USING SOUNDSCAPES TO MEASURE BIODIVERSITY, HABITAT CONDITION, AND ENVIRONMENTAL CHANGE IN AQUATIC ECOSYSTEMS

by

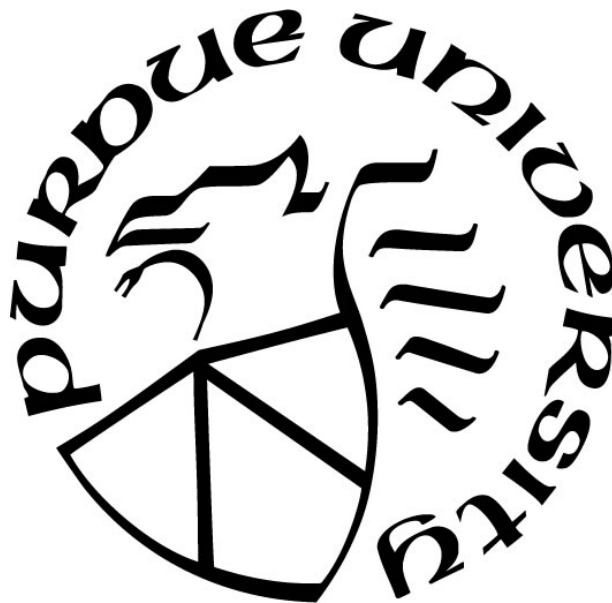**Benjamin L. Gottesman**

A Dissertation

Submitted to the Faculty of Purdue University
In Partial Fulfillment of the Requirements for the degree of

Doctor of Philosophy

Department of Forestry and Natural Resources

West Lafayette, Indiana

December 2019

THE PURDUE UNIVERSITY GRADUATE SCHOOL
STATEMENT OF COMMITTEE APPROVAL

Dr. Bryan Pijanowski, Chair
> Department of Forestry and Natural Resources

Dr. Barny Dunning
> Department of Forestry and Natural Resources

Dr. Jeff Lucas
> Department of Biology

Dr. Tomas Höök
> Department of Forestry and Natural Resources

Approved by:
> Dr. Linda Lee and Dr. Robert Wagner
>> Head of the Graduate Program

For my Grandma, a life-long learner with a golden ear

FOREWORD

" A picture is worth a thousand words, and a soundscape is worth a thousand pictures"
—Bernie Krause

"The polyphonic prairies here, it's all around you"

—Damon Albarn

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Author: Gottesman, Benjamin, L. PhD
Institution: Purdue University
Degree Received: August 2019
Title: Using Soundscapes to Measure Biodiversity, Habitat Condition, and Environmental
      Change in Aquatic Ecosystems
Committee Chair: Bryan Pijanowski

Biodiversity loss is the silent crisis of the 21st century. Human activities are drastically altering the diversity of life on Earth, yet the extent of this transformation is shrouded by our limited information on biodiversity and how it is changing. Emerging technologies may be suited to fill this information gap, and as a result increase our capacity to measure and manage natural systems. Acoustic monitoring is a remote sensing technique that is rapidly reshaping the temporal and spatial scales with which we can assess animal biodiversity. Through recording and analyzing soundscapes—the collection of sounds occurring at a given place and time—we can assess biodiversity, habitat condition, and environmental change. However, the relationships between soundscapes and these three ecological dimensions are still in the early phases of categorization, especially in aquatic systems.

This dissertation investigates how soundscapes can be used to measure biodiversity, habitat condition, and environmental change in aquatic habitats. It addresses several knowledge gaps: First, I develop a framework for classifying unknown sounds within a soundscape, which I use to measure the acoustic diversity and dynamics within a tropical freshwater wetland. Second, I demonstrate that soundscapes can reflect the resilience of animal communities following disturbance events. Altered soundscapes revealed that Hurricane Maria, which swept through Puerto Rico in September 2017, impacted dry forest animal communities more than adjacent coral reef communities. Third, in kelp forest habitats off the coast of California, USA, I showed that soundscape variables correlated with ecological variables associated with regime shift in kelp forests, including urchin density, kelp cover, and fish diversity. Overall, this dissertation demonstrates that soundscape recording and analysis is a promising way to assess the ecological conditions of aquatic systems.

CHAPTER 1: **INTRODUCTION**

1.1 Biodiversity decline

We live in a time of rapid and widespread environmental change (Cardinale et al., 2012; Vos, Joppa, Gittleman, Stephens, & Pimm, 2015). Humans have significantly altered 75% of terrestrial environments and 66% of marine environments (Díaz et al., 2019). As a result, biological diversity is declining at unprecedented rates, estimated at 100-1000 times greater than historical levels (Butchart et al., 2010). Approximately, one million species face extinction this century (Díaz et al., 2019). In addition, animal populations are dwindling in number and geographic extent, with vertebrate populations declining approximately 60% since the 1970s according to the most recent *Living Planet Index* (Dirzo et al., 2014; McCauley et al., 2015; McRae, Freeman, & Marconi, 2016). The five primary drivers of this biodiversity loss are, in order of their importance, habitat loss, exploitation of organisms, climate change, pollution, and invasive species (Sala et al., 2000).

Preserving biodiversity, the variation of life at scales from genes to species to ecosystems, is necessary to support human society (Chapin III et al., 2000; Haines-Young & Potschin, 2010). Humans rely on intact natural systems to clean our air and water, sustain us with food, pollinate our crops, give us life-saving medicines, and protect our cities from extreme weather events (Daily, 1997; Worm et al., 2006). In order to prevent catastrophic losses in biodiversity by the end of the 21st century, swift and transformative changes are needed not only in governance, public awareness, and economic systems, but also in our capacity to measure biodiversity and how it is changing (Pimm et al., 2015; Stoms & Estes, 1993).

Measuring biodiversity is a challenging endeavor due to its irreducible complexity, the different scales at which it needs to be measured, and the different methods required to measure it (Butchart et al., 2010). Biodiversity has three main dimensions: phylogenetic (taxonomic), genetic, and functional diversity (Loreau, Naeem, & Inchausti, 2002; Purvis & Hector, 2000; Gaston & Spicer, 2013). While the Linnaean system for classifying biodiversity has remained consistent for almost 300 years, methods to measure biodiversity in the field remain quite varied; they can differ based on ecosystem type, species of interest, and the human and economic resources available. One

commonality though, at least in most cases, is that these methods are employed by humans in the field. In this way, humans are part of all these biodiversity measurement systems. Our knowledge of biodiversity and how it is changing is therefore shaped by practical, human-based constraints (Pimm et al., 2015). Since humans cannot endure the field indefinitely, biodiversity surveys are often conducted at sparse temporal intervals and only at particular times of the year and hours of the day (Gasc et al., 2018). Researchers in the field are also limited in the number of different taxa that they can measure at a given time and the number of sites where they can replicate these measurements. Moreover, due to the short-term nature of most research grants and the prohibitive cost of long-term monitoring, biodiversity surveys tend to be short-term, though there are many established long-term monitoring programs. For this reason, measuring trends in biodiversity across large temporal and spatial scales becomes difficult via *in situ* surveys alone (Anderson, 2018).

As a result, some steep, long-term declines in biodiversity have evaded detection from the scientific community until only recently. For example, in 2017, in what helped spark the global interest in the "insect apocalypse," a small-town, German entomological society used its decades-long archive to demonstrate that overall insect abundance (measured by weight) across 63 sites in Germany dropped 75% in 27 years (Hallmann et al., 2017). Since then, researchers around the world have sought after similar datasets to show similar long-term patterns (Lister & Garcia, 2019). In response, Europe ratified its first ever initiative for protecting pollinators, illustrating the importance of standardized long-term datasets in galvanizing conservation outcomes (European Commission, 2019). In a similar case, Rosenberg et al. (2019) utilized bird survey data collected since the 1970s to discover a 29% overall decline in the abundance of 529 North American bird species over the last 48 years. However, these long-term datasets are quite rare for most taxa and for most regions of the world (Wepprich, Adrion, Ries, Wiedmann, & Haddad, 2019).

1.2 Importance of monitoring and assessment

Key to measuring biodiversity change in the future will be developing systematic approaches that autonomously collect data at relevant spatiotemporal scales and yield meaningful indicators of biodiversity. In the most recent United Nation's Convention on Biological Diversity, the conference of parties outlined 20 biodiversity-oriented policy benchmarks, known as the Aichi

targets. Reaching these targets would constitute a conservation success for the 196 countries involved (Tittensor et al., 2014). All of these targets are assessed by "monitoring and reviewing implementation of the national biodiversity strategies and action plans and national targets, using indicators" (Collen et al., 2009). Indeed, judging conservation outcomes is only possible if we find measurable indicators through ecological monitoring.

Ecological monitoring is essential for measuring change in the environment. It consists of long-term, systematic collection of ecological data to determine changes in the environment and the causes of these changes (Spellerberg, 1991). One type of ecological monitoring is biodiversity monitoring. Collecting information on a subset of animals can serve as an indicator of the overall biodiversity because the abundance, productivity, and reproductive success of these animals integrate the impacts of numerous environmental factors (Spellerberg, 1991). Common measurements of biodiversity include species richness, the number of different species within an ecological community, and species abundance, the total number of individuals per species within an ecological community. However, monitoring by itself is oftentimes not enough (McDonald-Madden et al., 2010). To be especially useful for habitat management, monitoring programs should be designed to answer explicit questions and produce data that informs the scientific researchers, resource managers, and policy makers that can benefit from this information (Niemelä, 2000). Even without specific questions, collecting biodiversity data can provide a critical baseline from which to evaluate long-term environmental change.

Despite the importance of ecological monitoring, traditional approaches are currently limited in the following respects (McDonald-Madden et al., 2010). First, the technical and financial resources to conduct *in situ* monitoring are oftentimes prohibitive, leading to large spatial and temporal gaps in our knowledge and a dearth of long-term monitoring programs (Pereira & David Cooper, 2006; Strayer & Dudgeon, 2010). Second, monitoring outcomes do not always inform natural resource management or policy, whether due to insufficient protocol design, a lack of pre-defined goals, or an inability to summarize results in a way that is accessible to managers or policy makers (McDonald-Madden et al., 2010). That monitoring is costly, difficult to conduct at scale, and not always tailored to inform management dictates that we need new methods to complement existing

approaches. This dissertation evaluates the potential for an emerging biodiversity monitoring technique—soundscape recording and analysis— to address these limitations.

1.3 Rise of soundscape monitoring

Soundscapes are now being recorded to monitor biodiversity and ecosystems (Pijanowski, Farina, Gage, Dumyahn, & Krause, 2011). Unlike biodiversity monitoring, soundscape monitoring measures assemblages of sounds (instead of species) in order to answer different ecological questions related to individual species, animal populations, community diversity, habitat condition, among others (Pijanowski et al., 2011a). In the last ten years, these relationships have been demonstrated in terrestrial, freshwater, and marine systems (Borker et al., 2014; Burivalova et al., 2018; Harris, Shears, & Radford, 2016; Towsey, Wimmer, Williamson, & Roe, 2014). The adoption of soundscape monitoring (also called passive acoustic monitoring) is accelerating at a rapid pace as practitioners incorporate this method into their monitoring programs (Sugai, Silva, Ribeiro, & Llusia, 2019).

Soundscape monitoring can help to address aforementioned limitations associated with current monitoring approaches (Deichmann, Hernández-Serna, Delgado, Campos-Cerqueira, & Aide, 2017). It is relatively low-cost compared to traditional field approaches and does not require local experts out in the field, which in some cases can be a limiting factor. Since it is a remote sensing technology, recorders can be deployed for long periods of time and across large spatial scales. Acoustic data has high-temporal resolution and is dense with information. It can be analyzed in a multitude of ways from human listening to fully automated approaches using machine-learning techniques (Bellisario & Pijanowski, 2019; Gottesman et al., 2018). Data are also preserved indefinitely for later analysis, making this method well-suited for long-term, standardized monitoring. In this way, recording soundscapes can help against the problem of shifting baselines, whereby slow and gradual changes evade detection and create new and false conceptions of what is normal (Knowlton & Jackson, 2008). In other words, recordings are "acoustic fossils" (B.C. Pijanowski, personal communication, 2016) that preserve the qualities of a place at a given time.

1.4 Soundscapes in aquatic environments

While soundscape ecology originated in the terrestrial sphere, there is both a need and opportunity to apply soundscape approaches in freshwater and marine habitats (Linke et al., 2018; Miksis-Olds, Martin, Tyack, & Tyack, 2018). Aquatic habitats are generally difficult to access and costly to survey. As a result, surveys conducted in these environments are often "snapshots" that have limited temporal resolution (i.e. annual surveys conducted each summer). This sampling scheme can lead to poor understanding of larger spatiotemporal patterns that evade these "snapshot" surveys (Adams, 2001). Furthermore, many aquatic organisms become active at night or at certain periods of the year where sampling is difficult, and so there is limited information on these fauna (Staaterman et al., 2017). Developing new monitoring systems that leverage digital technologies to exceed the temporal and/or spatial scales possible with human divers would provide insight into longer-term trends, make visible formerly unseen patterns, and offer a standardized stream of data on marine biodiversity.

New approaches are needed because aquatic ecosystems, in many ways, are undergoing even more extreme changes than their terrestrial counterparts. In freshwater habitats, biodiversity is declining faster than in any other ecosystem (Dudgeon et al., 2006). Given that lakes, rivers, and ponds host at least 6% of all species (while only occupying 0.01% of the Earth's surface), and that this biodiversity supports essential freshwater ecosystem services (Daily, 2012), obtaining information on its status is crucial. However, as Dudgeon (2006) reports: "knowledge of the total diversity of fresh waters is woefully incomplete – particularly among invertebrates and microbes, and especially in tropical latitudes that support most of the world's species. It is likely that numerous freshwater species are going extinct before they become known to science.

Similar large-scale changes are occurring in marine environments. Overfishing has removed 90% of large predatory fish in the last 50-100 years (Myers & Worm, 2005). Approximately 33% of fish stocks are currently being harvested at unsustainable levels (Díaz et al., 2019). Stark declines also have occurred for marine mammals (Baylis et al., 2015; Lotze, Coll, Magera, Ward-Paige, & Airoldi, 2011) and benthic invertebrates (Hobday, Tegner, & Haaker, 2000). Beyond the declines of individual species, anthropogenic stressors including climate change, pollution, and overharvesting are resulting in the collapse of entire marine ecosystems (Steele, 1998). For

example, under current warming scenarios, the majority of coral reefs are slated for destruction by the end of the 21st (Bellwood, Hughes, Folke, & Nyström, 2004; Hughes et al., 2017). Kelp forests, another valuable coastal habitat, are undergoing regime shifts due to overfishing and nutrient pollution (Krumhansl et al., 2016). Complicating the task of conserving aquatic ecosystems is the lack of comprehensive information on them. More than 80% of the ocean still is unmapped and unexplored (National Oceanographic and Atmospheric Administration [NOAA], 2018a). Passive acoustic monitoring is one emerging technology that can help to fill this information gap.

In these low-visibility environments, "sound is a way of life" for aquatic organisms (Schack, 2018). Many aquatic organisms use sound to communicate within or navigate through submerged environments, where sound travels 5X faster and farther than on land (Brekhovskikh, Lysanov, & Beyer, 1991; Larsen & Radford, 2018). Of the "five senses" (touch, smell, taste, hearing, and sight), only sound avails itself for long-distance information transfer (>300 meters) underwater (though some organisms utilize senses that humans do not have, like electroreception; Gordon et al., 2018; Lohmann, Lohmann, & Endres, 2008).

A startling diversity of aquatic fauna produce sound, whether intentionally for communication or unintentionally as the result of some other behavior (Au & Hastings, 2008; Webb, Fay, & Popper, 2008). More than 800 fish species from 109 families are known to be soniferous, but this is likely a vast under-estimate (Rountree et al., 2006). Crustacean species from more than 20 families and 50 genera produce sound through stridulatory and snapping mechanisms (Schmitz, 2002). A notable soniferous crustacean group is the snapping shrimp (Family: Alpheidae), which produces one of the loudest and most pervasive sounds in coastal waters of tropical and temperate regions (Bohnenstiehl, Lillis, & Eggleston, 2016). From humpback whales in Hawaii to Weddell and harp seals at the poles, marine mammals are among the most prolific sound producers in the ocean. They utilize sound to communicate over thousands of kilometers (Tyack & Clark, 2000) and to detect prey through echolocation (Caldwell & Caldwell, 1969). Compared to the marine environment, producers in freshwater habitats are relatively understudied, but it is known that hundreds of freshwater fish species, amphibians, macroinvertebrates from four orders, and even plants, produce sound underwater (Linke et al., 2018).

In addition to the biological portion of aquatic soundscapes, there are also significant contributions from anthropogenic and geological sources. Anthropogenic noise in its various forms is audible across most of the ocean (Hildebrand, 2009), and has important consequences for the fitness and behavior of marine mammals, fish, and invertebrates (Slabbekoorn et al., 2010; Tyack, 2008). Geological sounds from wind-caused wave action and weather events like earthquakes and hurricane also have characteristic acoustic signatures (Hildebrand, 2009). As a result, aquatic soundscapes convey information on the composition of biological, geological, and anthropogenic elements (Miksis-Olds et al., 2018). Together, these three groups of sound comprise the soundscape, which is the total collection of sounds occurring at a given place at a given time (Pijanowski, Farina, et al., 2011).

Assessing marine soundscapes can provide useful information on the status of species populations, animal communities, and habitats (Harris et al., 2016; Kaplan et al., 2015; Rowell et al., 2017). Soundscapes can be quantified in many different ways, including by their amplitude, frequency, temporal dynamics, sound types, among other dimensions. One commonly used method consists of measuring the intensity of different frequency bands that contain sounds from animals in different taxonomic groups. Fish generally vocalize in the 'low' frequency portion of the soundscape (<1000 Hz). Invertebrates tend to produce sound in the 'high' frequency portion of the soundscape (>1000 Hz). In some cases, soundscape-ecological relationships have been demonstrated for both the low- and high-frequency portions of the soundscape. Kennedy et al. (2010) analyzed 2 min snapshots collected from 40 reefs in Panama and found that fish diversity, fish density, and coral cover positively correlated with low-frequency sound levels. Benthic invertebrate diversity correlated with high-frequency sound levels, likely because increased reef complexity offered more niches to soniferous invertebrates like snapping shrimp. Other marine soundscape studies have found ecological associations only with low-frequency components. Kaplan (2015) found that diel patterns in low-frequency sound (100-1000 Hz) correlated with the density of fish and coral cover, while high-frequency sound levels were not significantly associated with biological variables of interest. Freeman & Freeman (2016) surveyed 23 Hawaiian reefs and found that lower-frequency sound levels (< 2 kHz) dominated in more protected and remote sites and correlated with fish abundance, benthic invertebrate abundance, and habitat complexity. High-frequency sound levels (2-20 kHz), in fact, were correlated with benthic fleshy macroalgae cover

associated with habitat degradation. In contrast with this study, other studies have found positive ecological relationships mainly with high-frequency components. Coquereau et al. (2017) found that trawled maerl beds off the coast of France contained 8 soniferous benthic invertebrates per square meter while unfished beds contained 49, and that these organisms mainly produced sound between 1-60 kHz. Additionally, broadband sound levels were 3-fold less intense in the fished maerl beds mainly because of differences in the 3-15 kHz range. Rossi (2017) compared kelp forests to nearby degraded algal turf and found that shrimp snaps per minute declined from approximately 290 to 90. Total sound levels (.3–10 kHz) also declined from 122 dB to 115 dB, mainly due to differences in high-frequency sound levels caused by snapping shrimp activity.

This summary illustrates that relationships between soundscapes and ecosystem condition are promising but still in their early phases of categorization. There remains great variability in the findings between different studies, potentially stemming from differences in study design, ecosystem type, measurements used, or confounding factors such as anthropogenic noise. Since soundscape ecology started in the terrestrial environment, most of the original tools and analyses were developed for and validated on terrestrial data. For example, acoustic indices—automated measurements of a soundscape generally intended to indicate ecological properties of interest— have received mixed success in the marine realm (Staaterman et al., 2017). Therefore, additional research is needed to understand soundscape-ecological relationships across different aquatic ecosystems and develop analysis methods that produce results that are consistent, interpretable, and useful. Relatedly, one under-researched area in this field is soundscape-disturbance relationships. Passive acoustic monitoring is well-suited for capturing the effects of gradual, long-term (5+ year) disturbances because recorders collect standardized data autonomously for months to years at a time. Their automated nature also makes this technology suitable for assessing the impacts of unexpected pulse disturbances like hurricanes or wildfire (Gasc et al., 2018). However, these two research areas are still in early phases, in part due to the lack of relevant datasets.

1.5 Key knowledge Gaps

My dissertation addresses several gaps in the field of soundscape ecology. Though each chapter addresses specific gaps, my dissertation sought to address the following overarching objectives:

1) Test soundscape-ecological relationships in different freshwater and marine environments

2) Investigate how disturbance events alter soundscapes

3) Develop new tools and methodologies to analyze soundscapes in aquatic habitats

All three of these themes improve the capacity of soundscape ecology to serve as a modern method for measuring biodiversity and ecological change in aquatic ecosystems.

Chapter 2: While soundscape-ecological relationships have been demonstrated in various terrestrial and marine ecosystems, relatively little is known about freshwater soundscapes and their potential to indicate freshwater biodiversity, especially in the tropics where they are almost completely undocumented (Linke et al., 2018). Desjonquères (2015) explored the diversity of three temperate ponds and found 43 sound types. Each pond had significantly different sound type richness and daily dynamics. Building upon this approach, Desjonquères (2018) showed that sound type diversity correlated with aquatic macro-invertebrate diversity, demonstrating that acoustic communities can reflect animal communities in temperate freshwater habitats. Since macro-invertebrates comprise the majority of sounds heard in many freshwater systems (Aiken, 1985a; Desjonquères et al., 2018), and are reliable bio-indicators (Johnson, Wiederholm, & Rosenberg, 1993), freshwater soundscapes could indicate the condition of these habitats. Whether or not this relationship holds in tropical environments is currently unclear, since little is known about tropical freshwater soundscapes in general. If these soundscapes are rich in biological sounds, then it is likely that soundscape monitoring could offer a much-needed window into the biodiversity of these hard-to-measure and fast-declining systems.

Chapter 3: Few practical methods exist to remotely measure disturbance impacts on animal communities. Soundscape monitoring has the potential to do so. Audio recorders are autonomous and can be left in the field for months or years, enabling the capture of unpredictable disturbance events. Audio data are also standardized so that disturbance-related impacts and long-term changes can be assessed with minimal observer bias. These data are also of high temporal resolution so that fine-scale disturbance dynamics can be properly determined. Despite this potential, soundscape-disturbance research is only in its early stages of development. Just a handful of studies (< 15) have explored the capacity of soundscapes to measure different dimensions of disturbance,

partially due to the scarcity of datasets that include a disturbance event midway through (but see Gordon et al., 2018 and Lee, Davies, & Struebig, 2017). There is a need to determine whether soundscapes can consistently reflect different dimensions of disturbance, including its magnitude, identity, and drivers. Relatedly, soundscapes could also reveal aspects of animal community resilience, both in terms of resistance to disturbance and time the community takes to recover, though these have yet to be explored in soundscape literature.

Chapter 4: Regime shifts are causing large, enduring and negative shifts in marine ecosystems (Steele, 1998). Developing early warning signs of regime shifts, ways to rapidly assess habitat condition, and ways to identify regime shift drivers, would improve the management of at-risk ecosystems (Carpenter et al., 2011; Dakos, Carpenter, van Nes, & Scheffer, 2015). There have been several recent studies on how soundscapes can indicate regime shifts and ecosystem functioning. Rossi et al. (2017) compared the soundscapes of healthy and degraded habitats in two systems: a kelp forest/algal turf complex in Southern Australia where the regime shift driver was nutrient pollution and a seagrass-macroalgal habitat near naturally occurring CO_2 vents off the coast of Italy where the regime shift driver was ocean acidification. Rossi et al. found similar decreases in sound pressure levels between healthy and shifted habitats regardless of ecosystem type or regime shift driver, leading Rossi et al. to posit that soundscape alterations due to regime shifts may be consistent regardless of their driver. However, as this pattern has been demonstrated only in two ecosystems and with only two drivers, more research is needed in order to more fully characterize soundscape-regime shift relationships.

1.6 Problem statement and research questions

In Chapters 2-4, we pose and answer research questions to address the aforementioned research gaps.

Chapter 2: Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes

Problem statement: Soundscapes from tropical freshwater habitats are almost completely undocumented, but could potentially serve as indicators of freshwater biodiversity. Furthermore, the soundscapes of most aquatic systems are still largely unknown. Developing standardized

methods of categorizing their components is needed. We analyzed recordings from a 21-day period in a Costa Rican freshwater wetland to better understand the acoustic diversity and dynamics of these systems. To do so, we developed a method for categorizing sound types based on their spectral and temporal features.

Research question 1: What is the acoustic diversity within the soundscapes of a tropical freshwater wetland?

Research question 2: Do automated metrics of acoustic diversity correlate with metrics obtained through intensive listening and labelling?

This chapter was published in *Freshwater Biology* as:

Gottesman, Benjamin L., Dante Francomano, Zhao Zhao, Kristen Bellisario, Maryam Ghadiri, Taylor Broadhead, Amandine Gasc, and Bryan C. Pijanowski. "Acoustic monitoring reveals diversity and surprising dynamics in tropical freshwater soundscapes." *Freshwater Biology* (2018).

Chapter 3: Assessing ecological resilience through sound

Problem statement: Few practical methods exist to measure animal community resiliency in real-world situations. Rigorous and replicable methods to assess ecological resilience are needed. We utilized soundscapes to measure different dimensions of animal community resilience in Puerto Rican coral reef and dry forest habitats in response to Hurricane Maria.

Research question 1: Which sound types were significantly impacted by Hurricane Maria and what were the magnitudes of these impacts?

Research question 2: Were the marine and terrestrial acoustic communities impacted by Hurricane Maria? If so, what were the magnitudes of these impacts, and how did these impacts differ across sites?

Research question 3: For sound types that were significantly impacted, what were their recovery trajectories?

This chapter is in preparation for submission to the peer-reviewed journal *Global Change Biology*.

Chapter 4: Soundscapes indicate kelp forest condition

Marine soundscapes have demonstrated potential to provide scalable and continuous information on habitat condition. However, there is still a sizeable knowledge gap concerning which soundscape features reflect different ecological properties and the mechanisms underlying these relationships. In this study, we tested the utility of soundscape recording and analysis in assessing the regime shifts occurring in kelp forests off the coast of California, USA, in Channel Islands National Park. We predicted that healthy kelp forests would have more intense, more dynamic low- and high-frequency portions of the soundscape than urchin-dominated, regime-shifted habitats.

Research question 1: Do soundscapes correlate with ecological variables associated with kelp forest regime shifts?

Research question 2: Do soundscapes differ inside and outside of marine protected areas?

This chapter is in preparation for submission to the *Journal of Applied Ecology*.

CHAPTER 2: ACOUSTIC MONITORING REVEALS DIVERSITY AND SURPRISING DYNAMICS IN TROPICAL FRESHWATER SOUNDSCAPES

Benjamin L. Gottesman (Corresponding Author), Dante Francomano, Zhao Zhao, Kristen Bellisario, Maryam Ghadiri, Taylor Broadhead, Amandine Gasc*, Bryan Pijanowski*

*Amandine Gasc and Bryan Pijanowski should be considered joint senior authors

1.7 Introduction

Globally, human activities are rapidly degrading freshwater systems, threatening the biodiversity they host and the ecosystem services they provide (Daniels & Cumming, 2008; Thomsen et al., 2012). Conservation of these systems depends on enhanced understanding of their ecological dynamics, especially in ecologically important and data-deficient regions like the tropics (Revenga, Campbell, Abell, de Villiers, & Bryer, 2005). In these difficult-to-access aquatic environments where visibility can be limited, sound is often a principle means of animal communication, and this acoustic communication presents an opportunity for researchers to conduct long-term, high-resolution acoustic monitoring (Jansson, 1974; Luczkovich, Mann, & Rountree, 2008). Thus far, almost all underwater acoustic studies that aim to evaluate biological diversity or habitat condition have focused on marine habitats (Coquereau, Lossent, Grall, & Chauvaud, 2017; Freeman et al., 2014; Harris et al., 2016; Miksis-Olds, 2013; Parks, Miksis-Olds, & Denes, 2014; cf. Desjonquères et al., 2015). Freshwater acoustic research has principally focused on characterizing the bioacoustics of individual species, as opposed to the diversity and dynamics of habitat soundscapes.

Soundscapes are collections of all sounds occurring at a place over a given time frame and are composed of biological, geophysical and anthropic sounds (Pijanowski et al., 2011b). Biological

sound sources represent a subset of the biological community present. By quantifying the diversity and occurrences of biological sounds, it is possible to assess animal activity patterns and in some cases evaluate biodiversity or habitat condition. Recent research has proven the utility of soundscape recording and analysis for monitoring biodiversity and habitat condition in terrestrial and marine systems (Fuller, Axel, Tucker, & Gage, 2015; Harris et al., 2016; Pekin, Jung, Villanueva-Rivera, Pijanowski, & Ahumada, 2012). Benefits of soundscape monitoring in contrast to more traditional survey methods include (1) non-invasive sampling, (2) high temporal resolution, (3) the ability to sample in remote locations, at night and through disturbance events, (4) digital data that are preserved for long-term studies or later reanalysis, (5) relatively low cost and (6) the ability to automate approaches to provide near-real-time assessments.

Soundscape approaches could enhance existing freshwater monitoring and assessment efforts. One aquatic habitat in need of biological monitoring advances is the forested freshwater area of Central America (15,000 km^2), which is located within the global biodiversity hotspot of Mesoamerica (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). These forested wetlands recharge aquifers, control floods, store nutrients and provide numerous other ecosystem services (Mitsch et al., 2008), but assessing this habitat is especially challenging due to a dearth of full species inventories (Ellison, 2004). A small portion of these 15,000 km^2 falls within La Selva Biological Station in northeastern Costa Rica (Figure 1). This wetland complex includes Cantarana Swamp, a small endorheic wetland that is the focus of this study in which we use underwater passive acoustic monitoring to assess the acoustic composition and dynamics of soniferous aquatic animals.

This study represents an early attempt at comprehensively describing tropical freshwater soundscapes in a systematic and quantitative manner. Our central goal was to measure Cantarana Swamp soundscapes and to evaluate the diversity and dynamics of biological sounds based on those measurements. To describe the soundscape diversity and dynamics, we (1) manually classified sound types and statistically evaluated this classification, (2) quantitatively measured soundscapes and their diversity using acoustic indices and sound type presence/absence, richness, and occupancy and (3) visualized and described the daily and longer-term soundscape dynamics based on these acoustic metrics. To assess how well acoustic indices captured sound type richness and occupancy, we compared these measurements. We interpreted soundscape diversity and

dynamics in the context of known present taxa, environmental conditions and theories of animal communication and soundscape ecology. As part of this discussion, we examined the nature and extent of temporal and spectral acoustic niche partitioning of the identified sound types.

1.8 Methods

1.8.1 Study area and time period

Cantarana Swamp is located in La Selva Biological Research Station (10.428683°N, 84.004767°W; hereafter referred to as "La Selva"), where the high biodiversity is noteworthy even with respect to other Costa Rican or Central American rainforests (McDade, Bawa, Hespenheide, & Hartshorn, 1994). The high richness of vertebrate species—48 amphibian species (Donnelly & Guyer, 1994), 412 bird species (McDade et al., 1994) and 120 mammal species (McDade et al., 1994)—is dwarfed by the invertebrate species richness, which has been estimated to be in the hundreds of thousands (De la Rosa, 2017a). The climate of La Selva is characteristic of Atlantic tropical wet forests. The 23-day study period (22 January–13 February 2015) occurred during La Selva's dry season (December–April) when monthly rainfall totals typically drop to approximately 80 mm below the monthly average of 330 mm (McDade et al., 1994). Sunrise ranged from 05:56 to 05:59, and sunset ranged from 17:36 to 17:44. Mean solar radiation, which was collected by La Selva in 30-min intervals, was above zero from 05:00 to 18:30 (see Supporting Information for further meteorological details; McDade et al., 1994). A new moon occurred on 27 January 2015.

Cantarana Swamp is situated in an area of old-growth forest about 600 m from the main campus of La Selva (Figure 1). When full, the swamp can measure 70 x 90 m and at least 1-m deep (De la Rosa, 2017b). It lacks an inlet or an outlet but fills from rainfall and occasional flooding from nearby rivers, and it drains through infiltration and evaporation. It can dry out intermittently for up to several months, usually between February and April.

As Cantarana Swamp is in a zero-extraction zone at La Selva, we were unable to obtain complete species inventories of animals that inhabit or frequent the swamp. Through communication with scientists who have worked near this swamp, however, we were able to obtain information based on personal observations and inferences based on other local studies. Generally speaking, aquatic animals that utilize the wetland include amphibians, fish, reptiles and insects. The further detail

that we have on 11 frog species, a single known family of fish, and insect taxa likely to be in Cantarana Swamp is presented in the discussion and Supporting Information (De la Rosa, 2017b; Whitfield, 2017).
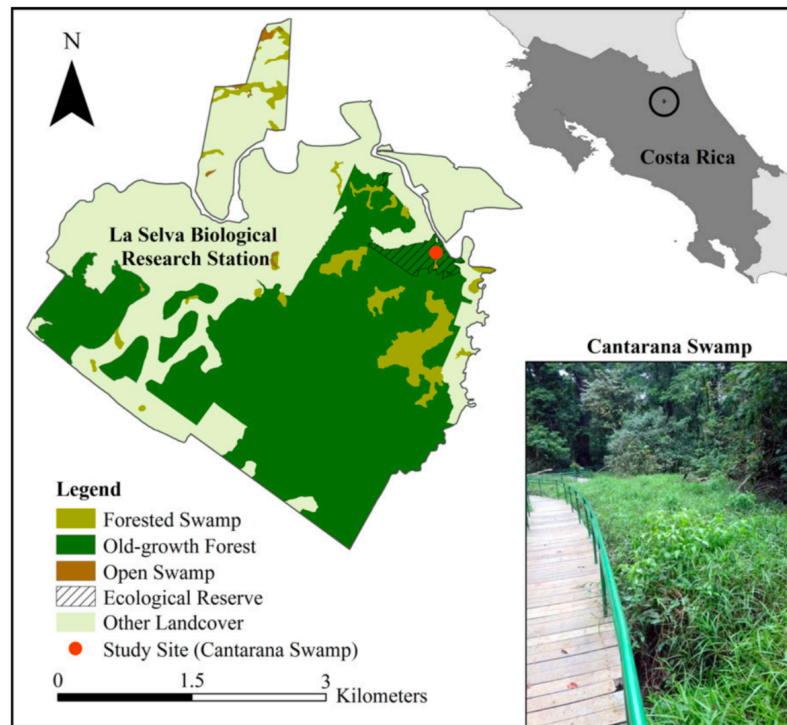
Figure 1: Maps of Costa Rica and La Selva Biological Research Station and a photograph of Cantarana Swamp where the acoustic recorder was deployed. On the map of Costa Rica, the encircled dot is La Selva Biological Research Station

1.8.2   Acoustic data collection and processing

BP and AG deployed a hydrophone (HTI-96-MIN, High Tech, Inc., Long Beach, MS, U.S.A.) 5 m from the edge of Cantarana Swamp on 22 January 2015. The depth of the swamp during the time of deployment was 0.5 m (B. Pijanowski and A. Gasc, personal observation), and the hydrophone was placed at the bottom of the swamp. An automated acoustic recorder (Song Meter SM2, Wildlife Acoustics, Maynard, MA, U.S.A.) was fastened to a wooden boardwalk that runs through the swamp, and the hydrophone was attached to one input port while a terrestrial microphone (SMX-II, Wildlife Acoustics, Maynard, MA, U.S.A.) was attached to the other port. Recordings were obtained in .wav file format at a 44.1 kHz sampling rate using 16 bits. The HTI

hydrophone had a factory-reported sensitivity of 165 dB V/lPa, and the SMX-II microphone had a factory-reported sensitivity of 36 dB V/Pa. A gain of +36 dB was applied to each track. The sensor was programmed to record 10 min every hour and 1 min every 15 min from 13:30 on 22 January–15:45 on 13 February 2015, producing 2,121 sound files. Each file was cropped to the first minute, and the hydrophone channel was separated from the terrestrial channel. Sound pressure levels (SPL) did not substantially decline over the course of the study period in the hydrophone channel, indicating that any hydrophone submersion in the swamp sediment was negligible in terms of acoustic dampening.

1.8.3 Analysis overview and audio library definition

To find and differentiate between sound types, BG listened to numerous files while viewing their spectrograms and then determined rules that could distinguish between the 18 found sound types (see section 2.3.1 and Figure 2 for more details). Clips of individual sound types were extracted and used to quantitatively evaluate the manual classification. Full sound files were used to assess soundscape diversity and dynamics by quantifying sound type occupancy and calculating acoustic indices. To perform these analyses, three audio libraries were created. Audio Library A consisted of ten instances of each sound type (n = 180) that had high signal-to-noise (SNR) ratios and were unmasked by other sound types. All clips were taken from separate audio files, unless there were not enough files with unmasked clips, in which case multiple sound type clips were taken from the same audio file. Audio Library B was a stratified-random subset of 240 files. Files with rain were excluded, and ten files were selected for each hour of the day (five from January and five from February). For each file, a clip of each sound type present in the file was selected to calculate additional acoustic measurements (as defined in 2.4.2). Audio Library C (1,699 files) was the full set of audio files excluding those containing rain. Prior to all analyses on libraries B and C, sound

files were reordered using a random number generator to ensure that temporal variation in sound type presence and occupancy was not influenced by listening order.
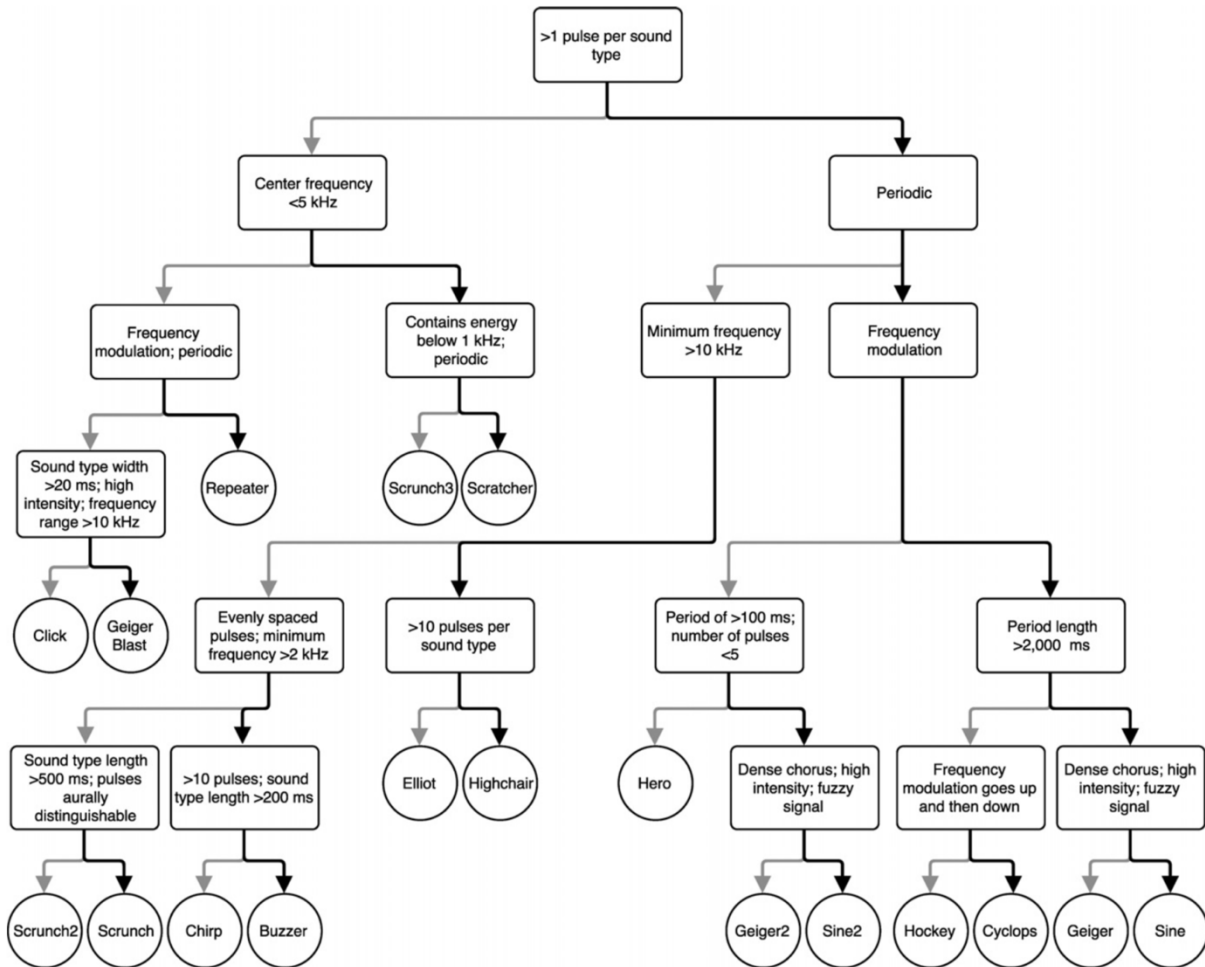
Figure 2: Decision tree used to classify the 18 sound types. Each node contains at least one binary classification rule. Sound types that satisfy a binary rule follow the black arrow, while sound types that do not satisfy a binary rule follow the grey arrow

1.8.3.1 Manual sound type classification

BG listened to a random collection of sound files to become acquainted with the data and to identify the various sound types present in these recordings. Since there was no existing sound library for aquatic animals from Costa Rica, or even for Central America, we could not classify sounds to any taxonomic level. Instead, we developed a classification system based on sound types, in a similar fashion to Desjonquères et al. (2015) and Anderson, Rountree, & Juanes (2008). Sound types were classified based on audible differences and visual inspection of spectrograms. While

there was a large degree of plasticity in most of the sound types identified, BG was able to develop rules from which classifications could be made. If no rule could distinguish between sets of sounds, they were grouped into one type (see Figure 2 and Supporting Information S2.0 for a hierarchical outline of classification rules and additional information on sound type classification). By comparing terrestrial recordings with the hydrophone recordings, it was possible to ascertain whether any sounds in the hydrophone channel originated from above water, and those sounds were not analyzed as sound types. All sound type classification was performed in Raven Pro (Raven Pro: Interactive Sound Analysis Software, 2016). BG listened to each file at least once while viewing the spectrogram (1,024-sample window length, 50% frame overlap and Hanning window type; following Warrington, McDonald, Rollins, & Griffith, 2014).

1.8.3.2 Quantitative analysis of sound types

Quantitative acoustic measurements were calculated for each sound type clip in libraries A and B to (1) validate the manual sound type classification, (2) test the utility of automated classification and (3) develop sound type-based measures of acoustic occupancy. We calculated the following 11 acoustic measurements (additional sound type measurements are provided in Table S1):

1. "Center frequency," the frequency at which the sound can be divided into two frequency intervals of equal energy;
2. "Peak frequency," the frequency with the highest average power;
3. "Bandwidth 90%," the difference between the 5% frequency (above which 95% of the energy is contained) and the 95% frequency (below which 95% of the energy is contained);
4. "High frequency," the highest frequency of the selection;
5. "Low frequency," the lowest frequency of the selection;
6. "Delta frequency," the difference between high frequency (4) and low frequency (5);
7. "Delta time," the length of the selection;
8. "Aggregate entropy," the proportion of energy in each frequency bin times its log (base 2), summed over all frequency bins;
9. "Average entropy," the aggregate entropy (8) divided by the number of discrete Fourier transform frames in the clip;

10. "Average power," the sum of the power spectral density of each spectrogram pixel divided by the number of pixels in the selection.

11. "Periodicity," the regular repetition of sounds—"true" if a sound type repeated at least five times in a recording with consistently spaced intervals.

We then performed a linear discriminant analysis (LDA) with leave-one-out cross-validation to determine whether these 11 features would differentiate between sound types in accordance with the manual classifications (Venables & Ripley, 2002). Due to misclassifications between two sound types, Geiger and Sine (Figure S1), we also quantified the period length, pulse width and inter-pulse distance for randomly selected Geiger and Sine clips from Library B. We determined whether these additional features would differentiate between these two sound types using a k-means test (Hartigan & Wong, 1979) and a logistic regression (McLeod & Xu, 2017). Please refer to Supporting Information for detailed protocol and source code for the LDA and the period and pulse quantification.

1.8.4 Sound type composition and dynamics

We evaluated the presence/absence of each sound type within each recording in Library C. We did not evaluate the abundance of each sound type within these files. We calculated the total number of occurrences of each sound type (maximum possible: one occurrence per file = 1,699 occurrences) and the total number of occurrences per hour of each sound type (maximum possible: 23 days of recording x 4 recordings made each hour = 92 occurrences). For each recording, we also calculated sound type richness—the number of sound types present in a file—within each hour and over the 23-day recording period. When calculating mean daily sound type richness, only full recording days (n = 21) were considered.

In addition to the above analyses, we employed a new acoustic measurement, "temporal occupancy," along with frequency and amplitude measurements, to quantify the occupancy of sound types within the acoustic space of each file in Audio Library B. Temporal occupancy refers to the proportion of time within a file that the amplitude of a sound type occurrence was non-negligible—spaces between pulses and between separate sound type instances were excluded from temporal occupancy. It was estimated for each sound type through visual examination of the spectrogram for each file. We consider the acoustic space at any location to have two dimensions:

time and frequency. The occupancy of acoustic space is a scalar field in which amplitude is the scalar value at each time– frequency point in acoustic space.

We developed three occupancy measures to quantify the use of acoustic space within each file in Library B. Occupancy 1 only considers the dimension of time. It is equal to the sum of sound types' temporal occupancies. Occupancy 2 considers the dimensions of time and frequency and is equal to the sum of the products of sound types' temporal occupancies and their delta frequencies. Occupancy 3 similarly considers the dimensions of time and frequency, but also accounts for amplitude. It is equal to the sum of the product of sound types' temporal occupancies, their delta frequencies and their average powers. Delta frequency and average power were calculated on at least one representative instance of each sound type present within a file. In cases when delta frequency and average power measures were calculated on multiple instances of a sound type within a file, these measures were averaged to attain one delta frequency and average power value per sound type per file.

1.8.5 Soundscape diversity and dynamics

Acoustic indices are measurements of a soundscape that yield ecologically meaningful information about biodiversity and biological activity patterns. They have been employed in many habitat types, including freshwater habitats (Desjonquères et al., 2015; Harris et al., 2016; Pieretti, Farina, & Morri, 2011). We computed 20 acoustic indices for each 1-min recording in Audio Library C. All acoustic indices (other than acoustic occupancy, SPL and the standard deviation of SPL) were from Towsey et al. (2014) and Sueur, Farina, Gasc, Pieretti, and Pavoine (2014), and all other than SPL and the Standard Deviation of SPL were calculated in the R statistical computing environment using version 3.2.4 (R Core Team, Vienna, Austria). Most of these indices are available in the R packages "seewave" (Sueur, Aubin, & Simonis, 2008) and "soundecology" (Villanueva-Rivera & Pijanowski, 2016), and others were coded by the authors (code available through GitHub; see Supporting Information for details). SPL and its standard deviation were calculated in MATLAB (The MathWorks, Inc., Natick, MA, U.S.A.) using PAMGuide (Merchant et al., 2015) with a frequency range of 1–22,050 Hz, a window length of 512 samples, a 50% overlap and a "Hann" window. For each file, there were 10,334 SPL values. We calculated the mean and standard deviation of these values for each recording. A table of all indices used in this analysis, their

original references, the chosen settings, and correlation coefficients and p values for tests described below is included in Supporting Information (Table S2).

We performed correlation tests to determine which acoustic indices were correlated with sound type richness and sound type occupancy. Since the sound type richness data and values for one acoustic index were not continuous, we employed Spearman's formula (Daniel, 1978). For each acoustic index, we performed one correlation test for Audio Library C comparing acoustic index values against sound type richness, and four correlation tests for Audio Library B comparing acoustic index values against sound type richness, Occupancy 1, Occupancy 2 and Occupancy 3. All p values were adjusted using a Bonferroni family-wise alpha correction (Holm, 1979). Prior to calculating the correlation tests for Library C, we employed first differencing on the acoustic index and sound type richness time-series in order to reduce autocorrelation in these series (Dickey & Pantula, 1987). We determined whether autocorrelation was adequately reduced by viewing the autocorrelation function plot for each time-series using a maximum lag of 530 (25% of the 2,212 files). We verified that time-series had fewer than 5% of the lag times outside of the 95% confidence interval bounds. Since the four correlation tests for Library B were performed on a stratified-random subset, we did not transform these data before performing these correlation tests. Six indices of the 20 calculated are included in the results and discussion based on their high correlation coefficients and the fact that they measure different aspects of a soundscape. These indices are the Bioacoustic Index (BI), background noise (BN), number of peaks (NP), SPL, the standard deviation of SPL (SDSPL) and the root mean square (RMS) amplitude. BI represents the energy between a mean spectrum curve and the minimum value of that curve (Boelman, Asner, Hart, & Martin, 2007). BN is the mode of windowed average amplitude values between a minimum dB threshold and 10 dB above that threshold (Towsey et al., 2014a). NP is the number of peaks in a mean spectrum (Gasc, Sueur, Pavoine, Pellens, & Grandcolas, 2013). RMS in the square root of the mean of squared recorded pressure values (Sueur et al., 2008). SPL is the mean RMS calculated for separate windows within a recording, and SDSPL is the standard deviation of those RMS values (Merchant et al., 2015).

1.9 Results

1.9.1 Sound type descriptions

The 18 sound types that were classified and named are presented in Figures 3 and 4. The frequencies of the sound types spanned the full spectrum of recordings (0–22.05 kHz). On the low end, Scratcher's broadband raps, which sounded like scratches against a substrate, contained energy reaching below 40 Hz. On the high end, Elliott was cut off at the top portion of the frequency spectrum. In this rich sonic environment, the acoustic space was dominated by four sound types: Geiger, Geiger2, Sine and Sine2. Sine and Sine2 occurred at night, while Geiger and Geiger2 were the most frequently occurring sound types during the daytime, although they were less intense than their night-time counterparts. Because the frequency ranges of ten sound types, including Geiger, Geiger2, Click, Geiger Blast, Sine, Sine2, Cyclops, Hockey, Hero and Buzzer, partially overlapped in the range of 7–15 kHz, this acoustic space was densely occupied. Repeater, Hockey and Cyclops were frequently masked by Geiger and Sine, while Buzzer, though short in duration, was prominent even amongst the dominant sound types.

All sounds were composed of single impulses or pulses. We define impulses as the smallest discernible temporal units of a sound type and pulses as groups of impulses. While several of the sound types were relatively simple, merely consisting of evenly spaced pulses or impulses that became closer together over the course of each pulse (as in the case of Scrunch and Scrunch2), some sound types had complex frequency and amplitude modulations. Geiger, Sine, Cyclops, Repeater and Hockey all exhibited dramatic frequency modulations with differences up to 9 kHz between the center frequencies of low- and high-frequency portions. Sometimes, the high-frequency portions of these sound types had a different pulse rate, pulse width, inter-pulse distance or amplitude than the low-frequency portions.

Some sound types may have originated from the same source. Geiger, Geiger2 and Geiger Blast frequently co-occurred in recordings and often immediately followed each other at similar amplitudes, suggesting that one animal may have produced these different sound types (see Figure 3 for spectrograms and oscillograms). Sine and Sine2 most likely come from the same producer because Sine was a frequency-modulated version of Sine2 and the two almost always co-occurred. Scrunch and Scrunch2 also occurred in the same frequency range, and both sound

37

types were single pulses in which the interval between impulses decreased over the course of the sound type. Scrunch, however, was much longer (1–2 s) and exhibited greater inter-impulse intervals than Scrunch2 (0.2 s), for which impulses were "scrunched" together and could not be aurally differentiated.
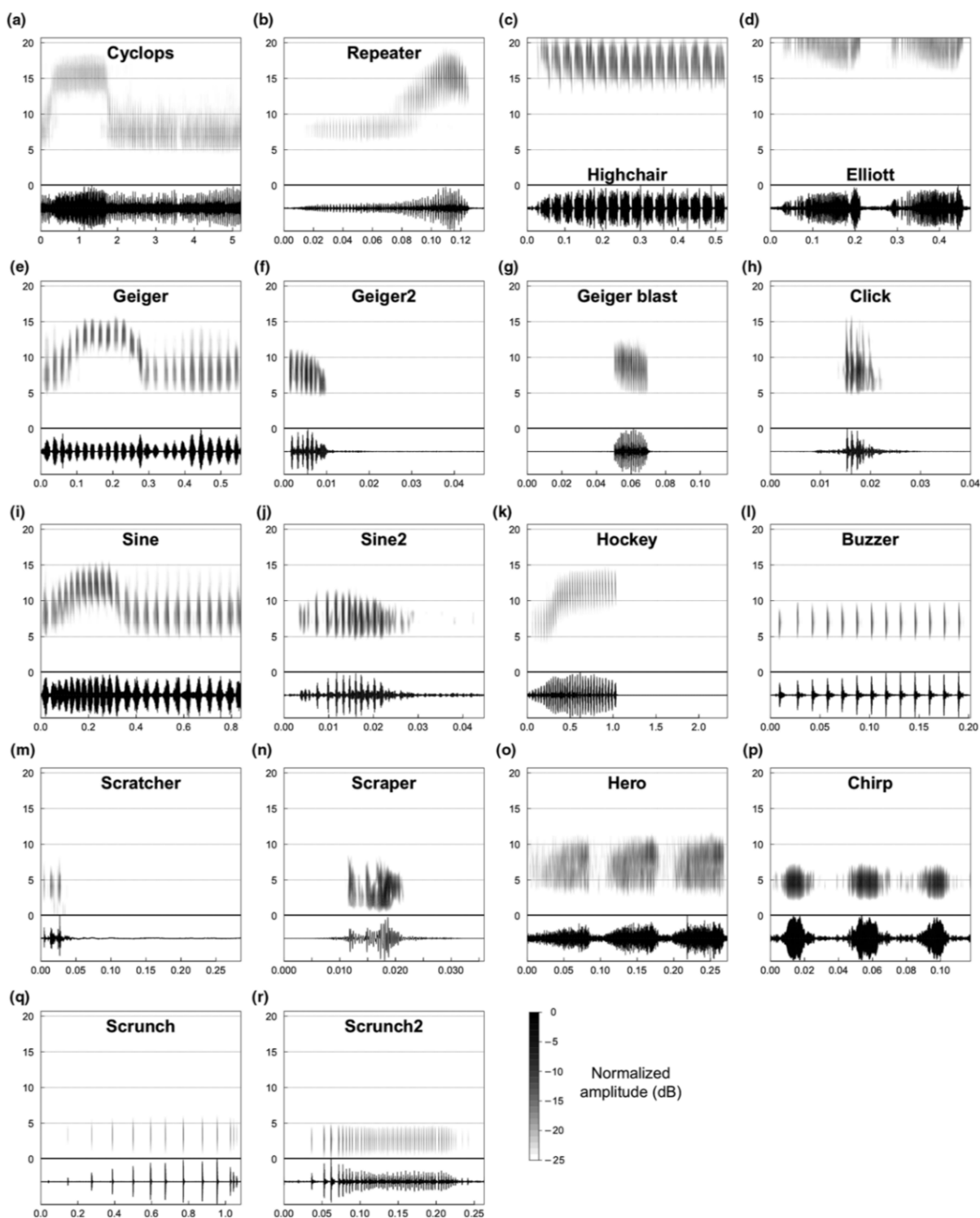
Figure 3: Spectrograms and oscillograms (below the spectrogram) of each sound type. Time (seconds) is presented on the *x*-axis. Frequency (kHz) is presented on the *y*-axis of spectrograms. Spectrogram normalized amplitude (dB) is indicated by the gradient at the far right of the figure
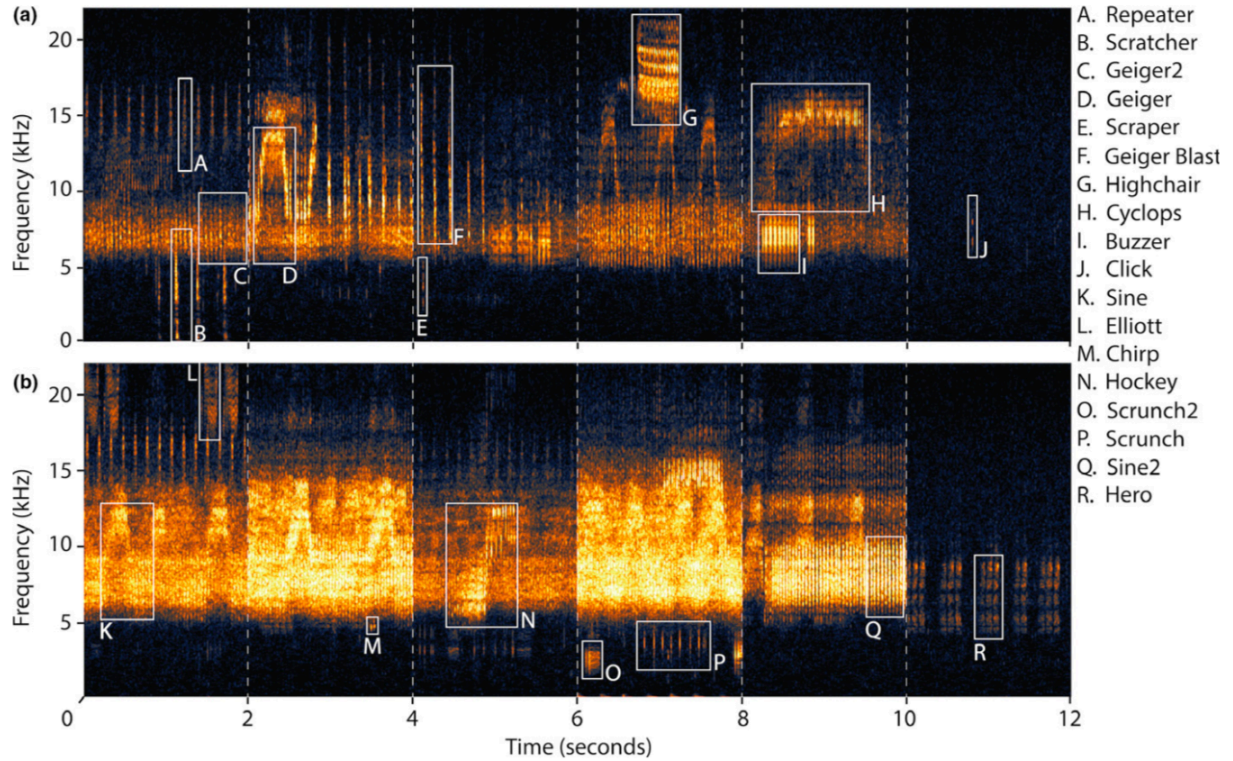
Figure 4: Spectrograms of 12 2-s clips that include all 18 sound types, each of which is outlined by a white rectangle. The top row of spectrograms contains recordings from during the daytime (from left to right: 08:00, 08:00, 11:15, 14:30, 16:30 and 18:00). The bottom row contains recordings taken from night-time (from left to right: 22:00, 22:00, 22:00, 03:30, 01:00 and 04:30). Spectrograms were produced using iZotope RX (iZotope RX, 2014) with a Hanning window of 1,024 samples

1.9.2 Sound type validation

The LDA correctly classified 87% of the observations in our feature set model (first and second axes accounting for 76% and 13% of variance) as opposed to our null model that correctly classified only 10% of observations. Excluding Geiger (20% accuracy), Click (60% accuracy) and Sine (60% accuracy), the other 15 sound types were classified with 95% accuracy. Click's four misclassifications were distributed across three groups; 75% of Geiger's eight misclassifications were attributed to Sine, and 100% of Sine's misclassifications were attributed to Geiger. Despite this apparent similarity, the period and pulse features differentiated between Geiger and Sine (see Figure 3 for spectrograms and oscillograms of these sound types). A k-means test differentiated between Geiger and Sine with 89% accuracy based on these features. A logistic regression revealed that "pulse interval of high-frequency portion" and "pulse width of low-frequency portion" differed significantly between Geiger and Sine (pulse interval of high-frequency portion: $Z = 2.07$,

p = .039; pulse width of low-frequency portion: Z = 3.12, p = .002). Due to these results, Geiger and Sine were considered as two different sound types.

1.9.3 Sound type occurrences

The most common sound type was Scrunch, which occurred in approximately 50% of the recordings (Figure 5). The least common was Hero, which was found in 0.3% of the recordings. Some sound types exhibited consistent diurnal patterns, while other sound types displayed no clear daily variation (example soundscape recordings from various times of day are provided in Supporting Information). Acoustic activity of Geiger, Geiger2, Geiger Blast, Hockey, Elliott, Buzzer and Scraper was highest between the hours of 06:00 and 17:00. Sine and Sine2 were present mainly between 19:00 and 04:00. Scrunch and Scrunch2 occurred considerably more at night and Chirp was detected almost exclusively during the night. Click occurred most at dawn (05:00–06:00) and dusk (17:30–18:30). Hero and Repeater had the highest activity just after dawn and dusk, while Scratcher intensified during morning hours (04:00–11:00). Cyclops and Highchair were active during the day and night.
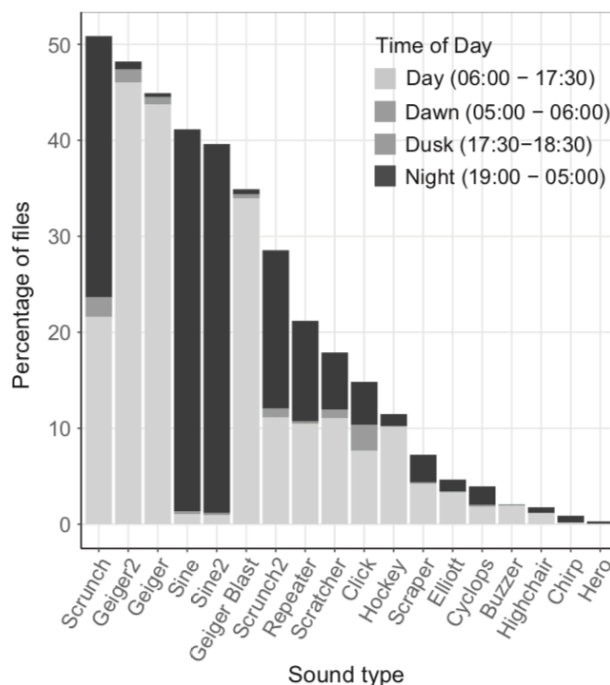
Figure 5: Percentage of files within which a sound type occurred. Shading denotes time of day

Over the 23-day recording period, some sound types exhibited wide variation in daily detection rates, while others were detected evenly (Figure 6). We calculated the standard deviation of the number of daily occurrences on all full recording days except for January 27–29, when heavy rains made it difficult to detect certain sound types. Of the 12 sound types with over 100 detections (Scrunch, Geiger2, Geiger, Sine, Sine2, Geiger Blast, Scrunch2, Repeater, Scratcher, Click, Hockey and Scraper), Sine2, Geiger, Geiger2, Scraper and Scratcher had the lowest standard deviation of daily abundance values (SD = 2.8–8.4), meaning that they had the most consistent

acoustic activity throughout the 23-day study period. Repeater, Hockey, Geiger Blast and Click were more variable in their abundances (SD = 9.5–11.5), and Scrunch and Scrunch2 had the highest variation in daily abundances (SD = 18.3–27.6). Following a 209-mm precipitation event from January 27–29, the occurrences of Scrunch, Scrunch2, Hockey and Repeater increased considerably. Similarly, for the sound types with fewer than 100 detections (Chirp, Highchair, Buzzer, Hero, Elliott and Cyclops), 89% of the detections occurred over a 15-day window after January 29.
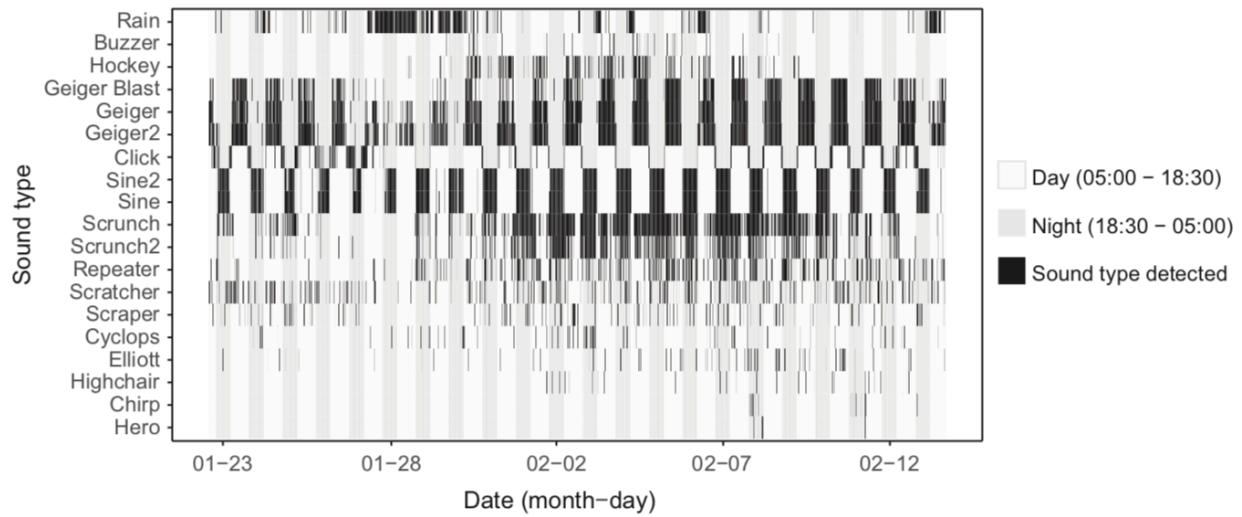
Figure 6: Detections of sound types and rain over the 23-day deployment. Light grey shading denotes daytime (05:00-19:00) and dark grey shading denotes night-time (19:00-05:00). The presence of rain is included because it could bias detection and influence the presence/ absence of some sound types

1.9.4   Sound type richness

Hourly sound type richness was highest from 06:00 to 10:00 with an average of 4.79 ± 1.50 (± notation denotes "mean ± standard deviation" throughout this article) sound types detected per recording. Fifty-four per cent of recordings with sound type richness greater than six occurred during this time period (as opposed to 17%, if such recordings had been uniformly distributed throughout the day). 05:00 and 18:00 had the fewest sound types present, with average sound type richness of 2.55 ± 1.41 and 2.57 ± 1.38 sound types, respectively (Figure 7). The average daily sound type richness was 3.64 ± 1.22. However, daily sound type richness varied considerably over the 23-day study period. From February 1–8, sound type richness peaked with a mean of 4.68 ± 0.26. Mean daily richness of the remaining days was 3.09 ± 0.52 (Figure 8).

42

1.9.5 Sound type occupancy

The three occupancy measurements displayed similar trends to each other, with the night-time acoustic space more occupied than that of the daytime (see Supporting Information and Figure S3 for more details). The acoustic space at dawn and dusk was almost unoccupied, with vacant temporal and frequency niches that were occupied during other times of day. Of daytime values for Occupancies 1 and 2 (which do not factor in the amplitude of the sound types), highest occupancy was generally between 06:00 and 10:00, which coincided with the period of highest sound type richness. Occupancy 3 had a larger difference between daytime and night-time occupancies because the intensity of the night-time soundscapes was higher than that of the daytime by approximately 12 dB. These daily occupancy trends were reflected by the average daily spectrogram (Figure 9).
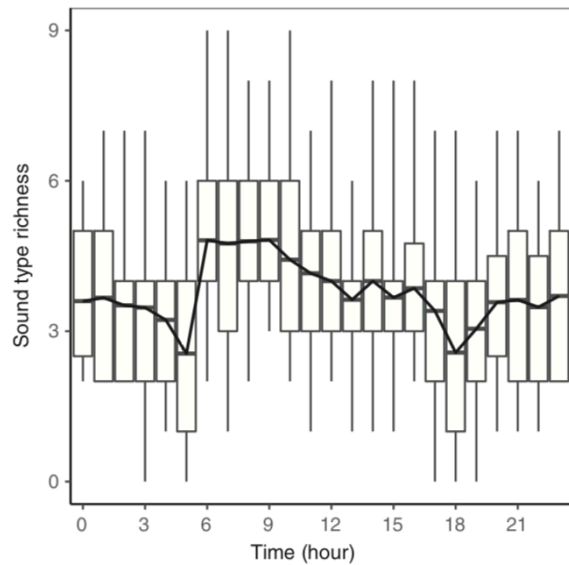
Figure 7: Mean sound type richness calculated for each hour. The lower bound of each box is the 25% quantile and the upper bound is the 75% quantile; whiskers extend to the minimum and maximum values for each hour

1.9.6 Sound type descriptions

Sound type richness was significantly correlated with the majority of the acoustic indices we tested. NP was most highly correlated with sound type richness in both Library B and Library C, with correlations of 0.35 ($p < .001$) and 0.15 ($p < .001$), respectively. The acoustic indices were much more related to sound type occupancy. The acoustic index mostly highly correlated with Occupancy 1 was BN, with a correlation of 0.79 ($p < .001$). For Occupancies 2 and 3, BI displayed the strongest relationship, with correlations of 0.85 ($p < .001$) and 0.92 ($p < .001$), respectively.

1.9.7 Soundscape diversity and dynamics

Over the course of an average day, NP crested with approximately 12–15 peaks between 06:00 and 08:00 (Figure 10), which coincided with the highest period of sound type richness. It declined gradually over the course of the day. NP was lowest at 05:15 (dawn) and 18:00 (dusk) with approximately 6 and 4 peaks, respectively. At night, NP values were consistently between 8 and 10 peaks. The BI, which was the most highly correlated index with Occupancies 2 and 3, was also the second most correlated index with Occupancy 1. Maximum values for BI occurred between 21:45 and 02:15, and were lowest between 04:45 and 06:00 and 17:45 and 18:45. After dusk, values rose steadily between 18:45 and 21:30, peaked and then declined rapidly from 02:15 to 05:30. Broadband SPL and RMS were highest at night. The wetland had median SPL of 20.1 ± 5.3 dB during the day, 8.6 ± 6.4 dB at night and 22.5 ± 7.2 dB at dawn

Figure 8: Mean sound type richness calculated for each day over the 23-day study period. The lower bound of each box is the 25% quantile. and the upper bound is the 75% quantile: whiskers extend to the minimum and maximum values for each day

and dusk. At 05:30 and 18:15, when BI levels were lowest, the SPL was 23.8 ± 6.4 dB and 21.6 ± 6.7 dB, respectively. This site exhibited a large amplitude range with an average 29.1 ± 4.2 dB difference between the daily minimum and maximum SPL values (based on per-file SPL averages). Since RMS is more visually illustrative of dawn and dusk differences in intensity, it is presented instead of mean SPL in Figure 10. SDSPL values, which illustrate the variability in intensity within a given file, were higher during the day when soundscapes were sparser than at night when there was near-constant sound composed primarily of Sine and Sine2.

44

Figure 9: Average spectrogram depicting the daily soundscape pattern. In this spectrogram, the intense night choruses, the sparser daytime soundscape and the silences at dawn and dusk, are all evident. The faint yellow band from 3 to 4 kHz represents the activity of sound types Scrunch and Scrunch2
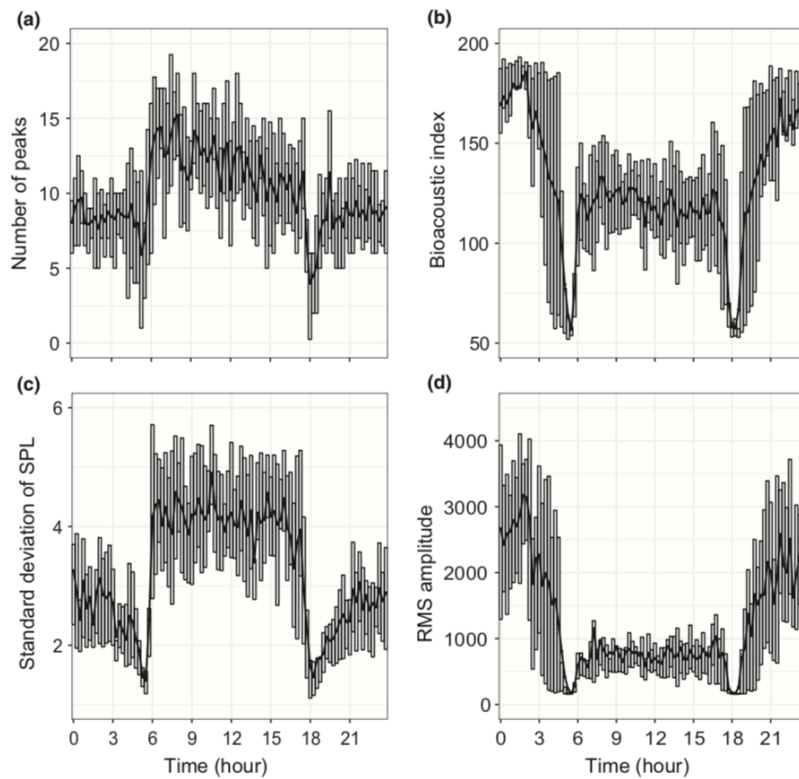
Figure 10: Quarter hourly mean acoustic index values including (a) number of peaks. (b) Bioacoustic Index, (c) standard deviation of the 10,334 sound pressure level (SPL) values for each 60-s file and (d) root mean square (RMS) amplitude across the full bandwidth (0–22.050 Hz). In each figure, the lower bound of each box is the 25% quantile and the upper bound is the 75% quantile

1.10   Discussion

In Cantarana Swamp, we discovered a rich soundscape composed almost entirely of biological sounds, which supports our argument that passive acoustic recording and principles from soundscape ecology can contribute to the assessment of tropical freshwater systems. These aquatic soundscapes exhibited two characteristics that enable or facilitate acoustic monitoring: a high SNR of biological sounds and a high occupancy of biological sound types. Our study demonstrates that soundscape analysis in a tropical freshwater habitat can reveal soundscape dimensions including sound type diversity and patterns of daily dynamics. By applying principles from soundscape ecology, we can relate these dimensions to biodiversity or habitat condition to enhance understanding and conservation of freshwater ecosystems. In the context of these principles, we discuss (1) likely sources of the Cantarana sound types, (2) soundscape composition and acoustic niche partitioning between sound types, (3) patterns of temporal soundscape dynamics and potential proximate causes, (4) the efficacy of soundscape measurements used in this study and (5) directions for future freshwater soundscape monitoring research.

1.10.1 Sound type attribution

We attribute all 18 sound types to aquatic insects. The sound types were all composed of multiple pulses, single pulses or impulses, suggesting that they may have been produced through some form of stridulation, which is the most common method of sound production in aquatic insects (Aiken, 1985b; Gerhardt & Huber, 2002). It is well known that many aquatic insect taxa from at least four orders utilize acoustic communication in freshwater habitats (Aiken, 1985b). Aquatic insects communicate to defend against predators, proclaim their territories, identify and discriminate between individuals and species and attract mates (Otte, 1974). In La Selva's lentic habitats, 12 aquatic insect families have been identified, including Aeshnidae, Lestidae, Libellulidae, Belostomatidae, Hebridae, Mesoveliidae, Naucoridae, Veliidae, Dytiscidae, Gyrinidae, Hydrophilidae and Noteridae (Springer, 2017). Six of these families (Belostomitidae, Naucoridae, Vellidae, Dystiscidae, Gyrinidae and Hydrophilidae) have been shown to produce sound for communication (Aiken, 1985b). Additionally, Schlagbauer (1995) documented the presence of 33 families of aquatic insects in a similar wetland within 1 km of Cantarana Swamp and more detailed information of the findings of that study is available through a Github repository detailed in Supporting Information. Neither the single documented fish family (Synbranchidae) nor any

present frog species have been shown to produce sound underwater, and we determined that no sound types in our classification originated above water.

1.10.2 **Sound type composition and acoustic niche partitioning**

The composition of soundscapes varied greatly over the course of the day, with some sound types detected almost exclusively during the day, and others only during the night. This trend has been documented across a wide range of ecosystems (Gasc et al., 2013; Ruppé et al., 2015). Certain times of day are advantageous for sound production for a number of reasons: increasing the likelihood of conspecific reception, optimizing propagation, reducing energy and time consumption, reducing predation risk and finding available acoustic niche space. For example, the night-time soundscapes composed of Sine and Sine2 consisted of multiple individuals overlapping and interlocking their sounds in an intense chorus. It appears that these signals were for courting females; Aiken (1982) explained that the density of the chorus is a characteristic of aquatic insect courtship sounds dictated by female preference. Diel periodicity—which Corbet (1966) defined as the "recurrent temporal pattern of an activity with a 24-hr period"—has been demonstrated in several aquatic insect species (Aiken, 1985a). Jansson (1973) found that within the genus Cenocorixa (Corixidae), different species had distinct peak sound production periods, including daytime, night-time, dusk and morning. He concluded that light intensity was regulating these temporal patterns. Sound types within Cantarana Swamp exhibited acoustic activity peaks at all of these times.

Acoustic niche partitioning refers to the minimization of temporal and spectral overlap between various sounds in acoustic space; the acoustic niche hypothesis (ANH) states that species in a species-rich community will evolutionarily or behaviorally modify their acoustic signals to produce sound in a manner that minimizes temporal and spectral overlap with other regularly present sounds in the environment (Krause, 1993; Ruppé et al., 2015; Villanueva-Rivera, 2014). The two pairs of dominant sound types (Sine/Sine2 and Geiger/Geiger2) offer evidence supporting the ANH. The Sine and Geiger pairs had very similar frequency ranges, yet they almost never co-occurred (see Figure 4). Sine and Sine2 occurred during the night, and Geiger and Geiger2 occurred during the day. Either Sine, Sine2, Geiger and Geiger2 originated from the same species, or there were two species with similar frequency ranges that produced sound in complete temporal

isolation from each other. The non-overlapping acoustic activity patterns of these sound types offer some support for the temporal dimension of the ANH, although their daily activity patterns could also be attributed to non-communicative reasons. In a related study, Jansson (1971) found that temporal isolation could help reduce masking between sympatric aquatic insect species with overlapping frequency ranges for Cenocorixa bifida and C. expleta in both laboratory and field conditions.

The extent to which the frequency dimension of the ANH plays a role here is less clear. Fundamental frequency correlates strongly with body length in aquatic insects (Theiß, 1982) and would therefore be difficult to change in order to occupy an open niche. Moreover, frequency modulation—changing the fundamental frequency over the course of a sound—is thought to be an ineffective communicatory strategy in shallow freshwater habitats because modulations within a range of several kHz would likely be distorted by environmental interference, which is pervasive in shallow freshwater systems (Aiken, 1985b). In contrast to studies that downplay the potential use of this strategy by aquatic insects, there was significant frequency modulation in five of the sound types in this wetland, namely Geiger, Sine, Hockey, Cyclops and Repeater, although these modulations generally exceeded several kHz. The different frequency modulations of these sound types aided our distinction between them, as their low-frequency portions often overlapped (except for Geiger and Sine, which were temporally isolated from each other and exhibited similar frequency modulations). Development of these distinct modulation patterns may aid differentiation between conspecifics and heterospecifics as well, and these differences represent a case of spectral acoustic niche partitioning.

1.10.3 Daily soundscape dynamics

As in many ecosystems, the soundscapes of Cantarana Swamp exhibited daily dynamics, but one pattern distinguished them from soundscapes in other ecosystems. The most unexpected aspect of the Cantarana Swamp soundscape was silence as opposed to sound. Unlike the rest of the day when there was constant acoustic activity, dawn and dusk were nearly silent. The fact that such a wide-open acoustic space was not more fully occupied is surprising, especially when compared to many other habitat types that have peaks of acoustic activity at dawn and dusk (Bertucci, Parmentier, Berten, Brooker, & Lecchini, 2015; Depraetere et al., 2012; Pijanowski et al. Krause,

2011a; Radford, Jeffs, Tindle, & Montgomery, 2008). In our study, the only sound type with abundance peaks at dawn and dusk was Click. Increased detection of this 0.013-s sound may only have occurred because dominant sound types masked it at other times of day. Alternatively, the sound type could have some communicative function germane to these time periods.

A proximate cause for these quiet times around dawn and dusk could be intermediate light levels that do not trigger communication amongst animals that otherwise produce sound at higher or lower light levels. However, this hypothesis is challenged by the fact that night-time sounds began to decline around 02:00, far before any uptick in solar radiation occurs. Similarly, daytime sounds began declining at around 17:15, which precedes the sunset by approximately 45 min. Air temperature during the pre-dawn period (00:00–06:00) was nearly constant, with an average range of less than 1°C. Pre-dusk (15:00–18:00) temperature was more variable, with an average range of approximately 3°C. To date, acoustic activity in aquatic insects has been demonstrated in laboratory settings to be purely controlled by exogenous factors, with light intensity as the main factor and temperature as a contributing factor (Aiken, 1985a; Jansson, 1968). However, in this wetland, acoustic activity changed before there was any major change in these factors, implying that there was an additional exogenous component, endogenous biological clock or extreme sensitivity to temperature changes that regulated acoustic activity.

Another potential explanation for these quiet periods around dawn and dusk is that these insects decrease their sound production in an attempt to reduce the risk of predator detection. Though many animals utilize this strategy (McGregor, 2005), so far there is no evidence that predators can use aquatic insect sounds to locate prey, primarily because aquatic insect sounds have been thought to have a limited range of detection that is less than 1 m (Aiken, 1982; Jansson, 1973). However, in this system, there is reason to suspect this range of detection might be larger. The dense night-time choruses of Sine and Sine2, by far the loudest sound types, were captured on the terrestrial microphone 50 cm above the wetland, suggesting that the detection range of these sounds could be larger than 1 m, especially since these detected sounds penetrated the highly reflective water–air boundary (Aiken, 1985b). A more in-depth investigation of this system that considers insect life histories is necessary to ascertain why these periods were so quiet.

1.10.4 **Longer-term soundscape dynamics**

The longer-term dynamics illustrate that soundscape diversity in this wetland varied over multiday periods. Since freshwater acoustic communities can change over daily and longer-term timescales, we caution that taking an acoustic snapshot (less than 1 day) of a freshwater community could underrepresent the acoustic diversity of a given site. In our study, Chirp and Hero did not occur until after 15 full days of sampling. Longer-term changes could be triggered by environmental events like precipitation. Some sound types, including nearly all of the rarer sound types, occurred more often immediately after the heavy precipitation event between January 27 and January 29. While our sampling window was relatively small, precipitation has been shown to cause changes in communication for many taxa (Ospina, Villanueva-Rivera, Corrada-Bravo, & Aide, 2013), so this correlation may not be anomalous. This observation offers evidence that precipitation might be an important cue regulating the acoustic communication of freshwater insects.

1.10.5 **Acoustic index- and sound type-based soundscape measurements**

Acoustic index values were significantly, but only moderately correlated with sound type richness at this site. This moderate correlation suggests that single acoustic indices and sound type richness highlight different aspects of acoustic diversity. This result is unsurprising, as some sound types barely occupied any acoustic space, while others were dominant with respect to frequency and time. It would be unrealistic to assume that an acoustic index could be equally sensitive to sound types that vary dramatically in spectral or temporal occupancy (Gasc, Pavoine, Lellouch, Grandcolas, & Sueur, 2015). In the case of this acoustic community, acoustic indices offered a much better window into overall sound type occupancy, which has recently been linked to sound type richness in terrestrial tropical habitats (Aide, Hernández-Serna, Campos-Cerqueira, Acevedo-Charry, & Deichmann, 2017). In a similar study on the soundscapes of temperate ponds, Desjonquères et al. (2015) found that only the acoustic index Acoustic Richness was marginally correlated with sound type richness (correlation of 0.2) and abundance (correlation of 0.19), once controlling for the SNR of the sound types. The lack of a strong relationship in that study was probably because the soundscapes of these ponds were composed of only sparse and faint biological sounds. In stark contrast, the biological sounds at Cantarana Swamp dominated the soundscapes on every rainless day and night.

Sound type classification offered information on acoustic diversity and dynamics that was not captured by the acoustic indices— and therefore represents an important component of the analysis of aquatic soundscapes. However, due to a lack of classification standards, this method produces results that are not currently comparable between studies or across different habitats. For example, Desjonquères et al. (2015) classified 48 sound types from three temperate ponds in France but that study found lower average sound type richness per minute (0.6, 1.0 and 2.2 in the different ponds) than we did in Cantarana Swamp (3.7). Overall sound type richness may be influenced by the classification choices of the human inspector. Sound type classification is still a subjective exercise, and in some studies, similar sounds can be lumped together, while in others, every unique temporal-spectral signal can be given its own sound type label. Devising best practices for defining sound types and developing automated sound type classification programs are important steps in addressing shortcomings in this approach. In Supporting Information S2, we have provided recommendations for conducting manual classification of sound types.

1.10.6 Future directions for freshwater soundscape monitoring research

Both the findings and limitations of our study highlight the ample opportunity to expand and refine freshwater acoustic monitoring and assessment techniques. Important foci for future research include (1) ground-truthing soundscape data with *in situ* field sampling of biota and environmental conditions, (2) matching sound types with species, (3) using sound types to assess other freshwater habitats, (4) assessing annual and interannual dynamics and (5) considering the role of soundscapes in revealing ecological disturbance gradients. In order for soundscape methods to be effective in freshwater environments, soundscape measurements must have a sufficiently strong positive correlation with at least one ecologically meaningful facet of biodiversity, be it the presence of an indicator species or species richness, abundance, evenness or composition. Given the rich diversity and dynamics identified in our study, we would encourage such future work because soundscape recording and analysis could be an effective tool for monitoring and assessing the biodiversity of tropical freshwater systems.

Acknowledgments

Benjamin Gottesman (Corresponding Author), Dante Francomano, Zhao Zhao, Kristen Bellisario, Maryam Ghadiri, Taylor Broadhead, Amandine Gasc*, Bryan Pijanowski*

*Amandine Gasc and Bryan Pijanowski should be considered joint senior authors.

Additional supporting information external to this document including example sound files can be found on Github (https://github.rcac.purdue.edu/PijanowskiGroup/Gottesman_et_al_2017)

S2.1 Biotic information

The wetland was dominated by the grass *Scleria microcarpa* (Cyperaceae). Other plant species include *Spathiphyllum friedrichsthalii* (Araceae), *Calyptrocarya poeppigiana* (Cyperaceae), *Calyptrogyne ghiesbreghtiana* (Arecaceae)*,* and *Clidemia japurensis* (Melastomaceae; Ramirez, 2017; Strieby, 1998).

Fauna that utilized this swamp included many anuran species, reptiles including Serpentes (snakes), Testudines (turtles), and *Caiman crocodilus* (Alligatoridae; spectacled caiman), mammals such as Chiroptera (bats), *Procyon lotor* (Procyonidae; raccoon), and *Leopardus pardalis* (Felidae; ocelot). The most common frog species that utilize the swamp are *Agalychnis callidryas* (Hylidae), *Leptodactylus pentadactylus* (Leptodactylidae), *Scinax eleaochroa* (Hylidae), *Dendropsophus ebraccatus* (Hylidae), *Smilisca baudinii* (Hylidae). Others include *Gastrophryne pictiventris* (Microhylidae), *Scinax boulengeri* (Hylidae), *Smilisca phaeota* (Hylidae), *Agalychnis saltator* (Phyllomedusidae), *Tlalacohyla loquax* (Hylidae), and *Dendropsophus phlebodes* (Hylidae; Whitfield, 2017). The only fish family that has been identified is Synbranchidae (swamp eels) (de la Rosa, personal communication, January 26, 2017).

In addition to the aquatic insect families reported in lentic habitats within La Selva (M. Springer, personal communication, March 21, 2017), Schlagbauer (Schlagbauer, 1995) documented the

presence of aquatic insects at a similar wetland to Cantarana Swamp within 1 km of Cantarana Swamp. All the insects she documented are reported in a .csv file in the Github repository mentioned at the beginning of this Appendix.

S2.2 Sound type classification methods and discussion

Soundscape recording is occurring in an increasing number of habitat types. Sometimes, and especially in the aquatic habitats, not all sounds can be attributed to known species or processes. In these cases, it is feasible to classify sounds into "sound types" based on discernable features. Classifying and analyzing all of the sounds types within a habitat is helpful in revealing 1) acoustic diversity, 2) soundscape composition dynamics, and 3) how acoustic space is occupied. A sound type taxonomy can also be paired with later species identification.

Several studies have utilized manual sound type classification (e.g., Anderson et al., 2008; Desjonquères et al., 2015; Ruppé et al., 2015). The most common method for manually classifying sound types is a combination of aural and visual inspection. While visually inspecting spectrograms is a faster classification method than aural inspection, listening to files in real time can provide additional information that can help to more accurately classify sound types. Listening is therefore advisable, especially at the beginning of classification analyses.

Several sources of variability make classifying sound types challenging. First, there is inherent variability in the signals produced by any individual organism and those of individuals within a species. Signals can also be altered due to a number of environmental factors, causing filtering patterns that create distorted versions of the emitted sounds. We attempted to account for this variability by spending a significant period of time listening and thinking before conducting a formal classification analysis. We listened to a range of files and considered the variability of recorded sounds as well as the environmental interference that might have played a role in the habitat.

Sound type classification is still a subjective exercise, and in some studies similar sound types are lumped together, while in others, every unique temporal-spectral signal has its own sound type label. Due to the subjectivity inherent in this process, it is important to decide what type of

classification leniency should be employed. In Cantarana Swamp, there was significant masking, a high degree of signal distortion, and inherent signal variability. For this reason, we tended to lump sounds together as opposed to considering them as distinct sound types. For example, Buzzer varied considerably in the number of impulses per pulse (from fewer than 15 to more than 40 impulses per pulse), but due to other sound type characteristics, such as the frequency range, impulse width, and inter-impulse distance, we still classified these sounds as Buzzer. Similarly, Repeater was often masked by other sound types, so that only the upper portion of the signal was audible/visible, but that signal was still classified as "Repeater". Scratcher's low-frequency content was sometimes partially filtered due to the acoustic properties of the shallow wetland, but we still attributed these filtered sounds to "Scratcher". The rules on which our classification was based are provided in Figure S1. With a more divisive classification strategy, there would have been hundreds or thousands of sound types because of the high variability within the sound types.

While this method is proficient in generating study-specific data that can be useful to answer localized questions, it is clear that sound type classification is too subjective to enable post-hoc across-study or inter-system comparisons. There are no existent standards for assessing what constitutes a sound type, and how stringent to be in demarcating boundaries between sound types. Other standardized metrics such as purely automated classification or acoustic indices are more readily comparable. Individual researchers will likely conduct manual classification for different studies in unique ways, and this may be merited given the diverse nature of acoustic datasets. Nonetheless, we propose several basic guidelines for sound type classification:

1. Generate a random subset of your data and aurally and visually inspect it for several hours. In this study, BG listened to 200 1-minute recordings. This exercise revealed the presence of 13 out of the 18 sound types eventually classified. While not the entire amount, it gave BG an approximate sense of the acoustic diversity, the variability within the common sound types, and the properties of the acoustic habitat.
2. As you recognize each new sound type, save an excerpt, note when it occurred, and create a description of its signal properties.
3. If possible, use a good sound visualization program that allows control of spectrogram settings and enables easy scrolling through numerous files.

4. When starting a sound type analysis, randomize the order of sound files you will analyze.

5. If in you are in the middle of an analysis and discover a new sound type, it is important to start from the beginning of the analysis and look for that sound type in earlier recordings.

6. Run some form of quantitative classification to validate manual sound type classification. If you decide to run a linear discriminant analysis, use either leave-one-out or k-fold cross-validation.

S2.3 Linear discriminant analysis methods and results

In order to run the linear discriminant analysis (LDA), we had to satisfy two assumptions: features had to be non-correlated and beta dispersion had to be homogenous between groups (Anderson, Ellingsen, & McArdle, 2006; Venables & Ripley, 2002). To avoid collinearity while retaining maximal feature content, features with Pearson correlations greater than 0.7 (low frequency, high frequency, aggregate entropy, average power, delta frequency, peak frequency) were combined using a principal component analysis (PCA). Only the first principal component was retained for inclusion in the LDA based on the comparison of principal component scores with a broken stick null model (Cangelosi & Goriely, 2007; MacArthur, 1957). To verify distinctness of groups, we employed a permutational analysis of variance ($F_{1,179} = 14.66$, $p = 0.001$, $R^2 = 0.08$), and to ensure homogeneity of beta dispersions, we used a beta dispersion permutation test ($F_{17,162} = 4.52$, $p = 0.01$; Anderson et al., 2006). We ran an LDA on the set of features associated with each sound type clip and also on a null model consisting of the same features with randomized sound type labels. The LDA results were assessed by confusion matrices that utilized leave-one-out cross-validation to quantify the classification accuracy for each sound type for both models (see Figure S2 for the confusion matrix of the alternative model).

S2.4 Pulse rate calculation description

In order to further analyze the sound types Geiger and Sine, the period length, inter-pulse distance, and pulse width were estimated. Period length refers to the length of one repetition of a periodic sound type. Pulse width refers to the average width of the sound produced by one "cycle of movement of the stridulatory surface" (Drosopoulos & Claridge, 2005). Within each sound type, the inter-pulse distance refers to the interval between consecutive pulses. Since Geiger and Sine

have frequency modulation, the pulse duration and inter-pulse distance were calculated separately for the high- and low-frequency portions of the signal.
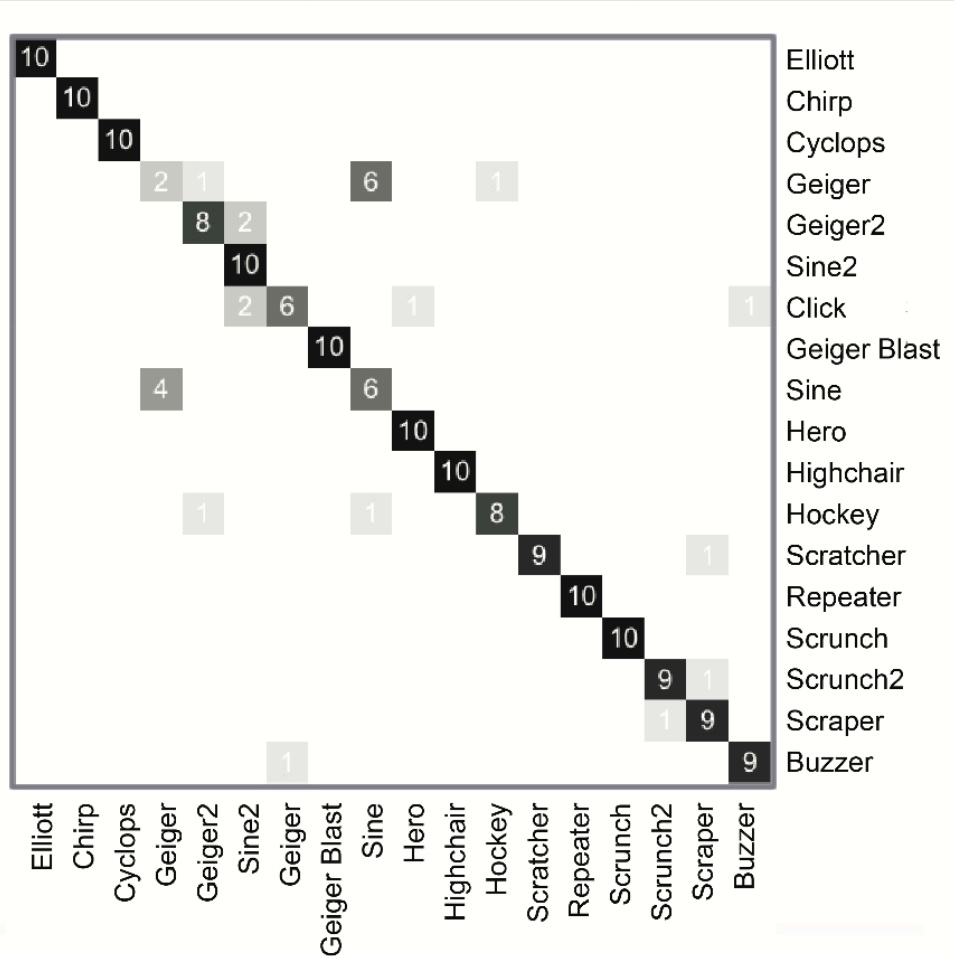
Figure 11: Confusion matrix displaying the linear discriminant analysis (LDA) results. The horizontal axis represents the group to which the sound belongs based on manual classification, and the vertical axis represents the group to which the sound was assigned by the model. Shading and numbers in each box denote the number of assignments to that box.

S2.4.1 Period length estimation

Each audio clip used in the analysis came from Library B, and contained 4 – 6 consecutive sound type occurrences of Geiger, Geiger2, Sine, or Sine2. The frequency range of interest was determined first in order to apply a low-pass filter that removed unrelated, concurrent sounds. Spectrograms were calculated for these filtered clips using a frame length of 1024 samples and a shift of 256 samples between adjacent frames. A Hamming window and a 1024-point FFT were used to implement the short-time Fourier transform (STFT). The corresponding spectrogram was denoted as $S(k, l)$, with k as the index of the Fourier coefficients and l as the index of temporal

frames. Within the frequency range of interest, a 2-D Wiener low-pass filter was applied to $S(k, l)$, using neighborhoods of size 6-by-6, which can help to remove grainy background noise. Motivated by Eichinski, Sitbon, and Roe (2015) and Towsey and Planitz (2011), we converted the output of the low-pass filter into a binary image. Unlike the user-defined fixed threshold used in their studies, an adaptive intensity threshold calculated by the Ostu method was applied (Otsu, 1979; Xu, Xu, Jin, & Song, 2011). Note that this binary image represented most of the time-frequency concentration areas within the frequency range of interest—that is, most energy of the signal of interest was preserved while noise was suppressed to some extent. Considering that the temporally-repeated, time-frequency concentration pattern corresponds to the period length information, we calculated the band-limited energy sequence $En(l)$, which is given as:

$$En(l) = \sum_{k=K_1}^{K_2} |S(k,l)|^2 \quad (1)$$

K_1 and K_2 correspond to the frequency range of interest. (For Geiger, K_1 and K_2 were set to a narrower frequency range containing only those components above 10 kHz.) A 9-point moving-average filter was applied to $En(l)$. Finally, period length estimates were obtained via spectral peak detection after the conventional Fourier transform on the output of the moving-average filter.

S2.4.2 Inter-pulse distance and pulse width estimation

To determine inter-pulse distance and pulse width, spectrograms were re-calculated for each sound clip with a frame length of 256 samples and a shift of 64 samples between adjacent frames to obtain finer temporal resolution. After applying a 2-D Wiener low-pass filter using neighborhoods of size 6-by-6, the band-limited energy sequence corresponding to the inter-pulse distance information, namely $FEn(l)$, was also calculated in a similar manner as described in S4.1. Then, an 11-point moving-average filter was applied to $FEn(l)$, which resulted in a smoothed output $SEn(l)$. It is worth remarking that quasi-periodicity can be observed in $SEn(l)$, owing to the fact that sample values in $SEn(l)$ were relatively large when located within each pulse and small in the gaps between pulses. Similarly, inter-pulse distance estimation was implemented by using the conventional Fourier transform on $SEn(l)$.

In order to calculate pulse width, a definition of "pulse width" must be established. Considering that a "3 dB width" is a very common definition in communication, radar, and sonar systems (Oppenheim, Schafer, & Buck, 1999), we calculated the pulse width in a similar manner—that is, the pulse width of each pulse in $SEn(l)$ refers to the temporal range in which every sample value was not less than this threshold value. Furthermore, due to the unrestricted aquatic environment, the pulses usually did not possess bilateral symmetry and $SEn(l)$ was non-stationary. Thus, we employed the threshold value that approximately corresponded to the 3 dB point and was equidistant to the nearest local maximum and minimum. We calculated the mean of the upper and lower envelopes of $SEn(l)$, namely $MEn(l)$. The values of the crosspoints between $MEn(l)$ and $SEn(l)$ were considered as the 3 dB points employed in estimating pulse width information. Then, for each pulse, the duration length within the two crosspoints between $MEn(l)$ and $SEn(l)$ was referred to as an individual pulse width measurement. A set of all the individual pulse width measurements was denoted as $\{IPW_i, i=1, 2\ldots K\}$, with K as the number of observations. An illustrative example of this procedure using a portion of a recording is given in Figure S3, in which (a) shows the original time-domain signal and spectrogram, and (b) presents the curves corresponding to the raw band-limited energy sequence $FEn(l)$, smoothed sequence $SEn(l)$, and mean sequence $MEn(l)$, respectively.

It is worth noting that the calculation of $MEn(l)$ relies on a cubic-spline interpolation of local maxima and minima of $SEn(l)$. Therefore, exceptional local maxima and/or minima originating from competing sound sources or environmental noise may evidently influence the performance of $MEn(l)$. This is expressed as distortion of $MEn(l)$ resulting in some outliers that have highly deviating measurements in the set $\{IPW_i, i=1, 2\ldots K\}$. Rejecting such outliers is not trivial work for fully automated processing due to the diversity in the unrestricted environment (Zoubir, et al., 2012). We designed a semi-automatic outlier rejection scheme to make the pulse width estimation more robust to real-world recordings. To be more specific, manual inspection of the plots containing $FEn(l)$, $SEn(l)$, and $MEn(l)$ (e.g. Figure S2(b)) was required first to decide whether or not there was distortion in $MEn(l)$. In the case of no distortion, the average of all elements in the set $\{IPW_i, i=1, 2\ldots K\}$ directly yielded the pulse width result of the clip. If distortion was confirmed, local maxima and minima of $SEn(l)$ were further refined—that is, a new $MEn(l)$ was calculated through a cubic-spline interpolation using those local maxima and minima without the

exceptional values. Finally, the pulse width result of the clip is the average of new individual pulse width measurements.
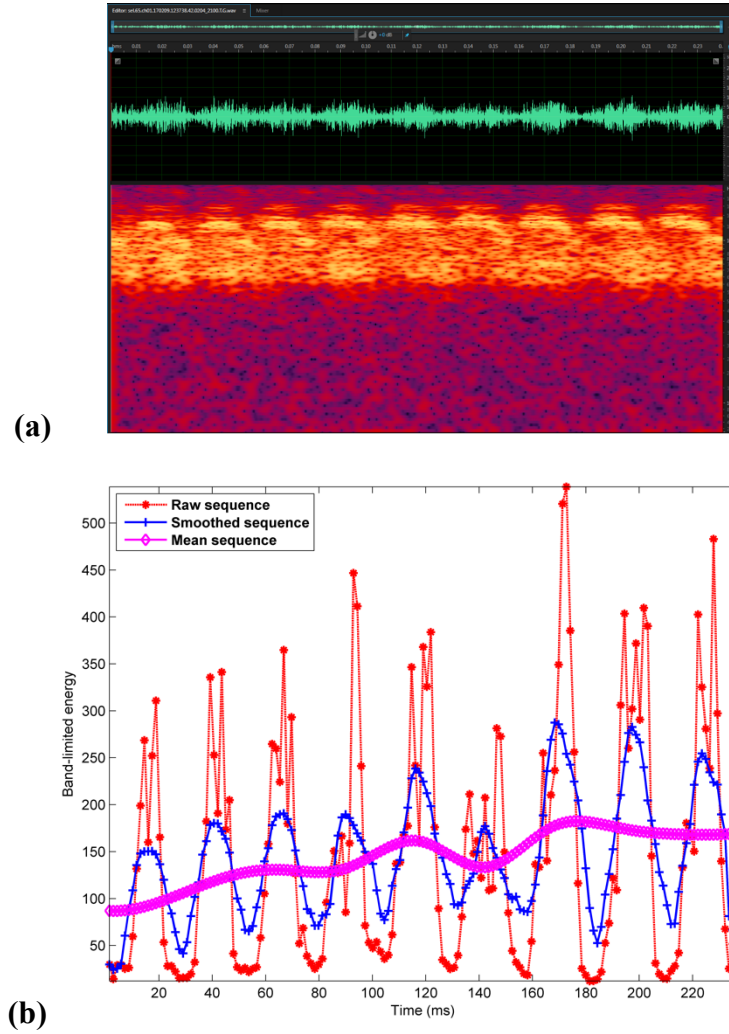
Figure 12: An illustrative example of pulse width estimation using a portion of a recording: (a) the original time-domain signal and spectrogram; (b) the curves corresponding to the raw band-limited energy sequence FEn(l), smoothed sequence SEn(l), and mean sequence MEn(l). There are 9 individual pulse width measurements in this figure.

S2.4.3 Statistical test of period and pulse rate features

K-means clustering (Hartigan & Wong, 1979) was used to cluster sound clips of Sine and Geiger (n = 81) into two groups using "period length", "inter-pulse distance of high-frequency portion",

"inter-pulse distance of low-frequency portion", and "pulse width of low-frequency portion" as features. A logistic regression (McLeod & Xu, 2017) was then carried out to determine which features significantly differed between these two sound types, with "sound type" (Sine or Geiger) as the dichotomous dependent variable and the four acoustic features as the independent variables.
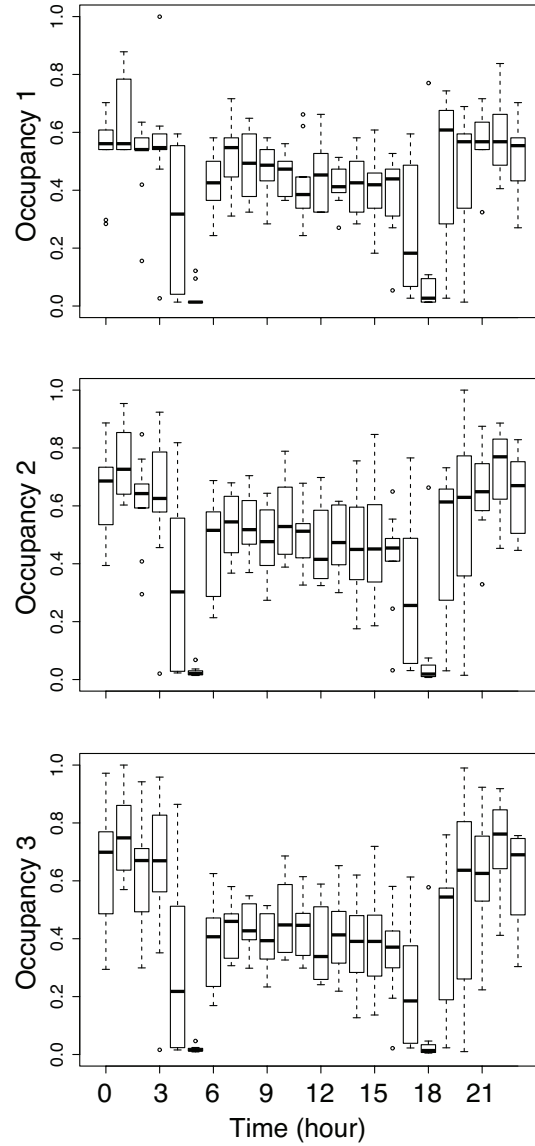
Figure 13: Plots of the three occupancy measurements. Occupancy 1 equals the sum of sound types' real percentages, Occupancy 2 equals the sum of sound types' real percentages * their delta frequencies, and Occupancy 3 equals the sum of sound types' real percentages * their delta frequencies * their average powers. In each box, the horizontal line represents the median value, the bottom represents the first quantile, the top represents the third quantile, and the whiskers extending from the top and bottom represent the maximum and minimum values, respectively type-based metric

Table 1: Sound type measurements. These values were determined from manually inspecting five files for each sound type that had high signal-to-noise ratios and were unmasked by other sound types. Measurements were calculated in iZotope RX using an FFT window of 64, "Hann" window, and "multi-resolution" spectrogram calculation algorithm.

Sound type	Periodicity	Frequency modulation	Minimum frequency (Hz)	Maximum frequency (Hz)	Frequency range (Hz)	Number of pulses	Pulse width (seconds)*	Pulse width (seconds; high)*	Inter-pulse distance (seconds)*	Inter-pulse distance (seconds; high)*	Sound type length (seconds)	Period length (seconds)
Buzzer	no	no	5,100 ± 105	9,620 ± 150	4,520 ± 171	1 ± 0	0.382 ± 0.072	N/A	N/A	N/A	0.382 ± 0.072	N/A
Chirp	no	no	3,820 ± 58	5,320 ± 86	1,500 ± 105	1 ± 0	0.089 ± 0.008	N/A	N/A	N/A	0.089 ± 0.008	N/A
Click	no	no	4,560 ± 421	12,520 ± 1339	7,960 ± 1194	1 ± 0	0.013 ± 0.004	N/A	N/A	N/A	0.013 ± 0.004	N/A
Cyclops	yes	yes	5,400 ± 550	18,200 ± 503	12,800 ± 726	94.2 ± 17.1	0.025 ± 0.002	0.011 ± 0.000	0.031 ± 0.001	0.017 ± 0.001	4.101 ± 0.657	4.101 ± 0.657
Elliott	no	no	16,240 ± 407	22,050 ± 0	5,810 ± 407	3.8 ± 1	0.179 ± 0.012	N/A	0.08 ± 0.009	N/A	1.194 ± 0.270	1.060 ± 0.780[†]
Geiger	yes	yes	4,880 ± 150	15,980 ± 431	11,100 ± 386	30.8 ± 3.7	0.021 ± 0.002	0.016 ± 0.001	0.011 ± 0.002	0.006 ± 0.002	0.909 ± 0.158	0.909 ± 0.158
Geiger Blast	no	no	3,840 ± 254	21,080 ± 538	17,240 ± 531	1 ± 0	0.027 ± 0.002	N/A	N/A	N/A	0.027 ± 0.002	N/A
Geiger2	yes	no	5,000 ± 130	10,660 ± 150	5,660 ± 209	1 ± 0	0.018 ± 0.003	N/A	0.024 ± 0.005	N/A	0.018 ± 0.003	0.043 ± 0.003
Hero	yes	no	3,860 ± 81	10,120 ± 107	6,260 ± 40	3 ± 0	0.074 ± 0.003	N/A	0.019 ± 0.001	N/A	0.254 ± 0.002	0.459 ± 0.013
Highchair	no	no	14,020 ± 193	20,500 ± 636	6,480 ± 664	18 ± 1.9	0.025 ± 0.001	N/A	0.006 ± 0.001	N/A	0.592 ± 0.083	N/A
Hockey	yes	yes	4,520 ± 222	14,060 ± 199	9,540 ± 144	26.2 ± 1.6	0.016 ± 0.001	0.018 ± 0.001	0.017 ± 0.002	0.019 ± 0.001	0.885 ± 0.044	2.369 ± 0.201
Repeater	yes	yes	6,200 ± 253	20,620 ± 744	14,420 ± 920	1 ± 0	0.139 ± 0.006	N/A	0.016 ± 0.002	N/A	0.139 ± 0.006	0.155 ± 0.008
Scraper	no	no	2,020 ± 177	6,800 ± 804	4,780 ± 807	1 ± 0	0.015 ± 0.003	N/A	N/A	N/A	0.015 ± 0.003	N/A
Scratcher	yes	no	0 ± 0	8,520 ± 601	8,520 ± 601	1 ± 0	0.126 ± 0.006	N/A	0.214 ± 0.089	N/A	0.126 ± 0.006	0.341 ± 0.092
Scrunch	no	no	1,840 ± 154	5,900 ± 235	4,060 ± 344	1 ± 0	1.170 ± 0.130	N/A	N/A	N/A	1.170 ± 0.130	N/A
Scrunch2	no	no	1,880 ± 222	4,240 ± 189	2,360 ± 236	1 ± 0	0.168 ± 0.016	N/A	N/A	N/A	0.168 ± 0.016	N/A
Sine	yes	no	5,100 ± 221	15,140 ± 250	10,040 ± 341	23.4 ± 1.2	0.022 ± 0.003	0.022 ± 0.001	0.018 ± 0.001	0.004 ± 0.001	0.769 ± 0.053	0.769 ± 0.053
Sine2	yes	yes	4,480 ± 183	11,780 ± 1235	7,300 ± 1379	1 ± 0	0.023 ± 0.002	N/A	0.022 ± 0.002	N/A	0.023 ± 0.002	0.044 ± 0.001

* "Pulse width" and "inter-pulse distance" were calculated separately on low-frequency and high-frequency portions of sounds with frequency modulation. Calculations for low frequency portions are presented under the "pulse width" and "inter-pulse distance" headings, while calculations for high-frequency portions are presented under the following headings with "high" in parentheses.
[†] Of the five clips used of Elliot, two were periodic, and this measurement is based on those two clips.

Table 2: List of acoustic indices used in this study including their sources, parameters, and correlations with sound type-based metrics

Index	Reference	Parameters	Library C Richness		Library B Richness		Occupancy 1		Occupancy 2		Occupancy 3	
			Spearman correlation	p value	Spearman correlation	p value	Spearman correlation	p value	Spearman correlation	p value	Spearman correlation	p value
Acoustic Complexity Index (ACI)	Sueur et al. 2014	cluster size (j) = 5 seconds	0.02	1.0	0.22	0.013	0.30	< 0.001	0.45	< 0.001	0.48	< 0.001
Acoustic Occupancy (AO)	Pijanowski & Gasc, unpublished	no modification to source code	-0.04	1.0	0.08	1.0	0.61	< 0.001	0.55	< 0.001	0.58	< 0.001
Acoustic Richness (AR)	Sueur et al. 2014	no modification to source code	-0.04	1.0	-0.25	0.003	0.04	1	-0.08	1	-0.09	1
Bioacoustic Index (BI)	Boelman et al. 2007	no modification to source code	0.03	1.0	0.16	0.208	0.70	< 0.001	0.85	< 0.001	0.92	< 0.001
H	Sueur et al. 2014	no modification to source code	0.01	1.0	-0.16	0.207	-0.22	0.016	-0.38	< 0.001	-0.44	< 0.001
H_f	Sueur et al. 2014	no modification to source code	0.03	1.0	-0.10	1.0	-0.47	< 0.001	-0.56	< 0.001	-0.65	< 0.001
H_t	Sueur et al. 2014	no modification to source code	-0.02	1.0	-0.23	0.006	0.08	1	-0.04	1	-0.04	1
Normalized Difference Soundscape Index (NDSI)	Sueur et al. 2014	High band = 5,000 – 22,050; low-band = 1,000 – 5,000	0.00	1.0	0.11	1.0	0.63	< 0.001	0.78	< 0.001	0.88	< 0.001
Acoustic Activity (AA)	Towsey et al. 2014	no modification to source code	-0.02	1.0	0.20	0.035	-0.13	0.826	-0.05	1	-0.06	1
Average Duration of Acoustic 6Events (ADAE)	Towsey et al. 2014	no modification to source code	0.02	1.0	0.15	0.383	-0.20	0.039	-0.11	1	-0.13	1
Acoustic Diversity Index (ADI)	Sueur et al. 2014	no modification to source code	-0.03	1.0	-0.05	1.0	-0.33	< 0.001	-0.53	< 0.001	-0.61	< 0.001
Acoustic Evenness Index (AEI)	Villanueva-Rivera et al. 2011	db_threshold = -40; freq_step = 1000	0.05	0.682	0.06	1.0	0.30	< 0.001	0.49	< 0.001	0.57	< 0.001
Average Signal Amplitude (ASA)	Towsey et al. 2014	no modification to source code	-0.07	0.073	0.14	0.625	0.69	< 0.001	0.82	< 0.001	0.91	< 0.001
Background Noise (BN)	Towsey et al. 2014	no modification to source code	-0.06	0.412	0.20	0.043	0.78	< 0.001	0.83	< 0.001	0.88	< 0.001
Median of Amplitude Envelope (MAE)	Sueur et al. 2014	no modification to source code	-0.02	1.0	-0.26	0.001	0	1	-0.13	0.989	-0.13	0.76
Number of Peaks (NP)	Sueur et al. 2014	frequency = 300 Hz, threshold = 0.4, f = NULL, nmax = NULL, amp = NULL	0.15	< 0.001	0.35	< 0.001	0.12	1	0.10	1	0.02	1
Signal-to-Noise Ratio (SNR)	Towsey et al. 2014	no modification to source code	0.06	0.357	-0.03	1.0	-0.57	< 0.001	-0.56	< 0.001	-0.61	< 0.001
Root Mean Squared (RMS) amplitude	Sueur et al. 2014	no modification to source code	-0.12	< 0.001	0.11	1.0	0.65	< 0.001	0.80	< 0.001	0.90	< 0.001
Broadband Sound Pressure Level (SPL)	Merchant et al. 2015	1-22050 Hz; fft = 512; "Hann" window	-0.07	0.067	0.04	1.0	0.60	< 0.001	0.58	< 0.001	0.64	< 0.001
Standard Deviation of Sound Pressure Level (SDSPL)	Merchant et al. 2015	1-22050 Hz; fft = 512; "Hann" window	0.03	1.0			0.03	1	0.15	0.387	0.16	0.286

CHAPTER 3: DIFFERENTIAL TERRESTRIAL AND MARINE ANIMAL COMMUNITY RESPONSES TO HURRICANE MARIA IN SW PUERTO RICO: QUANTIFYING ECOSYSTEM RESILIENCE THROUGH SOUND

Benjamin L. Gottesman (Corresponding Author), Jack Olson, Soohyun Yang, Orlando Acevedo-Charry, Dante Francomano, Felix Martinez, Richard Appeldoorn, Doran Mason, Steve Ruberg, Ernesto Weil, Bryan Pijanowski. *In prep.*

1.11   Introduction

Patterns of disturbance and response shape ecosystem dynamics (Foley et al., 2005; Rockström et al., 2009; Turner, 2010). Ecosystems have developed high resilience to historical disturbance regimes, meaning that they retain their essential structure and functioning after perturbation (Holling, 1973). Despite their remarkable natural resilience, the stability of ecosystems is increasingly being tested by human activities, which are altering historical disturbance regimes and the capacity of ecosystems to recover (Johnstone et al., 2016). Increasing frequency and intensity of disturbances in combination with decreased response capacity can trigger enduring shifts into novel states that may fail to provide comparable ecosystem services (Folke et al., 2004). In this time of rapid environmental change, quantifying the resilience of ecosystems can improve our abilities to predict disturbance impacts, estimate the loss of ecosystem services, and conduct adaptive management. While resilience theories are becoming more refined, few practical methods exist to measure ecosystem resiliency in real-world contexts (Bennett, Cumming, & Peterson, 2005). Rigorous and replicable methods to measure ecological resilience are needed in order to better understand where, when, and how altered disturbance regimes will fundamentally transform ecosystems.

One measurable and important contributor to ecosystem resilience is biodiversity (Folke et al., 2004; Oliver, et al., 2015; Peterson, Allen, & Holling, 1998). Biodiversity-related mechanisms operating at the species, community, and landscape levels can bolster resistance to and recovery from perturbations (Oliver et al., 2015).

Individual species vary in their ability to withstand perturbations, adapt to environmental changes, and maintain or expand populations following disturbance (Peterson et al., 1998). At the community level, resilience is strengthened by functional response diversity, i.e. when multiple species perform similar functional roles but exhibit differing disturbance responses (Elmqvist et al., 2003). In this way, biodiversity has an insurance effect that has been demonstrated theoretically and empirically, whereby resilience is improved with greater richness and evenness of species across trait-response space (Chillo, Anand, & Ojeda, 2011; Kissick, Dunning, Fernandez-Juricic, & Holland, 2018; Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Peterson et al., 1998). At the landscape level, higher environmental heterogeneity (and also beta diversity, see Mellin, Bradshaw, Fordham, & Caley, 2014) increases the spatial heterogeneity of disturbance impacts, which bolsters resilience by creating refugia where organisms can persist through disturbance events (Oliver, Roy, Hill, Brereton, & Thomas, 2010). Refugia also preserve pockets of ecological legacy from which organisms can subsequently colonize more disturbed parts of the diverse landscape (Adger, Hughes, Folke, Carpenter, & Rockström, 2005).

Biodiversity is often measurable, but traditional techniques of biodiversity assessment are typically limited in the taxa that are surveyed and are costly and impractical to conduct long-term, especially over long durations and following pulse disturbance events (Sueur, Pavoine, Hamerlynck, & Duvail, 2008). As a result, biodiversity datasets that contain pulse disturbances are usually temporally disparate (monthly or bi-monthly), which increases the risk of Type I Error when observed changes are caused by seasonality or longer-term stressors as opposed to the disturbance of interest (the false snapshot effect; Adams, 2001). Low temporal resolution also fails to capture finer-scale changes in temporal variability that signal instability and approaching regime shifts (Carpenter & Brock, 2006). Furthermore, these survey efforts are usually short-term (< 2 years post-disturbance), and so they miss any longer-term response patterns. While human-led survey efforts will always constitute an essential part of biodiversity monitoring, especially to identify the processes and drivers linked with observed ecosystem changes, some of their shortcomings are being addressed through more novel technological applications.

Remote sensing technologies that are automated and standardized can measure ecosystems at unprecedented temporal and spatial scales. Visual remote sensing (satellites, LiDAR, drones, etc.)

has emerged as an effective method for capturing changes in vegetation and habitat structure at fairly high temporal resolution (with measurements every few days), but it has limited applications for direct animal community monitoring (Gasc et al., 2018, but see Spaan et al., 2019). Audio recordings, however, are comparably effective at capturing changing patterns in wildlife presence or behavior (Gasc et al., 2018; Villaneuva-Rivera et al., 2011), and can deliver data with temporal resolutions of milliseconds. With recent advances in storage capacity and energy efficiency, acoustic recorders can now capture months or years of data between servicing periods (Gage & Axel, 2014; Gibb, Browning, Glover-Kapfer, & Jones, 2019; Hill et al., 2018), making this technology highly useful for assessing the animal impacts of unpredictable pulse disturbances.

Soundscape recordings are increasingly being used to assess the impact of disturbance on animal communities (Indeck, Simard, Gowans, Lowerre-Barbieri, & Mann, 2015; Lee, Davies, & Struebig, 2017). Because animal diversity and abundance have been shown to correlate with soundscape complexity and amplitude (Buxton, Agnihotri, Robin, Goel, & Balakrishnan, 2018; Buxton, McKenna, et al., 2018; Harris et al., 2016; Rowell et al., 2017; Sueur et al., 2014), soundscapes could potentially reveal the magnitude of environmental disturbances through the changes in soundscape complexity and amplitude after disturbance events. Several studies have already employed soundscape recordings to evaluate disturbance impacts in different terrestrial and marine ecosystems (Coquereau et al., 2017; Deichmann et al., 2017; Gasc et al., 2018; Lee et al., 2017). However, whether soundscape-disturbance relationships are generalizable across disturbance types and ecosystems is still unclear. Furthermore, identifying which soundscape components indicate different dimensions of disturbance ecology is critical to unlocking the potential of this emerging method.

We posit that soundscapes can be used to measure three components of ecological resilience: impact magnitude (resistance), functional response diversity (recovery), and the spatial patterns of disturbance and recovery (impact heterogeneity). In ecosystems where animals from different taxonomic and functional groups produce sound, it is possible to acoustically assess the resistance and response of individual species, functional groups, and animal communities (Butler, Stanley, & Butler, 2016; Buxton, Brown, Sharman, Gabriele, & McKenna, 2016; Coquereau et al., 2017). If multiple acoustic recorders are deployed within a habitat, analyzing the variability in acoustic

responses across sites can also provide insight into impact heterogeneity (Browning et al., 2017). Overall system resilience can be evaluated as the degree of initial alteration (resistance) and by the time it takes for post-disturbance altered soundscapes to resume similar composition and dynamics to pre-disturbance soundscapes (recovery) (Angeler et al., 2014).

Here, we analyzed soundscape resilience in two coastal ecosystems in Puerto Rico following Hurricane Maria, which swept across the island on September 20, 2017. While hurricanes are a natural, foundational disturbance in tropical coastal ecosystems, there is growing consensus that climate change is increasing the frequency of intense storms, especially in the Atlantic Ocean (Holland & Bruyère, 2014; Knutson et al., 2010, Pielke et al. 2003). Since at least 1995, we have entered a multi-decade period of heightened storm activity in the Atlantic, with 2005 and 2017 as exceptionally hyperactive years (Chylek & Lesins, 2008). Hurricane Maria was the strongest Atlantic storm in 2017 and the second most powerful storm to affect Puerto Rico in its documented history (Feng et al., 2018). The storm killed over 2,000 people, caused $90 billion in damages, and drastically altered natural systems across the island (Halverson, 2018; Kishore et al., 2018; Van Beusekom, Álvarez-Berríos, Gould, Quiñones, & González, 2018). There was mass defoliation, with 23 to 31 million trees severely damaged or killed (Feng et al., 2018). Animal responses are still largely uncharacterized, though several studies have noted declines in granivorous, frugivorous, and nectivorous birds following Hurricane Maria and Hurricane Irma, which also struck the island in September 2017 (Schraffner et al. 2018; Lloyd, Rimmer, & Faría, 2019). Coral reefs in Puerto Rico suffered severe damage during Hurricane Maria, with wave-exposed sites receiving large swells which overturned, broke, or buried an estimated 11% of the island's corals (NOAA, 2018b). Although the effects of Caribbean hurricanes has been studied in traditional ways regarding the responses of plants, animals, and ecosystem structure and function (Tanner, Kapos, & Healey, 1991), soundscape ecology could reveal other dimensions of ecosystem responses in an integrative way (Deichmann et al., 2017).

We took advantage of three terrestrial and three marine automated recorders that we deployed in dry forest and coral reef habitats in coastal Puerto Rico that recorded soundscapes from March 2017, six months before Hurricane Maria struck the island, to January 2018. To assess the hurricane impacts on the terrestrial and marine communities, we identified eight sound types

representing different functional groups and measured 1) which sound types were significantly impacted by the storm and the magnitude of these impacts, 2) whether the marine and terrestrial acoustic communities were impacted by the storms, the magnitude of these impacts, and how these impacts differed across sites, and 3) the recovery rates of sound types that were significantly impacted. We hypothesized that acoustic activity across all sound types would decline following Hurricane Maria because of a combination of direct mortality, dispersal, and behavioral change (Waide, 1991a). We also hypothesized that the terrestrial impacts would be greater and more prolonged than the marine impacts, given field observations that there was greater physical modification to the dry forest sites than to the coral reefs sites after the storms.

1.12   Materials and methods

1.12.1 Site descriptions

This study was conducted in dry forest and coral reef habitats in southwest Puerto Rico, the driest part of the island (Figure 14a; Ewel & Whitmore, 1973). La Parguera Natural Reserve (LPNR), where we recorded coral reef soundscapes, is a marine protected area offshore of the southwest coast of Puerto Rico (Figure 14b). This 10-km portion of the Puerto Rico insular shelf contains one of the most well-developed coral reef systems on the island. It is large with respect to other reef systems around the island, has better defined reef zonation (fore reef, reef crest, back reef, lagoon), and contains extensive mangroves and seagrass beds that are nursery habitats for many reef fish species (Morelock, Schneiderman, & Bryant, 1977). Approximately 20 km east of the sensors in LPNR, Guanica State Forest, where we recorded dry forest soundscapes, is considered the best preserved subtropical dry forest in the Caribbean (Figure 14c; Ewel & Whitmore, 1973). Approximately half of Puerto Rico's bird species and 15 of its 17 endemic bird species inhabit Guanica State Forest (Arendt, Faaborg, Canals, & Bauer, 2015). It has four main forest types: upland deciduous, semi-evergreen, scrub, and coastal mangroves (Lugo, Gonzalez-Liboy, Cintron, & Dugger, 1978).
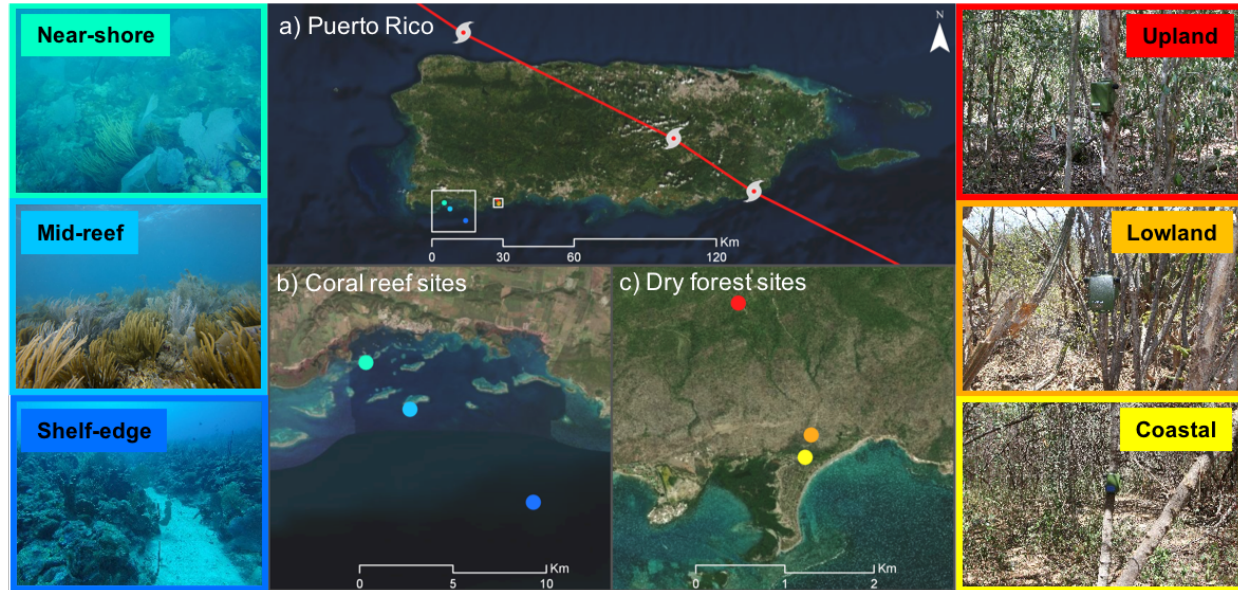
Figure 14: Map of the study region including a) the island of Puerto Rico and the path of Hurricane Maria, b) the three marine recorder sites in La Parguera Reserve, PR, and c) the three terrestrial recorder sites in Guanica Dry Forest, PR. The six images on the left and right of the figure portray the six study sites. The frame color of each site photo is used to represent these sites in subsequent figures.

1.12.2 Acoustic Data collection

From March 2017 to January 2018, we deployed three acoustic recorders in each of these two systems (coral reef and dry forest) to capture and compare their annual soundscape dynamics. At the coral reef sites in LPNR, three Wildlife Acoustics SM3M recorders equipped with HTI-96-MIN hydrophones were installed across an inshore to offshore gradient. The most landward site, Pelotas (near-shore; 17.957367, -67.0696), was located 1.8 km offshore and is distinguished by a steeply sloping linear reef formation to 14 m depth, with adjacent seagrass beds and soft sediment. Media Luna (mid-reef; 17.934883, -67.04885), located 4.5 km offshore, is a linear, octocoral-dominated forereef extending to 18 m depth. The shelf-edge zone of LPNR, represented here by Weinberg (shelf-edge; 17.890483, -66.988667), is typified by spur and groove coral formations found between 18 and 30m depth. Each marine recorder was fastened to a rebar rod approximately 1 m above the substrate. Sensors recorded continuously, with a sampling rate of 48 kHz, a bit depth of 16 bits, and a gain of 18 dB. The arrival of the storm coincided with one of the recorder servicing periods, and, as a result, data were not obtained in the 17 days immediately after the storm for the marine sites.

Concurrently, three Wildlife Acoustics SM4 terrestrial recorders were installed across a coastal gradient in the Guanica Dry Forest, including three of the four main forest types: 1) upland deciduous forest (17.97004, -66.86971), 2) lowland scrub forest (17.95676, -66.86234), and 3) coastal mangrove forest (17.95451, -66.86295). Each recorder was fastened to a tree at a height of 1.5 m. Sensors recorded 10 minutes every 30 minutes using built-in SM4 microphones, with a sampling rate of 48 kHz, a gain of 18 dB, and a bit depth of 16 bits.

1.12.3 Soundscape analysis

To prepare recordings for analysis, marine recordings that were shorter than 59 minutes, captured during recorder servicing periods, or corrupted during data offloading, were removed from the dataset. Each hour-long recording was divided into 60 1-minute-long files. The percentage of days with incomplete or no data over the course of the study period (March 9, 2017–January 1, 2018) was 23% at the near-shore site, 14% at the mid-reef site, and 20% at the shelf-edge site. Terrestrial recordings were converted to mono by selecting the audio channel with the greatest preservation of high frequency content following Hurricane Maria. The percentage of days with incomplete or missing data for terrestrial sites was 22% at the coastal site, 25% at the lowland site, and 24% at the upland site.

1.12.3.1   Identifying biological components of the soundscape

Especially in a system with uncharacterized soundscapes, it is important to become familiar with the soundscape composition and dynamics prior to analysis (Gottesman et al., 2018). To identify the main biological sound types, BG listened to more than 200 recordings from each site (20 hours) from different times of the day and different times of the year while reviewing their spectrograms. We also generated long-term spectrograms (Merchant et al., 2015) and false color spectrograms (Towsey et al., 2014b) to better understand soundscape dynamics over longer timeframes (code and example spectrograms available through GitHub; see Supporting Information for details). In the marine soundscapes, fish and snapping shrimp were the primary sound producers, and their sounds were easily distinguishable in the time and frequency domains. Similarly, in the terrestrial environment, insects and birds were the primary sound producers, and their sounds were distinguishable as well. For the fish and insects, we identified different frequency bands containing

fish and insect sounds when spectrograms were viewed with a window length of 8,192 samples. On the basis of these taxonomic and frequency distinctions, we defined distinct sound types.

Across all sites, we identified eight broad biological sound types, four for the coral reef and four for the dry forest, and quantified their frequency ranges and temporal dynamics (Table 3). In the marine system, sound types included a low-frequency fish (LFF) chorus that occurred around dusk, a high-frequency fish (HFF) chorus that occurred at night, sporadic fish pulses (FP) that generally peaked at dawn and dusk, and broadband snaps from snapping shrimp (*Alphidae* sp.; SS) that were ever-present but exhibited peaks at dawn and dusk. In the terrestrial system, sound types included bird vocalizations (BV) that peaked at dawn, and low-, mid-, and high-frequency insect (LFI, MFI, HFI) choruses that peaked at night. We sought to measure the daily acoustic activity of each sound type that we identified. For sound types that dominated their respective frequency bands (e.g. fish choruses, shrimp snaps, insect choruses), we measured sound pressure levels (SPLs) in those frequency bands. For sound types that did not dominate their frequency bands (bird vocalizations and fish pulses), we calculated other acoustic metrics that better measured these sounds (described in Section 2.3.3). We consulted experts in Puerto Rican taxa and bioacoustics (Michelle Umpierre, David Mann, and RA for fish sounds, OAC for birds, and OAC and Carl Strang for insects) to identify the producers of these sound types when possible.

Table 3: Sound types and their measurement parameters including: frequency range, daily activity period, acoustic measurement selected, and references to previous work that employed similar measurements for similar purposes. For six of the eight sound types, measurements were based on sound type sound pressure levels (SPLs).

	Sound types	Symbol	Frequency range (kHz)	Daily activity	Measurement	References
	Low-frequency fish chorus	LFF_{SPL}	150–450	18:00-22:00	Peak SPL	Rowell et al., 2017; Kaplan et al., 2018
	High-frequency fish chorus	HFF_{SPL}	900–2000	22:00 – 05:00	Peak SPL	Rowell et al., 2017; Kaplan et al., 2018
	Snapping shrimp	SS_{SPL}	3,000–24000	All hours	Median SPL	Lillis et al., 2014; Rossi et al., 2016
	Fish pulses	FP	50–800	All hours	Spectral cross-correlation	Knight et al., 2017
	Low-frequency insect chorus	LFI_{SPL}	2,500–4,300	18:00 – 05:00	Median SPL	Staaterman et al., 2017;
	Mid-frequency insect chorus	MFI_{SPL}	4300–5,250	18:00 – 05:00	Median SPL	Staaterman et al., 2017;
	High-frequency insect chorus	HFI_{SPL}	5,500–10,000	18:00 – 05:00	Median SPL	Staaterman et al., 2017
	Bird vocalizations	BV	1,000–10,000	06:00 – 08:00	Spectral saturation	Towsey et al. 2017; Burivalova et al. 2018

1.12.3.2 Dominant sound type analysis

To measure the six dominant sound types (fish choruses, snapping shrimp, and insect choruses), we first calculated SPLs in R (R Core Team, 2012) using "PAMGuide" (Merchant et al., 2015). Audio files were converted into the spectral domain with a short-term Fourier transform (STFT) using a Hann window, a window length of 0.5 seconds, and zero overlap. For each sound type, the output of the STFT (12,000 frequency bins x 120 time windows) was cropped to the upper and lower bounds of the sound type's frequency range, summed, and then converted into calibrated dB values using the hydrophone sensitivities calculated for each marine unit (NS: -164.3; MR: -164.6; SE: -164.4 (dB re: 1V/μPa)) and the default microphone sensitivity for SM4 units (-35 dB re: 1V/Pa) that was provided in the Wildlife Acoustics SM4 documentation. This analysis yielded 120 SPL values per sound type per recording. We calculated the median SPL value of these 120 values to obtain one SPL measurement per recording.

To then obtain a measurement of daily acoustic activity for each of these sound types, we applied a 1-hour moving average and then calculated either the peak or median value of the multiple values for each daily activity period, depending on the sound production dynamics of each sound type. For the low- and high-frequency fish choruses, we calculated the peak value of each activity period (LFF$_{SPL}$, HFF$_{SPL}$) since peak levels have been shown to correlate with fish abundance (Rowell et al., 2017) and also because these choruses did not always span the entire nighttime period. For the shrimp-dominated frequency band, in which snaps were always present, we calculated the median daily SPL value (SS$_{SPL}$). For the low-, mid-, and high-frequency insect bands, which typically spanned nighttime chorusing periods, we also utilized the median value (LFI$_{SPL}$, MFI$_{SPL,}$ and HFI$_{SPL}$)

1.12.3.3 Non-dominant sound type analysis

1.12.3.3.1 Birds

To measure the acoustic activity of birds, we calculated the saturation of soundscapes at dawn (06:00 – 08:00). Since a diverse assemblage of bird species produced sound during this period with minimal masking from insects or other sources, we followed previous work (Burivalova et al., 2018; Depraetere et al., 2012; Towsey et al., 2014b) that showed that measuring the saturation of dawn soundscapes positively correlates with bird community diversity. Soundscape saturation

refers to the percentage of frequency bins that are acoustically "active" within a recording. Our methods followed those of Burivalova et al. (2018) and are detailed in Supplementary Information (S3.1).

To validate the bird vocalizations, we manually surveyed the calling activity of different avian species in 45 recordings. We randomly selected five 1-minute recordings from dawn (06:00–08:00) for each of the three sites at three time periods: before Hurricane Maria (August 30–September 15 excluding September 6–September 7 due to the passage of Hurricane Irma), soon after the storm (September 25–October 11), and 8–10 weeks after the storm (November 20–December 11). All surveys were conducted by a single observer (OAC) who is proficient in acoustic bird identification and an expert in Puerto Rican avifuana. OAC listened to the recordings and counted the number of calls and the number of songs produced per species as in an avian point count (Brinley Buckley et al., 2018). We did not correct for potential double counting in these tallies because oftentimes the individual producer was unclear and because we reasoned that a greater abundance of songs and calls would still be a valid index of the avian community diversity. We then used R and "rmcorr" (Bakdash & Marusich, 2017) to conduct a repeated measures correlation analysis on the relationship between the dawn saturation index and 1) the total number of songs and calls and 2) the species richness of vocalizing species, including site as a random effect. We validated model assumptions by performing a Shapiro-Wilk test to check for normality of residuals and a Levene's test to check for homogeneity of variance. We also confirmed that relationships between the dependent and independent variables were linear and parallel across conditions. This analysis revealed a significant correlation between the dawn saturation index and the total number of songs and calls per recording ($r = 0.48$, $p = 0.001$) and the species richness of calling species ($r = 0.31$, $p = 0.040$), indicating that soundscape saturation was an adequate index of bird species diversity in this context. We present additional results on changes in species-specific and community-wide acoustic activity following Maria in S3.2.

1.12.3.3.2 Fish

We detected sounds produced by fish by performing spectral cross-correlation, which measures the pixel-by-pixel similarity between the spectrogram of a template call and windowed selections of a spectrogram of a recording (Hafner & Katz, 2017). We reviewed approximately 20 randomly-

selected recordings from each site and selected fish pulses with high signal-to-noise ratios, different fundamental frequencies, and diverse call structures in order to best account for the variety of fish calls present in these recordings. This process produced 24 representative call templates. Within the R programming environment, we used the R package "monitoR" to perform the spectral cross-correlation (Hafner & Katz, 2017). We removed all correlation peaks below a cutoff threshold of 0.5. Since we utilized 24 call templates, multiple templates could detect the same fish call, leading to an inflation of fish pulse counts. To address this potential inflation of counts, we divided each recording into 120 0.5-second windows and counted as detections the 0.5-second windows that contained a fish pulses present. We assessed the false positive rate of this call detection method by evaluating the presence / absence of fish sounds in 150 randomly selected 0.5-second clips with detections present (50 clips for each site). BG aurally and visually reviewed clips in Izotope Rx (*iZotope RX 4 Advanced*, 2014). We added one second before and after each file in order to make the sounds more discernable, but a clip was only considered "positive" if a biological sound was present during the middle 0.5-second portion. We assessed the false negative rate by this same method on clips with no detections present. This detector had a true positive rate of 86% (near-shore: 90%, mid-reef: 84%, shelf-edge: 84%), and a false negative rate of 76% (near-shore: 64%, mid-reef: 72%, shelf-edge: 92%), which was in part due to the prevalence of fish pulses with varying signal-to-noise ratios in these recordings.

1.12.4 **Statistical analysis:**

We applied statistical tests to determine 1) which sound types were significantly impacted by the storm and the magnitude of these impacts, 2) whether the marine and terrestrial acoustic communities were impacted by the storms, the magnitude of these impacts, and how these impacts differed across sites, and 3) the recovery rates of sound types that were significantly impacted.

We first defined pre-storm and post-storm periods of 15 or 20 days depending on data availability. This period length was chosen in order to include inherent short-term variation due to diel and lunar periods and minor weather events, while minimizing seasonal variation or long-term trends that could potentially confound the measurement of hurricane impacts. In the marine environment, the pre-storm period spanned from August 17–September 5 (20 days) and the post-storm period spanned from October 7–October 26 (20 days). In the terrestrial environment, the pre-storm period

spanned from August 22–September 5 (15 days) and the post-storm period spanned from September 26–October10 (15 days). We assumed that sound production patterns across these time periods were relatively consistent, and that acoustic differences between periods were due to the storm. We elaborate on and provide justification for these assumptions in the Discussion.

1.12.4.1 Impact assessment–sound type level

We performed linear mixed effects analyses in R using lme4 (Bates, Maechler & Bolker, 2012) to determine if Hurricane Maria significantly impacted the daily acoustic activity of each sound type. In these models, "period" (pre-storm or post-storm) was considered as a fixed effect and site was considered as a random effect. For marine sound types, since sound production in shrimp and fish can vary in accordance with the lunar phase, we also included daily lunar luminosity as a fixed effect. For all sound types, we validated model assumptions using methods described in Section 2.3.3.2. To satisfy these assumptions, we performed a log_{10} transform on LFI_{SPL} to meet the normality assumption. We also rank transformed $MFI_{SPL,}$ LFF_{SPL}, and HFF_{SPL} because they failed to meet the normality assumption. Therefore, it was not possible to obtain model coefficients for these three sound types. We obtained p values by performing ANOVAs that compared the models to null models that lacked period as a fixed effect. We considered the period coefficient as indicative of the impact magnitude (lack of resistance) and direction.

1.12.4.2 Impact assessment–community level

To visualize community level impacts, we plotted marine and terrestrial acoustic communities in ordination space. For each system, we conducted a principal coordinates analysis (PCoA) based on the Bray-Curtis distance matrix of daily sound type values using the *vegan* package in R (Oksanen et al., 2017). Prior to the ordination, to standardize the magnitudes of the different acoustic metrics, we rescaled values for each sound type between 0 and 1. Since LFI_{SPL} and MFI_{SPL} were highly correlated *(r = 0.86)*, we summed them prior to community analyses ($LMFI_{SPL}$). We measured two dimensions of community-level impacts. We assessed the magnitude of community alteration by calculating the distance between pre- and post-storm site centroids. To measure the relative influences of period and site on the PCoA values, we conducted an analysis of variance using distance matrices with the "adonis" function in *vegan*. To obtain another index of soundscape disturbance, we assessed changes in average daily soundscape variability by calculating the

dispersion of points around their respective site-period centroid. To determine whether there were significant changes in variability, we conducted pairwise comparisons of pre- and post-storm dispersions for each site using the "permutest" function in *vegan*.

1.12.4.3 Recovery response quantification

We also sought to estimate the response trajectories of impacted sound types, so we employed a logistic curve that has been broadly applied for modeling population growth (Lambert, Jennings, Kaiser, Davies, & Hiddink, 2014; Pitcher, Poiner, Hill, & Burridge, 2000):

$$Z(t) = \frac{Z_o Z_K}{Z_o + (Z_K - Z_o) \exp(-rt)} \quad (1)$$

where $Z(t)$ is the estimated value for the acoustic index Z (i.e., LFI$_{SPL}$, MFI$_{SPL}$, or BV) at a date t, Z_o is the initial value of Z at the initial date t_o declared as $t = 0$, Z_K is the equilibrium Z targeted as the converging value as time variable t approaches infinity, and r is the recovery per day. Only the coastal terrestrial site had sufficient data for this temporal analysis, as the marine sites had temporal gaps following the storm and the midland and upland units did not record from mid-October to early-November. Furthermore, at the coastal site, the HFI did not decline after the storm, and so there was no scope for assessing the recovery of this sound type.

To minimize the effect of seasonal soundscape changes, we restricted our analysis from an initial date (t_o) to December 31, 2017. The three sound types we evaluated (BV, LFI, and MFI) had lagged declines in the days following Maria, and so we defined t_o for each sound type as the date with the minimum value during the post-storm period (October 9 for LFI, October 1 for MFI, and October 2 for BV). For the LFI, we observed a strong lunar cycle of approximately 8 dB. To better measure impacts caused by the hurricane, we removed this lunar component by decomposing the time series using the *decompose* function in the "stats" R package. Prior to decomposition, we linearly interpolated missing values using the *na.interpolation* function in "stats", but these interpolated values were removed prior to calculating the logistic growth function. We considered recovery as when the sound type reached pre-storm levels (Z_K), which we defined as the median of pre-storm values. The recovery growth rate *(r)* was found through Matlab's *nlinfit* function, which aims to minimize the sum of the square of the residuals for the fitted equation (Eq. (1)) over

a defined time period (t_o – December 31, 2017). Required recovery time to reach quasi-equilibrium status (t^*, [days]) was calculated through the analytical expression inversely derived from Eq. (1) as:

$$t^* = \frac{1}{r} \ln\left(\frac{\alpha(Z_K - Z_o)}{(1 - \alpha)Z_o}\right) \quad (2)$$

where α is the threshold ratio for determining the quasi-equilibrium status. α values theoretically range from 0 to 1, and we employed $\alpha = 0.9$ for t^* estimation.

1.13   Results

1.13.1 Impact assessment—sound type level

All four of the terrestrial sound type occurrences declined significantly following Maria (Figure 16b). BV declined from 53% to 22% (Chi Sq. = 104.63, $p < 0.001$). The LFI$_{SPL}$ declined from 63.2 dB to 57.4 dB, which represents almost a halving of sound pressure levels (Chi Sq. = 42.88, $p < 0.001$). The MFI$_{SPL}$ declined significantly ($p < 0.001$) from 58.2 to 53.0. The HFI$_{SPL}$ declined 1.9 dB, from 82.9 dB to 81.0 dB (Chi Sq. = 6.80, $p = 0.009$), though this difference was driven primarily by the decrease at the lowland site (Figure 17b).

In the marine environment, sound types exhibited mixed responses to Hurricane Maria (Figure 16a). The SS$_{SPL}$ exhibited a small but significant increase of 0.5 dB (Chi Sq. = 32.53. $p < 0.001$) that was driven by the two more inland sites, near-shore and mid-reef, where SS$_{SPL}$ increased 1.1 dB and 0.8 dB, respectively. This increase at the two inland sites was sizeable with respect to the SS$_{SPL}$ range from March 2017–January 2018, which was approximately 3 dB (including the increase after Hurricane Maria). Though a relatively small increase, it was statistically significant in part due to the negligible within-group variation for the pre- and post-storm periods. The LFF$_{SPL}$ significantly increased (Chi Sq. = 4.28 , $p = 0.039$), mainly because of its appearance at the shelf-edge following Hurricane Maria. FP decreased by 8.86 detections per minute (Chi Sq. = 21.36, $p < 0.001$). There was no statistical difference in LFF$_{SPL}$, though there was a 3.4 dB increase at the near-shore site, minimal change at the mid-reef site, and a 4.8 dB decrease at the shelf-edge site (Chi Sq. = 0.39, $p = 0.531$; Figure 17a).
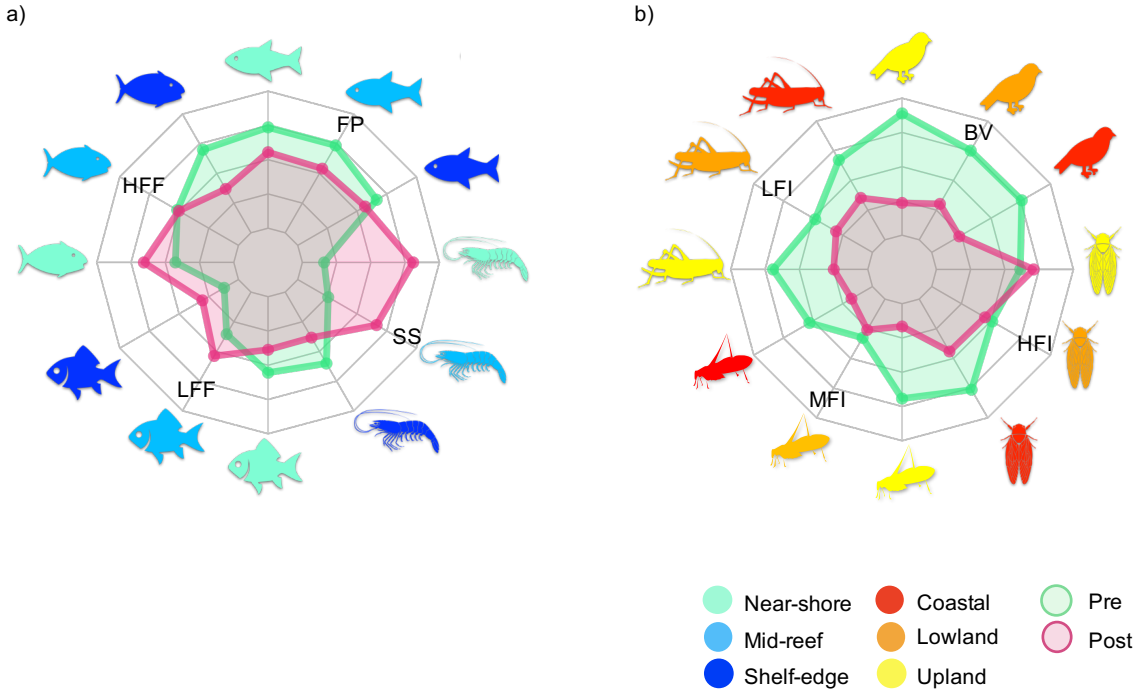
Figure 15: Short term (15 – 20-day) soundscape change in a) the three coral reef sites in La Parguera and b) the three dry forest sites of Guanica. The values in this radar diagram represent the pre- and post-storm means for each sound type. Prior to calculating these means, sound type values at each site were scaled between 0 and 1. In a) SS = snapping shrimp; LFF = low-frequency fish chorus; HFF = high-frequency fish chorus; FP = fish pulses. In b) LMFI = low- and medium-frequency insect choruses; HFI = high-frequency insect chorus; BV = bird vocalizations.
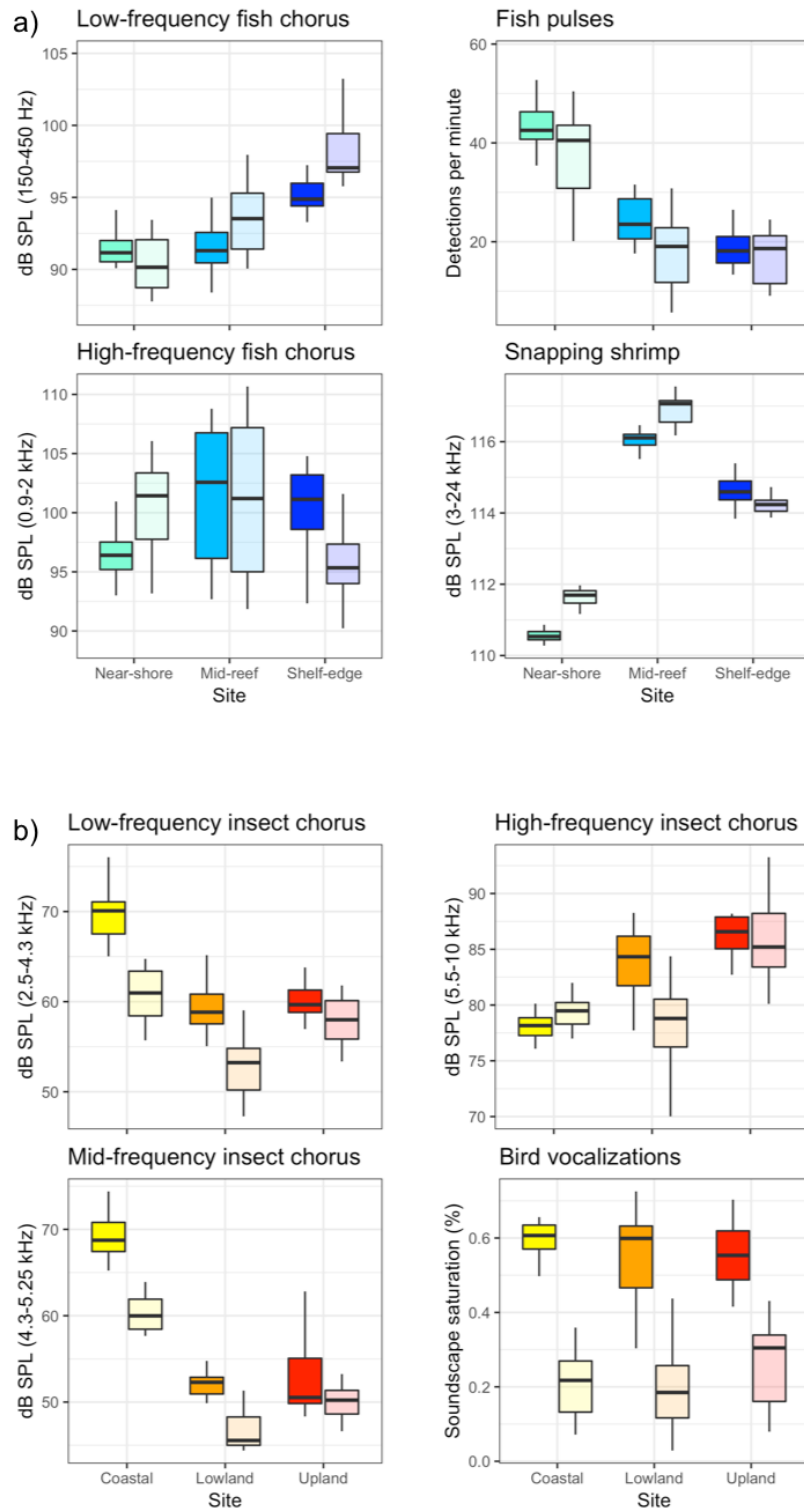
Figure 16: Boxplots of sound types before (opaque boxes) and after (translucent boxes) Hurricane Maria at the coral reef and dry forest sites. The middle band of each box represents the median value. The upper and lower hinges represent the upper and lower quartiles, respectively. The upper and lower whiskers extend to the largest and smallest values no further than 1.5 times the inter-quartile range.

1.13.2 Impact assessment—Community Level

The PCoA plots illustrate divergent community responses in the dry forest and coral reef ecosystems (Figure 18). In the dry forest, the effect of the storm appears to dwarf site-specific differences (period: $R^2 = 0.33$, $p = 0.001$; site: $R^2 = 0.26$, $p = 0.001$), while the reverse appears true for the marine realm (period: $R^2 = 0.03$, $p = 0.001$; site $= R^2 = 0.65$, $p = .001$). In the dry forest PCoA plot, the six site-period clusters divided into pre- and post-storm regions, with pre-storm points appearing toward the upper-left quadrant of the plot (towards the BV eigenvector) and post-storm points appearing toward the right side of the plot (away from sound type eigenvectors). While the upland and lowland sites were similar to each other prior to the storm, they became distinct after the storm; coastal site points were tightly clustered in pre- and post-storm periods, but in the post-storm period, they experienced newfound overlap with the lowland site polygon. In the coral reef PCoA plot, points were first clustered by site, with the near-shore site clusters located on the right side of the plot towards the FP eigenvector, the mid-reef clusters located towards the bottom-left of the plot near the SS and HFF eigenvectors, and the shelf-edge clusters located toward the upper left of the plot near the LFF eigenvector. There also appeared to be a secondary clustering effect of the storm, evidenced by the separation between pre/post points within the three larger site clusters.
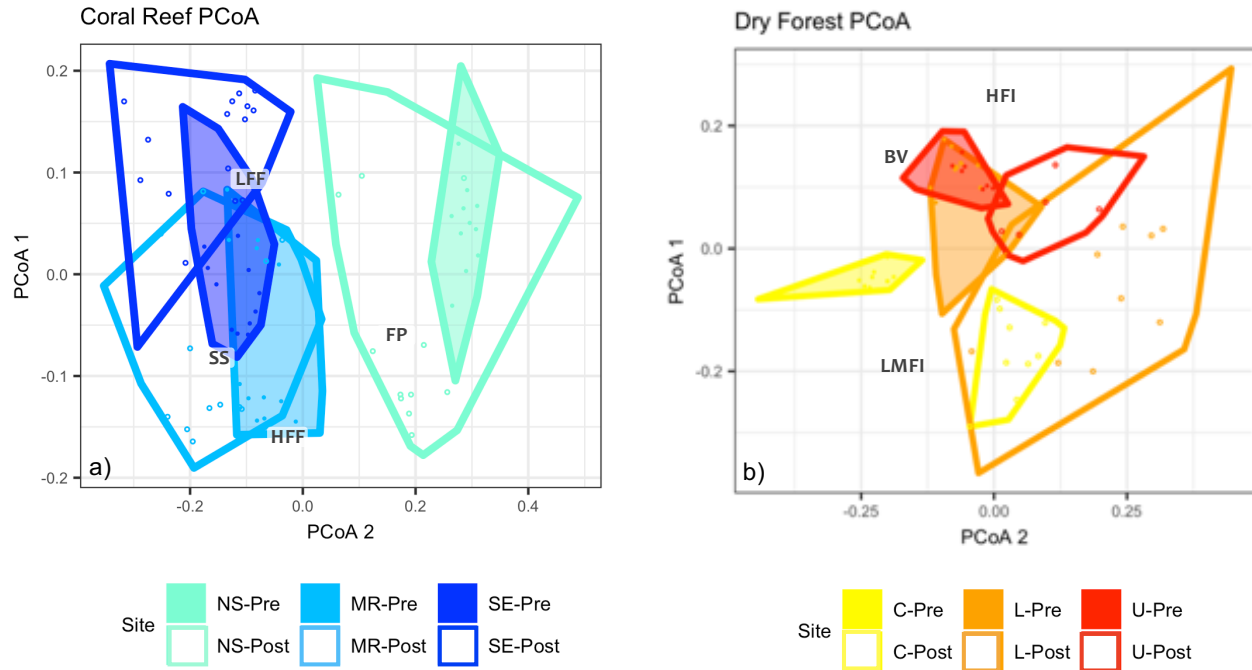
Figure 17: Principle coordinates analysis plots illustrating the acoustic communities in the a) coral reef and b) dry forest sites. Pre-storm days are filled circles and post-storm days are empty circles. Pre-storm clusters are shaded polygons and post-storm clusters are outlined polygons. In (a), NS = Near-shore, MR = Mid-reef, and SE = Shelf-edge. In (b) U = Upland; L = Lowland; C = Coastal. Sound type text labels are located at the termini of their respective eigenvectors. In (a) SS = snapping shrimp; LFF = low-frequency fish chorus; HFF = high-frequency fish chorus; FP = fish pulses. In (b) LMFI = low- and mid-frequency insect choruses; HFI = high-frequency insect chorus; BV = bird vocalizations.

In both terrestrial and marine systems, the distance between pre- and post-storm site centroids in the PCoA plot was generally higher at sites closer to the coastline. In the terrestrial environment, the largest difference was coastal (Bray-Curtis distance = 0.33), followed by lowland (0.32), and then by upland (0.22). In the marine environment, the largest difference was near-shore (0.20), followed by shelf-edge (0.16), followed by mid-reef (0.12).

Soundscape variability increased at all sites following the storms. In the terrestrial environment, mean soundscape variability increased 119% (0.07 to 0.16 increase in spatial median distance to centroid). In the marine environment, mean soundscape variability increased 36% (0.10 to 0.13). Unlike impact magnitude, changes in variability did not always increase with proximity to the coast. In the terrestrial environment, the lowland habitat exhibited the greatest change in variability ($\Delta 0.16$ in spatial median distance to centroid; 168% increase; $p < 0.001$), followed by the coastal ($\Delta 0.06$; 110% increase; $p < 0.001$) and upland sites ($\Delta 0.05$; 67% increase; $p < 0.001$). In the marine

environment, the near-shore site had the greatest change in variability (Δ0.06; 72.9% increase; p = 0.004). Both the mid-reef (Δ0.02; 19.9% increase; p = 0.027) and shelf-edge (Δ0.03; 19.6% increase; p = 0.260) increased moderately, though the change in the shelf-edge was not significant.

1.13.3 Recovery responses assessment

The bird community, as measured by BV, reached pre-storm levels (Z_K = 0.61) after approximately 67 days. The LFI (with the lunar component removed) reached pre-storm levels (Z_K = 69.6) after 34 days. The MFI reached pre-storm levels (Z_K = 68.7) after 56 days (Figure 19). In the discussion, we discuss how lunar and seasonal soundscape changes impact the estimation of recovery trajectories.
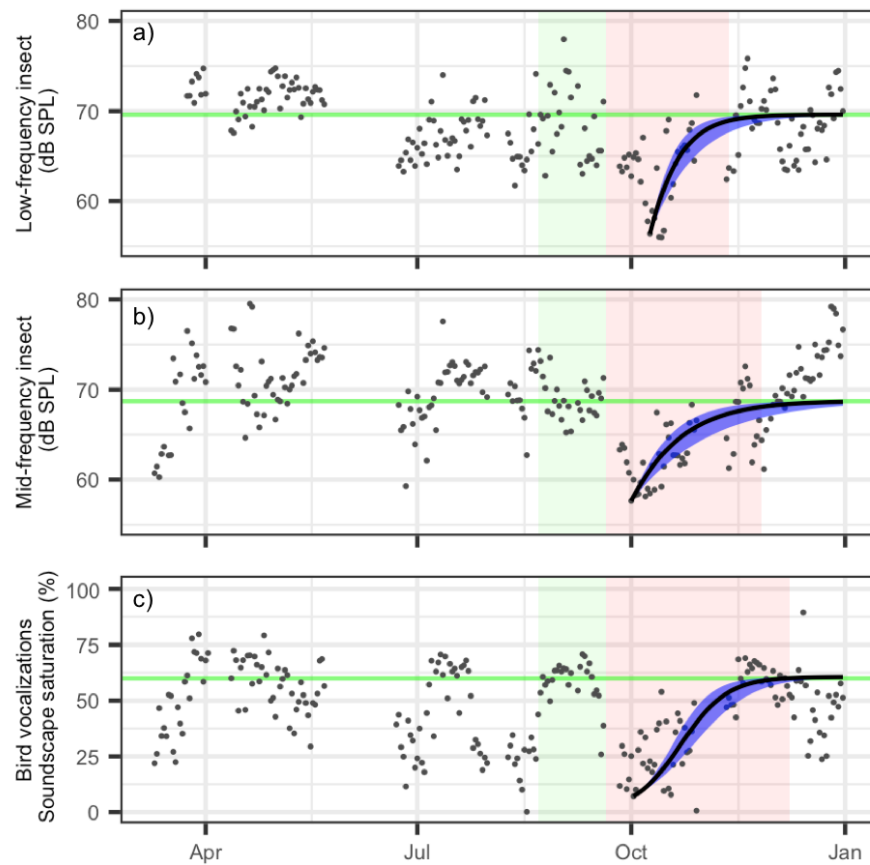
Figure 18: Recovery dynamics of the a) mid-frequency insect chorus, and b) bird vocalizations at the coastal dry forest site from March 2017 to April 2018. Gray circles represent daily index values. The green horizontal line indicates the equilibrium threshold. The black line represents the logistic curve. The blue shading estimate the upper and lower values of the growth rate estimated with 95% confidence level. The green shaded area encompasses the 'pre' period. The red shaded area represents the period after Maria and until the system "recovered".

1.14   Discussion

Our study provides evidence that soundscapes can measure three dimensions of ecological resilience: impact magnitude (resistance), functional response diversity (recovery), and the heterogeneity of disturbance impacts. We hypothesized that the activity of all sound types would decline following Hurricane Maria due to a combination of direct mortality from the storm and altered behavior and post-storm movement that resulted in less calling activity. Our findings did not entirely support this hypothesis. In the terrestrial sites, we observed significant declines in the four sound types and in eight of the twelve sound type/site pairs. Contrastingly, in the marine realm, only FP significantly declined following the storms, and two sound types, LFF and SS, significantly increased. We also predicted that the magnitude of soundscape alteration would correlate with the degree of environmental alteration, which was greater in the terrestrial system compared with the nearby marine environment. This prediction was validated, at least with respect to short-term impacts (< 2 months), for individual sound types and also acoustic communities. Distances between pre/post cluster centroids were 45% greater in the dry forest than in the coral reef. Below we explain the implications of our results on understanding the effects of Hurricane Maria on species, habitats, and ecosystems in more detail. Moreover, we provide some insight on the future use of soundscape research approaches to evaluate ecological resilience and also present some caveats about our study.

1.14.1 Effect of habitat

Our study demonstrates that habitat type can mediate species disturbance responses. Apart from the BV, where declines were relatively consistent across sites, the direction and/or magnitude of sound type alteration appeared to be influenced by habitat type, especially for the three insect choruses, LFF, and SS. For example, the LFI chorus exhibited steeper declines at the coastal (9.6 dB) and upland sites (6.4 dB; the two sites with greater vegetation density) than the lowland scrub site (3.1 dB). These two vegetation-dense sites likely had more diverse insect communities prior to the storm, and also suffered greater defoliation and downed trees that could have damaged insect habitats and resulted in insect mortality. In the marine realm, the LFF chorus appeared around Hurricane Maria and after Hurricane Irma. Apart from these times, it was only observed on one occasion in mid-November out of the whole study period. The emergence of this chorus around the storms could be due to the movement of mobile marine species that relocate during disturbance

events (Bongaerts, Ridgway, Sampayo, & Hoegh-Guldberg, 2010). That this chorus was at the shelf-edge location could offer anecdotal support of the deep reef refugia hypothesis (Bongaerts et al., 2010), which states that deeper-water reefs may be less susceptible to local and global disturbances than shallow-water reefs, and therefore can offer potential refuges for coral and fish species. While support for this theory is mixed and dependent on system, disturbance type, and species (Bongaerts & Smith, 2019), we did observe that in these reefs, the shelf-edge was the most stable site with respect to pre/post soundscape alterations. This pattern has been observed previously for fish species after Hurricane Allen in Jamaica (Kaufman, 1983). In both the marine and terrestrial systems, the magnitude of soundscape alteration generally increased toward the coast, likely reflecting more extreme effects of the hurricane closer to the coast. Wave impacts can be expected to be greater in shallow water, and coastal vegetation is highly exposed to untempered ocean winds.

1.14.2 **Effect of species**

Resistance levels and response trajectories were also sound type dependent, likely reflecting underlying taxonomic differences. For example, the HFI chorus exhibited minimal change at two of the three terrestrial sites, indicating high resistance from species that produced sound within this frequency band, which included members of Tettigoniidae (7.4 – 8.2 kHz), Gryllidae (5.5 – 6.0 kHz; 6.8 – 7.4 kHz) and Hemiptera cicadomorpha (6.0 – 6.6 kHz). In contrast, the insect choruses choruses and bird vocalizations experienced similar, sizeable alterations across sites (50-60% decline), but also all showed signs of recovery in the weeks following the storm. The insect choruses reached pre-storm levels prior to the bird vocalizations. One hypothesis for this difference is that taxonomic groups that are less mobile (e.g., arthropods) would need to adapt traits that enhance their short-term resistance to perturbations, while mobile species (e.g., birds) could adapt traits that exploit their dispersal abilities. For example, hurricane-induced natural selection resulted in changes to morphological traits that enhanced clinging capacity in a small-bodied lizard, *Anolis scriptus,* following Hurricanes Irma and Maria in the Turks and Caicos (Donihue et al., 2018). Conversely, it has recently been shown that some bird species like the golden-winged warbler (*Vermivora chrysoptera*) can detect large storm events several days before their arrival in order to pre-emptively avoid them (Streby et al., 2015). Here, we did observe a decrease in BV in the two

days before Maria struck. From Sept 8–17, BV ranged from 64–73%. It decreased to 26% on Sept. 18 and 39% on Sept. 19.

Our results are consistent with previous studies that investigated hurricane responses across the following taxonomic groups.

Fishes: The response of fishes to hurricanes is dependent on storm magnitude, habitat type, and species. Changes can include decreased species richness, decreased abundance, shift in community composition, and altered behavior. These short-term impacts can persist for several weeks (Paperno et al., 2006) or longer than one year (Kaufman, 1983). For fish that produce sound, their acoustic activity can provide an index of their resilience to hurricanes. Two recent studies, one that recorded sand seatrout (*Cynoscion arenarius)* around Hurricane Charley off the coast of Florida and one that recorded Spotted Seatrout *(Cynoscion nebulosus)* in Aransas Bay in Texas, have shown that fish continued chorusing directly after the passage of Category 4 hurricanes. While data were unavailable after Hurricane Maria, in the 3–4 days after Hurricane Irma, the high-frequency fish chorus reached its highest measured levels. Another interesting pattern is the appearance of one chorus type at the shelf-edge site in the days surrounding Hurricanes Irma and Maria, potentially from fish movement from more coastal reef habitats into the refuges of deeper water. While the number of detected fish calls did decline slightly after the storm, this could have resulted in elevated background noise levels during several days following the storm event and not a reduction in fish calling activity.

Shrimp: There was a small but significant increase in the high-frequency band dominated by shrimp snaps due to elevated levels over the five weeks that followed Hurricane Maria at the two near shore sites. This pattern did not correspond with changes in water temperature during this time period, and so explanations for this change likely stem from biological or environmental factors. Shrimp could have potentially become more active if prey was more available after the storm damaged their habitats or if altered seawater conditions caused them to increase. Their snapping rates. Alternatively, this slight increase could result from increased wave action following the storm, which would have elevated high frequency sound levels.

Insects: The low-, mid-, and high-frequency insect choruses declined for at least several weeks following Hurricane Maria at some or all of the sites. These impact and response dynamics likely reflect taxa- and guild-level traits that mediate hurricane responses (Schowalter, Willig, & Presley, 2017). Hurricanes trigger a rapid restructuring of resources (i.e., foliage to litter) that can benefit detrivores and negatively impact arboreal herbivores.

Birds: Bird vocalizations, measured by dawn chorus saturation, declined 59% in the weeks following Hurricane Maria. This reduced saturation likely reflects a combination of dispersal from the coast and mortality following the storm due to a lack of resources. Frugivore and nectivorous birds declined by 30–70% in the months after hurricanes in Mexico, St. John, and Puerto Rico, while insectivore and omnivorous birds lacked similar guild-wide patterns (Askins & Ewert, 1991; Lynch, 1991; Waide, 1991a, 1991b), suggesting that the effects of hurricanes could be mediated by resource availability and dispersal from affected sites instead of direct mortality (Waide et al. 1991b). Hurricanes remove flowers, fruits, and seeds, so the greatest stress could come after the storm when resources are scarce. Supporting this hypothesis, the bird with the greatest number of sounds detected at our sites, the bananaquit *Coereba flaveola* (n=235), is a nectivorous bird. It was likely greatly impacted by the defoliation caused by the storm and likely contributed to the desaturation trend apparent in the dawn soundscapes. The Puerto Rican tanager *Nesospingus speculiferus* (n=203), the bird with the second-highest number of detections, is an omnivore that feeds mainly on invertebrates (Pérez-Rivera 1997), yet understory fruit gleaning accounted for 63% in its foraging behavior at a study site in Rio Chiquito, Luquillo Experimental Forest in Puerto Rico (Cruz 1987), and so it could have also declined after the storm. Of the eight species with more than ten detections, seven of these species fed at least partially on fruits and nectar. Therefore, it would be reasonable to expect these species to be affected by the storm (Waide et al. 1991b). An alternative explanation for sparser dawn choruses could be behavioral changes, rather than changes in abundance. For example, birds' nests and territories may have been destroyed by the storm in which case there would be no point in defending them with vocal territorial displays. This hypothesis could explain a shift from mostly songs to mostly calls in our annotated dataset.

1.14.3 **Effect of ecosystem**

Dry forest sites were more impacted than the coral reef sites. While we observed sizeable short-term effects on the dry forest animal community, several studies have recently demonstrated the remarkable resiliency of dry forest systems to disturbance, including the intensifying hurricane regimes that are plausible toward the end of the 21st century (Álvarez-Yépiz, Martínez-Yrízar, & Fredericksen, 2018; Bhaskar et al., 2018; Holm, Van Bloem, Larocque, & Shugart, 2017; Imbert & Portecop, 2008). However, these studies have mainly focused on the resilience of vegetation and soil, not the animal communities. Given the important functional roles of animals with maintaining ecosystem structure and function (e.g., seed dispersal and herbivory) assessing the resiliency of animals to changing disturbance regimes is a necessary aspect of predicting overall ecosystem resiliency. Similar to dry forests, Caribbean coral reefs can be highly resilient to hurricanes, though large storm events can cause major damage to coral reefs (NOAA, 2018b). However, it remains unclear whether or not hurricanes exacerbate coral reef degradation in combination with other threats. A recent study found that while hurricanes caused short-term damage in some Atlantic reefs, these effects did not exacerbate longer-term trends in coral reef condition, suggesting that hurricanes are not a multiplicative stressor (Mumby, Hastings, & Edwards, 2007). This coral resilience could be in part because fish and invertebrates are resilient to hurricane impacts, and can maintain critical reef-sustaining functions after these events to facilitate reef recovery. The relatively little change in the marine soundscapes at these sites indicates such resiliency.

1.14.4 **Study limitations**

The first main challenge of our study was separating hurricane-related soundscape impacts from seasonal dynamics that could have also contributed to soundscape changes. In the dry forest habitat there were long-term phenological patterns including increased dry season (December-March) activity for some insect sound types. In the coral reefs, there were both annual and lunar cycles. Fish chorusing activity and snapping shrimp sound levels generally increased during the summer months, a pattern which is consistent with other studies (Staaterman et al., 2014). The high-frequency chorus also peaked around new moons and bottomed out around full moons. Despite these annual and lunar cycles, the soundscape changes following Hurricane Maria appeared highly distinct from these patterns. Post-storm changes were relatively sudden decreases followed by a

return toward its prior state over a time period that did not correspond with trends in seasonal variation. In the terrestrial realm, evaluating short-term recovery was complicated by the prevalence of lunar and seasonal soundscape changes, particularly for the low-frequency insect chorus. For this reason, going forward, reference data spanning previous years would enable the direct comparison of post-disturbance soundscapes with baseline conditions and facilitate the detangling of disturbance-related impacts from monthly or annual cycles. Such comparisons should become more achievable as passive acoustic monitoring becomes incorporated into environmental monitoring platforms, open-access soundscape databases proliferate, and acoustic phenologies for different habitat types are described in the scientific literature. Increased knowledge of the acoustic composition and dynamics of different ecosystems will enable researchers to understand inherent sources of soundscape variability in order to better measure presence and magnitude of stressors.

The second challenge involved data lapses at key time periods, including directly after Hurricane Maria at the three marine sites. These holes in the acoustic record prevented anecdotal descriptions of community responses immediately after Maria, and also reduced our ability to build recovery models for most of the sites. Despite this challenge, we were able to evaluate the short-term impacts (15–20 days) and responses (4 months) that enabled us to measure resilience to the hurricane.

The third challenge can also be conceived of as an opportunity. Some of the broad sound types measured in this study could be split into more distinct sound types that each likely represent different soniferous species, each with their own recovery dynamics and ecological significance. Most soundscape studies still employ broad measurement types like band-level measurements or acoustic indices (Sugai et al. 2019). These methods are relatively easy to employ and suitable for characterizing large community shifts, but they are likely only accessing a fraction of the informational content encoded in soundscape recordings. Developing automated sound-type based analyses will propel this field towards a better understanding of ecosystem dynamics and disturbance response (Lin, Fang, & Tsao, 2017). As more sound types are ascribed to taxa, particularly in the marine realm, we can compliment existing knowledge of functional roles and community structure with information on species-level contributions to soundscape dynamics.

Regarding soundscape metrics, one contribution of this study is the suggestion that increased soundscape variability may be an indicator of a disturbed landscape. Thus far, soundscape studies have mainly focused on measuring complexity or amplitude within a single recording, and from these values comparing sites or temporal periods (but see Francomano et al. *in press*). Changes in the variability of soundscape components across different temporal scales appears to be a meaningful indication of disturbance level. Direct comparison of soundscape variability with measures of physical habitat alteration would help corroborate this point. Of course, some systems are inherently more variable than others. The coral reef sites contained sound types that were influenced by the lunar phase and therefore these soundscapes contain more short-term (day-to-day) variability than the dry forest soundscapes, where soundscape patterns mainly were driven by daily and annual phenologies. That said, time-series modeling can account for temporal patterns and separate natural sources of variation from ones that signify disturbance and potentially anticipate regime shifts.

1.14.5 Conclusions

In conclusion, this study illustrates the ways in which Hurricane Maria impacted dry forest animal communities and to a lesser extent those of nearby coral reefs. Furthermore, it serves as a proof of the concept that soundscape recording and analysis can measure different aspects of ecological disturbance and resilience. In this time of rapid environmental change, soundscapes can signal the ways in which altered disturbance regimes are transforming ecosystems.

Supporting information for:

Terrestrial and marine animal communities exhibited differential responses to Hurricane Maria in SW Puerto Rico: Quantifying Ecosystem Resilience Through Sound

Additional supporting information external to this document including example sound files can be found on Github (https://github.rcac.purdue.edu/PijanowskiGroup/Gottesman_et_al_2019)

S3.1 Bird vocalization index

For each audio file, we calculated its spectrogram using a STFT with a Hann window, a window length of 1024 samples, and 0% overlap, which produced 512 bins spanning 1–24,000 Hz. Prior to calculating the bird vocalization index (BV), we denoised the spectrogram to remove background noise and near-continuous sounds produced by insects and wave action. To do so, we calculated the background noise present in each of the 512 frequency bins by creating a 100-bin histogram of the amplitude values for each frequency bin, smoothing the histogram with a 5-point moving average, and then selecting the amplitude bin one under the modal value. Background noise was then subtracted from each frequency bin to obtain the denoised spectrogram. Denoised spectrograms were then cropped between 1–10 kHz, the frequency region containing most avian vocalizations. Spectrograms were then converted into binary matrices, whereby values that were above a threshold value were made equal to 1, and values below this threshold were made equal to 0. The binary matrix was summed and divided by the total number of cells to produce a saturation percentage between 0 and 1. We tested different thresholds from 2–4 dB in increments of 0.1 dB and selected the threshold that that yielded a normal distribution of values while retaining a large saturation range across values (0.0–70.8), which was 2.9 dB. We then took the average of the four dawn saturation values calculated on the four dawn recordings to obtain the daily BV index.

BV significantly correlated with the two biodiversity metrics calculated on the annotated avian dataset. BV was weakly correlated with species richness of calling species ($r = 0.31$, $p = 0.040$) and more strongly correlated with the total number of songs and calls ($r = 0.48$, $p = 0.001$). The manual analysis also revealed differences in the bird community before and after the storm. There

were 22.9 ± 4.5 (mean ± SE) songs and calls detected in the Pre-storm (August 30–September 15) recordings, and 12.3 ± 5.0 and 14.3 ± 4.5 detections in the Post-storm I (September 25–October 11) and Post-storm II (November 20–December 11) phases, respectively. The coastal area had the most songs and calls per file detected (23.5 ± 4.8), followed by lowland (20.6 ± 5.6), and upland (5.4 ± 1.8). Following Maria, the upland site declined 86% in songs and calls, the lowland site declined 85%, and the coastal site increased 37%. However, this increase at the coastal site was driven by an increase in calls, as there was a 56% decrease in songs there. The species most impacted was *Coereba flaveola*, which was detected in 80% of recordings prior to the storm and 40% of recordings post storm. *Elaenia martinica* was detected in 47% recordings pre-storm and 13% in Post-storm I, and 13% in Post-storm II. As for species richness, 13 species were detected in the Pre-storm, 10 in Post-storm I, and 12 in Post-storm II. *Zenaida aurita* and *Setophaga americana* were only detected prior to the storms. *Tyrannus dominicensis*, *Tiaris bicolor*, *Spindalis portoricensis*, and *Euphonia musica* were only detected after the storms.

CHAPTER 4: **SOUNDSCAPES INDICATE KELP FOREST CONDITION**

Ben Gottesman (Corresponding Author), Joshua Sprague, David Kushner, Kristen Bellisario, David Savage, Megan McKenna, Dave Conlin, Mary Jo Barkaszi, Michele Halvorsen, Eva DiDonato, Bryan Pijanowski. *In prep.*

1.15   Introduction

Human activities are causing large, abrupt, and enduring changes in the structure and function of ecosystems, also known as regime shifts (Scheffer & Carpenter, 2003). Generally, habitats that have undergone regime shifts support less biodiversity and produce fewer ecosystem services (Folke et al., 2004). While the ecological theory of regimes shifts is becoming more refined, ways to empirically measure regime shifts remain elusive (Quinlan, Berbés-Blázquez, Haider, & Peterson, 2016). To do so in a real-world context, it is necessary not only to identify meaningful variables to measure, but also develop a measurement system that can obtain this information at appropriate spatial and temporal scales at low cost. Developing and implementing such methods to measure ecosystem condition would improve the management and conservation of systems on the brink, especially if they also provide insights into regime shift drivers (Anderson, 2018; Carpenter et al., 2011).

Soundscapes (in sensu Pijanowski, 2011a; Pijanowski et al., 2011b) are emerging as a potential stream of information from which we can measure habitat condition and potentially regime shifts (Rossi et al., 2017). Soundscape ecology originated in the terrestrial realm (Pijanowski et al. 2011b), but holds particular promise for surveying freshwater (Gottesman et al., 2018) and marine ecosystems (Miksis-Olds et al., 2018), which can be impractical to access regularly. While most marine monitoring programs perform biodiversity surveys once or twice per year, passive acoustic recorders can collect soundscape data continuously for months or years (Staaterman et al., 2014). This fine-scale temporal resolution improves the assessment of rare and cryptic species (Staaterman et al., 2017; Wade et al., 2006), understanding temporal dynamics (McWilliam, McCauley, Erbe, & Parsons, 2018), and evaluation of disturbance impacts (Biggs, Lowerre-Barbieri, & Erisman, 2018; Locascio & Mann, 2005). For example, some early warning signals of

regime shifts, such as rising variance or slowing rate of recovery after a disturbance, are detectable with the high temporal resolution provided by long-term soundscape recordings (Carpenter et al., 2011).

In this study, we tested whether soundscape recording and analysis could indicate the condition of kelp forests off the coast of California, USA, in Channel Islands National Park. Kelp forests (Order: Laminariales) are structurally complex, highly productive, and biologically diverse ecosystems that form on rocky marine coastlines in temperate and sub-arctic regions (Steneck et al., 2002). Recent evidence suggests that the resilience of these forests is eroding due to a number of stressors, including overfishing, ocean warming, pollution, and disease (Krumhansl et al., 2016). As a result, kelp forests can undergo regime shifts into degraded, alternative states that support fewer fish and invertebrate species, sequester less carbon, and provide scant ecosystem services (Krumhansl et al., 2016; Miller et al., 2018). One main pathway toward regime shift in kelp forests is the removal of apex predators through overfishing and overharvesting. When keystone predators become scarce, populations of prey species, like sea urchins (Class: Echinoidea), increase rapidly. In a healthy kelp forest, sea urchins inhabit rocky crevices and feed on drift kelp that sloughed off plants. At higher urchin densities, drift kelp becomes scarcer, causing sea urchins to venture out of these cryptic refuges in search of food. Upon finding a kelp plant, sea urchins consume the holdfasts that tether the plant to the reef, causing the kelp to drift away (Kriegisch, Reeves, Flukes, Johnson, & Ling, 2019). At high densities, sea urchins can vanquish a kelp forest in several weeks, at which point the system shifts into an urchin-dominated barren from which it is difficult to recover.

1.15.1 Background

1.15.1.1 Soundscapes as indicators of biodiversity and ecosystem health

Several recent studies have demonstrated strong positive relationships between soundscapes and marine habitat condition (Bertucci, Parmentier, Lecellier, Hawkins, & Lecchini, 2016; Coquereau et al., 2017; Gordon et al., 2018), fish diversity (Harris et al., 2016), and fish abundance (Rowell et al., 2017). One emerging pattern is that the low and high portions of the soundscape contain information on different ecological dimensions. Fish generally vocalize in the low-frequency portion of the soundscape (<1000 Hz; Lindseth & Lobel, 2018; Staaterman et al., 2017). Acoustic

metrics calculated on the low-frequency portion have correlated with fish diversity and density in coral reefs in Panama (Kennedy et al., 2010), Hawaii (Freeman & Freeman, 2016; Kaplan et al. 2015), and French Polynesia (Bertucci et al., 2016), as well as rocky reefs in New Zealand (Harris et al., 2016) and France (Desiderà et al., 2019). Measurements of the high-frequency portion of the soundscape (>1000 Hz), in which many invertebrates produce sound (Bohnenstiehl et al., 2016), have correlated with invertebrate richness and abundance in maerl beds off the coast of France (Coquereau et al., 2017) and invertebrate density in Panama (Kennedy et al., 2010). Beyond indexing taxonomic diversity, low- and high-frequency portions of the soundscape can also indicate habitat condition, including coral cover (Bertucci et al., 2016; Freeman & Freeman, 2016; Kennedy et al., 2010), degradation level (Gordon et al., 2018; Lillis, Eggleston, & Bohnenstiehl, 2014; Rossi et al., 2017), and ecosystem functions (Elise et al., 2019). However, other studies that have employed similar measurements in similar ecosystems have found no such correlations between soundscapes and these dimensions of biodiversity and habitat condition. For example, Kaplan et al. (2015) found no significant difference in high-frequency sound levels between healthy and destroyed reefs in Hawaii, while Freeman & Freeman (2016) actually found a negative relationship between habitat condition and the intensity of high-freqeuncy sound levels. Anthropogenic noise can obfuscate these soundscape-ecological relationships by influencing soundscape metrics, especially in areas with high shipping traffic. Therefore, there are still sizeable knowledge gaps regarding 1) the relationships between soundscape and ecological variables, 2) the consistency of these relationships under different anthropogenic noise conditions, and 3) the mechanisms underlying these relationships.

1.15.1.2   Kelp forest health

Regional drivers rather than global forces dictate the direction and magnitude of recent changes in the condition of kelp forests (Krumhansl et al., 2016). Currently, local stressors including overfishing and overharvesting, nutrient pollution, and disease are the primary drivers of kelp forest regime shifts (Krumhansl et al., 2016). Effective habitat management at the local to regional level can improve the condition of vulnerable kelp forests. No-take marine reserves have increased the density, diversity, and size of targeted fauna (such as California spiny lobster, *Panulirus interruptus*, kelp bass, *Paralabrax clathratus*, and California sheephead, *Semicossyphus pulcher*), decreased urchin density, and increased kelp cover by correcting the trophic imbalance that results

from overfishing and over-harvesting (Caselle, Rassweiler, Hamilton, & Warner, 2015). Given the impact of local stressors and management decisions on kelp forest condition, developing ways to measure the status of kelp forests and regime shift drivers at local to regional scales may improve management of these systems. Diver surveys are instrumental for this reason, but they are costly and limited across spatial and temporal scales. Satellite remote sensing can measure kelp extent and biomass across entire coastlines, though detection is limited to kelp near the surface (Nijland, Reshitnyk, & Rubidge, 2019). However, it provides no information on the ecological mechanisms dictating kelp dynamics. A remote sensing approach that can measure these ecological drivers at scale would fill the gap between these two existing approaches.

1.15.1.3   Sound in kelp forest

Soundscapes could provide such information in kelp forest systems. For example, in the Channel Islands, kelp forest species associated with regime shifts are well-documented sound-producers. Several of its apex predators are soniferous. For example, the giant black seabass (*Stereolepis gigas*) produces low-frequency "booms" and "drum-rolls" associated with courtship (Clark & Allen, 2018). Some key urchin predators also produce sound. The California spiny lobster (*Panulirus interruptus*) produces an anti-predator "rasp" made by rubbing its antennae (Patek, Shipp, & Staaterman, 2009). In addition, another species in the Palinuridae family, the European spiny lobster (*Palinurus elephas*), was recently found to produce low-frequency, high-amplitude buzzes and rattles (154.2—160.6 dB re 1 µPa2) that are suitable for acoustic monitoring. These sounds were missed in previous studies that were performed in tanks (Jézéquel, Bonnel, Coston-Guarini, & Chauvaud, 2019; Jézéquel, Bonnel, Coston-Guarini, Guarini, & Chauvaud, 2018). The sunflower seastar (*Pycnopodia helianthoides*) has been shown to produce low-amplitude sounds as its spines scrape along rocky substrate (Kitting, 1979). The now extirpated southern sea otter *(Enhydra lutris)*, which was once the dominant controller of sea urchin populations, may have also communicated underwater (Ghoul & Reichmuth, 2012). Sea urchins make sounds when they feed and move that are amplified by their resonant calcareous skeletons (Radford et al., 2008). In coastal waters around New Zealand, urchins increased ambient sound energy by 2–3 orders of magnitude around dusk by making sounds between 400–4000 Hz (Radford et al., 2008). Even fishing pressure could be roughly approximated through measuring patterns in boat noise.

In addition to the main kelp forest drivers, numerous other fish, invertebrate, and marine mammal species contribute to the biological portion of the soundscape. Soniferous fish include the white seabass (*Atractoscion nobilis;* Aalbers & Drawbridge, 2008), garibaldi (*Hypsypops rubicundus*; Parmentier, Lecchini, Mann, Lecchini, & Mann, 2016; Sikkel, 1990), plainfin midshipman (*Porichthys notatus*; Ibara, Penny, Ebeling, van Dykhuizen, & Cailliet, 1983), and bocaccio rockfish (*Sebastes paucispinis*; Širović, Cutter, Butler, & Demer, 2009). Many invertebrate species likely produce sound across the frequency spectrum. Snapping shrimp (Family: Alpheidae) produce high-amplitude, broadband snaps above 1 kHz (Bohnenstiehl et al., 2016). Due to their high density, snap rate, and snap amplitude, these snaps are the most pervasive sound in kelp forests. Importantly, shrimp snap rates can serve as an indicator of habitat transformation. Decreased snap rates have been linked with habitat degradation in coral reefs (Gordon et al., 2018), hard-bottom (Butler et al., 2016), oyster reef (Lillis et al., 2014), and kelp forest habitats (Rossi et al., 2017). Other benthic invertebrate groups that likely produce sound include Echinodermata, Mollusca, and Crustacea. Kitting (1979) recorded feeding sounds from 14 species of mollusks (limpets, chitons, barnacles, crabs, urchins, sea stars, sea snails) and was able to discriminate from these sounds not only the species but also what it was feeding on. Lastly, 3 species of pinniped and 33 cetacean species, of which around 18 are considered residents, have been reported in the Channel Islands (United States Coast Guard, 2008). Because kelp forest condition in this system is driven by the density of sea urchins and their fish and invertebrate predators, and because members within these groups produce characteristic sounds, soundscapes present an opportunity to evaluate the status of regime shift drivers and evaluate overall kelp forest condition.

1.15.2 **Research questions**

In this study, we addressed two principle questions: 1) do soundscape features correlate with ecological drivers of regime shift in kelp forests and 2) do soundscapes differ inside and outside of marine protected areas, where there is a known difference in habitat condition? We were most interested in identifying acoustic features that linked with fish diversity, urchin abundance, and kelp cover, as this information may provide information on the dynamics of regime shift drivers**.** We hypothesized that the intensity and dynamics of the low- and high-frequency portions of the soundscape would be positively correlated with fish, invertebrate, kelp cover and negatively with urchin density due to increased abundance of soniferous fish and invertebrate species in more

forested areas. In this way, we predicted that marine protected areas would have more intense, more dynamic low- and high-frequency portions of the soundscape than unprotected areas.

1.16   Methods

1.16.1   Study area

This study was carried out in Channel Islands National Park, which is located off the coast of Southern California. The park encompasses the five northernmost of the eight California Channel Islands (Figure 20). Its surrounding waters comprise the Channel Islands National Marine Sanctuary, which as of 1968 contained 1/3 of California's kelp forests (Davies, 1968). More than 1,000 species of macro-flora and fauna depend on these forests for food, shelter, and substrate (Davis, Richards, & Kushner, 1996). In 2003, in response to the observed steady degradation of kelp forests and fish populations within the park, a network of 13 marine protected areas (MPAs) was established (Gleason et al., 2010). Research has shown that these reserves increased the biomass and diversity of targeted fish and invertebrate species (Caselle et al., 2015), increased kelp cover, and reduced urchin density, and ultimately improved the resilience and recovery of these kelp forests (Kushner, Rassweiler, McLaughlin, & Lafferty, 2013).
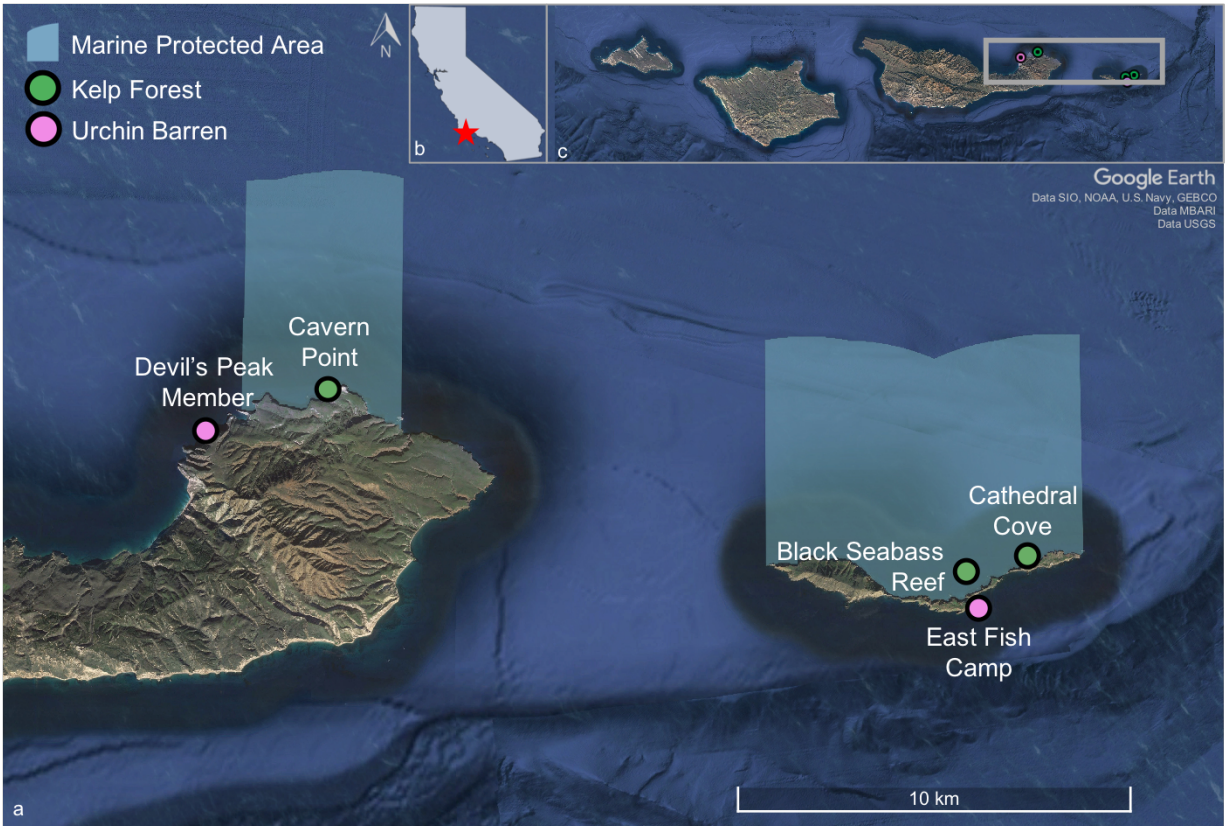
Figure 19: Map depicting (a) the five study sites in Channel Islands National Park, including Cathedral Cove, Cavern Point, Black Seabass Reef, Devil's Peak Member, and East Fish Camp, (b) location of the Channel Islands in California, USA, and (c) four of the five southern Channel Islands.

1.16.2 Acoustic data collection

We collected acoustic recordings over a 42-day period from May 12–June 23, 2018 at five sites off the coasts of Anacapa and Santa Cruz Islands. Both islands had MPAs on their northern coasts that were established in 2003. One site, Cathedral Cove, had been protected since 1978. Recorders were deployed inside and adjacent to these MPAs (Table 4). Recorders were a minimum distance of 1.4 km from other recorders and MPA boundaries, except for East Fish Camp, an unprotected site that was acoustically buffered from other recorders and MPAs because it was the only recorder on the south side of the island chain. We selected sites with similar bathymetry, biogeography, and depth in order to measure better the ecological differences caused by habitat condition and protection status. Recordings were collected with SoundTrap 300 STD underwater sound recorders, which had a working frequency range from 20 Hz–60 kHz (Ocean Instruments NZ,

2017). Four of the five units had 256 GB of storage and an external battery pack. They recorded 5 minutes every 15 minutes with a sampling rate of 48 kHz, a bit depth of 16 bits, and a gain setting of "high." The fifth unit that was deployed at Cathedral Cove had 128 GB of storage with no external battery pack. This unit recorded 1 minute every 15 minutes with a sampling rate of 96 kHz, which was selected in order to assess the prevalence of ultrasonic sounds, and was down-sampled to 48 kHz prior to this analysis. It had the same bit depth and gain settings as the other recorders. Recorders were enclosed in a PVC housing, fastened to a concrete block, and installed on the seafloor with the hydrophone approximately 20 cm above the substrate (Figure 21). While we considered other deployment designs in which the hydrophone was suspended at least 1 meter above the substrate, installing the unit closer to the seafloor was preferable due to the dynamic and high-energy wave conditions in these shallow water habitats.

Table 4: Information on the five study sites, including their location, whether or not they occured within a marine protected area (MPA), and the year the MPA was established.

Site	Island	Latitude	Longitude	Depth (m)	MPA	Year Protected
Cathedral Cove	Anacapa	34.016	-119.372	8	Inside	1978
Cavern Point	Santa Cruz	34.054	-119.567	12	Inside	2003
Black Sea Bass Reef	Anacapa	34.013	-119.389	16	Inside	2003
Devil's Peak Member	Santa Cruz	34.045	-119.601	12	Outside	NA
East Fish Camp	Anacapa	34.005	-119.386	12	Outside	NA
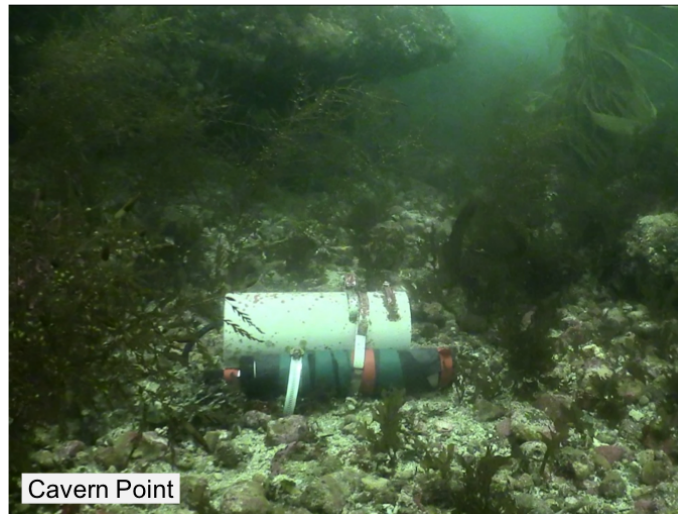
Figure 20: Photograph of the SoundTrap recorder deployed at Cavern Point off the island of Santa Cruz in the Channel Islands.

1.16.3 Biodiversity data collection

Biodiversity data were collected as part of the Channel Islands Kelp Forest Monitoring Program (KFMP), one of the oldest ongoing marine monitoring programs in the United States, which started in 1982-85 at 16 sites (Davis et al., 1996). The KFMP was expanded following the establishment of the Channel Islands MPAs in 2003. Now, the KFMP monitors 33 sites each summer by conducting surveys along 100-meter permanent transects. The five acoustic recorders were deployed at five of these fixed 100-meter transects. We utilized five different survey methods to assess the diversity and abundance of fish, invertebrate and kelp species. Kelp abundances (% cover) were acquired via the KFMP random point contact survey (Kushner & Sprague, 2018). Urchin densities were acquired by combining the KFMP 1m quadrat survey and KFMP 5m quadrat survey (Kushner & Sprague, 2018). Invertebrate abundances were acquired through integrating KFMP 1m quadrat survey, KFMP 5m quadrat survey, and KFMP band transect survey (Kushner & Sprague, 2018). Fish species abundances were acquired via the KFMP visual roving survey (Kushner & Sprague, 2018). We utilized surveys from 2016–2018 (instead of just 2018) to reduce any biasing effects of spatiotemporal sampling differences between survey years so that biodiversity data were more robust representations of recent kelp forest condition. We aggregated species-specific count data to generate the following six biodiversity metrics that summarized taxonomic groups of interest: kelp cover, urchin density, invertebrate density, invertebrate species richness, fish abundance, and fish species richness. For density and count values, we computed the

means over these three years. For fish and invertebrate species richness, we pooled values across years, and calculated the total number of fish and invertebrate species identified during this period.

1.16.4 Soundscape analysis

To assess kelp forest soundscapes, we calculated nine soundscape variables using three complimentary acoustic analyses that measured different dimensions of biological sounds within these sites, including: 1) high-frequency shrimp snaps, 2) low- and high-frequency sound levels, and 3) low- and high-frequency sound dynamics. Our dataset consisted of 20,196 recordings that were 56 seconds in length (96 recordings per day x 42 days x 5 sites). Prior to analysis we visually and aurally reviewed the recordings and removed 851 files that contained noise from nearby boats (4% of dataset). East Fish Camp had 318 files containing boat noise, followed by Cathedral Cove (272), Black Seabass Reef (107), Devil's Peak Member (85), and Cavern Point (69). We include example spectrograms of files containing boat noise in Supplementary Information. We linearly interpolated these missing values using the *na.interpolation* in the R package "imputeTS" (Moritz & Bartz-Beielstein, 2017) because a subsequent analysis required complete time series and because there were negligible differences on soundscape metrics between interpolating and leaving missing values as NA.

1.16.4.1 High-frequency shrimp snaps

We detected the number of shrimp snaps in the recordings by employing a shrimp snap detector following the methods of Bohnenstiehl et al. (2016). Prior to analysis, we band-pass filtered recordings from 2–20 kHz and trimmed them to the first 30 seconds. Then, we performed a shrimp snap detector function that correlated windowed selections of the time-series with the stereotypical shape of a snapping shrimp snap that was generated in Matlab (Bohnenstiehl et al., 2016). Correlations above 0.75 were considered detections. We visually verified the accuracy of this detector by inspecting spectrograms and oscillograms annotated with snap detections. To measure shrimp snaps only produced within 100m of the hydrophones and the biodiversity transects, we retained snaps that had an amplitude of at least 130 dB. We determined this threshold by modeling the propagation of these sounds based on the estimated source level of shrimp snaps and how sound spreads in this shallow water. The source level of shrimp snaps was stamped to be approximately 150 dB (99% percentile SPL_{rms} from 2-20 kHz for detected snaps was 150.3 dB).

We used the cylindrical geometric spreading model that is commonly applied in coastal ocean acoustics (Lillis et al., 2014; Urick, 1983). We applied the equation $SL - 10 \cdot \log_{10}(d) = RL$, where SL is the snap source level (150 dB), d is the distance between the sound source and the receiver (100 m), and RL is the received level of a snap that was produced at 100 m. The threshold of 130 dB also exceeded the ambient noise floor by approximately 14 dB (mean SPL_{rms} from 2-20 kHz = 116.2 dB). In addition to calculating the number of snaps per minute, we also measured the peak frequency of each snap to try to better understand the biological and environmental effects that could cause differences in snapping shrimp activity across these five sites.

1.16.4.2   Low- and high-frequency sound levels

To measure the intensity of low- and high-frequency sound levels, we calculated sound pressure levels (SPLs) across three different frequency bands. After aurally and visually reviewing recordings and their spectrograms, we selected three frequency bands, 20–80 Hz, 50–750 Hz and 2–24 kHz, which contained most biological sounds and partitioned them into broad groups containing different sound producers. The low frequency bands (20–80 Hz and 50–750 Hz) contained sounds from fish, marine mammals, and invertebrates. We measured both of these bands because the 50–750 Hz was dominated at some sites by the plainfin midshipman, which had a fundamental frequency of approximately 100 Hz and strong harmonics to approximately 700 Hz. The 20–80 Hz frequency band contained sounds from larger-bodied fish and organisms that produced low-frequency sounds associated with body movement against substrate. The high-frequency band (2000–24000 Hz) contained sounds from snapping shrimp, echolocating dolphins, and potentially other soniferous invertebrates (Lillis et al., 2014; Staaterman et al., 2017).

We calculated calibrated sound pressure levels within these frequency bands using custom scripts written in R and the hydrophone sensitivities provided by SoundTrap for each hydrophone (R Core Team, 2018). To do so, we first converted recordings into the spectral domain using a Discrete Fourier Transform with a window length of 8,192 samples, 0% overlap and a Hann window. For each recording and frequency band, we calculated the upper quartile SPL value, which we selected because it measured continuous biological choruses as well as more discrete sound events better than commonly used metrics such as root-mean-square or median amplitude. Root-mean-square amplitude was overly sensitive to short-duration, high-amplitude sounds (some over 150 dB) that

confounded the measurement of all other biological patterns 12/6/19 3:21:00 PM. The median amplitude was mainly reflective of ambient soundscape levels, which were influenced by the noise from ships, many of which were likely passing through the Santa Barbara Channel. In supplementary information, we provide visualizations to illustrate the utility of the upper quartile SPL value for measuring biological components of these kelp forest soundscapes.

1.16.4.3   Diel dynamics of soundscape variables

We measured the daily variation of snap rates and the low-and high-frequency sound levels, since the magnitude of diel soundscape patterns was correlated with fish density (low-frequency diel pattern) and coral cover (high-frequency diel pattern) in previous studies (Kaplan et al. 2018). Peak frequency was omitted as we did not expect its diel dynamics to yield meaningful information pertaining to our research questions. To measure the magnitude of the diel trends in these soundscapes, we first utilized the *decompose* function in the "stats" R package to decompose the time series of the four of the five soundscape variables (excluding peak snap frequency) into their seasonal, trend, and irregular components (R. Core Team, 2018). We extracted the diel component, smoothed it with a 4-point moving average, and cropped it to one-day length (96 values). To quantify the "magnitude" of the daily variation, we plotted the diel pattern, and calculated the area above and below its mean using the *AUC* function from the "DescTools" package in R, with the assumption that more dynamic sites would have a greater area under the curve measurement (AUC; Kaplan et al. 2018).

1.16.4.4   Long-term dynamics of soundscape variables

To better understand the biological sounds that influenced the soundscape metrics, we generated long-term spectrograms. We did so by calculating the power spectral density of each recording using a window length of 8,192, a Hann window, and 0% overlap using custom scripts in R that were based off of "PAMGuide" (Merchant et al., 2015). For each recording, we calculated the 75th percentile SPL value. We then stitched together these power spectral density values together using custom scripts in R to create long-term spectrograms for each site (Figure 24).

1.16.5 **Statistical analysis**

1.16.5.1 **Correlation between soundscapes and drivers of kelp forest regime shifts**

We conducted correlation tests between soundscape variables (n=9) and biological variables (n=6) associated with kelp forest regime shifts to test our predictions that the intensity and dynamics of the low- and high-frequency portions of the soundscape would be positively correlated with fish, invertebrate, and kelp cover diversity and negatively correlated with urchin density. Instead of testing all possible combinations between these variables, to avoid generating spurious results, we only computed tests for combinations that we predicted a relationship would exist *a priori*. We predicted that fish density and abundance would be positively correlated with the four low-frequency sound variables. We also predicted that kelp cover, invertebrate density, and invertebrate richness would be positively correlated with high-frequency variables (including shrimp-derived metrics), while urchin density would be negatively correlated with high-frequency variables. To prepare data for these correlation tests, we calculated the mean value of band-level SPLs and shrimp snap rates to obtain one value for each site. We conducted Pearson correlation tests since all variables passed the Shapiro-Wilk test for normality of residuals. Some variables first needed transformation. "Fish abundance" first needed to be squared in order to meet the normality assumption. "Urchin density" needed to be $\log_{10}(x)$ transformed to meet the linearity assumption. We considered as significant correlations where $p < 0.1$ and the correlation coefficient (r) > 0.85 to further investigate potentially important soundscape-ecological relationships despite the low statistical power that resulted from our limited sample size (n = 5).

1.16.5.2 **Effect of MPAs on biological and soundscape components**

To determine if soundscapes and biological variables differed depending on protection status, we computed linear models in R using the *lm* function in the "stats" package (R. Core Team, 2018). Prior to performing these models, we reduced the dimensionality of the soundscape and biological variables by conducting separate principle components analyses on scaled variables using the *prcomp* function from the "stats" package in R (R. Core Team, 2018). For both the soundscape and biological variables, we retained the first two principle components because their eigenvalues were > 1.0 and together they captured > 80% of the variability. We computed two multivariate regression models in which the two principle components were the dependent factors and time

since protection was the independent factor (CC=40 years; BSBR=15 years, CVP=15 years; EFC=0 years, DPM=0 years). Model assumptions were validated by performing Shapiro-Wilk tests for normality of residuals.

1.17 Results

1.17.1 Ecological patterns

Kelp cover varied greatly between sites (Table 5). Cathedral Cove, which had been protected for forty years, had the highest kelp cover (34.8%). The other two protected sites, Cavern Point and Black Seabass Reef, had coverages of 23.5% and 7.7%. The two unprotected sites, Devil's Peak Member and East Fish Camp, had coverages of 0.0% and 0.05% kelp stipes per m^2. Of the four kelp species recorded at these sites, the dominant species was giant kelp, *Macrocystis pyrifera*, which comprised 57% of the total.

Urchin density was inversely related with kelp cover. Cathedral Cove had the lowest urchin density (0.4 m^{-2}), followed by Cavern Point (2.3 m^{-2}) and Black Seabass Reef (3.95 m^{-2}). As expected, Devil's Peak Member (10.5 m^{-2}) and East Fish Camp (26.8 m^{-2}) had more urchins than the protected sites. Of the four urchin species (*Centrostephanus coronatus, Lytechinus anamesus, Strongylocentrotus franciscanus, Strongylocentrotus purpuratus*), the species most associated with regime shifts, *S. purpuratus*, comprised 69% of the urchin community. While East Fish Camp had between 17.7-24.5 urchins per m^{-2} from 2016-2018, Devil's Peak Member was more variable, with 22.91 m^{-2} in 2018, 0.9 m^{-2} in 2016, and 1.5 m^{-2} in 2017.

Invertebrate density tracked similarly with urchin density. Invertebrate abundance was lower at protected sites (1.2–1.6 m^{-2}) than the unprotected sites (2.6–3.6 m^{-2}). Invertebrate richness also peaked at East Fish Camp (15 m^{-2}) and was lowest at Cathedral Cove (10 m^{-2}).

Fish abundance was similar at four of the five sites, ranging from 1285 fish per transect at Cathedral Cove to 1132 at Cavern Point. The anomalous fifth site, East Fish Camp, only had an abundance of 620 fish. Its richness was also at least 7 species fewer than the other four sites. The two Santa Cruz sites had the highest species richness values, with Devil's Peak Member and

Cavern Point having 31 and 33, respectively. The Anacapa sites, Black Seabass Reef and Cathedral Cove, had 27 and 30, respectively. The five most abundant fish species were *Chromis punctipinnis* (2716), *Lythrypnus dalli* (749), *Halichoeres semicinctus* (244), *Paralabrax clathratus* (236), and *Oxyjulis californica* (192).

Table 5: Table of the six biodiversity variables obtained from Kelp Forest Monitoring Program surveys conducted from 2016–2018.

Site	Fish Abundance (#)	Fish Richness (#)	Kelp Cover (%)	Urchin Density (m^{-2})	Invertebrate Density (m^{-2})	Invertebrate Richness (#)
Cathedral Cove (MPA 1978)	1285	30	34.8	0.4	1.6	10
Black Seabass Reef (MPA 2003)	1132	31	23.5	2.3	1.4	14
Cavern Point (MPA 2003)	1195	27	7.7	4.0	1.2	12
Devil's Peak Member (Unprotected)	1244	33	0.0	10.5	3.6	13
East Fish Camp (Unprotected)	620	20	0.1	26.8	2.6	15

1.17.2 Soundscape patterns

1.17.2.1   Snapping shrimp snaps

The three protected sites had fewer snaps per minute (220–803) and higher peak snap frequencies (3.8–4.4 kHz) than the unprotected sites, where snapping rates ranged from 889–1071 and peak frequencies ranged from 3.4–3.8 kHz. Snaps per minute were greatest at East Fish Camp (1071 snaps per minute) and lowest at Cathedral Cove (220 snaps per minute; Figure 22). Peak snap frequency exhibited the opposite trend, with the highest snap frequency at Cathedral Cove (4.4 kHz) and the lowest snap frequency at East Fish Camp 3.4 kHz).

1.17.2.2   Low-frequency sound levels

East Fish Camp had the lowest SPLs for both the 20-80 Hz and 50-750 Hz frequency bands. Fish chorusing events were fewer and less intense at this site compared to the other four sites. The lower recorded levels of fish choruses at East Fish Camp could indicate that the chorusing fish were far from the hydrophone, and potentially outside of this urchin barren. Devil's Peak Member had the highest SPLs for both the 20–80 Hz and the 50-750 Hz frequency bands due to nightly fish choruses from multiple species, but especially the plainfin midshipman. The long, wide tails for

Devil's Peak Member, East Fish Camp, and Black Seabass Reef in the 50–750 Hz violin plot (Figure 22) are due to regular plainfin midshipman choruses at these sites. The wider distribution of values at Cathedral Cove and Black Seabass Reef are the result of low-frequency fish choruses (<80 Hz), possibly from white seabass and kelp seabass, and also high-amplitude sounds that appeared to be produced by body movement against the substrate.

1.17.2.3 High-frequency sound levels

High-frequency SPLs at Cathedral Cove (112.4 ± 1.6 dB) were 4–7 dB lower than the other four sites. The two Santa Cruz sites, Devil's Peak Member and Cavern Point, had the highest high-frequency SPLs of 118.2 ± 1.3 dB and 119.6 ± 0.8 dB, respectively. Protected sites had a wider distribution of high-frequency SPLs than the unprotected sites. Standard deviation of these SPLs ranged from 1.3–1.6 in protected and 0.81–0.85 in unprotected areas. The shapes of the 2-24 kHz violin plots reflect this pattern.
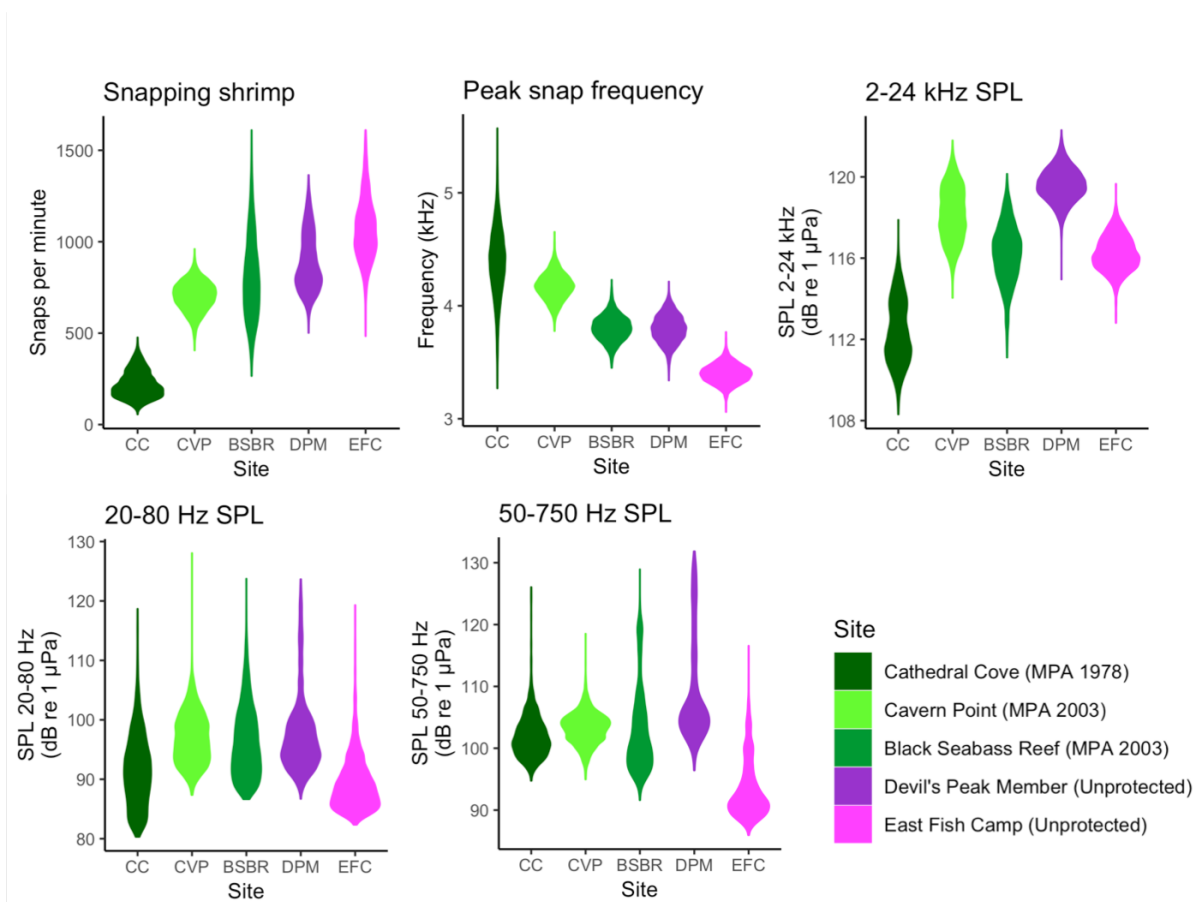
Figure 21: Violin plots of the five soundscape variables. CC = Cathedral Cove; CVP = Cavern Point; BSBR = Black Seabass Reef; DPM = Devil's Peak Member, and EFC = East Fish Camp. Green shading denotes kelp forest sites and purple and pink shading denotes urchin barren sites.

1.17.3 **Diel dynamics of soundscape variables**

1.17.3.1   Snapping shrimp diel dynamics

Snap rates were generally high at night, peaked around dawn, and decreased over the course of the day until just before dusk, upon which time rates increased again (Figure 23). Four of the five sites displayed pronounced peaks at dawn. While Black Seabass Reef had the largest diel dynamics (AUC=10,635), East Fish Camp had the steepest crepuscular peak and the second highest AUC (8,991). Cathedral Cove had discernable day-night patterns in snapping shrimp dynamics, but had the 2nd lowest AUC for shrimp snaps (4,687) likely because it had the lowest overall snap rate and we did not rescale values prior to this analysis.

1.17.3.2   Low-frequency diel dynamics

In general, the 20–80 Hz band was lowest during the day, peaked around sunset, and sustained moderately high levels throughout the night. At Black Seabass Reef, there were crepuscular peaks that coincided with activity of species that produced high-amplitude, low-frequency sounds. Starting just before dawn and subsiding in late morning, sounds that often exceeded 160 dB re 1 uPa, occurred every 5-15 seconds, and durations spanning 0.25–5 seconds. We could not identify the producer but suspect that sounds were produced via body movement against the substrate. The peak at dusk was caused by chorusing fish. While four of the sites had strong daily dynamics (AUC=144–303), East Fish Camp had negligible daily dynamics within this band (AUC=39).

The 50–750 Hz band peaked at night. The general shape of this diel pattern was associated with fish chorusing activity, and the magnitude of the pattern depended mainly on the prevalence of the plainfin midshipman. Devil's Peak Member had the most intense and consistent chorusing from this fish species and the highest AUC (549). At Cathedral Cove (164) and Cavern Point (84), its contributions were relatively faint and infrequent and so these sites had the lowest AUC values. Cavern Point was also the only site where levels increased during the daytime. This increase could be due to wave action elevating background noise within this band (Hildebrand, 2009).

1.17.3.3   High-frequency dynamics

The 2–24 kHz sound levels were lowest during the daytime There were pronounced peaks at dusk at four of the five sites. The two urchin barren sites also had slight peaks at dawn. The biggest

difference between the protected and unprotected sites was that sound levels increased considerably at night at the protected sites (+2.3 dB) but only minimally at the urchin barren habitats (+0.7 dB). This difference in day-night dynamics was reflected in the AUC values, which ranged from 95-110 in protected habitats and 39-52 in unprotected habitats.
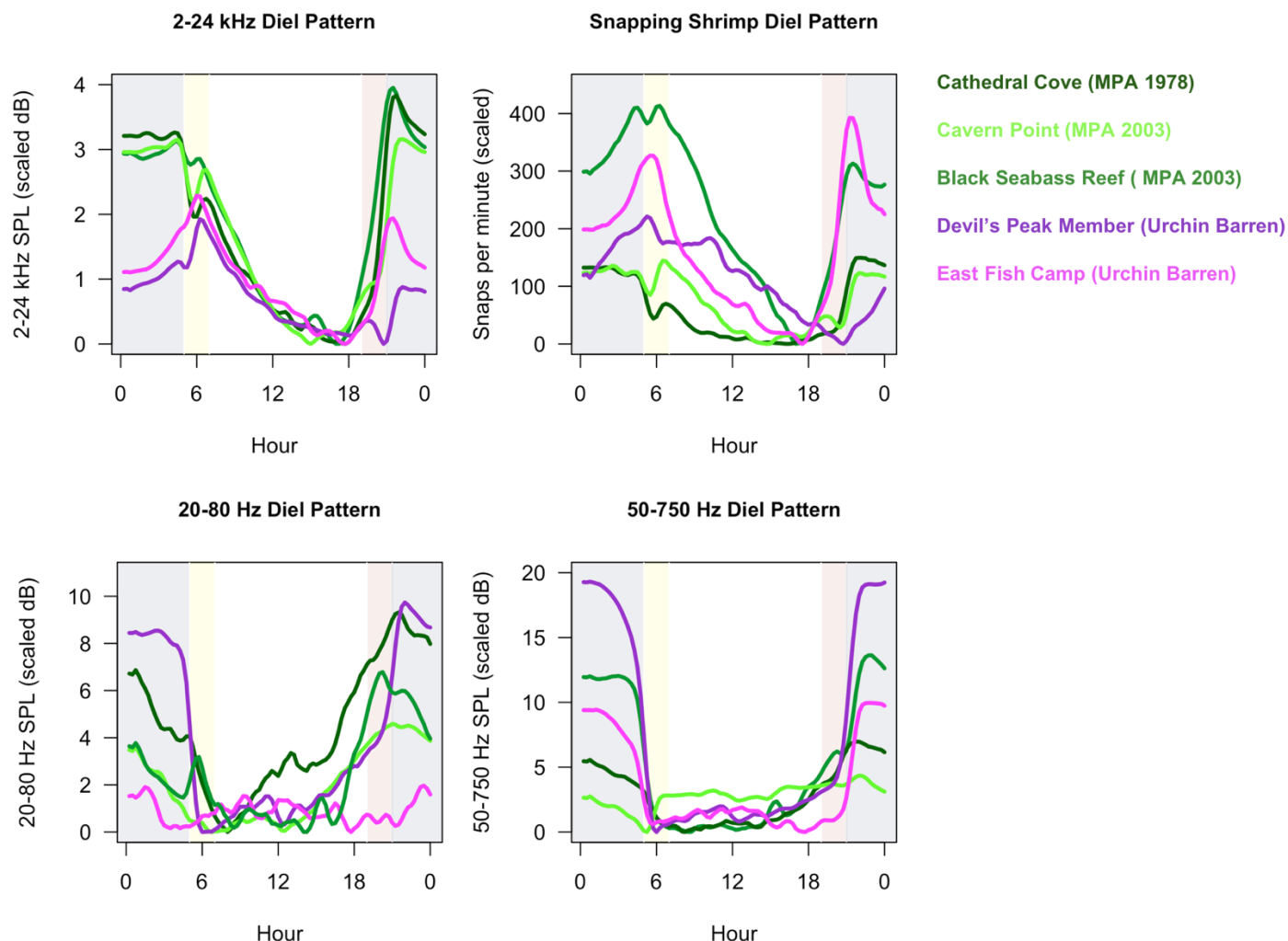
Figure 22: Daily dynamics for four of the five soundscape variables. Values were scaled relative to the minimum of the 96 daily values, and thus represent dB or shrimp snaps above the minimum daily value.

1.17.4 Longer-term dynamics in soundscape variables:

Over this 42-day period, sites exhibited different longer-term soundscape patterns. Most apparent were the plainfin midshipman choruses at Devil's Peak Member, Black Seabass Reef, East Fish Camp, and Cathedral Cove, which chorused at night from 21:30–04:00, and peaked from 22:00–01:45. While the production of the plainfin midshipman was consistent across days during this

time period, other fish choruses were more variable, with multi-day upticks in activity (i.e. 5/17–5/19 for Devil's Peak Member, Black Seabass Reef and 5/26–5/27 for Cavern Point). Figure 24 also illustrates the relative lack of low-frequency intensity and dynamics at East Fish Camp. While individual fish pulses at East Fish Camp were quite common, the lower levels here likely reflected the dearth of chorusing fish at this site. In supplementary information, we provide sound files of different key biological sounds that occurred within these soundscapes.
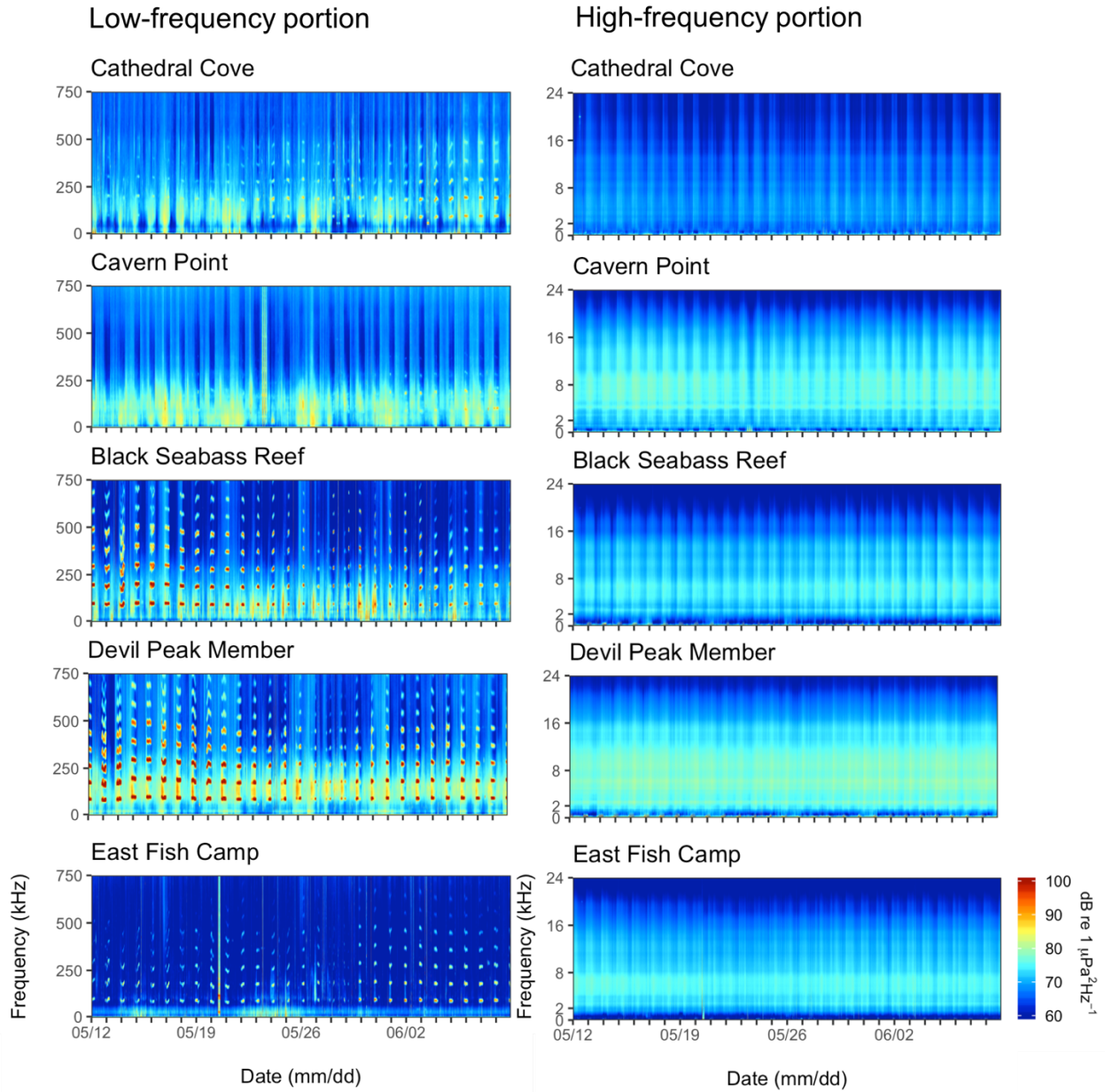
Figure 23: Long-term power spectral density plots depicting low- and high-frequency trends for these five sites PSD were calculated on median sound levels. Power spectral density values were calculated based on the upper quantile of sound pressure levels for each recording.

1.17.5 **Correlation between soundscapes and ecological drivers of kelp forest regime shifts**

Three main drivers of regime shifts in kelp forests—the density of kelp, the density of urchins, and the diversity and abundance of fish—significantly related to different soundscape variables (Figure 25). Invertebrate richness and density were significantly related with soundscape variables as well.

Kelp cover negatively correlated ($r(3) = -.93$, $p = .022$) with the number of snapping shrimp snaps per minute and positively correlated with the peak frequency of snaps ($r(3)= .93$, $p = .024$). Kelp cover was also negatively correlated with high-frequency sound pressure levels ($r(3) = -.85$, $p = .070$).

Sea urchin density positively correlated ($r(3) = .98$, $p = .004$) with the number of snapping shrimp snaps per minute and negatively correlated with the peak frequency of snaps ($r(3)= -.93$, $p = .010$). While it was not significantly correlated with high-frequency SPL, sea urchin density was negatively correlated with high-frequency SPL diel dynamics ($r(3)= -.87$, $p = .058$).

Fish species richness ($r(3)= .94$, $p = .017$) and fish abundance ($r(3)= .86$, $p = .065$) positively correlated with sound levels from 50-750 Hz, but not the daily dynamics within this frequency band. Conversely, fish species richness ($r(3)= .87$, $p = .054$) and fish abundance ($r(3)= .88$, $p = .047$) were highly correlated with the daily dynamics of the 20-80 Hz band, but not with its sound levels.

Invertebrate density was negatively correlated with the diel trend of the 2–24 kHz frequency band ($r(3)= -.92$, $p = .027$). Invertebrate richness was significantly correlated with the number of snaps per minute ($r(3)= .86$, $p = .060$).
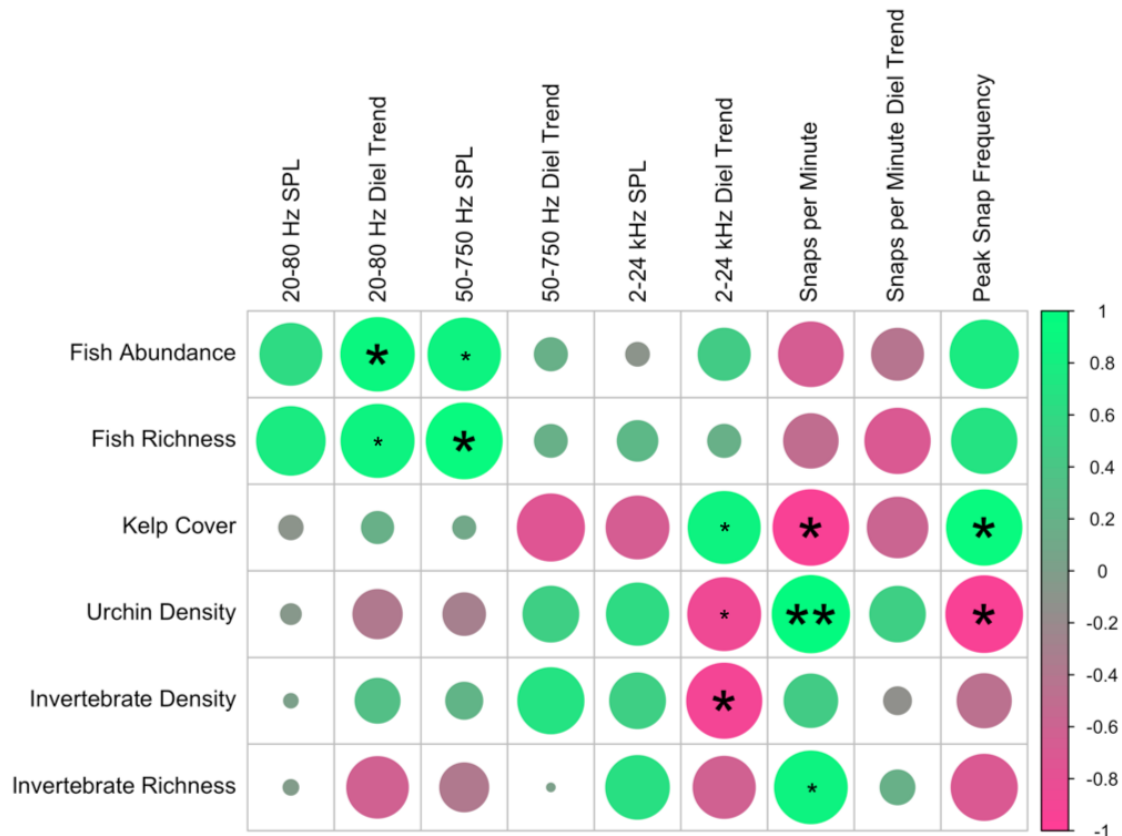
Figure 24: Correlation plot between soundscape and biological variables. $p < 0.1$ (*), $p < 0.05$ (✱) and $p < 0.01$ (✱✱). The color of the circles reflects the direction of the correlation, while the size of the circles indicates the magnitude of the correlation.

1.17.6 Effect of MPAs on biological and soundscape components

While time since protection was not significant for either PCA axis representing the biological variables, there was a significant positive relationship between the first soundscape PCA axis (adj. $R^2 = .82$, $F_{1,3} = 19.6$, $p = .022$). The soundscape variables that contributed most to this axis were peak snap frequency (0.50), number of snaps (0.49), and diel dynamics in the high-frequency band. These three variables all increased with greater time since protection. Regarding the biological variables, only kelp cover and urchin density showed such a monotonic pattern. Other biological variables varied in ways that could reflect MPA effects. Invertebrate density was more than doubled in unprotected habitats (Gottesman, unpublished data). At East Fish Camp, the site with the highest urchin density and devoid of kelp, fish abundance (620) was approximately half as high as the other four sites and fish richness (20) was 40% lower.

1.18 Discussion

1.18.1 Overview

This study demonstrates that marine soundscapes can indicate the condition of kelp forests, which are increasingly vulnerable to destruction from sea urchin overgrazing. Our results suggest that several ecological variables associated with regime shifts in kelp forests, including urchin (and invertebrate) density, kelp cover, and fish richness and abundance correlated with measurable soundscape components. Soundscapes also indicated the ecological legacy of these five sites, with time since protection significantly related to some soundscape variables. The biological variables did not significantly correlate with time since protection, potentially because fish, kelp, and invertebrates have nonlinear and asynchronous recovery trajectories. The primary finding of this study—that degraded sites exhibited increased snapping shrimp activity and, to a lesser degree, increased high frequency sound levels—runs counter to our hypothesis and also to a previous study that found decreased shrimp activity in kelp forest sites degraded from nutrient pollution (Rossi et al., 2017). The contrasting results between these two studies is important because it illustrates that different disturbances can alter soundscapes in characteristic and sometimes divergent ways, even in similar ecosystems. We explore potential explanations for this contrast in the body of this discussion. To unify our results into a cohesive framework, we propose the concept of a sound web, which refers to evaluating trophic structure, habitat condition, or regime shifts through the relative abundance of sounds made by different functional groups, for example predators (carnivorous fish, lobster) and prey (snapping shrimp, sea urchins).

A main finding of this study is that certain forms of habitat degradation may actually *increase* sound production from dominant soniferous taxa (snapping shrimp), possibly causing an associated increase sound levels. In our study, snapping shrimp rates at the two urchin barren habitats were four times greater than at Cathedral Cove, which had been protected since 1978. The two sites that had been protected since 2003 had intermediate snapping rates. Similarly, Cathedral Cove also had high frequency sound levels (SPL 2-24 kHz) that were 4–7 dB lower than the other four sites.

Thus far, in almost all soundscape studies that have reported significant relationships between ecological variables (species abundance, species richness, and habitat condition) and soundscape

variables (sound pressure levels, soundscape complexity, sound type diversity), these relationships have been positive (Butler et al., 2016; Buxton, et al., 2018b; Harris et al., 2016; Pieretti et al., 2011, but see Freeman & Freeman, 2016). Here, we see that a regime shift caused by overfishing was associated with an *increase* in sounds from snapping shrimp (and potentially other invertebrates) and elevated high-frequency sound levels. Reasons for this observed difference in snapping shrimp acoustic activity can be ecological, environmental, or a combination of the two.

The ecological explanation is that the removal of apex predators in unprotected habitats resulted in an increase in invertebrates, including sea urchins, mollusk species, and potentially snapping shrimp. At the two urchin-dominated habitats, invertebrate density was 220% greater than at protected sites. While snapping shrimp were not directly measured in these surveys, the overall increase in invertebrates suggests that shrimp density could be greater in regime-shifted habitats due to the lack of predators. Bolstering this suggestion, we observed a weakly significant correlation between snapping shrimp snaps and invertebrate richness. In addition to an increase in invertebrate density, there also could be accompanying changes in invertebrate behavior resulting in soundscape alteration. For example, in healthy kelp forests, urchins usually stay hidden and protected in reef crevices during the day to avoid predation (Kenner, 1992; Ling et al., 2015). However, if predator abundance declines substantially, sea urchins become active during the daytime and drastically increase their locomotion in search of kelp, which could lead to a corresponding increase of sounds associated with these activities and a flattening of the diel dynamics. At the urchin barren sites, we did observe the dissolution of day-night patterns in the high frequency band, which could indicate behavior change from other invertebrate species including shrimp in these degraded, predator-scarce habitats (Figure 26). In general, for species that produce sound at night and crepuscular periods to avoid detection by predators, it is unclear how their patterns might change when predators are removed. This study produced results consistent with the hypothesis that soundscapes can encode behavioral changes induced by the removal or reintroduction of apex predators. Rather than impoverishing soundscapes, the removal of apex predators appears to have resulted in an influx of snapping shrimp activity and a flattening of the diel soundscape dynamics.
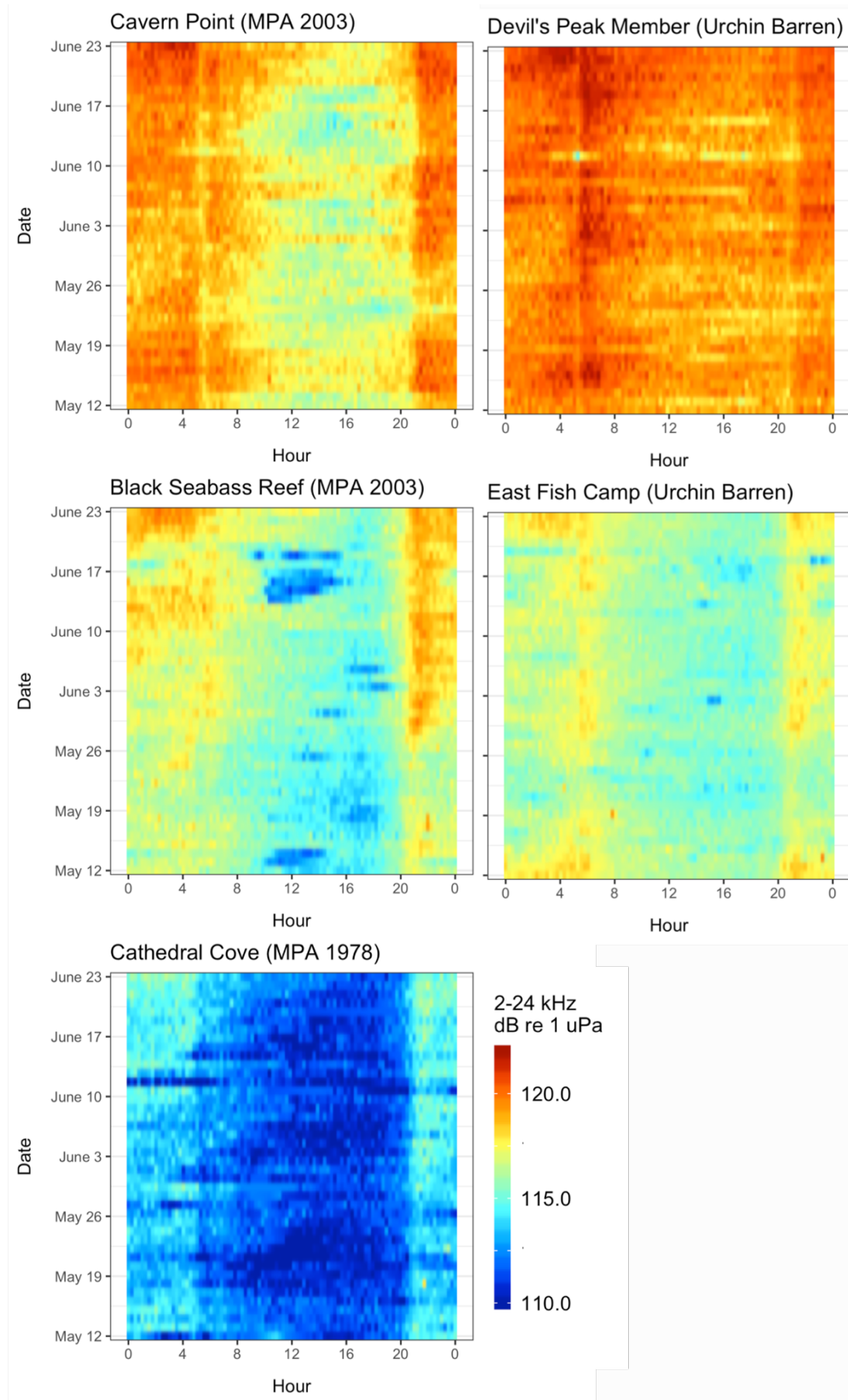
Figure 25: Diel dynamics of the high-frequency band (2–24 kHz) for the five sites. From these plots, the day-night dynamics within the protected areas (left column) are greatly reduced in the unprotected sites (right column).

The environmental explanation for the increased snapping shrimp activity observed in the degraded sites is due to how sound propagates differently in kelp forests versus urchin barrens. Kelp forests can attenuate low- and high-frequency sound, particularly in summer months when kelp plants are dense and have high leaf areas (Wilson, 2011). Therefore, we would expect healthy kelp forests to have an environmental quieting effect that would result in decreased sound levels. This environmental explanation is potentially supported by the strong inverse relationship between kelp cover and peak snap frequency, which could result if kelp attenuates sound waves between 2–4 kHz more than sound waves between 4–6 kHz, but additional research is needed to determine the nature and extent of how kelp density impacts biological sound transmission. In ecosystems like kelp forests, where regime shifts also trigger major changes in habitat structure and therefore the propagation environment, assessing biodiversity changes through soundscape analysis is made more complex because these physical changes need to be accounted.

The strong relationship between snapping shrimp activity and urchin density is a relatively surprising finding in that it contrasts with the results of Rossi et al. (2017). They recorded in healthy kelp forests and adjacent habitats that had shifted into algal-turf due to excessive nutrient pollution (different driver than sea urchin over-grazing). They found that from kelp forest habitats to adjacent algal turf, shrimp snaps declined from 290 to 90 snaps per minute and that total sound levels (300–10,000 Hz) declined from 122 dB to 115 dB. Their hypothesis for these reduced shrimp snap rates and sound levels was that habitat simplification decreased the niches for shrimp to inhabit. Since they observed a similar soundscape alteration in macroalgae-seagrass habitats in Italy on an ocean acidification gradient (different regime shift), they concluded that "modified cues of shifted ecosystems are similar regardless of spatial scale and type of environmental driver" (Rossi et al., 2017). Our study illustrates that different pathways toward kelp forest degradation may result in different soundscape impacts. Shrimp density may decline in a kelp forest degraded through nutrient pollution (because of fewer niches) but increase in a kelp forest degraded through overfishing (due to fewer predators). This is an important result because it shows that different disturbance types may have characteristic soundscape impacts, even if the degree of alteration or ecosystem is similar.

Another unexpected result of the study was the lack of discernable urchin sounds in the urchin barren habitats. A recent study has shown that urchin species produce sounds associated with movement and feeding. Reported frequency ranges for these sounds have included 3–6 kHz (Coquereau et al., 2016), .4–4 kHz (Radford et al., 2008), and ultrasonic components including an initial broadband transient at 37–49 kHz (Coquereau et al., 2016). Urchins in rocky coastal reefs in Northern New Zealand generated a 20 dB increase in ambient sound levels at dusk (Harris et al., 2016). In our study, we detected no comparable increase in sound levels in this frequency range at dusk, though there were crepuscular peaks of about 1 dB at the two urchin barren sites. One reason for this lack of urchin sounds is that soon after a habitat shifts into an urchin barren, urchins quickly exhaust the food supply, cease feeding, reduce activity, and slowly decompose (David Kushner, personal communication, 2019). This inactivity could result in minimal sound production during this period. We did detect repeated scrape-like sounds that occurred mostly at the barren sites, but an expert in urchin bioacoustics thought that they were produced too rapidly to be from a feeding urchin, and were likely produced by a turbin snail or similar mollusk (Natalie Soars, personal communication, 2018). Also from reviewing the spectrograms of all recordings, we observed an increase in ambient noise levels from 400-1000 Hz, though we could not identify the source of this elevation in background noise. Therefore, soundscape monitoring could potentially play a role in detecting the onset of urchin overgrazing, but after a forest has transformed into a barren, the sounds from urchins may not be a usable indicator of their presence.

1.18.2 **Study Limitations**

While this study does illustrate the strong relationships between soundscape components and kelp forest condition at these sites, it is important to regard these results in proper context. First, with only five sites surveyed, it is difficult to know for certain whether these results are generalizable to other habitats within the Channel Islands and similar kelp forest systems. While we selected sites with similar environmental and biogeographical characteristics, it is possible that some external factors could have contributed to differences in these soundscape. For example, East Fish Camp, which had 50–750 Hz sound levels at least 9 dB less than the other sites, was also the only site on the south side of the island chain. Therefore, it could have been buffered from the Santa Barbara Channel shipping lanes approximately 10–20 km north of Santa

Cruz and Anacapa, thus reducing ambient low-frequency sound levels. Despite the anomalous location of East Fish Camp, we are confident that the low-frequency differences between East Fish Camp and the other sites were largely driven by reduced biological sound production. The other four sites had more frequent and intense fish choruses and 20-80 Hz daily dynamics that were 3–8 times greater than at East Fish Camp. The nocturnal peaks in low-frequency sound levels did not correspond to the daytime peaks in commercial fishing activity or the noon and midnight peaks in commercial shipping on the Santa Barbara Channel (Mckenna, Soldevilla, Oleson, Wiggins, & Hildebrand, 2009), though this recorder was deployed at a different location within the Santa Barbara Channel and so daily shipping dynamics would likely be different at this location.

In addition to anthropogenic noise, another confounding factor could have been the acoustic activity of whale species that inhabit the waters surrounding the Channel Islands, including the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), and humpback whale (*Megaptera novaeangliae*). However, the daily and seasonal patterns of these species do not cleanly match the patterns observed in this study. Blue whales migrate through this area from June–November and peak in September. They typically sing during dawn and dusk (type "A" and "B" calls) and emit sounds that may be associated with feeding (type "D" calls) throughout the day (Oleson, Wiggins, & Hildebrand, 2007; Širovic et al., 2015). These temporal patterns do not match the diel patterns in low-frequency sound observed at these sites. Humpback whales arrive in late summer and therefore were not contributing to soundscapes during our study period. Fin whales are present year round but their peak calling period is from September–December (Širovic et al., 2015). Nonetheless, sampling additional sites and implementing metrics not based directly on SPLs within frequency bands will elucidate relationships between soundscapes and fish biodiversity more clearly.

Relatedly, while the methods employed here measure the main soundscape components, including shrimp snaps, fish choruses, and to a lesser extent pulsed fish and invertebrate sounds, these measurements likely unlock only a fraction of the informational content encoded in marine soundscapes. In order to advance our understanding of soundscape patterns and ecological relationships, it is important to 1) continue to develop automated sound-type based

measurements, 2) identify the species producing these different sound types, and 3) understand the environmental and physical conditions that include these measures. In addition to these sound-type based measurements, this study illustrates that the magnitude of diel patterns is also an ecologically-relevant component of soundscapes.

To conclude, this study demonstrates that marine soundscapes can indicate the condition of kelp forests. Furthermore, species associated with kelp forest regime shifts correlate strongly with soundscape variables. However, some of these relationships—like the inverse relationship between kelp cover and snapping shrimp activity—were unexpected, and illustrate how different disturbance pathways can cause distinct soundscape impacts. Based on this finding, it appears that not all ecological disturbance types cause a decrease in soundscape levels. If soundscapes are a reliable indicator of kelp forest condition, then managers have a tool to rapidly assess these habitats at far greater spatial and temporal scales than is currently possible with diver surveys.

Appendix C

Supporting Information for Soundscapes Indicate Kelp Forest Condition

S4.1 Selection of sound pressure level measurements

We measured sound pressure levels across three frequency bands in order to obtain indices of the diversity and abundance of animals that produced sound within these frequency ranges as well as habitat condition. To obtain one sound pressure level value per recording for each frequency band, it was necessary to average the 328 SPL values that were output from the Discrete Fourier Transform. There are several methods to average series of sound level measurements. To determine which method was suitable in this system, we tested the root-mean-square, median, 75th percentile, and 95th percentile and investigated how these values reflected biological patterns by inspecting comparing SPL values with spectrograms.

We selected the Q75 amplitude for several reasons. First, it effectively indicated chorusing events and also more discrete biological sound pulses. In contrast, the median mainly measured the ambient soundscape levels, while the root-mean-square and Q95 mainly reflected the high-amplitude sounds that may have been short-duration and not indicative of overall soundscape patterns. RMS in particular was highly biased by short-duration, high amplitude sound events, and as a result was incapable of measuring other aspects of the soundscape. While we are confident that this method is appropriate for measuring sound patterns in these frequency bands, one drawback is that it underrepresents the diel and between site variation, as median or RMS values had wider ranges than the Q75.

The following visualization illustrates the different qualities of these four measurements.
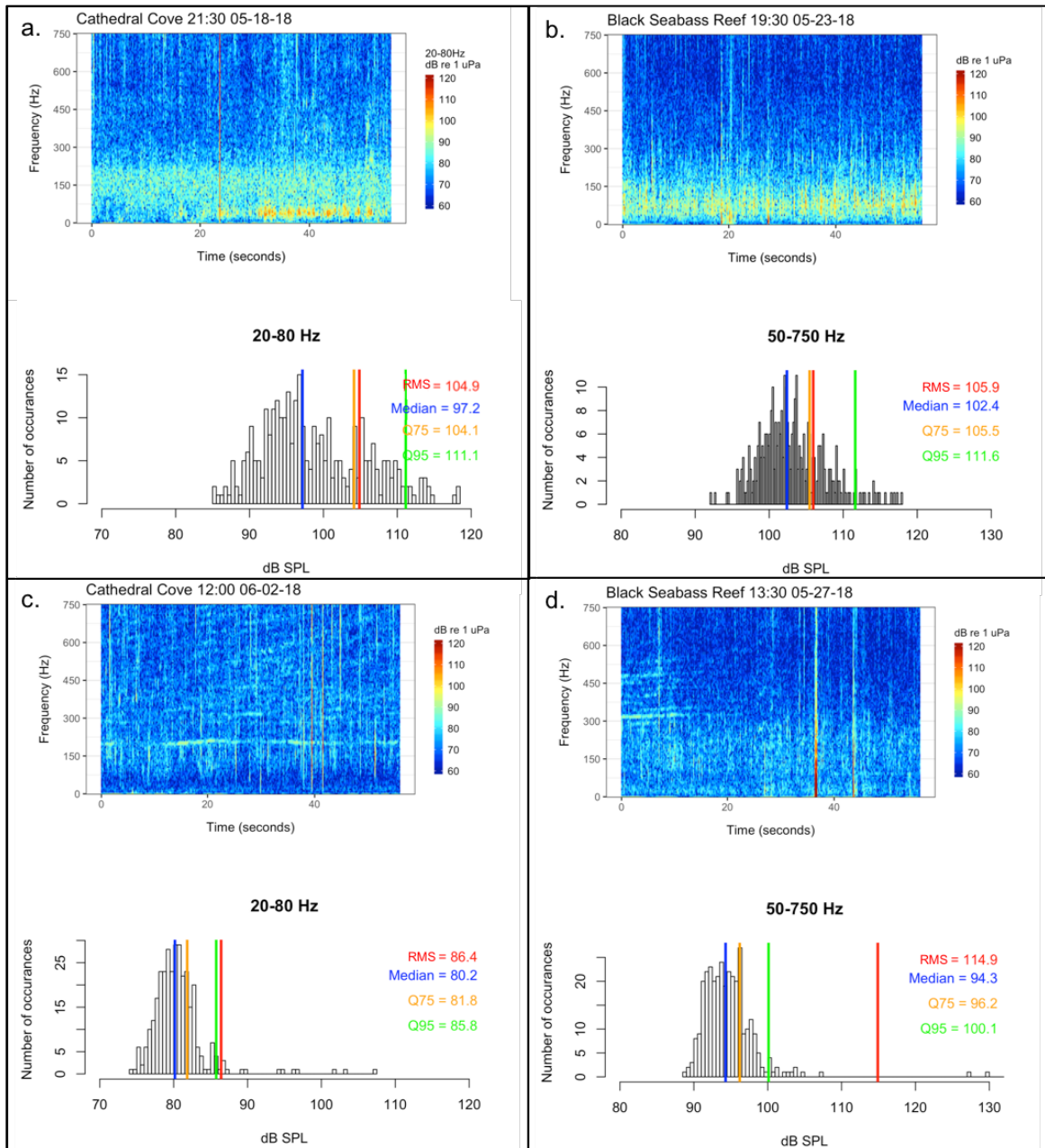
Figure 26: Spectrograms and corresponding histograms of the 328 sound pressure level values generated for each sound file. These four visualizations demonstrate why the Q75 measurement selected: a) More sporadic fish sounds start midway through the recording and influence Q75, Q95, and mean, but not median, b) continuous fish chorus influences all four measurement types, c) Though biological sounds in this recording are relatively low-intensity and sparse, a. single high-amplitude pulse results in higher RMS and Q95 values but not median and Q75 values, d) a single high-amplitude sound results in the very high RMS value, while the other three metrics better reflect the overall soundscape.

S4.1 Spectrograms of recordings containing boat noise
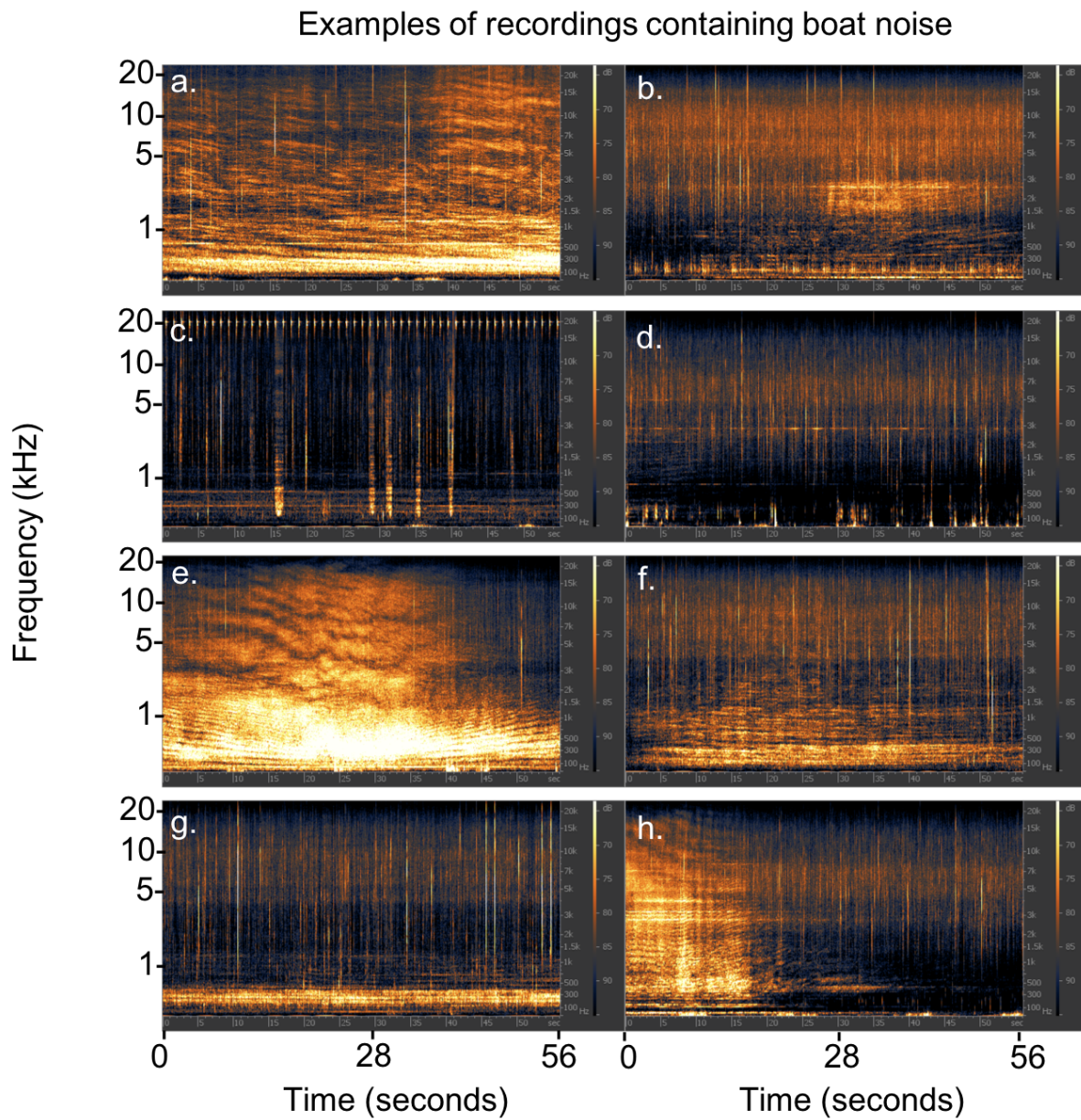
Figure 27: Spectrograms of eight recordings that contained boat noise, including a) Cathedral Cove (May 12, 2018, 14:45), b) Cathedral Cove (May 12, 2018, 14:45), c) Cavern Point (June 16, 2018, 12:00), d) Cathedral Cove (May 12, 2018, 09:45), e) East Fish Camp (June 20, 2018, 09:30), f) Black Seabass Reef (June 18, 2018, 15:00), g) Cavern Point (June 14, 2018, 10:45), h) Cavern Point (June 15, 2018, 12:45), i) Cathedral Cove (May 12, 2018, 14:45).

CHAPTER 5: **CONCLUSION**

1.19   Conclusion objectives

This dissertation aimed to assess biodiversity, habitat condition, and disturbance impacts in aquatic systems using emerging soundscape recording and analysis techniques. The overarching goal of this dissertation was to investigate how soundscapes could be used to measure short- and long-term environmental change. This Conclusion presents the major findings from each chapter with respect to this central objective, and discusses future directions for these projects and also the field of soundscape ecology as a whole.

1.20   Chapter 2 conclusions and future directions

1.20.1 **Rich soundscapes of tropical freshwater habitats**

The Costa Rican swamp we recorded for 21 days teemed with biological sounds. We identified eighteen sound-types likely produced by freshwater invertebrate species. This exploratory study illustrates the ample opportunity to assess biodiversity and habitat condition in tropical freshwater environments through sound. The primary finding here was that these wetland soundscapes were diverse and dynamic, even when compared to the air-borne sounds emanating from the adjacent forest. Several other patterns are worth noting, too. First, the structure of biological sounds within these soundscapes supports the acoustic niche hypothesis, which states that animals within a community will evolutionarily or behaviorally modify their acoustic signals to minimize overlap with other regularly occurring environmental and biological sounds. This hypothesis had been demonstrated in terrestrial (Villanueva-Rivera, 2014) and marine ecosystems (Ruppé et al., 2015), but not yet in a freshwater context. In Cantarana Swamp, we observed clear day-night partitioning between two sound types with very similar frequency ranges, "Geiger" and "Sine". Their non-overlapping diel patterns supported the temporal dimension of the ANH, which has been empirically demonstrated elsewhere (Hart, Hall, Ray, Beck, & Zook, 2015). Relatedly, there was a greater diversity of sound types within the 3-15 kHz range during the early morning (a pseudo "dawn chorus), potentially because sound types were less masked during this period than during the nighttime when "Sine" dominated the soundscapes.

Regarding the frequency dimension of the ANH, we did observe multiple sound types that exhibited frequency modulation, enabling them to temporarily exceed the background din of other sound types. Up until this point, frequency modulation was not believed to be an effective communicatory strategy in shallow-water freshwater habitats (Aiken, 1985b). This study offers preliminary evidence of frequency modulation in freshwater insects, potentially to aid in the differentiation between sounds of conspecifics and heterospecifics.

1.20.2 **Value of sound-type based approaches**

To analyze these soundscapes, we first created a taxonomy of all regularly occurring sound types based on their spectral and temporal features. Then we counted the occurrences of these sound types within each recording. This method yielded comprehensive and interpretable measurements of soundscape diversity and dynamics. Had we only utilized automated acoustic indices, most of the information regarding sound type diversity and diel patterns in community composition would have been lost. The sound-type based approach utilized in Chapter 2 is a robust way to analyze soundscapes from unexplored places. However, for large datasets, this method requires more analysis time than fully- or semi-automated approaches. However, new supervised and unsupervised automated sound-type based approaches are emerging, and offer much promise in increasing the potency of soundscape-based approaches (Lin et al. 2017).

1.20.3 **Future directions of freshwater soundscape monitoring and assessment:**

Since our study identified rich diversity and dynamics in these tropical wetland soundscapes, we would encourage future work that investigates the linkages between biodiversity, habitat condition, and soundscape diversity and dynamics in similar systems. To do so, we would recommend (1) ground-truthing soundscape data with in-situ biodiversity surveys, (2) matching sound types with species, (3) testing soundscape approaches across different freshwater ecosystems and disturbance gradients, and (4) determining annual and interannual dynamics.

1.21   Chapter 3 conclusions and future directions

1.21.1 Soundscape-disturbance relationships

Chapter 3 was one of two chapters to investigate how soundscapes may reflect impacts from ecological disturbance. By analyzing recordings before and after Hurricane Maria, we determined that Hurricane Maria had significant short-term impacts on the dry forest animal community of Guanica, Puerto Rico, and minimal impact on nearby coral reef community at La Parguera, Puerto Rico. This study demonstrated that the magnitude of soundscape alterations following an ecological disturbance can indicate the magnitude of impacts on the animal community. Furthermore, this study illustrated that long-term soundscape recording could be used to measure multiple dimensions of ecological resilience, including resistance to perturbation, the recovery trajectories of individual species, taxonomic groups, and animal communities, and how disturbance impacts vary across spatial scales. However, we did observe that lunar and seasonal patterns can confound the accurate measurement of recovery trajectories, especially if multi-year data is unavailable. In light of increasingly unpredictable disturbance phenomena, soundscape approaches can bolster our understanding of how ecosystems (and their resiliency) are changing.

1.21.2 Future directions for soundscape-disturbance research

Future work should investigate soundscape-disturbance relationships across ecosystems and disturbance types. Right now, the shape, slope, and consistency of these relationships are largely unknown. To determine these factors, we recommend that future studies evaluate multi-year soundscape response dynamics and validate soundscape data with *in situ* biodiversity surveys. Multi-year data is particularly useful to detangle temporal phenomena including lunar and seasonal cycles. Further research that develops methods to identify and decompose the different temporal components within a soundscape would advance soundscape-disturbance research. If successful, then we encourage the incorporation of long-term soundscape monitoring into pre-existing ecological monitoring stations like the National Ecological Observatory Network.

1.22   Chapter 4 conclusions and future directions

1.22.1 **Soundscape-biodiversity relationships**

We found strong correlations between soundscape and ecological variables in this kelp forest ecosystem. Fish abundance and density positively correlated with low-frequency sound pressure levels and the magnitude of low-frequency diel dynamics. Kelp cover, urchin density, and invertebrate density and richness were correlated with high-frequency soundscape metrics including snapping shrimp counts, peak snap frequency, and the magnitude of high frequency diel dynamics. Some of these results— such as the link between low-frequency sound levels and fish diversity—echo previous studies (Desiderà et al., 2019; Kaplan et al., 2018; Kennedy et al., 2010). Other findings, namely the inverse relationship between habitat condition and snapping shrimp snaps and high-frequency sound levels, are significant because they run counter to prior work but demonstrate counterintuitive ways that soundscapes can signify habitat change in marine systems.

1.22.2 **Soundscape-regime shift relationships**

Regime shift from kelp forest to urchin barren is driven by the relative abundance of sea urchins, sea urchin predators, and kelp. By measuring the sounds associated with different regime shift drivers, we were able to assess habitat condition. In these kelp forests, sites that were protected for longer had more kelp and fewer urchins, and less snapping shrimp activity, higher peak snap frequencies, and greater high-frequency diel dynamics. The higher snapping shrimp activity outside protected areas could have resulted a decrease in fish predator abundance in these heavily fished areas. In a prior study on kelp forest soundscapes, Rossi (2017) found that excessive nutrient pollution led to a reduction in snapping shrimp activity in kelp forests that shifted into algal turf habitats. This differing results between these two studies illustrates that regime shift pathways and types of disturbance may alter soundscapes in characteristic ways and may not always be associated with a decrease in biological sound levels.

1.22.3 **Future directions for Chapter 4**

We aim to deploy acoustic recorders in 2-8 more kelp forest monitoring sites within the Channel Islands. Increasing the sample size will enable us to determine whether the relationships between soundscape and biological variables that we found for these five sites apply to other kelp forest habitats. Secondly, we aim to improve our measurements of fish sounds. The low-frequency

portion of the soundscape at the Channel Islands is a complex combination of biological, anthropogenic, and geological sounds. While we found significant relationships between fish abundance and richness and low-frequency levels and dynamics, applying more sound-type based analyses will be necessary to increase confidence that biological sounds emanating from these kelp forest habitats are driving the soundscape metrics. Lastly, snapping shrimp activity could be a relatively straightforward way to obtain a snapshot of kelp forest condition, but currently we still need to improve our knowledge of how snapping shrimp activity varies across different spatial scales within kelp forests. One way to ascertain this would be to use marine gliders to survey the coasts of the Channel Islands. From these data, we would link snapping shrimp activity to benthic structure, ecological variables, and environmental variables. Another important future direction for this study, and for marine soundscape ecology in general, is matching sounds to species. In these Channel Island recordings, we were not able to identify the producers for most of the biological sounds. Developing databases of fish, invertebrate and marine mammal sounds will be critical to advancing this emerging discipline.

1.23   Broad dissertation conclusions

Biodiversity is decreasing at unprecedented rates, especially in aquatic ecosystems. In these difficult to access environments, emerging technologies can improve our understanding of environmental change within these systems. Modernizing the way that we assess natural systems is vital toward improving conservation efforts. Soundscape-based approaches are still in their early stages, especially in aquatic systems, but already they are providing information on habitat condition, biodiversity, and ecosystem resilience in vulnerable habitats. Going forward, much like weather stations improved our understanding of climate patterns, and satellites enabled us to measure land use change, the soundscape observatories could provide much-needed streams of data from which we can assess animal biodiversity and environmental change.

REFERENCES

Aalbers, S. A., & Drawbridge, M. A. (2008). White Seabass Spawning Behavior and Sound Production. *Transactions of the American Fisheries Society*, *137*(2), 542–550. https://doi.org/10.1577/T04-058.1

Adams, A. (2001). Effects of a hurricane on two assemblages of coral reef fishes: Multiple-year analysis reverses a false 'snapshot' interpretation. *Bulletin of Marine Science*, *69*(2), 341-356.

Adger, W. N., Hughes, T. P., Folke, C., Carpenter, S. R., & Rockström, J. (2005). Social-Ecological Resilience to Coastal Disasters. *Science*, *309*(5737), 1036–1039. https://doi.org/10.1126/science.1112122

Aiken, R. B. (1982). Shallow-water propagation of frequencies in aquatic insect sounds. Canadian Journal of Zoology, 60(12), 3459–3461. https://doi.org/10.1139/z82-436

Aiken, R. B. (1985a). Diel periodicity of song type in an aquatic insect (Palmacorixa buenoi: Heteroptera: Corixidae). Canadian Entomologist. Retrieved from http://agris.fao.org/agris-search/search.do?recordID= US201301450394

Aiken, R. B. (1985b). Sound Production by Aquatic Insects. *Biological Reviews*, *60*(2), 163–211. https://doi.org/10.1111/j.1469-185X.1985.tb00714.x

Álvarez-Yépiz, J. C., Martínez-Yrízar, A., & Fredericksen, T. S. (2018). Special Issue: Resilience of tropical dry forests to extreme disturbance events. *Forest Ecology and Management*, *426*, 1–6. https://doi.org/10.1016/j.foreco.2018.05.067

Anderson, C. B. (2018). Biodiversity monitoring, earth observations and the ecology of scale. *Ecology Letters*, *21*(10), 1572–1585. https://doi.org/10.1111/ele.13106

Anderson, K. A., Rountree, R. A., & Juanes, F. (2008). Soniferous Fishes in the Hudson River. *Transactions of the American Fisheries Society*, *137*(2), 616–626. https://doi.org/10.1577/T05-220.1

Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*(6), 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x

Angeler, D. G., Allen, C. R., Birgé, H. E., Drakare, S., McKie, B. G., & Johnson, R. K. (2014). Assessing and managing freshwater ecosystems vulnerable to environmental change. *AMBIO*, *43*(1), 113–125. https://doi.org/10.1007/s13280-014-0566-z

Arendt, W. J., Faaborg, J., Canals, M., & Bauer, J. (2015). *Bird Checklist Guánica Biosphere Reserve Puerto rico*. 32.

Askins, R. A., & Ewert, D. N. (1991). Impact of Hurricane Hugo on Bird Populations on St. John, U.S. Virgin Islands. *Biotropica*, *23*(4), 481–487. https://doi.org/10.2307/2388270

Au, W. W. L., & Hastings, M. C. (2008). Introduction. In W. W. L. Au & M. C. Hastings (Eds.), *Principles of Marine Bioacoustics* (pp. 3–25). https://doi.org/10.1007/978-0-387-78365-9_1

Bakdash, J. Z., & Marusich, L. R. (2017). Repeated Measures Correlation. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.00456

Bates, Douglas, Maechler, Martin, Bolker, Ben , Walker, Steve (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Baylis, A. M. M., Orben, R. A., Arnould, J. P. Y., Christiansen, F., Hays, G. C., & Staniland, I. J. (2015). Disentangling the cause of a catastrophic population decline in a large marine mammal. *Ecology*, *96*(10), 2834–2847. https://doi.org/10.1890/14-1948.1

Bellisario, K. M., & Pijanowski, B. C. (2019). Contributions of MIR to soundscape ecology. Part I: Potential methodological synergies. *Ecological Informatics*, *51*, 96–102. https://doi.org/10.1016/j.ecoinf.2019.02.009

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833. https://doi.org/10.1038/nature02691

Bennett, E. M., Cumming, G. S., & Peterson, G. D. (2005). A Systems Model Approach to Determining Resilience Surrogates for Case Studies. *Ecosystems*, *8*(8), 945–957. https://doi.org/10.1007/s10021-005-0141-3

Bertucci, F., Parmentier, E., Lecellier, G., Hawkins, A. D., & Lecchini, D. (2016). Acoustic indices provide information on the status of coral reefs: An example from Moorea Island in the South Pacific. *Scientific Reports*, *6*. https://doi.org/10.1038/srep33326

Bertucci, F., Parmentier, E., Berten, L., Brooker, R. M., & Lecchini, D. (2015). Temporal and Spatial Comparisons of Underwater Sound Signatures of Different Reef Habitats in Moorea Island, French Polynesia. *PLOS ONE*, *10*(9), e0135733. https://doi.org/10.1371/journal.pone.0135733

Bhaskar, R., Arreola, F., Mora, F., Martinez-Yrizar, A., Martinez-Ramos, M., & Balvanera, P. (2018). Response diversity and resilience to extreme events in tropical dry secondary forests. *Forest Ecology and Management*, *426*, 61–71. https://doi.org/10.1016/j.foreco.2017.09.028

Biggs, C. R., Lowerre-Barbieri, S. K., & Erisman, B. (2018). Reproductive resilience of an estuarine fish in the eye of a hurricane. *Biology Letters*, *14*(11), 20180579. https://doi.org/10.1098/rsbl.2018.0579

Boelman, N. T., Asner, G. P., Hart, P. J., & Martin, R. E. (2007). Multi-trophic invasion resistance in Hawaii: Bioacoustics, field surveys, and airborne remote sensing. Ecological Applications, 17(8), 2137–2144. https://doi.org/10.1890/07-0004.1

Bohnenstiehl, D. R., Lillis, A., & Eggleston, D. B. (2016). The Curious Acoustic Behavior of Estuarine Snapping Shrimp: Temporal Patterns of Snapping Shrimp Sound in Sub-Tidal Oyster Reef Habitat. *PLoS ONE*, *11*(1). https://doi.org/10.1371/journal.pone.0143691

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the 'deep reef refugia' hypothesis: Focus on Caribbean reefs. *Coral Reefs*, *29*(2), 309–327. https://doi.org/10.1007/s00338-009-0581-x

Bongaerts, Pim, & Smith, T. B. (2019). Beyond the "Deep Reef Refuge" Hypothesis: A Conceptual Framework to Characterize Persistence at Depth. In Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), *Mesophotic Coral Ecosystems* (pp. 881–895). https://doi.org/10.1007/978-3-319-92735-0_45

Borker, A. L., McKown, M. W., Ackerman, J. T., Eagles-Smith, C. A., Tershy, B. R., & Croll, D. A. (2014). Vocal activity as a low cost and scalable index of seabird colony size. *Conservation Biology: The Journal of the Society for Conservation Biology*, *28*(4), 1100–1108. https://doi.org/10.1111/cobi.12264

Brekhovskikh, L. M., Lysanov, Yu. P., & Beyer, R. T. (1991). Fundamentals of Ocean Acoustics. *The Journal of the Acoustical Society of America*, *90*(6), 3382–3383. https://doi.org/10.1121/1.401411

Brinley Buckley, E. M. (2016). *Applications of Time-lapse Imagery for Monitoring and Illustrating Ecological Dynamics in a Water-stressed System*.

Brinley Buckley, E. M., Caven, A. J., Gottesman, B. L., Harner, M. J., Pijanowski, B. C., & Forsberg, M. L. (2018). Assessing biological and environmental effects of a total solar eclipse with passive multimodal technologies. *Ecological Indicators*, *95*, 353–369. https://doi.org/10.1016/j.ecolind.2018.07.017

Burivalova, Z., Towsey, M., Boucher, T., Truskinger, A., Apelis, C., Roe, P., & Game, E. T. (2018). Using soundscapes to detect variable degrees of human influence on tropical forests in Papua New Guinea. *Conservation Biology*, *32*(1), 205–215. https://doi.org/10.1111/cobi.12968

Butchart, S. H. M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J. P. W., Almond, R. E. A., … Watson, R. (2010). Global Biodiversity: Indicators of Recent Declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Butler, J., Stanley, J. A., & Butler, M. J. (2016). Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. *Journal of Experimental Marine Biology and Ecology*, *479*(Supplement C), 89–96. https://doi.org/10.1016/j.jembe.2016.03.006

Buxton, R. T., Agnihotri, S., Robin, V. V., Goel, A., & Balakrishnan, R. (2018). Acoustic indices as rapid indicators of avian diversity in different land-use types in an Indian biodiversity hotspot. *Journal of Ecoacoustics*, *2*, GWPZVD. https://doi.org/10.22261/JEA.GWPZVD

Buxton, R. T., Brown, E., Sharman, L., Gabriele, C. M., & McKenna, M. F. (2016). Using bioacoustics to examine shifts in songbird phenology. *Ecology and Evolution*, *6*(14), 4697–4710. https://doi.org/10.1002/ece3.2242

Buxton, R. T., McKenna, M. F., Clapp, M., Meyer, E., Stabenau, E., Angeloni, L. M., … Wittemyer, G. (2018). Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. *Conservation Biology*, *0*(ja). https://doi.org/10.1111/cobi.13119

Caldwell, D. K., & Caldwell, M. C. (1969). *Echolocation-type signals by two dolphins, genus Sotalia* (No. TR-4). Retrieved from Los Angeles County Museum Calif. website: https://apps.dtic.mil/docs/citations/AD0693198

Cangelosi, R., & Goriely, A. (2007). Component retention in principal component analysis with application to cDNA microarray data. *Biology Direct*, *2*, 2. https://doi.org/10.1186/1745-6150-2-2

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59–67. https://doi.org/10.1038/nature11148

Carpenter, S. R., & Brock, W. A. (2006). Rising variance: A leading indicator of ecological transition. *Ecology Letters*, *9*(3), 311–318. https://doi.org/10.1111/j.1461-0248.2005.00877.x

Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, R., Brock, W. A., Cline, T., … Weidel, B. (2011). Early Warnings of Regime Shifts: A Whole-Ecosystem Experiment. *Science*, *332*(6033), 1079–1082. https://doi.org/10.1126/science.1203672

Caselle, J. E., Rassweiler, A., Hamilton, S. L., & Warner, R. R. (2015). Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Scientific Reports*, *5*, 14102. https://doi.org/10.1038/srep14102

Chapin III, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., … Díaz, S. (2000). Consequences of changing biodiversity. *Nature*, *405*(6783), 234–242. https://doi.org/10.1038/35012241

Chillo, V., Anand, M., & Ojeda, R. A. (2011). Assessing the Use of Functional Diversity as a Measure of Ecological Resilience in Arid Rangelands. *Ecosystems*, *14*(7), 1168–1177. https://doi.org/10.1007/s10021-011-9475-1

Chylek, P., & Lesins, G. (2008). Multidecadal variability of Atlantic hurricane activity: 1851–2007. *Journal of Geophysical Research: Atmospheres*, *113*(D22). https://doi.org/10.1029/2008JD010036

Clark, B. L. F., & Allen, L. G. (2018). Field Observations on Courtship and Spawning Behavior of the Giant Sea Bass, Stereolepis gigas. *Copeia*, *106*(1), 171–179. https://doi.org/10.1643/CE-17-620

Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R., & Baillie, J. E. M. (2009). Monitoring change in vertebrate abundance: The living planet index. *Conservation Biology: The Journal of the Society for Conservation Biology*, *23*(2), 317–327. https://doi.org/10.1111/j.1523-1739.2008.01117.x

Coquereau, L., Grall, J., Chauvaud, L., Gervaise, C., Clavier, J., Jolivet, A., & Iorio, L. D. (2016). Sound production and associated behaviours of benthic invertebrates from a coastal habitat in the north-east Atlantic. *Marine Biology*, *163*(5), 127. https://doi.org/10.1007/s00227-016-2902-2

Coquereau, L., Lossent, J., Grall, J., & Chauvaud, L. (2017). Marine soundscape shaped by fishing activity. *Open Science*, *4*(1), 160606. https://doi.org/10.1098/rsos.160606

Corbet, P. S. (1966). Diel patterns of mosquito activity in a high arctic locality: Hazen Camp, Ellesmere Island, N.W.T. The Canadian Entomologist, 98(12), 1238–1252. https://doi.org/10.4039/Ent981238-12

Daily, G. C. (1997). *Nature's Services: Societal dependence on natural ecosystems.* Retrieved from http://agris.fao.org/agris-search/search.do?recordID=XE20122002413

Daily, Gretchen Cara. (2012). *Nature's Services: Societal Dependence On Natural Ecosystems*. Island Press.

Daniel, W. W. (1978). Applied nonparametric statistics. Houghton Mifflin. Retrieved from http://agris.fao.org/agris-search/search.do?recordID= US201300557893

Daniels, A. E., & Cumming, G. S. (2008). Conversion or conservation? Understanding wetland change in northwest Costa Rica. Ecological Applications, 18(1), 49–63. https://doi.org/10.1890/06-1658.1

Davies, D. H. (1968). *Statistical analysis of the relation between kelp harvesting and sportfishing in the California kelp beds.* (No. 139; pp. 151–212). California Deptartment of Fish and Game.

Davis, G. E., Richards, D. V., & Kushner, D. (1996). *Kelp forest monitoring design review* (No. 96–01).

De la Rosa, C. L. (2017a). *Re: Question about La Selva Insect Diversity.*

De la Rosa, C. L. (2017b, January 26). *Re: Purdue Soundscapes: La Selva Frogs and Aquatic Insects Question*.

Deichmann, J. L., Hernández-Serna, A., Delgado C., J. A., Campos-Cerqueira, M., & Aide, T. M. (2017). Soundscape analysis and acoustic monitoring document impacts of natural gas exploration on biodiversity in a tropical forest. *Ecological Indicators*, *74*(Supplement C), 39–48. https://doi.org/10.1016/j.ecolind.2016.11.002

Depraetere, M., Pavoine, S., Jiguet, F., Gasc, A., Duvail, S., & Sueur, J. (2012). Monitoring animal diversity using acoustic indices: Implementation in a temperate woodland. *Ecological Indicators*, *13*(1), 46–54. https://doi.org/10.1016/j.ecolind.2011.05.006

Desiderà, Elena, Guidetti, P., Panzalis, P., Navone, A., Valentini-Poirrier, C.-A., Boissery, P., … Iorio, L. D. (2019). Acoustic fish communities: Sound diversity of rocky habitats reflects fish species diversity. *Marine Ecology Progress Series*, *608*, 183–197. https://doi.org/10.3354/meps12812

Desjonquères, C., Rybak, F., Castella, E., Llusia, D., & Sueur, J. (2018). Acoustic communities reflects lateral hydrological connectivity in riverine floodplain similarly to macroinvertebrate communities. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-31798-4

Desjonquères, C., Rybak, F., Depraetere, M., Gasc, A., Le Viol, I., Pavoine, S., & Sueur, J. (2015). First description of underwater acoustic diversity in three temperate ponds. *PeerJ*, *3*, e1393. https://doi.org/10.7717/peerj.1393

Díaz, S., Settele, J., Brondízio, E., Ngo, H. T., Guèze, M., Agard, J., … Vilá, B. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. 44.

Dickey, D. A., & Pantula, S. G. (1987). Determining the order of differencing in autoregressive processes. Journal of Business & Economic Statistics, 5(4), 455–461. https://doi.org/10.1080/07350015.1987. 10509614

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Donihue, C. M., Herrel, A., Fabre, A.-C., Kamath, A., Geneva, A. J., Schoener, T. W., … Losos, J. B. (2018). Hurricane-induced selection on the morphology of an island lizard. *Nature*, *560*(7716), 88. https://doi.org/10.1038/s41586-018-0352-3

Donnelly, M. A., & Guyer, C. (1994). Patterns of reproduction and habitat use in an assemblage of Neotropical hylid frogs. *Oecologia*, 98(3–4), 291–302. https://doi.org/10.1007/BF00324217

Drosopoulos, S., & Claridge, M. F. (2005). *Insect Sounds and Communication: Physiology, Behaviour, Ecology, and Evolution*. CRC Press.

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., … Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. https://doi.org/10.1017/S1464793105006950

Eichinski, P., Sitbon, L., & Roe, P. (2015). Clustering Acoustic Events in Environmental Recordings for Species Richness Surveys. *Procedia Computer Science*, *51*(Supplement C), 640–649. https://doi.org/10.1016/j.procs.2015.05.178

Elise, S., Urbina-Barreto, I., Pinel, R., Mahamadaly, V., Bureau, S., Penin, L., … Bruggemann, J. H. (2019). Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs. *Ecological Indicators*, *107*, 105623. https://doi.org/10.1016/j.ecolind.2019.105623

Ellison, A. M. (2004). Wetlands of Central America. *Wetlands Ecology and Management*, 12(1), 3–55. https://doi.org/10.1023/B:WETL. 0000016809.95746.b1

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, *1*(9), 488–494. https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2

European Commission. (2019). *The EU approach to tackle pollinator decline.* Retrieved September 19, 2019, from https://ec.europa.eu/environment/nature/conservation/species/pollinators/index_en.htm

Ewel, J. J., & Whitmore, J. L. (1973). The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands. *USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018*, *018*. Retrieved from https://www.fs.usda.gov/treesearch/pubs/5551

Feng, Y., Negron-Juarez, R. I., Patricola, C. M., Collins, W. D., Uriarte, M., Hall, J. S., … Chambers, J. Q. (2018). *Rapid remote sensing assessment of impacts from Hurricane Maria on forests of Puerto Rico* (No. e26597v1). https://doi.org/10.7287/peerj.preprints.26597v1

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., … Snyder, P. K. (2005). Global Consequences of Land Use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., & Holling, C. S. (2004). Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 557–581. https://doi.org/10.1146/annurev.ecolsys.35.021103.105711

Francomano, D., Gottesman, B. L., Pijanowski, B. C. *In press.* Biogeographical and analytical implications of temporal variability in geographically diverse soundscapes. *Ecological Indicators.*

Freeman, L. A., & Freeman, S. E. (2016). Rapidly obtained ecosystem indicators from coral reef soundscapes. *Marine Ecology Progress Series*, *561*, 69–82. https://doi.org/10.3354/meps11938

Freeman, S. E., Rohwer, F. L., D'Spain, G. L., Friedlander, A. M., Gregg, A. K., Sandin, S. A., & Buckingham, M. J. (2014). The origins of ambient biological sound from coral reef ecosystems in the Line Islands archipelago. The Journal of the Acoustical Society of America, 135(4), 1775– 1788. https://doi.org/10.1121/1.4865922

Fuller, S., Axel, A. C., Tucker, D., & Gage, S. H. (2015). Connecting soundscape to landscape: Which acoustic index best describes landscape configuration? Ecological Indicators, 58, 207–215. https://doi.org/10. 1016/j.ecolind.2015.05.057

Gage, S. H., & Axel, A. C. (2014). Visualization of temporal change in soundscape power of a Michigan lake habitat over a 4-year period. *Ecological Informatics*, *21*, 100–109. https://doi.org/10.1016/j.ecoinf.2013.11.004

Gasc, A., Pavoine, S., Lellouch, L., Grandcolas, P., & Sueur, J. (2015). Acoustic indices for biodiversity assessments: Analyses of bias based on simulated bird assemblages and recommendations for field surveys. *Biological Conservation*, 191, 306–312. https://doi.org/10.1016/j.biocon.2015.06.018

Gasc, A., Sueur, J., Pavoine, S., Pellens, R., & Grandcolas, P. (2013). Biodiversity sampling using a global acoustic approach: Contrasting sites with microendemics in New Caledonia. *PLoS ONE*, 8(5), e65311. https://doi.org/10.1371/journal.pone.0065311

Gasc, A., Gottesman, B. L., Francomano, D., Jung, J., Durham, M., Mateljak, J., & Pijanowski, B. C. (2018). Soundscapes reveal disturbance impacts: Biophonic response to wildfire in the Sonoran Desert Sky Islands. *Landscape Ecology*, *33*(8), 1399–1415. https://doi.org/10.1007/s10980-018-0675-3

Gaston, K. J., & Spicer, J. I. (2013). *Biodiversity: An Introduction*. John Wiley & Sons.

Gerhardt, H. C., & Huber, F. (2002). *Acoustic communication in insects and anurans: Common problems and diverse solutions.* Chicago, IL: University of Chicago Press.

Ghoul, A., & Reichmuth, C. (2012). Sound production and reception in southern sea otters (Enhydra lutris nereis). *Advances in Experimental Medicine and Biology*, *730*, 157–159. https://doi.org/10.1007/978-1-4419-7311-5_35

Gibb, R., Browning, E., Glover-Kapfer, P., & Jones, K. E. (2019). Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. *Methods in Ecology and Evolution*, *10*(2), 169–185. https://doi.org/10.1111/2041-210X.13101

Gleason, M., McCreary, S., Miller-Henson, M., Ugoretz, J., Fox, E., Merrifield, M., … Hoffman, K. (2010). Science-based and stakeholder-driven marine protected area network planning: A successful case study from north central California. *Ocean & Coastal Management*, *53*(2), 52–68. https://doi.org/10.1016/j.ocecoaman.2009.12.001

Gómez, W. E., Isaza, C. V., & Daza, J. M. (2018). Identifying disturbed habitats: A new method from acoustic indices. *Ecological Informatics*, *45*, 16–25. https://doi.org/10.1016/j.ecoinf.2018.03.001

Goold, J. C. (1996). Acoustic Assessment of Populations of Common Dolphin Delphinus Delphis In Conjunction With Seismic Surveying. *Journal of the Marine Biological Association of the United Kingdom*, *76*(3), 811–820. https://doi.org/10.1017/S0025315400031477

Gordon, T. A. C., Harding, H. R., Wong, K. E., Merchant, N. D., Meekan, M. G., McCormick, M. I., … Simpson, S. D. (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. *Proceedings of the National Academy of Sciences*, *115*(20), 5193–5198. https://doi.org/10.1073/pnas.1719291115

Gottesman, B. L., Francomano, D., Zhao, Z., Bellisario, K., Ghadiri, M., Broadhead, T., …
Pijanowski, B. C. (2018). Acoustic monitoring reveals diversity and surprising dynamics
in tropical freshwater soundscapes. *Freshwater Biology*, *0*(0).
https://doi.org/10.1111/fwb.13096

Hafner, S. D., & Katz, J. (2017). *MonitoR: Acoustic template detection in R*. Retrieved from
http://www.uvm.edu/rsenr/vtcfwru/R/?Page=monitoR/monitoR.htm

Haines-Young, R., & Potschin, M. (2010). The links between biodiversity, ecosystem services
and human well-being. In D. G. Raffaelli & C. L. J. Frid (Eds.), *Ecosystem Ecology* (pp.
110–139). https://doi.org/10.1017/CBO9780511750458.007

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., … Kroon, H. de.
(2017). More than 75 percent decline over 27 years in total flying insect biomass in
protected areas. *PLOS ONE*, *12*(10), e0185809.
https://doi.org/10.1371/journal.pone.0185809

Harris, S. A., Shears, N. T., & Radford, C. A. (2016). Ecoacoustic indices as proxies for
biodiversity on temperate reefs. *Methods in Ecology and Evolution*, *7*(6), 713–724.
https://doi.org/10.1111/2041-210X.12527

Hart, P. J., Hall, R., Ray, W., Beck, A., & Zook, J. (2015). Cicadas impact bird communication
in a noisy tropical rainforest. *Behavioral Ecology*, *26*(3), 839–842.
https://doi.org/10.1093/beheco/arv018

Hartigan, J. A., & Wong, M. A. (1979). Algorithm AS 136: A K-Means Clustering Algorithm.
Journal of the Royal Statistical Society. Series C (Applied Statistics), *28*(1), 100–108.
https://doi.org/10.2307/2346830

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean.
Marine Ecology Progress Series, *395*, 5–20. https://doi.org/10.3354/meps08353

Hill, A. P., Prince, P., Covarrubias, E. P., Doncaster, C. P., Snaddon, J. L., & Rogers, A. (2018).
AudioMoth: Evaluation of a smart open acoustic device for monitoring biodiversity and
the environment. *Methods in Ecology and Evolution*, *9*(5), 1199–1211.
https://doi.org/10.1111/2041-210X.12955

Hobday, A. J., Tegner, M. J., & Haaker, P. L. (2000). Over-exploitation of a broadcast spawning
marine invertebrate: Decline of the white abalone. *Reviews in Fish Biology and Fisheries*,
10(4), 493–514. https://doi.org/10.1023/A:1012274101311

Holland, G., & Bruyère, C. L. (2014). Recent intense hurricane response to global climate change. *Climate Dynamics*, *42*(3), 617–627. https://doi.org/10.1007/s00382-013-1713-0

Holling, C. S. (1973). Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics*, *4*(1), 1–23. https://doi.org/10.1146/annurev.es.04.110173.000245

Holm, J. A., Van Bloem, S. J., Larocque, G. R., & Shugart, H. H. (2017). Shifts in biomass and productivity for a subtropical dry forest in response to simulated elevated hurricane disturbances. *Environmental Research Letters*, *12*(2), 025007. https://doi.org/10.1088/1748-9326/aa583c

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., … Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), 373–377. https://doi.org/10.1038/nature21707

HTI-96-MIN (n.d.). Long Beach, MS: High Tech, Inc.

Jansson, A. (1968). Diel periodicity of the stridulating activity of Callicorixa producta Reuter (Heteroptera, Corixidae). *Annales Zoologici Fennici*, 5(3), 265–269.

Ibara, R. M., Penny, L. T., Ebeling, A. W., van Dykhuizen, G., & Cailliet, G. (1983). The mating call of the plainfin midshipman fish, Porichthys notatus. In D. L. G. Noakes, D. G. Lindquist, G. S. Helfman, & J. A. Ward (Eds.), *Predators and prey in fishes: Proceedings of the 3rd biennial conference on the ethology and behavioral ecology of fishes, held at Normal, Illinois, U.S.A., May 19–22, 1981* (pp. 205–212). https://doi.org/10.1007/978-94-009-7296-4_22

Imbert, D., & Portecop, J. (2008). Hurricane disturbance and forest resilience: Assessing structural vs. functional changes in a Caribbean dry forest. *Forest Ecology and Management*, *255*(8), 3494–3501. https://doi.org/10.1016/j.foreco.2008.02.030

Indeck, K. L., Simard, P., Gowans, S., Lowerre-Barbieri, S., & Mann, D. A. (2015). A severe red tide (Tampa Bay, 2005) causes an anomalous decrease in biological sound. *Royal Society Open Science*, *2*(9). https://doi.org/10.1098/rsos.150337

IZotope RX 4 Advanced (Version 4.01.512). (2014).

IZotope RX (Version 4). (2014). Combridge, MA: iZotope, Inc.

Jansson, A. R. I. (1971). *Stridulation and its significance in the waterbug genus Cenocorixa* (Doctoral dissertation, University of British Columbia)

Jansson, A. (1973). Diel periodicity of stridulating activity in the genus Cenocorixa (Hemiptera, Corixidae). *Annales Zoologici Fennici,* 10(2), 378–383.

Jansson, A. (1974). Annual periodicity of male stridulation in the genus Cenocorixa (Hemiptera, Corixidae). *Freshwater Biology*, 4(1), 93–98. https://doi.org/10.1111/j.1365-2427.1974.tb00941.x

Jézéquel, Y., Bonnel, J., Coston-Guarini, J., & Chauvaud, L. (2019). Revisiting the bioacoustics of European spiny lobsters Palinurus elephas: Comparison of antennal rasps in tanks and in situ. *Marine Ecology Progress Series*, *615*, 143–157. https://doi.org/10.3354/meps12935

Jézéquel, Y., Bonnel, J., Coston-Guarini, J., Guarini, J.-M., & Chauvaud, L. (2018). Sound characterization of the European lobster Homarus gammarus in tanks. *Aquatic Biology*, *27*, 13–23. https://doi.org/10.3354/ab00692

Johnson, R. K., Wiederholm, T., & Rosenberg, D. M. (1993). *Freshwater Biomonitoring Using Individual Organisms, Populations, and Species Assemblages of Benthic Macroinvertebrates*. 128.

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., … Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, *14*(7), 369–378. https://doi.org/10.1002/fee.1311

Kaplan, M. B., Lammers, M. O., Zang, E., & Aran Mooney, T. (2018). Acoustic and biological trends on coral reefs off Maui, Hawaii. *Coral Reefs*, *37*(1), 121–133. https://doi.org/10.1007/s00338-017-1638-x

Kaplan, M. B., Mooney, T. A., Partan, J. W., & Solow, A. R. (2015). *Coral reef species assemblages are associated with ambient soundscapes*. Retrieved from http://darchive.mblwhoilibrary.org/handle/1912/7527

Kaufman, L. S. (1983). Effects of Hurricane Allen on reef fish assemblages near Discovery Bay, Jamaica. *Coral Reefs*, *2*(1), 43–47. https://doi.org/10.1007/BF00304731

Kennedy, E. V., Holderied, M. W., Mair, J. M., Guzman, H. M., & Simpson, S. D. (2010). Spatial patterns in reef-generated noise relate to habitats and communities: Evidence from a Panamanian case study. *Journal of Experimental Marine Biology and Ecology*, *395*(1–2), 85–92. https://doi.org/10.1016/j.jembe.2010.08.017

Kenner, M. C. (1992). Population dynamics of the sea urchin Strongylocentrotus purpuratus in a Central California kelp forest: Recruitment, mortality, growth, and diet. *Marine Biology*, *112*(1), 107–118. https://doi.org/10.1007/BF00349734

Kissick, A. L., Dunning, J. B., Fernandez-Juricic, E., & Holland, J. D. (2018). Different responses of predator and prey functional diversity to fragmentation. *Ecological Applications*, *28*(7), 1853–1866. https://doi.org/10.1002/eap.1780

Kitting, C. L. (1979). The use of feeding noises to determine the algal foods being consumed by individual intertidal molluscs. *Oecologia*, *40*(1), 1–17. https://doi.org/10.1007/BF00388806

Knight, E., Hannah, K., Foley, G., Scott, C., Brigham, R., & Bayne, E. (2017). Recommendations for acoustic recognizer performance assessment with application to five common automated signal recognition programs. *Avian Conservation and Ecology*, *12*(2). https://doi.org/10.5751/ACE-01114-120214

Knowlton, N., & Jackson, J. B. C. (2008). Shifting Baselines, Local Impacts, and Global Change on Coral Reefs. *PLOS Biology*, *6*(2), e54. https://doi.org/10.1371/journal.pbio.0060054

Knutson, T. R., McBride, J. L., Chan, J., Emanuel, K., Holland, G., Landsea, C., … Sugi, M. (2010). Tropical cyclones and climate change. *Nature Geoscience*, *3*(3), 157–163. https://doi.org/10.1038/ngeo779

Krause, B. L. (1993). The niche hypothesis: A virtual symphony of animal sounds, the origins of musical expression and the health of habitats. *The Soundscape Newsletter*, 6, 6–10.

Kriegisch, N., Reeves, S. E., Flukes, E. B., Johnson, C. R., & Ling, S. D. (2019). Drift-kelp suppresses foraging movement of overgrazing sea urchins. *Oecologia*, *190*(3), 665–677. https://doi.org/10.1007/s00442-019-04445-6

Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., … Byrnes, J. E. K. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences*, *113*(48), 13785–13790. https://doi.org/10.1073/pnas.1606102113

Kushner, D. J., Rassweiler, A., McLaughlin, J. P., & Lafferty, K. D. (2013). A multi-decade time series of kelp forest community structure at the California Channel Islands. *Ecology*, *94*(11), 2655–2655. https://doi.org/10.1890/13-0562R.1

Kushner, D., & Sprague, J. (2018). *Channel Islands National Park Kelp Forest Monitoring Handbook*. Channel Islands National Park.

McDade, L. A., Bawa, K. S., Hespenheide, H. A., & Hartshorn, G. S. (Eds.). (1994). *La Selva: ecology and natural history of a neotropical rain forest*. University of Chicago Press.

Lambert, G. I., Jennings, S., Kaiser, M. J., Davies, T. W., & Hiddink, J. G. (2014). Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. *Journal of Applied Ecology*, *51*(5), 1326–1336. https://doi.org/10.1111/1365-2664.12277

Larsen, O. N., & Radford, C. (2018). Acoustic Conditions Affecting Sound Communication in Air and Underwater. In H. Slabbekoorn, R. J. Dooling, A. N. Popper, & R. R. Fay (Eds.), *Effects of Anthropogenic Noise on Animals* (Vol. 66, pp. 109–144). https://doi.org/10.1007/978-1-4939-8574-6_5

Lee, B. P. Y.-H., Davies, Z. G., & Struebig, M. J. (2017). Smoke pollution disrupted biodiversity during the 2015 El Niño fires in Southeast Asia. *Environmental Research Letters*, *12*(9), 094022. https://doi.org/10.1088/1748-9326/aa87ed

Lillis, A., Eggleston, D., & Bohnenstiehl, D. (2014). Estuarine soundscapes: Distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. *Marine Ecology Progress Series*, *505*, 1–17. https://doi.org/10.3354/meps10805

Lin, T.-H., Fang, S.-H., & Tsao, Y. (2017). Improving biodiversity assessment via unsupervised separation of biological sounds from long-duration recordings. *Scientific Reports*, *7*(1), 4547. https://doi.org/10.1038/s41598-017-04790-7

Lindseth, A., & Lobel, P. (2018). Underwater Soundscape Monitoring and Fish Bioacoustics: A Review. *Fishes*, *3*(3), 36. https://doi.org/10.3390/fishes3030036

Ling, S. D., Scheibling, R. E., Rassweiler, A., Johnson, C. R., Shears, N., Connell, S. D., … Johnson, L. E. (2015). Global regime shift dynamics of catastrophic sea urchin overgrazing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659). https://doi.org/10.1098/rstb.2013.0269

Linke, S., Gifford, T., Desjonquères, C., Tonolla, D., Aubin, T., Barclay, L., … Sueur, J. (2018). Freshwater ecoacoustics as a tool for continuous ecosystem monitoring. *Frontiers in Ecology and the Environment*, *16*(4), 231–238. https://doi.org/10.1002/fee.1779

Lister, B., & Garcia, A. (2019). Reply to Willig et al.: Long-term population trends in the Luquillo Rainforest. *Proceedings of the National Academy of Sciences*, *116*(25), 12145–12146. https://doi.org/10.1073/pnas.1904582116

Lloyd, J. D., Rimmer, C. C., & Faría, J. A. S. (2019). Short-term effects of hurricanes Maria and Irma on forest birds of Puerto Rico. *BioRxiv*, 578336. https://doi.org/10.1101/578336

Locascio, J. V., & Mann, D. A. (2005). Effects of Hurricane Charley on fish chorusing. *Biology Letters*, *1*(3), 362–365. https://doi.org/10.1098/rsbl.2005.0309

Lohmann, K. J., Lohmann, C. M. F., & Endres, C. S. (2008). The sensory ecology of ocean navigation. *Journal of Experimental Biology*, *211*(11), 1719–1728. https://doi.org/10.1242/jeb.015792

Loreau, M., Naeem, S., & Inchausti, P. (2002). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press.

Lotze, H. K., Coll, M., Magera, A. M., Ward-Paige, C., & Airoldi, L. (2011). Recovery of marine animal populations and ecosystems. *Trends in Ecology & Evolution*, *26*(11), 595–605. https://doi.org/10.1016/j.tree.2011.07.008

Luczkovich, J. J., Mann, D. A., & Rountree, R. A. (2008). Passive acoustics as a tool in fisheries science. Transactions of the American Fisheries Society, 137(2), 533–541. https://doi.org/10.1577/T06-258.1

Lugo, A. E., Gonzalez-Liboy, J. A., Cintron, B., & Dugger, K. (1978). Structure, Productivity, and Transpiration of a Subtropical Dry Forest in Puerto Rico. *Biotropica*, *10*(4), 278–291. https://doi.org/10.2307/2387680

Lynch, J. F. (1991). Effects of Hurricane Gilbert on Birds in a Dry Tropical Forest in the Yucatan Peninsula. *Biotropica*, *23*(4), 488–496. https://doi.org/10.2307/2388271

MATLAB. (Version R2015a). Natick, MA: The MathWorks, Inc. McDade, L. A., Bawa, K. S., Hespenheide, H. A., & Hartshorn, G. S. (Eds.). (1994).

MacArthur, R. H. (1957). On the relative abundance of bird species. *Proceedings of the National Academy of Sciences*, *43*(3), 293–295.

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, *347*(6219), 1255641. https://doi.org/10.1126/science.1255641

McDonald-Madden, E., Baxter, P. W. J., Fuller, R. A., Martin, T. G., Game, E. T., Montambault, J., & Possingham, H. P. (2010). Monitoring does not always count. *Trends in Ecology & Evolution*, *25*(10), 547–550. https://doi.org/10.1016/j.tree.2010.07.002

McGregor, P. K. (2005). *Animal Communication Networks*. Cambridge, U.K.: Cambridge University Press.

McKenna, M. F., Soldevilla, M. E. L. I. S. S. A., Oleson, E. R. I. N., Wiggins, S. E. A. N., Hildebrand, J. A., Damiani, C., & Garcelon, D. (2009). Increased underwater noise levels in the Santa Barbara Channel from commercial ship traffic and the potential impact on blue whales (Balaenoptera musculus). In *Proceedings of the 7th California Islands Symposium* (pp. 141-149). Institute for Wildlife Studies, Arcata, Calif, USA.

McLeod, A. I., & Xu, C. (2017). bestglm: Best subset GLM. Retrieved from https://CRAN.R-project.org/package=bestglm

McRae, L., Freeman, R., & Marconi, V. (2016). *Living Planet Report 2016: Risk and Resilience in a New Era*. Retrieved from http://www.deslibris.ca/ID/10066038

McWilliam, J. N., McCauley, R. D., Erbe, C., & Parsons, M. J. G. (2018). Soundscape diversity in the Great Barrier Reef: Lizard Island, a case study. *Bioacoustics*, *27*(3), 295–311. https://doi.org/10.1080/09524622.2017.1344930

Mellin, C., Bradshaw, C. J., Fordham, D. A., & Caley, M. J. (2014). Strong but opposing β-diversity-stability relationships in coral reef fish communities. *Proceedings. Biological Sciences*, *281*(1777), 20131993–20131993. https://doi.org/10.1098/rspb.2013.1993

Merchant, N. D., Fristrup, K. M., Johnson, M. P., Tyack, P. L., Witt, M. J., Blondel, P., & Parks, S. E. (2015). Measuring acoustic habitats. *Methods in Ecology and Evolution*, *6*(3), 257–265. https://doi.org/10.1111/2041-210X.12330

Miksis-Olds, J. L., Martin, B., & Tyack, P. L. (2018). Exploring the ocean through soundscapes. *Acoust. Today*, *14*, 26-34.

Miksis-Olds, J. L. (2013). Comparison of soundscapes across the Bering Sea shelf, a biological perspective. The Journal of the Acoustical Society of America, 134(5), 4147–4147. https://doi.org/10.1121/1. 4831202

Miller, R. J., Lafferty, K. D., Lamy, T., Kui, L., Rassweiler, A., & Reed, D. C. (2018). Giant kelp, Macrocystis pyrifera, increases faunal diversity through physical engineering. *Proc. R. Soc. B*, *285*(1874), 20172571. https://doi.org/10.1098/rspb.2017.2571

Mitsch, W. J., Tejada, J., Nahlik, A., Kohlmann, B., Bernal, B., & Hernández, C. E. (2008). Tropical wetlands for climate change research, water quality management and conservation education on a university campus in Costa Rica. Ecological Engineering, 34(4), 276–288. https://doi.org/10.1016/j.ecoleng.2008.07.012

Moore, P. W. B., & Au, W. W. L. (1975). Underwater localization of pulsed pure tones by the California sea lion (Zalophus californianus). *The Journal of the Acoustical Society of America*, *58*(3), 721–727. https://doi.org/10.1121/1.380720

Morelock, J., Schneiderman, N., & Bryant, W. R. (1977). Shelf Reefs, Southwestern Puerto Rico: Modern and Ancient Reefs. In *SG 4: Reefs and Related Carbonates—Ecology and Sedimentology*.

Moritz, S., & Bartz-Beielstein, T. (2017). *imputeTS: Time Series Missing Value Imputation in R*. https://doi.org/10.32614/rj-2017-009

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, *28*(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mumby, P. J., Hastings, A., & Edwards, H. J. (2007). Thresholds and the resilience of Caribbean coral reefs. *Nature*, *450*(7166), 98–101. https://doi.org/10.1038/nature06252

Myers, R. A., & Worm, B. (2005). Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1453), 13–20. https://doi.org/10.1098/rstb.2004.1573

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. https://doi.org/10.1038/ 35002501

Niemelä, J. (2000). Biodiversity monitoring for decision-making. *Annales Zoologici Fennici*, *37*(4), 307–317.

Nijland, W., Reshitnyk, L., & Rubidge, E. (2019). Satellite remote sensing of canopy-forming kelp on a complex coastline: A novel procedure using the Landsat image archive. *Remote Sensing of Environment*, *220*, 41–50. https://doi.org/10.1016/j.rse.2018.10.032

National Oceanographic and Atmospheric Administration. (2018a). How much of the ocean have we explored? Retrieved September 19, 2019, from https://oceanservice.noaa.gov/facts/exploration.html

National Oceanographic and Atmospheric Administration. (2018b). *Status of Puerto Rico's Coral Reefs in the Aftermath of Hurricanes Irma and Maria* [FEMA Assessment Report]. National Oceanic and Atmospheric Administration.

Ocean Instruments NZ. (2017). *Soundtrap 300 STD*. Auckland, New Zealand.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Stevens, M. H. H. (2017). vegan: Community Ecology Package (Version R package version 2.4-5). Retrieved from https://CRAN.R-project.org/package=vegan

Oleson, E. M., Wiggins, S. M., & Hildebrand, J. A. (2007). Temporal separation of blue whale call types on a southern California feeding ground. *Animal Behaviour*, *74*(4), 881–894. https://doi.org/10.1016/j.anbehav.2007.01.022

Oliver, T. H., Heard, M. S., Isaac, N. J. B., Roy, D. B., Procter, D., Eigenbrod, F., … Bullock, J. M. (2015). Biodiversity and Resilience of Ecosystem Functions. *Trends in Ecology & Evolution*, *30*(11), 673–684. https://doi.org/10.1016/j.tree.2015.08.009

Oliver, T. H., Isaac, N. J. B., August, T. A., Woodcock, B. A., Roy, D. B., & Bullock, J. M. (2015). Declining resilience of ecosystem functions under biodiversity loss. *Nature Communications*, *6*(1), 1–8. https://doi.org/10.1038/ncomms10122

Oliver, T., Roy, D. B., Hill, J. K., Brereton, T., & Thomas, C. D. (2010). Heterogeneous landscapes promote population stability. *Ecology Letters*, *13*(4), 473–484. https://doi.org/10.1111/j.1461-0248.2010.01441.x

Oppenheim, A. V., Schafer, R. W., & Buck, J. R. (1999). *Discrete-time Signal Processing* (2nd ed.). Upper Saddle River, NJ, USA: Prentice-Hall, Inc.

Ospina, O. E., Villanueva-Rivera, L. J., Corrada-Bravo, C. J., & Aide, T. M. (2013). Variable response of anuran calling activity to daily precipitation and temperature: Implications for climate change. *Ecosphere*, 4 (4), 1–12. https://doi.org/10.1890/ES12-00258.1

Otte, D. (1974). Effects and functions in the evolution of signaling systems. *Annual Review of Ecology and Systematics*, 5(1), 385–417. https://doi.org/10.1146/annurev.es.05.110174.002125

Otsu, N. (1979). A Threshold Selection Method from Gray-Level Histograms. *IEEE Transactions on Systems, Man, and Cybernetics*, *9*(1), 62–66. https://doi.org/10.1109/TSMC.1979.4310076

Paperno, R., Tremain, D. M., Adams, D. H., Sebastian, A. P., Sauer, J. T., & Dutka-Gianelli, J. (2006). The disruption and recovery of fish communities in the Indian River Lagoon, Florida, following two hurricanes in 2004. *Estuaries and Coasts*, *29*(6), 1004–1010. https://doi.org/10.1007/BF02798662

Parks, S. E., Miksis-Olds, J. L., & Denes, S. L. (2014). Assessing marine ecosystem acoustic diversity across ocean basins. *Ecological Informatics*, 21, 81–88. https://doi.org/10.1016/j.ecoinf.2013.11.003

Parmentier, E., Lecchini, D., Mann, D. A., Lecchini, D., & Mann, D. A. (2016). Sound Production in Damselfishes. https://doi.org/10.1201/9781315373874-18

Patek, S. N., Shipp, L. E., & Staaterman, E. R. (2009). The acoustics and acoustic behavior of the California spiny lobster (Panulirus interruptus). *The Journal of the Acoustical Society of America*, *125*(5), 3434. https://doi.org/10.1121/1.3097760

Pekin, B. K., Jung, J., Villanueva-Rivera, L. J., Pijanowski, B. C., & Ahumada, J. A. (2012). Modeling acoustic diversity using soundscape recordings and LIDAR-derived metrics of vertical forest structure in a Neotropical rainforest. *Landscape Ecology*, 27(10), 1513–1522. https://doi.org/10.1007/s10980-012-9806-4

Pereira, H. M., & David Cooper, H. (2006). Towards the global monitoring of biodiversity change. *Trends in Ecology & Evolution*, *21*(3), 123–129. https://doi.org/10.1016/j.tree.2005.10.015

Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological Resilience, Biodiversity, and Scale. *Ecosystems*, *1*(1), 6–18. https://doi.org/10.1007/s100219900002

Pieretti, N., Farina, A., & Morri, D. (2011). A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). *Ecological Indicators*, *11*(3), 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005

Pijanowski, B. C., Farina, A., Gage, S. H., Dumyahn, S. L., & Krause, B. L. (2011). What is soundscape ecology? An introduction and overview of an emerging new science. *Landscape Ecology*, *26*(9), 1213–1232. https://doi.org/10.1007/s10980-011-9600-8

Pijanowski, B. C., Villanueva-Rivera, L. J., Dumyahn, S. L., Farina, A., Krause, B. L., Napoletano, B. M., … Pieretti, N. (2011). Soundscape Ecology: The Science of Sound in the Landscape. *BioScience*, *61*(3), 203–216. https://doi.org/10.1525/bio.2011.61.3.6

Pimm, S. L., Alibhai, S., Bergl, R., Dehgan, A., Giri, C., Jewell, Z., … Loarie, S. (2015). Emerging Technologies to Conserve Biodiversity. *Trends in Ecology & Evolution*, *30*(11), 685–696. https://doi.org/10.1016/j.tree.2015.08.008

Pitcher, C. R., Poiner, I. R., Hill, B. J., & Burridge, C. Y. (2000). Implications of the effects of trawling on sessile megazoobenthos on a tropical shelf in northeastern Australia. *ICES Journal of Marine Science*, *57*(5), 1359–1368. https://doi.org/10.1006/jmsc.2000.0911

Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, *405*(6783), 212–219. https://doi.org/10.1038/35012221

Quinlan, A. E., Berbés-Blázquez, M., Haider, L. J., & Peterson, G. D. (2016). Measuring and assessing resilience: Broadening understanding through multiple disciplinary perspectives. *Journal of Applied Ecology*, *53*(3), 677–687. https://doi.org/10.1111/1365-2664.12550

R. Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Radford, C. A., Jeffs, A. G., Tindle, C. T., & Montgomery, J. C. (2008). Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia*, *156*(4), 921–929. https://doi.org/10.1007/s00442-008-1041-y

Radford, C., Jeffs, A., Tindle, C., & Montgomery, J. C. (2008). Resonating sea urchin skeletons create coastal choruses. *Marine Ecology Progress Series*, *362*, 37–43. https://doi.org/10.3354/meps07444

Ramirez, O. (2017, January 27). *Purdue Soundscapes: La Selva Frogs and Aquatic Insects Question*.

Raven Pro: Interactive Sound Analysis Software (2016). (Version 2.0). Ithaca, NY: Bioacoustic Research Program, Cornell Laboratory of Ornithology.

Revenga, C., Campbell, I., Abell, R., de Villiers, P., & Bryer, M. (2005). Prospects for monitoring freshwater ecosystems towards the 2010 targets. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 360(1454), 397–413. https://doi.org/10.1098/rstb.2004.1595

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S. I., Lambin, E., … Foley, J. (2009). Planetary Boundaries: Exploring the Safe Operating Space for Humanity. *Ecology and Society*, *14*(2). https://doi.org/10.5751/ES-03180-140232

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., … Marra, P. P. (2019). Decline of the North American avifauna. *Science*, *366*(6461), 120–124. https://doi.org/10.1126/science.aaw1313

Rossi, T., Connell, S. D., & Nagelkerken, I. (2016). Silent oceans: Ocean acidification impoverishes natural soundscapes by altering sound production of the world's noisiest marine invertebrate. *Proc. R. Soc. B*, *283*(1826), 20153046. https://doi.org/10.1098/rspb.2015.3046

Rossi, T., Connell, S. D., & Nagelkerken, I. (2017). The sounds of silence: Regime shifts impoverish marine soundscapes. *Landscape Ecology*, *32*(2), 239–248. https://doi.org/10.1007/s10980-016-0439-x

Rountree, R. A., Gilmore, R. G., Goudey, C. A., Hawkins, A. D., Luczkovich, J. J., & Mann, D. A. (2006). Listening to Fish. *Fisheries*, *31*(9), 433–446. https://doi.org/10.1577/1548-8446(2006)31[433:LTF]2.0.CO;2

Rowell, T. J., Demer, D. A., Aburto-Oropeza, O., Cota-Nieto, J. J., Hyde, J. R., & Erisman, B. E. (2017). Estimating fish abundance at spawning aggregations from courtship sound levels. *Scientific Reports*, *7*(1), 3340. https://doi.org/10.1038/s41598-017-03383-8

Ruppé, L., Clément, G., Herrel, A., Ballesta, L., Décamps, T., Kéver, L., & Parmentier, E. (2015). Environmental constraints drive the partitioning of the soundscape in fishes. *Proceedings of the National Academy of Sciences*, *112*(19), 6092–6097. https://doi.org/10.1073/pnas.1424667112

Sala, O. E., Chapin, F. S., Iii, Armesto, J. J., Berlow, E., Bloomfield, J., … Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Schack, H. (2018). The rising tide of underwater noise. *The Circle*, (3.2018).

Schaffner, F. C., Camacho-Fontánez, N. M., Colón-Cruz, M., Flusa, S. L., Pérez-Cruz, I. J., Rodríguez-Colón, I., ... & Torres-López, A. (2018). A First Assessment of the Effects of Hurricanes Irma and Maria Habitat on the Habitats and Terrestrial Bird Communities in the Coastal Dry Forest of Jobos Bay, Puerto Rico.

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution*, *18*(12), 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Schlagbauer, A. (1995). *Floristische und faunistische Aspekte eines tropischen Sumpfgewässers—Bestimmungen von Pflanzen und Wasserinsekten eines flussnahen Feuchtgebietes am Rio Puerto Viejo, Costa Rica* (Master's). University of Munich, LMU.

Schmitz, B. (2002). Sound Production in Crustacea with Special Reference to the Alpheidae. In K. Wiese (Ed.), *The Crustacean Nervous System* (pp. 536–547). Springer Berlin Heidelberg.

Schowalter, T. D., Willig, M. R., & Presley, S. J. (2017). Post-Hurricane Successional Dynamics in Abundance and Diversity of Canopy Arthropods in a Tropical Rainforest. *Environmental Entomology*, nvw155. https://doi.org/10.1093/ee/nvw155

Sikkel, P. C. (1990). *Factors influencing spawning site choice by female Garibaldi, Hypsypops rubicundus (Pisces: Pomacentridae)*. Oregon State University.

Širović, A., Cutter, G. R., Butler, J. L., & Demer, D. A. (2009). Rockfish sounds and their potential use for population monitoring in the Southern California Bight. *ICES Journal of Marine Science*, *66*(6), 981–990. https://doi.org/10.1093/icesjms/fsp064

Širovic, A., Rice, A., Chou, E., Hildebrand, J., Wiggins, S., & Roch, M. (2015). Seven years of blue and fin whale call abundance in the Southern California Bight. *Endangered Species Research*, *28*(1), 61–76. https://doi.org/10.3354/esr00676

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., & Popper, A. N. (2010). A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends in Ecology & Evolution*, *25*(7), 419–427. https://doi.org/10.1016/j.tree.2010.04.005

SMX-II. Maynard, MA: Wildlife Acoustics.

Song Meter SM2. Maynard, MA: Wildlife Acoustics.

Spaan, D., Burke, C., McAree, O., Aureli, F., Rangel-Rivera, C. E., Hutschenreiter, A., … Wich, S. A. (2019). Thermal Infrared Imaging from Drones Offers a Major Advance for Spider Monkey Surveys. *Drones*, *3*(2), 34. https://doi.org/10.3390/drones3020034

Spellerberg, I. F. (1991). *Monitoring Ecological Change*. Cambridge University Press.

Springer, M. (2017, March 21). *Purdue Soundscapes: La Selva Frogs and Aquatic Insects Question*.

Staaterman, E., Ogburn, M., Altieri, A., Brandl, S., Whippo, R., Seemann, J., … Duffy, J. (2017). Bioacoustic measurements complement visual biodiversity surveys: Preliminary

evidence from four shallow marine habitats. *Marine Ecology Progress Series*, *575*, 207–215. https://doi.org/10.3354/meps12188

Staaterman, E., Paris, C. B., DeFerrari, H. A., Mann, D. A., Rice, A. N., & D'Alessandro, E. K. (2014). Celestial patterns in marine soundscapes. *Marine Ecology Progress Series*, *508*, 17–32. https://doi.org/10.3354/meps10911

Steele, J. H. (1998). Regime Shifts in Marine Ecosystems. *Ecological Applications*, *8*(sp1), S33–S36. https://doi.org/10.1890/1051-0761(1998)8[S33:RSIME]2.0.CO;2

Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future. *Environmental Conservation*, *29*(4), 436–459. https://doi.org/10.1017/S0376892902000322

Stoms, D. M., & Estes, J. E. (1993). A remote sensing research agenda for mapping and monitoring biodiversity. *International Journal of Remote Sensing*, *14*(10), 1839–1860. https://doi.org/10.1080/01431169308954007

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, *29*(1), 344–358. https://doi.org/10.1899/08-171.1

Streby, H. M., Kramer, G. R., Peterson, S. M., Lehman, J. A., Buehler, D. A., & Andersen, D. E. (2015). Tornadic Storm Avoidance Behavior in Breeding Songbirds. *Current Biology*, *25*(1), 98–102. https://doi.org/10.1016/j.cub.2014.10.079s

Strieby, A. M. (1998). *A multispecific frog chorus: Calls, calling sites, and acoustical interference in a complex forest habitat.* (California State University at Northridge (USA)). Retrieved from http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=oet.xis&method=post&formato=2&cantidad=1&expresion=mfn=018363

Sueur, J., Farina, A., Gasc, A., Pieretti, N., & Pavoine, S. (2014). Acoustic Indices for Biodiversity Assessment and Landscape Investigation. *Acta Acustica United with Acustica*, *100*(4), 772–781. https://doi.org/10.3813/AAA.918757

Sueur, J., Aubin, T., & Simonis, C. (2008). Seewave: A free modular tool for sound analysis and synthesis. Retrieved from http://isyeb.mnhn.fr/IMG/pdf/sueuretal_bioacoustics_2008.pdf

Sueur, J., Pavoine, S., Hamerlynck, O., & Duvail, S. (2008). Rapid Acoustic Survey for Biodiversity Appraisal. *PLOS ONE*, *3*(12), e4065. https://doi.org/10.1371/journal.pone.0004065

Sugai, L. S. M., Silva, T. S. F., Ribeiro, J. W., & Llusia, D. (2019). Terrestrial Passive Acoustic Monitoring: Review and Perspectives. *BioScience*, *69*(1), 15–25. https://doi.org/10.1093/biosci/biy147

Tanner, E. V. J., Kapos, V., & Healey, J. R. (1991). Hurricane Effects on Forest Ecosystems in the Caribbean. *Biotropica*, *23*(4), 513–521. https://doi.org/10.2307/2388274

Theiß, J. (1982). Generation and radiation of sound by stribulating water insects as exemplified by the corixids. *Behavioral Ecology and Sociobiology*, 10(3), 225–235. https://doi.org/10.1007/BF00299689

Thomsen, P. F., Kielgast, J., Iversen, L. L., Wiuf, C., Rasmussen, M., Gilbert, M. T. P., ... Willerslev, E. (2012). Monitoring endangered freshwater biodiversity using environmental DNA. *Molecular Ecology*, 21(11), 2565–2573. https://doi.org/10.1111/j.1365-294X.2011.05418.x

Tittensor, D. P., Walpole, M., Hill, S. L. L., Boyce, D. G., Britten, G. L., Burgess, N. D., … Ye, Y. (2014). A mid-term analysis of progress toward international biodiversity targets. *Science (New York, N.Y.)*, *346*(6206), 241–244. https://doi.org/10.1126/science.1257484

Towsey, M. W., & Planitz, B. (2011). *Technical report: Acoustic analysis of the natural environment* [Report]. Retrieved from Queensland University of Technology website: http://eprints.qut.edu.au/41131/

Towsey, M., Wimmer, J., Williamson, I., & Roe, P. (2014). The use of acoustic indices to determine avian species richness in audio-recordings of the environment. *Ecological Informatics*, *21*, 110–119. https://doi.org/10.1016/j.ecoinf.2013.11.007

Towsey, M., Zhang, L., Cottman-Fields, M., Wimmer, J., Zhang, J., & Roe, P. (2014). Visualization of Long-duration Acoustic Recordings of the Environment. *Procedia Computer Science*, *29*, 703–712. https://doi.org/10.1016/j.procs.2014.05.063

Towsey, M. W. (2017). *The calculation of acoustic indices derived from long-duration recordings of the natural environment* [Report]. Retrieved from https://eprints.qut.edu.au/110634/

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849. https://doi.org/10.1890/10-0097.1

Tyack, P. L. (2008). Implications for marine mammals of large-scale changes in the marine acoustic environment. *Journal of Mammalogy*, *89*(3), 549–558. https://doi.org/10.1644/07-MAMM-S-307R.1

Tyack, P. L., & Clark, C. W. (2000). Communication and acoustic behavior of dolphins and whales. In *Hearing by whales and dolphins* (pp. 156-224). Springer, New York, NY.

Urick, R. J. (1983). *Principles of Underwater Sound*. Peninsula Publishing.

Vasilis, D., Carpenter S.R., van Nes, E., & Scheffer, M. (2015). Resilience indicators: Prospects and limitations for early warnings of regime shifts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1659), 20130263. https://doi.org/10.1098/rstb.2013.0263

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S* (Fourth). Retrieved from http://www.stats.ox.ac.uk/pub/MASS4

Villanueva-Rivera, L. J. (2014). Eleutherodactylus frogs show frequency but no temporal partitioning: Implications for the acoustic niche hypothesis. *PeerJ*, *2*, e496. https://doi.org/10.7717/peerj.496

Villanueva-Rivera, L. J., & Pijanowski, B. C. (2016). soundecology: Soundscape ecology. R. Retrieved from https://CRAN.R-project.org/package=soundecology

Vos, J. M. D., Joppa, L. N., Gittleman, J. L., Stephens, P. R., & Pimm, S. L. (2015). Estimating the normal background rate of species extinction. *Conservation Biology*, *29*(2), 452–462. https://doi.org/10.1111/cobi.12380

Wade, P., Heide-Jørgensen, M. P., Shelden, K., Barlow, J., Carretta, J., Durban, J., … Stinchcomb, C. (2006). Acoustic detection and satellite-tracking leads to discovery of rare concentration of endangered North Pacific right whales. *Biology Letters*, *2*(3), 417–419. https://doi.org/10.1098/rsbl.2006.0460

Waide, R. B. (1991a). Summary of the Response of Animal Populations to Hurricanes in the Caribbean. *Biotropica*, *23*(4), 508–512. https://doi.org/10.2307/2388273

Waide, R. B. (1991b). The Effect of Hurricane Hugo on Bird Populations in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, *23*(4), 475–480. https://doi.org/10.2307/2388269

Warrington, M. H., McDonald, P. G., Rollins, L. A., & Griffith, S. C. (2014). All signals are not equal: Acoustic signalling of individuality, sex and breeding status in a cooperative breeder. *Animal Behaviour*, 93, 249–260. https://doi.org/10.1016/j.anbehav.2014.05.007

Webb, J. F., Fay, R. R., & Popper, A. N. (2008). *Fish Bioacoustics*. Springer Science & Business Media.

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., & Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE*, *14*(7), e0216270. https://doi.org/10.1371/journal.pone.0216270

Whitfield, S. (2017, January 23). *Purdue Soundscapes: La Selva Frogs and Aquatic Insects Question*.

Wilson, C. J. (2011). *The acoustic ecology of submerged macrophytes* (Thesis). Retrieved from https://repositories.lib.utexas.edu/handle/2152/ETD-UT-2011-12-4742

Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., … Watson, R. (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, *314*(5800), 787–790. https://doi.org/10.1126/science.1132294

Xu, A. I. M. and C. (2017). bestglm: Best Subset GLM (Version 0.36). Retrieved from https://cran.r-project.org/web/packages/bestglm/index.html

Xu, X., Xu, S., Jin, L., & Song, E. (2011). Characteristic analysis of Otsu threshold and its applications. *Pattern Recognition Letters*, *32*(7), 956–961. https://doi.org/10.1016/j.patrec.2011.01.021