduction

Passive acoustic monitoring is an emerging tool to assess ecosystem state (Sueur and Farina, 2015). In the fields of bioacoustics and ecoacoustics, researchers have developed methods to assess biophonic patterns in relation to land use and landcover gradients (e.g. Deichmann et al., 2017; Pieretti et al., 2011; Pijanowski et al., 2011; Sugai and Llusia, 2019; Towsey et al., 2014; Zhang et al., 2016). Acoustic monitoring is a cross-taxa approach capable of assessing landscape level changes by sampling and analyzing soundscape patterns across space and time (Zhao et al., 2019). Study objectives span from changes in vocalizations of single species, to changes in communities (Ben-David et al., 2019; Forsman and Mönkkönen, 2001; Jorge et al., 2018a;

Mammides et al., 2017; Ng et al., 2018; Sethi et al., 2020), or changes in soundscapes, defined as the acoustic environment comprising all sounds in a given space and time (Pijanowski et al., 2011).

There are advantages and challenges associated with acoustic monitoring. One advantage is the ability to collect data simultaneously across large areas without the need to account for observer bias (Gibb et al., 2019). A second advantage is data collection can occur over longer time periods with minimum disturbance to wildlife (Deichmann et al., 2018; Gibb et al., 2019). The main challenges are data storage and processing, owing to the massive quantities of audio data accumulated at relatively low costs (Pavan et al., 2010; Wimmer et al., 2013). Furthermore, algorithms for specific call identification require extensive data collections for training of models (Pavan et al., 2010;

Abbreviations: BI, Bioacoustic Index; AEI, Acoustic Evenness Index; ADI, Acoustic Diversity Index; ACI, Acoustic Complexity Index

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Wimmer et al., 2013).

Many studies use acoustic indices to assess bird communities, and birds are considered an ideal taxon to study using acoustic methods because: 1) nearly all bird species produce communication calls (Sueur and Farina, 2015); 2) calls can be identified to species level by human surveyor (Gaston and O'Neill, 2004); 3) calls can sometimes be classified to specific behaviors (Ben-David et al., 2019); and 4) birds are sensitive to land use and land cover change (Londe et al., 2019), and therefore are frequently used as bioindicators for ecosystem integrity assessments across diverse habitats (Francis, 2017; Padoa-Schioppa et al., 2006; Paillisson et al., 2002).

Acoustic indices are numerical summaries of acoustic energy structure and frequency distributions (Towsey et al., 2014). In recent years, a number of acoustic indices have been developed for rapid, automated assessments of ecosystem condition or as a proxy for richness/diversity (Gasc et al., 2013; Rajan et al., 2019; Sugai and Llusia, 2019). Several studies report inconclusive relationships between different indices and measures of species richness/diversity such that conclusions with regards to the “best” performing index differ between ecosystems (Fairbrass et al., 2017; Fuller et al., 2015; Gasc et al., 2015; Mammides et al., 2017; Myers et al., 2019; Zhao et al., 2019). These uncertainties warrant ecosystem-specific assessments of the performance of acoustic indices (Gasc et al., 2015).

Here we assess the ability of 4 commonly used acoustic indices to predict grassland bird species richness in an effort to determine the best performing index for a Northern Great Plains grassland ecosystem. Grassland birds are one of the most imperiled avian groups in North America, where 74% of all grassland birds species are in decline (Rosenberg et al., 2019; Sauer et al., 2017). Therefore, there is a critical need to find a systematic cost-effective way to survey grassland birds at large scales. Ecoacoustics has a potential to simplify bird surveys, reduce their costs in time and money, and promote identification of changes in bird communities, species declines, and areas of conservation concern. Further, we assess the relationship of acoustic indices with landscape level covariates and use the best performing indices to explain grassland bird richness trends in relation to landscape gradients.

2. Study area

Work was conducted in a mixed-grass prairie ecosystem in north-central Montana within the Northern Great Plains (48°N , 108°W). This region is a breeding stronghold for several imperiled grassland bird species and is categorized as an area of high conservation priority for grassland birds (Pool and Panjabi, 2011, Fig. 1). The climate is characterized as arid and changes dramatically between seasons, from extremely cold winters (average temp -7.6°C) to warm to hot summers (average temp 33.8°C) (Whitlock et al., 2017). Average annual precipitation ranges from 325 to 384 mm (Whitlock et al., 2017). Vegetation is a mix of native perennial grasses, annual grasses (many non-native) and shrubs (*Artemisia cana*, *Artemisia tridentata*, *Juriparus horizontalis*, and *Krascheninikovia lanata*) (Charboneau, 2013). Seasonal streams run through the site with woody riparian vegetation comprised mainly of *Acer negundo*, *Populus angustifolia* and *Salicaceae* (Charboneau, 2013). The study area is a mixture of private and public lands used mostly for cattle ranching operations. The southern part of the study region is the Charles M. Russell Wildlife Refuge managed by US-Fish and Wildlife Service. It is a 1.1-million-acre refuge that surrounds the Fort Peck Reservoir on the Missouri River (Fig. 1).

3. Methods

3.1. Sampling design

We recorded morning soundscapes across 47 grassland sites during the grassland bird breeding season (May–June 2019). Sites were

randomly selected based on predetermined criteria specified for identifying grassland bird habitat within the overall study area. We first gridded the area to 0.8 km^2 cells and classified each cell based on vegetation structure and soil composition. Vegetation structure was determined using the Montana Spatial Data Infrastructure (MSDI) 2016 compiled by the Montana Natural Heritage Program (http://geoinfo.msl.mt.gov/home/msdi/land_use_land_cover.aspx). Soil composition was classified according to clay, sand and silt composition using Natural Resources Conservation Service (NRCS) soil dataset and classification based on soil texture triangle (NRCS, n.d.). We extracted cells with over 80% grass cover and soils characterized as either clay or loam. We selected 47 sampling sites from the resulting pool of grid cells that fit our criteria. We recorded morning chorus starting one hour before sunrise until one hour after sunrise (approximately 04:30–06:30 am) on 12–14 consecutive days. Sound was recorded in 10-minute segments, and we analyzed only the first minute of each segment, resulting in 12 1-minute recordings per day, per site for a total of 7313 recordings.

We collected acoustic data using AudioMoth recorders (Hill et al., 2018). Recorders were mounted on rebar stakes, 50 cm above ground, facing south. AudioMoth recorders were set for 192 kHz sampling rate, and medium gain.

3.2. Species and sound identification

We randomly selected 10 1-min recordings from each site, resulting in a subset of 470 1-min recordings that were used to assess acoustic index performance in relation to species richness. A trained ornithologist (EC) listened to each recording (full frequency range) and identified bird species vocalizations and recorded the number of species for each recording. We also recorded the presence of rain, wind, orthoptera and amphibian morphospecies occurrence during each recording. We recorded overall sound richness (all species including orthoptera, amphibians morphospecies and physical sound of wind or rain), bird richness (all bird species), and grassland bird specialist richness for 470 samples of 1-minute recordings. These data were used to evaluate acoustic indices.

3.3. Statistical analysis

3.3.1. Acoustic indices

We calculated four acoustic indices: Bioacoustic Index (BI) (Boelman et al., 2007); Acoustic Diversity Index (ADI) (Villanueva-Rivera et al., 2011); Acoustic Complexity Index (ACI) (Pieretti et al., 2011); and Acoustic Evenness Index (AEI) (Villanueva-Rivera et al., 2011). Calculations were within the 2–8 kHz range (BI and ACI) and 0–8 kHz range (ADI, AEI). Frequencies between 2 and 8 kHz are typical for grassland bird vocalizations in our study area (see Fig. 4, for species sonograms see Supplementary Materials). Indices were calculated using the package *soundecology* version 1.3.3 (Villanueva-Rivera and Pijanowski, 2018) in R version 3.5.1 (R Core Team, 2015).

BI is considered a proxy for bird richness and abundance (Boelman et al., 2007). It calculates the total of sonic energy using fast-Fourier transform (FFT) of each acoustic segment (Boelman et al., 2007). ACI measures the variability of sounds by measuring the intensities of frequencies registered within bins in each audio segment (Pieretti et al., 2011). FFT window size was set to 512 for BI and ACI. ADI is a diversity index that applies the Shannon Index to each acoustic segment (Pielou, 1966; Villanueva-Rivera et al., 2011). Each segment is divided into spectrogram bins (default 10 Hz) and the proportion of the signals in each bin above an amplitude threshold was extracted (default -50 dBFS). AEI is considered a proxy for species diversity, but its result is an inverse relationship (Villanueva-Rivera et al., 2011). AEI setting were set as ADI settings. AEI applies the Gini index, which measures inequality among sounds (Villanueva-Rivera et al., 2011). In this case a higher score would mean the soundscape is dominated by one or few

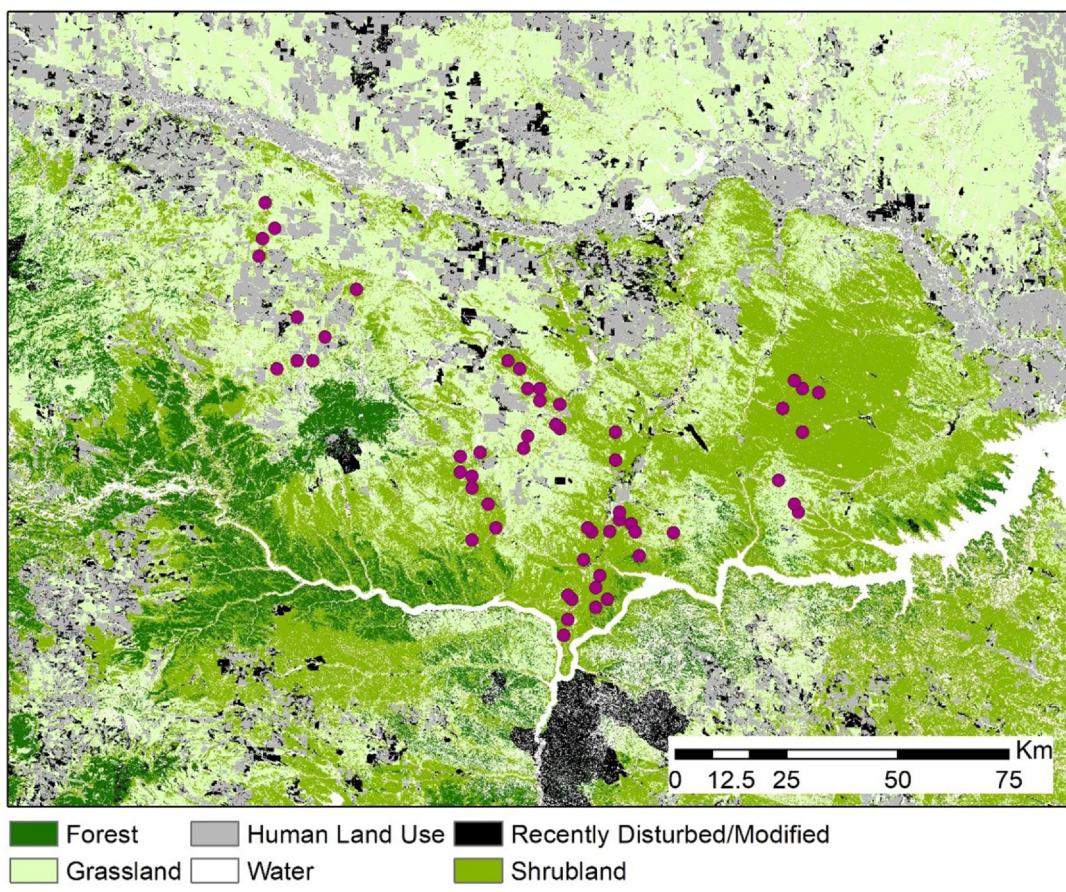


Fig. 1. Study area land cover map (National Landcover Dataset 2016). Survey sites are shown as red circles.

species.

3.3.2. Evaluation of indices

We extracted three components of richness from each recording (see Section 3.2 *Species and sound identification*). The first included grassland obligate birds, the second included all bird species and the third included all identifiable natural sounds, including insects, amphibians, wind, and rain. Wind and rain were included because they have the potential to compromise the relationship between acoustic indices and richness. We further tested the relationship between indices and bird richness by eliminating recordings with rain sounds to assess the contribution of rain to indices computations. We tested the correlation between species richness (identified manually) and acoustic indices, using Spearman correlation test using ‘*cor()*’ function from the ‘*stats*’ R package (R Core Team, 2015).

3.3.3. Explanatory variables

We further explore acoustic indices relationship with landscape gradient attributes with the goal to assess grassland bird richness responses to spatial covariates (Table 1). We extracted land cover percentages within a 500 m buffer (Boyce et al., 2020) for each site. Covariates included ground cover, herbaceous cover, and shrub cover from the National Land Cover Dataset (NLCD) (Xian et al., 2015; Yang et al., 2018). NLCD uses regression tree models to classify land cover categories based on Landsat 8 imagery (Yang et al., 2018). Clay and sand content % (kg/kg) were extracted from the OpenLandMap dataset available on Google Earth Engine (Gorelick et al., 2017). This layer is based on machine learning predictions from a global compilation of soil profiles and samples (Tomislav, 2018). Elevation was extracted from the National Elevation Dataset (NED) provided by U.S. Geological Survey (USDA) (Gesch et al., 2002). Slope and topographic roughness

were calculated using the ‘*train*’ function from the ‘*raster*’ v3.0-12 R package (Jacob van et al., 2020). Roughness is quantified using a moving window function that calculates the absolute mean differences between a centroid cell and the value of its 8 surrounding cells. The value indicates how variable elevation is in a given location. We extended the use of this function to calculate “roughness” of percent herbaceous cover and percent shrub cover. This variable results in a measurement of the heterogeneity of vegetation cover at a given site.

3.3.4. Association between acoustic index and landscape variables

We modeled indices against landcover gradients. We used a generalized linear mixed effects model (GLMM) with a nested design, where acoustic index is a function of site level covariates and repeated measures are nested in site and day. We used the ‘*lmer*’ v1.1-21 package (Bates et al., 2015). Random effects used in models were site ID and precipitation (m of water/3-hours) extracted from European Centre for Medium-Range Weather Forecasts datasets via Env-DATA tool (Dodge et al., 2013). We used a gamma distribution using link ‘*identity*’ which is suitable for the data distribution skew. We selected the leading model for each index using Akaike information criterion (AIC) score (Burnham and Anderson, 2004).

4. Results

4.1. Correlation of acoustic indices and sound richness

We manually identified 37 species among 1351 bird detections in a subsample of 470 1-minute recordings. This sample was used to assess acoustic indices correlation to bird richness. Among these, 14 species were grassland specialists (Fig. 2). Three species, western meadowlark (*Sturnella neglecta*), vesper sparrow (*Pooecetes gramineus*), and

Table 1
Landscape data layers. Data layers were manipulated to desired calculation and scales as detailed in methods.

Variable	Source	Type	Description	Resolution
Percent shrub cover	NLCD 2016	Numeric, trunked 0–100	The U.S. Geological Survey (USGS), based on Landsat imagery and geospatial ancillary datasets	30 m
Percent herbaceous cover (grass and others)	NLCD 2016	Numeric, trunked 0–100	The U.S. Geological Survey (USGS), based on Landsat imagery and geospatial ancillary datasets	30 m
Percent bare ground cover	NLCD 2016	Numeric, trunked 0–100	The U.S. Geological Survey (USGS), based on Landsat imagery and geospatial ancillary datasets	30 m
Clay content	OpenLandMap	Numeric, trunked 0–100	The U.S. Geological Survey (USGS), based on Landsat imagery and geospatial ancillary datasets	250 m
Sand content	OpenLandMap	Numeric, trunked 0–100	%Clay content kg/m ³	250 m
Elevation/Slope/Roughness	USGS National Elevation Dataset	Numeric, trunked 0–100	%Sand content kg/m ³	30 m
			USGS National Elevation Dataset courtesy of the U.S. Geological Survey.	

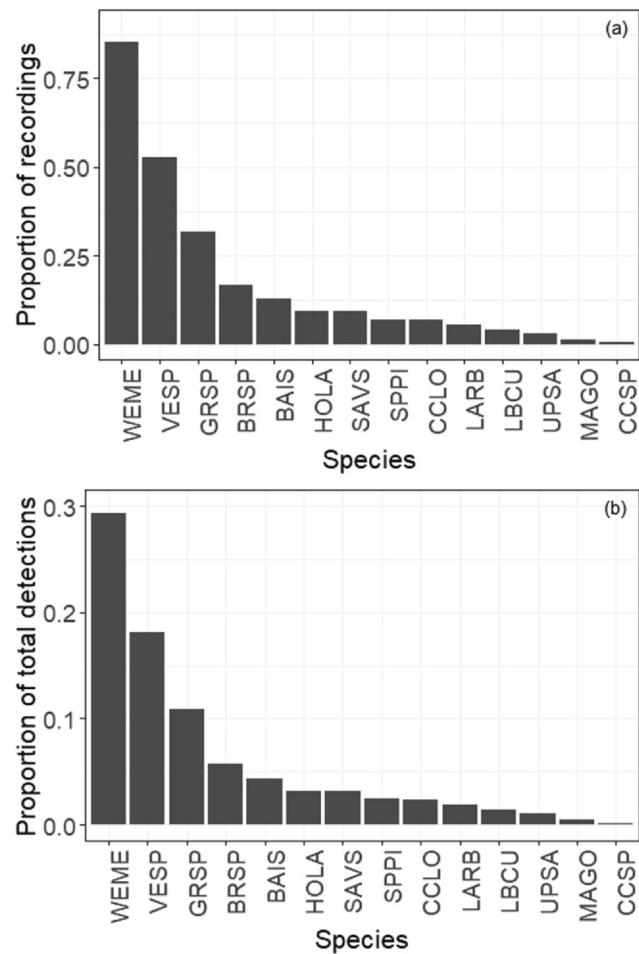


Fig. 2. (a) Proportion of species detections of grassland bird specialists detected in 470 1-min recordings from 47 sites. (b) Proportion of species detections from total species detections. Data collected May-June 2019, Montana, USA. Baird's sparrow (*Ammodramus bairdii*) (BAIS), Brewer's sparrow (*Spizella breweri*) (BRSP), Chestnut collared longspur (*Calcarius ornatus*) (CCLO), Clay colored sparrow (*Spizella pallida*) (CCSP), Grasshopper sparrow (*Ammodramus savannarum*) (GRSP), Horned lark (*Eremophila alpestris*) (HOLA), Lark bunting (*Calamospiza melanocorys*) (LARB), Long-billed curlew (*Numenius americanus*) (LBCU), Marbled godwit (*Limosa fedoa*) (MAGO), Savannah sparrow (*Passerculus sandwichensis*) (SAVS), Sprague's pipit (*Anthus spragueii*) (SPPI), Upland sandpiper (*Bartramia longicauda*) (UPSA), Vesper sparrow (*Pooecetes gramineus*) (VESP), Western meadowlark (*Sturnella neglecta*) (WEME).

grasshopper sparrow (*Ammodramus savannarum*) were dominant in this study area and were identified in 85, 52 and 32% of the recordings respectively (Fig. 2). Western meadowlark calls are mostly within 2–3 kHz, vesper sparrow 4–5 kHz, and grasshopper sparrow 7–9 kHz (Fig. 3). The overall soundscape was characterized by 5 distinct amplitude peaks at ~2, 3.5, 4, 5, 7 kHz, a trend that was found in most samples (curves are based on 7313 1-min recordings, Fig. 4).

Of the four indices, BI and ACI had the strongest absolute relationship with grassland bird richness. The latter had the opposite direction from the 'theoretical' prediction. ADI and AEI were not correlated with grassland bird richness BI was positively and significantly correlated with bird richness (*Spearman ρ correlation coefficient*: = 0.34, $p < 0.001$), grassland specialists' richness ($\rho = 0.31, p < 0.001$), and overall sound richness ($\rho: 0.17, p < 0.001$), however the latter was a weak relationship (Fig. 5). Acoustic Complexity Index was negatively correlated with total bird richness ($\rho = -0.31, p < 0.001$) and grassland specialist richness ($\rho = -0.34, p < 0.001$) (Fig. 3). Acoustic Diversity Index was significantly and negatively correlated with all sounds ($\rho = -0.17, p < 0.001$) (Fig. 3). Acoustic Evenness Index was

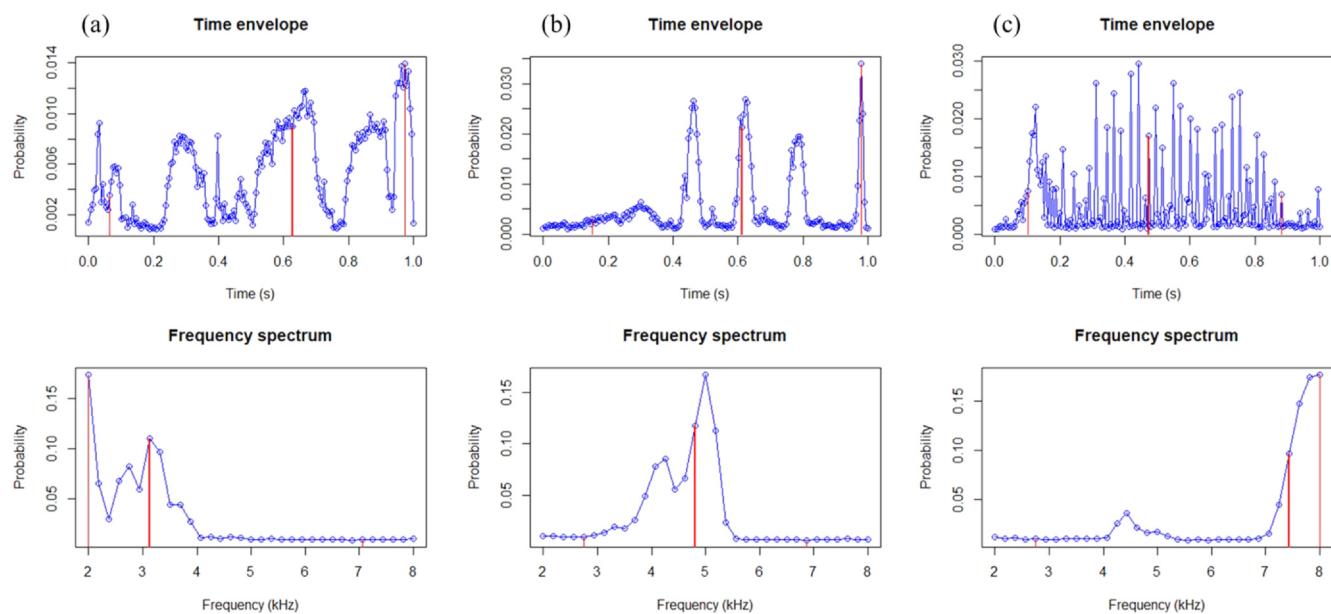


Fig. 3. Example of short-term Fourier transform presented for the three most dominant grassland bird species presented as the time contour and the frequency contour using the ‘*acoustat()*’ function from the ‘*seewave*’ R package (Simonis et al., 2020). (a) Western meadowlark (*Sturnella neglecta*), (b) Vesper sparrow (*Pooecetes gramineus*), (c) Grasshopper sparrow (*Ammodramus savannarum*).

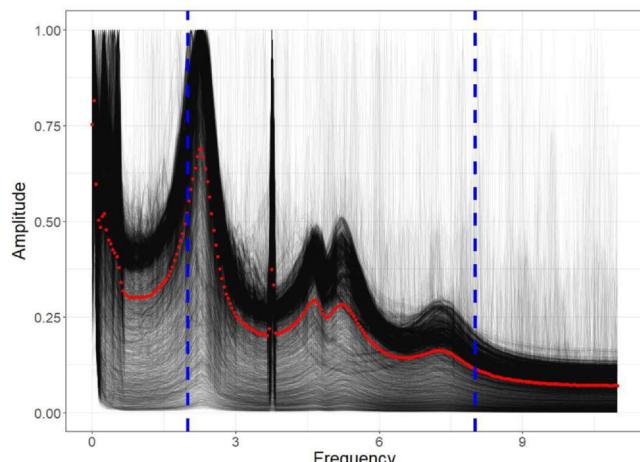


Fig. 4. Median frequency spectrum of 7313 acoustic recordings (1 min long each) sampled across 47 sites between May-June 2019, Phillips County, Montana. Mean frequency in red, 2 and 8 kHz marked with blue dashed line.

positively correlated with overall sound richness ($\rho = 0.17$, $p < 0.001$) (Fig. 3).

Eliminating recordings with rain sounds yielded similar trends, but correlation with bird specialists was stronger for both BI and ACI (Spearman ρ coefficient: 0.38 and -0.42 respectively, p -value: < 0.001). ADI and AEI relationship remained the same and the indices are significantly correlated with bird richness or grassland bird specialists.

4.2. Acoustic indices in relation to landscape gradients

The four indices were modeled against landscape level covariates (Table 2). BI showed a positive quadratic relationship with grass cover, and was lowest in intermediate grass cover, but it was skewed towards lower grass cover (based on linear relationship). BI had a negative quadratic relationship with shrub cover and was higher in intermediate shrub cover values. BI had a negative relationship with topographic roughness (Table 2). ACI was negatively correlated with grassland bird richness and should be interpreted accordingly. We note that we report

here the mathematical relationship of ACI with landscape covariates. ACI had a negative quadratic relationship with grass cover, meaning ACI was higher in intermediate grass cover. ACI had a negative relationship with topographic roughness (Table 2).

Despite the fact that the other two indices, ADI and AEI, were not correlated with grassland bird richness, we report their relationship with landscape gradients. Both indices had nonlinear relationships with vegetation cover (Table 2). ADI was higher at lower and higher grass cover. ADI was higher at intermediate shrub cover. AEI was higher at intermediate grass cover and lower with higher grass cover heterogeneity. AEI was higher at lower and higher shrub cover (Table 2).

5. Discussion

We assessed the use of four common acoustic indices as proxies of grassland bird richness in the North Great Plains short-grass system. We found that Bioacoustic Index (BI) and Acoustic Complexity Index (ACI) were most strongly correlated with grassland bird richness. However, in the case of ACI, the correlation with grassland bird richness was negative, and trends should be interpreted accordingly. The other two indices tested (ADI, AEI) were poor predictors of bird richness.

5.1. Comparisons of the study outcomes and previous studies

The relationship between bird richness and the four indices tested in this study have been assessed in other habitats and results vary amongst studies (Table 3). Acoustic indices are influenced by range of occupied frequencies, overlap of sounds, song structure and transmission. Choosing an acoustic index depends on the aims of the study, and should be based on good understanding of the relationship between each index and the biological variable of interest (Bradfer-Lawrence et al., 2019). Because habitat specific sound characteristics differentially affect indices, understanding the underlying soundscape characteristics may help interpret the results of this study and inconsistencies between previous studies.

The acoustic adaptation hypothesis holds that species’ sound characteristics are a product of natural selection, shaped by the acoustic properties of their habitat (Boncoraglio and Saino, 2007). According to this hypothesis, the frequency range used by birds is an evolutionary

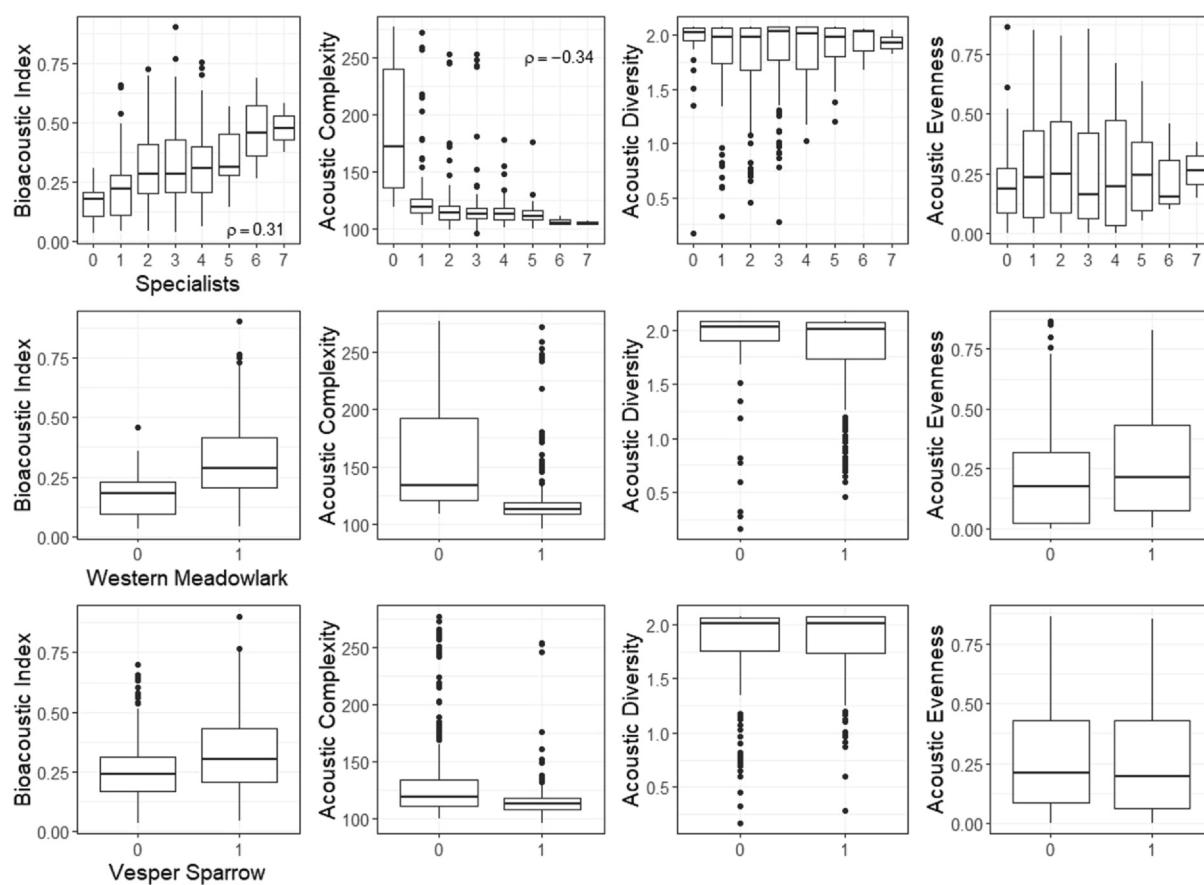


Fig. 5. Boxplots of four acoustic indices (Bioacoustic Index; Acoustic Diversity Index; Acoustic Evenness Index; Acoustic Complexity Index) in relation to: (a) the number of grassland bird specialist species recorded within 1-min samples. ρ is the Spearman correlation coefficient between acoustic indices and number of grassland bird specialists; only significant coefficients are presented ($P < 0.05$); (b) Acoustic indices values in the absence (0) or presence (1) of western meadowlark (*Sturnella neglecta*); (c) Acoustic indices values in the absence (0) or presence (1) of vesper sparrow (*Pooecetes gramineus*).

adaptation that allows for efficient sound transmission given their specific habitat conditions such as temperature, landscape configuration, or vegetation structure (Barker, 2008; Boncoraglio and Saino, 2007). This theory has been tested in several habitats and there is compelling evidence that bird species use similar frequencies in similar habitats. For example, in open habitats such as grasslands, birds use higher frequencies because sound is reflected from the ground, distorting calls in lower frequencies (Cossens and Falls, 1984; Piercy et al., 1977), whereas in dense vegetation habitats birds are bounded to lower frequencies because sound is reverberated, limiting birds from using higher frequencies (Barker, 2008; Boncoraglio and Saino, 2007). Studies have also shown that bird calls in mixed habitats are more flexible and occupy a wider range of frequencies in comparison to homogeneous habitats (Ryan and Brenowitz, 1985).

The above is consistent with studies that shown that spatial heterogeneity promotes bird diversity (Hovick et al., 2014). This suggests that indices that are more sensitive to the range of occupied frequencies, such as ADI and AEI, might be more suitable for studies in mixed habitats where species richness can be represented by the range of frequencies used (Ryan and Brenowitz, 1985), but not necessarily in homogenous habitats where species sounds are characterized by high frequency overlap (Eldridge et al., 2018; Luther, 2009). Indeed, AEI was found to be a good proxy of bird richness in relation to elevational gradients and vegetation structure in temperate rainforests of Chile or the Atlantic tropical rainforest (Jorge et al., 2018b; Moreno-Gómez et al., 2019). Fuller et al. (2015) reported that AEI is good predictor of habitat configuration in forest systems in Australia. Similar results were obtained in tropical savannas in Brazil, where the authors suggested the use of ADI and AEI are suited as proxies for birds, anurans, and insects

(Ferreira et al., 2018). In contrasts, ADI and AEI were not good proxies for grassland birds in this study. This could be due to the homogenous nature of this habitat which limits the relatively low number of grassland bird species to use a small range of frequencies (Fig. 4). Together with the dominant presence of one species throughout 85% of all recordings (western meadowlarks, Fig. 2) makes ADI and AEI not applicable in habitats with seldom differences in soundscapes between survey sites.

Another aspect to consider when interpreting indices is the potential of bias caused by other biophonic or physical sounds that overlap with the group of interest. While neotropical habitats are characterized by high overlap of bird occupied frequencies in a given site (Luther, 2009), they are also characterized by high overlap with more taxonomic groups that include anurans and insects that mask bird calls (Aide et al., 2017). For example, Eldridge et al. (2018) tested the performance of acoustic indices in relation to bird species and found a strong correlation between all the indices tested here and bird species richness in temperate habitats, but found a weaker correlations in neotropical habitats; the authors suggest that additional biophonic sounds (insects and anurans) may cause bias. Similar issues can arise in systems dominated by anthropogenic noise where additional man-made sounds mask biophonic sounds and skew acoustic indices outcomes (Fairbrass et al., 2017).

Additional sounds occurred in our study area and we assessed their contribution to correlation with acoustic indices. We found rain sounds slightly affected indices and masked bird sounds, but trends remained the same with or without rain recordings (analysis of subset excluding recordings with rain). In terms of biophonic sounds, the soundscape recorded in this study was primarily comprised by bird morning chorus,

Table 2

Top models for four acoustic indices: Bioacoustic Index (BI); Acoustic Complexity Index (ACI); Acoustic Diversity Index (ADI); Acoustic Evenness Index (AEI). Presented models with lowest AIC scores as defined by a generalized linear mixed effects model analysis with random effects terms for precipitation (m/3 h) and site ID. Saturated model covariates: Clay content; Grass cover²; Grass roughness; Ground cover; Shrub; Shrub roughness; Shrub cover²; Sand content; Slope; Topographic roughness. Audio data collected May – June 2019, Montana, USA.

	(Intercept)	Grass Cover	Grass roughness	Shrub cover	Shrub roughness	Shrub cover ²	Grass ²	Ground cover	Clay content	Sand content	Topographic roughness	Slope	AIC	logLik	
BI	Estimate	2.19E + 00	-1.08E -01	-1.02E -02	3.10E -02	.	-1.17E -03	1.26E -03	.	-1.95E -02	-2.22E -02	-6.84E -03	.	-6675.7	3348.8
SE	SE	3.89E -01	1.24E -02	2.76E -03	6.37E -03	.	2.19E -04	1.30E -04	.	5.22E -03	4.85E -03	1.86E -03	.	.	.
t-value	t-value	5.636	-8.752	-3.687	4.867	.	-5.359	9.685	.	-3.736	-4.576	-3.675	.	.	.
Pr(> z)	Pr(> z)	1.74E -08	< 2.00-16	2.27E -04	1.13E -06	.	8.36E -08	< 2.00-16	.	1.87E -04	4.75E -06	2.38E -04	.	.	.
ACI	Estimate	4.02E + 00	2.37E -02	.	.	.	-2.47E -04	.	4.76E -03	3.64E -03	-3.57E -03	.	54265.1	-27124.5	
SE	SE	1.17E -01	3.72E -03	.	.	.	3.89E -05	.	1.54E -03	1.51E -03	5.86E -04	.	.	.	
t-value	t-value	34.318	6.38	.	.	.	-6.349	.	3.09	2.42	-6.096	.	.	.	
Pr(> z)	Pr(> z)	< 2.00-16	1.77E -10	.	.	.	2.17E -10	.	0.002	0.0155	1.09E -09	.	.	.	
ADI	Estimate	1.44E + 00	-4.81E -02	1.69E -02	2.34E -02	-5.56E -03	-7.61E -04	4.57E -04	-4.94E -03	8.62E -03	-1.36E -02	1.49E -02	.	-2587.7	
SE	SE	1.75E -01	7.30E -03	2.86E -03	3.54E -03	2.09E -03	1.14E -04	7.50E -05	1.23E -03	1.50E -03	3.72E -03	7.10E -03	.	.	
t-value	t-value	8.213	-6.597	5.922	6.616	-2.658	-6.653	6.095	-4.017	5.732	-3.655	2.099	.	.	
Pr(> z)	Pr(> z)	< 2.00-16	4.19E -11	3.18E -09	3.68E -11	0.00785	2.87E -11	1.09E -09	5.89E -05	9.91E -09	0.0003	0.0358	.	.	
AEI	Estimate	-2.15E + 00	1.09E -01	-4.75E -02	-4.38E -02	.	1.76E -03	-9.25E -04	1.29E -02	-1.86E -02	-4.26E -02	2.81E -02	-4.16E -02	-6150.1	3088
SE	SE	6.37E -01	1.95E -02	5.87E -03	9.61E -03	.	3.30E -04	1.95E -04	3.36E -03	7.81E -03	7.32E -03	1.07E -02	2.07E -02	.	.
t-value	t-value	-3.382	5.608	-8.085	-4.554	.	5.333	-4.747	3.827	-2.377	-5.821	2.623	-2.011	.	.
Pr(> z)	Pr(> z)	7.20E -04	2.05E -08	6.21E -16	5.27E -06	.	9.67E -08	2.06E -06	1.30E -04	1.75E -02	5.86E -09	8.72E -03	4.43E -02	.	.

Table 3
List of publications which tested or used the indices evaluated in this study.

Index	Study area	Frequency range	Tested proxy	References
BI	Hawaii; tropical forest	2-8 kHz	Bird richness	(Boelman et al., 2007)
ACI	Glacier Bay National Park, Alaska	1.25-6.3 kHz	Bird community complexity	(Buxton et al., 2016)
ACI, ADI, AEI, BI	Sussex, in SE England; woodland	0.3-24 kHz; 0-10 kHz; 2-8 kHz	Bird richness	(Eldridge et al., 2018)
ACI, ADI, BI	Greater London, UK; urban	0-12 kHz	Biotic diversity	(Fairbrass et al., 2017)
ACI	Italy; Mediterranean maquis	1.5-15 kHz	Bird richness	(Farina et al., 2011)
ACI, ADI, AEI, BI	Brazil; tropical savanna ecoregion	0.3-48 kHz; 0-48 kHz; 0-48 kHz; 0.3-48 kHz;	Insects, anurans, bird richness	(Ferreira et al., 2018)
ACI, ADI, AEI, BI	South-east Queensland, Australia; subtropical climate	0-11 kHz; 0-11 kHz; 2-8 kHz	Landscape configuration, species richness	(Fuller et al., 2015)
ACI, ADI	Haute Vallée de Chevreuse Regional Natural Park, France; Woodland	0.02-20 kHz	Bird richness	(Gasc et al., 2015)
ACI, ADI, AEI, BI	Atlantic tropical rainforest	0-12 kHz; 0-12 kHz; 0-12 kHz; 0.05-12 kHz	Bird richness	(Jorge et al., 2018a)
ACI, ADI, AEI, BI	China; rubber plantations and tropical rainforest	0-10 kHz; 0-10 kHz; 0-10 kHz; 2-8 kHz;	Bird richness and diversity	(Mammides et al., 2017)
ACI, ADI, AEI, BI	Chile; temperate rainforest	0-10 kHz	Bird and anuran species richness	(Moreno-Gómez et al., 2019)
ACI, ADI, AEI, BI	Greece; Mediterranean olive grove	0-11 kHz; 0-11 kHz; 2-8 kHz	Bird and anuran species richness	(Myers et al., 2019)
ACI, ADI, AEI, BI	Queensland, Australia; rural, woodland	0-9 kHz; 0-9 kHz; 0-9 kHz; 2-9 kHz;	Biodiversity and ecosystem health	(Ng et al., 2018)
ACI, ADI, AEI, BI	Italy; Turkey oaks by highway	1.5-22.05 kHz	Bird call response to anthropogenic disturbance	(Pieretti and Farina, 2013)
ACI, ADI, AEI, BI	India; forest	22.05 kHz	Number of bird vocalizations	(Pieretti et al., 2011)
ACI, ADI, AEI, BI	Kerala, India; Urban gradient	0-UNK; 0-UNK; 2-8 kHz	Bird diversity	(Rajan et al., 2019)
ACI, ADI, AEI, BI	Costa Rica; wet and tropical dry forest	2-11 kHz	Bird richness	(Retamosa Izaguire et al., 2018)
ACI, AEI	Brisbane Australia; open forest and woodland	night 0-4 kHz; morning 0-6 kHz	Species diversity and evenness	(Towsley et al., 2014)
ACI, ADI, AEI, BI	Indiana, USA; oak-hickory forest	0-16 kHz; 0-8 kHz; 2-8 kHz	Bird richness	(Villanueva-Rivera et al., 2011)
ACI, ADI, AEI, BI	Jiangxi Province, China	0-16 kHz	Bird richness	(Zhao et al., 2019)

a time of day when insects (mainly Orthoptera) and anurans are less vocal (Paraskevopoulou et al., 2020), therefore, we are confident that other taxa had little influence on the results presented here.

To carry over longer distances, grassland bird calls favor higher amplitudes and are considered relatively repetitive, whereas birds in dense vegetation are characterized by short, complex and unique sounds where species partition time and signal space (Brown and Handford, 2000; Luther, 2009; Morton, 1975; Naguib, 2003). ACI measures sound complexity by measuring the difference of amplitude between consecutive frequency bins relative to the total amplitude (Farina et al., 2011). Therefore, we expect higher ACI values when sounds are characterized by short warbles and phrases calls in comparison to longer sounds of series or trills calls (i.e. open habitat sounds). BI computes the total sound energy by measuring the area under the curve (Boelman et al., 2007), so we would expect it to be higher when amplitudes are higher and across a wider range of frequencies. We found that increase in grassland bird richness decreased the collective sound complexity (lower ACI) and increased the overall sound energy (BI). This could be due to high overlap between bird calls, the type of calls typical for this habitat (less complex), and the low number of species with one dominant.

ACI was found as a good proxy for different biotic groups in other habitats (Myers et al., 2019; Rajan et al., 2019; (Fuller et al., 2015; Buxton et al., 2016) or when assessing seasonal differences in the same habitat (Buxton et al., 2016). These suggest that ACI is better suited for identifying differences in bird assemblages in mixed habitats or when comparing sites with extreme differences in habitat conditions. This is further supported by the fact that very dominant species may hinder ACI from detecting differences in bird richness (Retamosa Izaguirre et al., 2018). The fact that bird calls in homogenous habitats such as grasslands are less complex, and the soundscape is similar across survey sites, could explain the inverse relationship we found between ACI and grassland bird richness.

BI results are harder to explain. BI was reported as a good predictor in a variety of habitats, with no clear common characteristics between these studies (Boelman et al., 2007; Fairbrass et al., 2017; Rajan et al., 2019). The main soundscape characteristics that differentiate between previous studies and this study is that the current study was conducted in a habitat and time of day with relatively low overlap with other biophonic sounds and no anthropogenic noises.

5.2. Using acoustic indices to explain grassland bird responses to landscape gradients

We assessed the utility of 4 commonly used bioacoustics indices in mixed-shortgrass prairie. We looked for a way to conduct rapid assessments of grassland birds as this group is considered a bioindicator for ecosystem integrity. After assessing the relationship of indices with grassland birds, we further tested the relationship of BI and ACI with landscape attributes and assessed if the relationships are consistent with what is known for grassland birds. We found BI to exhibit similar spatial trends to what is known about grassland birds. In grasslands, birds maintain fine-scale associations with vegetation structure and ground-cover (Johnson et al., 2019; Knopf, 1996). These associations facilitate the use of grassland bird diversity in assessing ecosystem health as a function of land use, human disturbance, and grazing practices. (Golding and Dreitz, 2017; Vold et al., 2019).

Previous studies have shown that topographic roughness (sometimes referred as terrain ruggedness) is a driver of grassland bird habitat selection and distribution and grassland birds select lower roughness (Duchardt et al., 2018; Grand et al., 2019). Both ACI and BI had a negative relationship with roughness, but ACI has an inverse relationship with grassland birds therefore this result is opposite to what is known from the literature. Grassland heterogeneity has a positive impact on grassland birds (Johnson et al., 2019; Londe et al., 2019; Luoto et al., 2004). BI captured this relationship with grass cover

heterogeneity whereas ACI did not. Based on these outcomes, BI was more consistent with known grassland bird trends in relation to landscape gradients.

6. Conclusion

Acoustic indices are a promising tool for rapid assessments of habitat change and for monitoring changes in species communities. However, it is difficult to draw conclusions about biological or physical components of interest without prior evaluation of the suitability of acoustics indices for a particular ecosystem or location. Despite the extensive literature on the performance of different indices, researchers should be cautious when choosing the right index and the performance of indices should be validated for each study. In short grass prairies, the Bioacoustic Index and Acoustic Complexity Index can be used to evaluate grassland bird richness, however, BI can better describe grassland bird responses to land cover and land-use gradients. In short-grass prairies, the Bioacoustic Index can be used to evaluate grassland bird richness. Acoustic Complexity Index had a negative relationship with bird richness. Given that ACI was constructed such that high values should indicate higher complexity, further research exploring acoustic indices relation to sound characteristics is needed to fully understand the mechanism underlying the correlation. The difference between the two indices was underscored by the fact that BI was positively correlated with landcover variables known to produce higher bird species richness, while ACI had the opposite response with these same variables (topographic roughness).

Declaration of Competing Interest

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

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Author contributions

Study design and fieldwork: HS, ZP, EC, AJB, WJM; data analysis: HS, ZP, EC, JK, JLD. Writing of the article: HS, ZP, WJM, JK, JLD, AJB.

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Ethics

The work was conducted in compliance with the journal's ethics code.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106928>.

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