WETLAND BIODIVERSITY IN GRAND TETON NATIONAL PARK

by

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DEDICATION

For Kinli

You are my world and through my love for you, I grow in curiosity and amazement. I would not have been able to do any of this without you in my life. Thank you for everything.

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ABSTRACT

Freshwater wetlands support high biodiversity, yet many wetlands are subject to shifts in precipitation and temperature under projected climate patterns. These changes can alter wetland hydrological regimes, potentially leading to longer or more frequent dry periods, with effects that differ among taxa. In this thesis we aim to build on the understanding about biodiversity in wetlands and how these species may be affected by climate change, in hopes of providing information for land management. To accomplish these goals, we first focused on macroinvertebrates, a group that employs diverse strategies for surviving wetland drying. We explored the roles of wetland size, spatial isolation, and temporal isolation on macroinvertebrate richness and community composition. In summer 2018, we collected macroinvertebrates from 18 wetlands in Grand Teton National Park. We found macroinvertebrate family richness increased with wetland depth and slower rates of drying. We also found the interaction between spatial and temporal isolation explained the most variation in community composition for all the life history strategies we examined. Second, we explored the utility of different automated tools to monitor biodiversity in wetlands. In 2017, we placed wildlife cameras, as well as acoustic (audible and ultrasonic) recorders at 4 permanent wetlands in Grand Teton National Park for a week in June and August; we also completed a visual survey during each of these time intervals. We compared the number and type of species detected by each method over the summer to evaluate the effectiveness of each method for monitoring. Using wildlife cameras, in addition to visual surveys, increased the observation time at surveyed wetlands, captured complementary species, and recorded dynamics in the water level during the summer. These two chapters provide insights about how changes resulting from increased drying may affect one of the most biodiverse taxa and offer methods that allow monitoring of many taxa simultaneously.

CHAPTER ONE

INTRODUCTION TO THESIS

Wetlands improve water quality, sequester carbon, and reduce floods, while also supporting disproportionately high biodiversity relative to their presence on the landscape (Zedler and Kercher 2005). Wetlands support unique ecological functions and species richness (Mitsch and Gosselink 2015). A continuum of groundwater inputs, solute concentrations, and topographic distance (spatial isolation) create varying habitats and niches influencing community composition (Mushet et al. 2015). Drying patterns also provide unique habitats for species ranging from macroinvertebrates to mammals and birds, but especially species that require terrestrial and aquatic habitat for their life history such as amphibians (Leibowitz 2003). Wetland networks offer differential water availability some species need for their complex life-history and provide rescue effects that sustain metapopulations (Semlitsch et al. 1998). This ecological connection also supports dispersal and connectivity through upland corridors (Semlitsch et al. 1998), with differential topography and distance facilitating variation in gene flow (Mushet et al. 2015).

Globally, wetlands are projected to disappear entirely in some regions by midcentury (Albert et al. 2021). Over 50% of wetland global area has declined (Zedler and Kercher 2005), however, in some areas losses exceed 90% (Dahl 2000). Threats including climate change, ditching, tilling, groundwater pumping, and draining for agriculture result in the degradation of wetlands (Rains et al. 2015). National parks are relatively protected from anthropogenic influences from agriculture and human development but, wetlands in protected areas remain subjected to the effects of climate change.

The Greater Yellowstone Area (GYA) is one of the largest intact ecosystems, which includes Yellowstone and Grand Teton national parks (Ray et al. 2016). Future climate conditions in the GYA are projected to be warmer and drier (Pederson et al. 2011, Sepulveda et al. 2015). Based on multi-year monitoring datasets, >40% of the region's isolated wetlands are dry in years when above average temperatures combine with reduced precipitation (Ray et al. 2015). Importantly, the probability of wetland drying may increase several-fold with future declines in runoff (Wilmoth et al. 2015). It is unclear how the effects of climate-induced drying will affect wetland biodiversity in the GYA, which includes nearly 70% of Wyoming bird species (Nicholoff 2003), all native amphibians in the GYA, and more than 40% of all of plant species in Yellowstone National Park (Elliot and Hektner 2000).

We attempted to understand how drying may affect patterns of wetland biodiversity in the GYA by studying wetlands in Grand Teton National Park. Chapter two focuses on wetland characteristics that may be affected by increased drying from climate change, namely wetland size, spatial, and temporal isolation. We looked at relationships between these wetland characteristics and the family richness and community composition of macroinvertebrates. In Chapter three, we expanded our focus from one taxon to the diverse groups of species that use wetlands. In this chapter, we demonstrate the utility of automated recording units (ARUs) in conjunction with in-field surveys. We deployed wildlife cameras, acoustic and ultrasonic monitoring equipment over one summer season to better understand the utility of these novel survey techniques to complement existing amphibian surveys to capture additional species and seasonal patterns. Wildlife cameras survey large mammals and birds, acoustic recorders survey birds, insects, amphibians, and mammals with audible signatures, and ultrasonic recorders survey bat species; all of these tools can be combined to better understand ecological communities (Buxton et al. 2018a). We hope these two chapters combine to contribute cross-taxon information that helps protect wetland biodiversity.

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CHAPTER TWO

SPATIAL AND TEMPORAL ISOLATION AND SIZE OF WETLANDS INFLUENCE RICHNESS AND FUNCTIONAL COMPOSITION OF AQUATIC MACROINVERTEBRATES

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CHAPTER TWO

SPATIAL AND TEMPORAL ISOLATION AND SIZE OF WETLANDS INFLUENCE RICHNESS AND LIFE HISTORY COMPOSITION OF AQUATIC MACROINVERTEBRATES

Abstract

Wetlands have unique hydrology that fluctuates between periods of inundation and drying. This dynamic affects wetland characteristics in space and time. We used Island Biogeography Theory (IBT) as a framework for understanding the roles of wetland size and spatial isolation for aquatic macroinvertebrate communities. We also considered the role of temporal isolation (rate of drying), given that wetlands are also insular in time during periods of drought. We estimated the influence of these characteristics on family richness and community composition of aquatic macroinvertebrates; we defined composition based on four strategies these species use to survive drying. During summer 2018, we collected macroinvertebrates and measured characteristics of 18 wetlands in Grand Teton National Park, Wyoming. We measured several different metrics to quantify wetland size, spatial isolation, and temporal isolation. Generally, we found patterns consistent with IBT; richness increased with wetland size, decreased with temporal isolation, but increased with spatial isolation. Depth (size) and the rate of depth drying (temporal isolation) explained the most variation in family richness. We also found that the interaction between spatial and temporal isolation best explained variation in community composition; the size and magnitude of the estimated effects varied based on the different strategies for tolerating wetland drying. Our work indicates that IBT, modified by

including temporal isolation, can elucidate basic influences on family richness and community composition of aquatic macroinvertebrates, but understanding the role of spatial isolation is more complex. As climate change modifies the range of variation in hydrological regimes, some wetland-dependent taxa may no longer persist when dry periods are too long or too frequent in arid regions.

Introduction

Freshwater wetlands are one of the most biologically diverse ecosystems in the world, in part because of their dynamic hydrology (Mitsch and Gosselink 2015). All wetlands have water at some point, but the hydrological regime – the amount, duration, and frequency of flooding – varies greatly from wetland to wetland, year to year, and season to season (Lee et al 2015, Mitsch and Gosselink 2015). This dynamic affects many wetland characteristics from size and permanence to water chemistry, creating an array of conditions that support numerous terrestrial and aquatic species (Gopal 2000, Junk et al. 2013). These species have developed diverse and complex adaptations to persist in the face of changing hydrologic conditions (Boix et al. 2019). For example, species that can migrate can colonize different wetland types to avoid predators in permanent wetlands or avoid desiccation by moving to flooded wetlands (Elliott et al. 2020). Species that tolerate drying may hibernate or aestivate until the next wetland inundation, benefiting from the niche created by drying (Wiggins et al. 1980). Although the unique hydrology of wetlands can enhance biodiversity, it is a double-edged sword, as biodiversity also may be constrained when dry periods are too long or too frequent (Mitsch and Gosselink 2015).

Climate change is altering the historical range of variation in wetland hydrological regimes (Burkett and Kusler 2000). The patterns of change vary regionally; some areas are experiencing increased wetland inundation, but other areas are subject to increased temperatures and decreased precipitation, where the hydrological pattern tends toward increased drying (Ray et al. 2019). In arid regions, such as the western United States, wetlands are particularly vulnerable to climate change due to their dependence on snowmelt (Ray et al 2019). With decreased snowpack resulting from warmer temperatures, wetlands have shortened hydroperiods (duration of inundation) and longer periods of drought between inundations (Brooks and Hayashi 2002). Warmer temperatures also are associated with increased evapotranspiration (Chandler et al. 2017), accelerating wetland drying. As wetlands dry, water depth and area decrease (Schook and Cooper 2014); some wetlands can disappear completely, leading to fewer wetlands on the landscape (Mitsch and Gosselink 2000). Decreases in wetland density may increase the distances species must travel between wetlands, increasing spatial isolation (Gibbs 1993). For species that depend on inundation, wetlands provide discrete aquatic refugia over time (between dry periods) and in space (Ripley and Simovich 2007).

As wetlands become more insular in space and time (Ripley and Simovich 2007), wetland-dependent species are at risk of altered distributions and biodiversity losses (Blaustein et al. 2010, Junk et al. 2013, Johnson et al. 2010, Quesnelle et al. 2013, Ray et al. 2016). Species that will be most affected rely on more stable conditions created by long hydroperiods, such as waterfowl, amphibians, and shorebirds (Johnson et al. 2010, Ray et al. 2016). Even for species adapted to shorter hydroperiods and wetland drying, such as invertebrates, changes in the timing and duration of drying can make persistence challenging (Stenert et al. 2020). Understanding the link between specific wetland characteristics and the associated biodiversity is critical to determining the ecological vulnerability of these systems to climate change (Poff et al. 2002).

Two theoretical frameworks may help us understand how wetland-dependent species may respond to changes that result from altered hydroperiods and accelerated drying. First, given that wetlands act as aquatic “islands” within a terrestrial matrix (March and Bass 1995), Island Biogeography Theory (IBT, MacArthur and Wilson 1967) may help predict how the spatial isolation and size of wetlands influence species richness. Under the IBT framework, wetlands that are less spatially isolated likely support more species because the proximity to sources of immigrants facilitates colonization (March and Bass 1995). Large wetlands also can support more species given the increased area and habitat heterogeneity; large wetlands also may be easier for immigrating individuals to detect and target for colonization (March and Bass 1995, Vanschoenwinkel et al. 2009, Vanschoenwinkel et al. 2015). However, IBT does not account for the dynamic nature of wetland hydrology, namely the idea that the wetland “island” is not only isolated in space, but also isolated in time (Ebert and Balko 1987). For example, wetlands that are inundated less frequently and for shorter durations, are more temporally isolated from sources of immigrants. Ebert and Balko (1987) built on IBT for wetlands, proposing a modified framework that also integrates temporal isolation. Second, based on this modified framework, wetlands with shorter hydroperiods (greater temporal isolation) that are farther from their neighbors (greater spatial isolation) likely support fewer species than permanent wetlands that are closer to neighbors (Ebert and Balko 1987). However, the degree to which spatial and temporal isolation influences biodiversity also likely depends on how species disperse through space and time (Bohonak and Jenkins 2003, Buoro and Carlson 2014).

Macroinvertebrates are one of the most taxonomically diverse and ubiquitous groups in freshwater wetlands (Batzer and Ruhí 2013, Batzer and Wissinger 1996). They have evolved diverse dispersal strategies to accommodate varying degrees of wetland drying, as well as spatial and temporal isolation (Bohonak and Jenkins 2003), making them ideal taxa to test this modified IBT framework (March and Bass 1995, Ripley and Simovich 2007). Macroinvertebrates navigate spatial isolation with active or passive dispersal strategies (Batzer 2013, Batzer and Ruhí 2013). To navigate temporal isolation, some macroinvertebrates can remain as residents in a dry wetland until the next inundation by being dormant as desiccated life forms in sediment (Stubbington et al. 2016). These mechanisms for spatial and temporal dispersal related to wetland drying can be categorized into four broad life history strategies (Wiggins et al. 1980, Gleason and Rooney 2018): drought tolerators, wet layers, dry layers, and active dispersers. Although some macroinvertebrates may combine strategies, these classifications focus on the primary strategy used (Gleason and Rooney 2018). Drought tolerators cannot actively disperse over space, but can passively disperse by wind and on animals (Bilton et al. 2001) and have adaptations to disperse temporally (Panov and Caceres 2007) via resting egg banks (Stubbington et al. 2016), hibernation, and aestivation (Wiggins et al. 1980, Ebert and Balko 1987). Wet layers oviposit on water and require longer hydroperiods to develop fully (Wiggins et al. 1980). In contrast, dry layers disperse to dry basins to oviposit, overwintering in these areas as eggs or larvae (Wiggins et al. 1980). Active dispersers swim through floodwaters or fly to colonize wetlands and exploit resources when water is present; given that this life history strategy requires permanent water to overwinter, decreasing water depth triggers dispersal (Bilton et al. 2001).

We used the modified IBT framework (Ebert and Balko 1987) to test how wetland drying affects biodiversity, with a focus on aquatic macroinvertebrates. Macroinvertebrates represent an important link in wetlands between primary production and higher trophic levels (Williams

2006) and insights about these organisms may extend to other taxa. We examined how family richness and community composition of macroinvertebrates changed as a function of wetland size, spatial isolation, and temporal isolation; we also explored different metrics to quantify these wetland characteristics.

Our predictions were based on IBT and modified IBT, meaning that we expected higher richness of macroinvertebrates in larger wetlands (March and Bass 1995) that were less spatially and temporally isolated (Ebert and Balko 1987). We also predicted changes in abundance of the different life history strategies that would shape community composition (Gleason and Rooney 2018). Specifically, we expected drought tolerators and dry layers would respond similarly to temporal isolation and size: increasing in abundance with drying (temporally isolated) and in smaller wetlands because these groups can persist in dry conditions. Conversely, we expected lower abundance of wet layers and active dispersers with drying and in smaller wetland because these groups need more permanent water. We also expected drought tolerators would respond differently to spatial isolation compared with the other life history strategies that can disperse actively; with increased spatial isolation, we predicted drought tolerators would be less abundant, but other groups would be more abundant.

Study Area

We focused our work in Grand Teton National Park (GTNP), northwestern Wyoming, which is part of the Greater Yellowstone Ecosystem (GYE) (Figure 2.1). GTNP spans approximately 1,256 km^2, with elevations ranging from 4,198 m in the Teton Range to 1,926 m in Jackson Hole Valley (NPS 2021). Winters are long and cold (average temperature in January = -3.61 C°) and summers are short and cool (average temperature in July = 25.3 C°). Vegetation ranges from high-elevation pine forests (*Pinaceae* spp.), to low-elevation sagebrush (*Artemisia tridentata*) steppe, with mesic areas consisting of willows (*Salix* spp.), deciduous trees (*Populus* spp.), and a diverse understory (Ray et al. 2016).

The largest water bodies in GTNP include the Snake River, its tributaries, and six large moraine lakes (Hotaling et al. 2017). The main source of surface water is snow (Pederson et al. 2011). Snowfall accumulates between November and April, melting and recharging water systems between May and June (Ray et al. 2019). Palustrine wetlands (inland, area <0.08 km^2, depth <2 m, salinity below 0.5%, and no wave-formed shoreline, Cowardin et al. 1979) cover approximately 3% of GTNP (Gould et al. 2012). Snowmelt fills these wetlands, which vary in area, depth, and hydroperiod (Elliot and Hektner 2000). Permanent wetlands are inundated throughout the year, whereas seasonal wetlands are typically full in mid-June to early July and dry by late August (Ray et al. 2019). Snowmelt runoff is the best predictor of wetland drying in the region (Ray et al. 2019).

National parks are less subject to anthropogenic disturbance, such that examining wetlands in GTNP and within the larger GYE may provide important reference information for insights in other areas. Research on wetland macroinvertebrates is limited in the GYE, especially in GTNP. To the best of our knowledge, the roles of size, spatial, and temporal isolation have not been studied simultaneously in macroinvertebrate communities inhabiting wetlands in this region.

Methods

Site Selection

Wetlands in this study are part of a larger, long-term monitoring effort by the National Park Service Greater Yellowstone Inventory and Monitoring Network (GRYN) (Figure 2.1). GRYN surveys wetlands in seven catchments (study areas containing multiple wetlands) in GTNP each year to study the relationship between climate drivers and amphibian occurrence (Gould et al. 2012). For our research, we selected four of these seven catchments (Figure 2.1c). The selected catchments were continually accessible throughout the summer, contained a varying number of wetlands (4 to 36 wetlands per catchment), and ranged in elevation from 2000 to 2500m.

Initially, we classified all wetlands in the selected catchments into coarse categories based on spatial and temporal isolation to aid in site selection. To categorize spatial isolation, we calculated the distances of each wetland to their nearest neighbor using the ArcToolbox NEAR tool (Gould 2010). We then categorized wetlands with above average distances to the nearest neighbor as spatially isolated and wetlands with below average distances as not spatially isolated. We used the USFS National Wetland Inventory (NWI) permanence class (Cowardin et al. 1979) to classify “temporarily flooded” or “seasonally flooded” wetlands as temporally isolated and those classified as “intermittently exposed” as not temporally isolated. We randomly selected one wetland in each catchment to represent each of four categories: 1) spatially and temporally isolated, 2) spatially isolated, but not temporally isolated, 3) not spatially isolated and temporally isolated, 4) not spatially or temporally isolated. We selected one additional wetland in two of the catchments due to concerns about reliable access, resulting in a total of 18 wetlands.

Macroinvertebrate Sampling, Sorting, and Identification

We sampled each wetland three times during summer 2018 (mid-June, mid-July, and mid-August) to capture variation in the composition of the macroinvertebrate community, as well as changes in area and depth. Macroinvertebrate samples were collected using a D-framed net (500-micron mesh) with one m-long sweeps (Swartz et al. 2019). To ensure we collected macroinvertebrates with different depth preferences, we sampled three areas of each wetland (the shore, midpoint depth, and deepest part of the wetland), taking three random sweeps in each area (3 areas * 3 sweeps = 9 total sweeps) (Swartz et al. 2019). We filtered samples to remove sediment and preserved macroinvertebrates in 95% ethanol.

Macroinvertebrate Response Variables

Family Richness. We identified most taxa to family (Thorp and Covich 2009, Merritt and Cummins 1996, Pennak 1955**,** Merrit et al. 2008). The remaining taxa were identified to order, due to a lack of taxonomic keys for this region (Swartz et al. 2019, Appendix Table 2.1). Based on these data, we computed raw family richness (total number of taxa present) from a combined sample of all nine sweeps from each wetland visit. Given that wetlands varied in size, we needed to account for differences in sampling effort. As such, we standardized family richness (hereafter family richness) with sample completeness as a function of abundance using the iNEXT package (Chao et al. 2016) in Program R (version 4.1.1, R Core Team 2020). We used these estimates of family richness as the response variable in models to explore predictions related to overall richness. Taxa assessed at the order level were treated the same as taxa assessed at the family level.

Community Composition. We characterized community composition based on a principal component analysis of the relative abundance of these four life history categories. We then used the subset of principal component axes that explained most of the variation as response variables in models to explore predictions related to changes in composition. We categorized macroinvertebrates based on strategies for tolerating or avoiding wetland drying using Wiggins et al. (1980), excluding rare taxa (taxa present at only one wetland with <5 individuals). We focused on four life history categories related to drying: overwintering residents (drought tolerators), overwintering spring recruits (wet layers), overwintering summer recruits (dry layers), and non-wintering spring migrants (active dispersers) (Wiggins et al. 1980, Batzer and Ruhí 2013, Gleason and Rooney 2018, Appendix Table 2.1). Although some families of some macroinvertebrates may make use of several strategies, we classified each family into one group that best represented the primary or dominant life history strategy.

Wetland Explanatory Variables

Size. We computed four covariates to characterize wetland size: depth, area, overall change in depth, and overall change in area (Appendix Table 2.2). We measured the maximum depth of the wetland, by taking ten measurements with a collapsible meter ruler and retaining the maximum value. To measure area, we used the area calculation tool on a Garmin Montana GPS while walking the perimeter of the wetland where surface water was visible. We measured depth and area during each wetland visit. We computed the overall change in depth as: $(\frac{maximum\ depth - minimum\ depth}{maximum\ depth})$, using values collected during the three wetland visits; the overall change in area followed a similar formula: $(\frac{maximum\ area - minimum\ area}{maximum\ area})$. The computation of overall change in depth and area resulted in only one value of each metric for each wetland, such that these covariates are constant over time. Based on literature reviews, we assumed drying would decrease wetland size by decreasing area and depth, but increase the overall change in area and depth (Brooks and Hayashi 2002, Lee et al 2015).

Spatial Isolation. We computed two covariates to characterize spatial isolation: average distance to all wetlands and distance to nearest wetland (Appendix Table 2.2). First, the average distance to all wetlands in a catchment (hereafter, average distance) was calculated using the ArcToolbox NEAR tool (Gould 2010). This tool averages the distances between the centroid of each sampled wetland to all wetlands in the catchment (Gould 2010). The calculations were completed for each wetland by year, over the survey record available from GRYN data, and averaged. The number of years of available data varied between catchments from two to six years. Second, we measured the distance to the nearest wetland with Google Earth from approximately the center of the sampled wetlands to the closest neighboring wetland. The values for average distance and the distance to the nearest wetland were computed at the start of our study, such that these covariates are constant over time.

Temporal Isolation. We initially used the NWI permanence class as a coarse assessment of temporal isolation during the process of site selection. In our analyses, we instead characterize temporal isolation by computing rates of drying (Chandler et al. 2017). The relationship between rates of drying and composition of macroinvertebrates is less known than the influences of hydroperiod. NWI classifications also did not seem to capture the temporal dynamics of our studied wetlands. We computed two rates of wetland drying: rate of depth drying and rate of area drying for each wetland (Appendix Table 2.2). First, we calculated the total percent change (in depth or area) between each pair of consecutive sample dates (i.e., June to July, July to August).

We divided this value by the number of days between sample dates, to convert to a daily rate. Finally, we averaged the daily rates of change (in depth or area) for each pair of consecutive sample dates. Six of the 18 wetlands dried before the August sampling date; for these wetlands, we used the rate of drying from June to July in models. Based on a review of the literature, we assumed the rate of change in area and depth increase with faster drying wetlands compared to more stable wetlands (Chandler et al. 2017).

Data Analysis

We analyzed our data in two steps - an exploratory step and an inferential step (DeVoe et al. 2015). During the exploratory step, we evaluated which of the measured covariates best characterized size, spatial isolation, and temporal isolation. To do this, we created three model suites: models including only size covariates, models including only spatial isolation covariates, and models including only temporal isolation covariates. We compared models within each suite using Akaike Information Criterion for small sample sizes (AICc) (Brewer 2016) and retained covariates from the most-supported models ($\Delta AIC_c \leq 2$) for the next step. During the inferential step, we tested our hypotheses about wetlands and macroinvertebrates. We used covariates identified during the exploratory step to create models that corresponded with our *a priori* predictions about the roles of size, spatial isolation, and temporal isolation on variation in family richness and community composition (as characterized by principal components analysis) of the four life history categories. We again compared models within each suite using AICc and made inferences based on competing models ($\Delta AIC_c \leq 4$).

We focused primarily on additive models based on our *a priori* predictions, but also considered two-way interactions that we hypothesized to be biologically important (Appendix

Table 2.7). For wet layers, dry layers, and active dispersers, we expected larger effects of spatial isolation in larger wetlands that may be easier to detect (size × spatial isolation). For overall richness and all life history strategies, we expected the benefits of large wetland size would decrease with increased temporal isolation (size × temporal isolation). We also expected wetlands that dry quickly and are far apart would have the fewest macroinvertebrate families and low relative abundance of all life history strategies, except dry layers (spatial isolation × temporal isolation).

In each step, we constructed general linear mixed models using the lme4 package in R (Bates and Martin 2018) and included a random intercept for each wetland to account for repeated measurements over time. Prior to building models, we examined correlations among pairs of covariates; where Pearson correlation coefficient exceeded 0.60, we included only one of the covariates from the pair to avoid collinearity (DeVoe et al. 2015). All statistical analyses were completed in Program R (version 4.1.1, R Core Team 2020).

Results

Family Richness

We identified 37,365 individual macroinvertebrates collected from 18 wetlands during 47 sampling visits (Appendix Table 2.1). Estimates of family richness ranged from 1.8 to 16.8 (average = 9.6, standard deviation = 3.8). Chironomidae, Daphnidae, and Dytiscidae occurred in all wetlands and Chironomidae was most abundant.

During the exploratory step, we found that depth, area, and overall change in area were among the most-supported models to characterize wetland size (Appendix Table 2.3). Both distance metrics were included in well-supported models to describe spatial isolation, whereas the rate of depth drying was the only variable included to characterize temporal isolation (Appendix Table 2.3). We retained these six variables (depth, area, overall change in area, distance to the nearest neighbor, average distance to all wetlands, and rate of depth drying) for inclusion in models in the inferential step.

During the inferential step, we found that size, spatial isolation, and temporal isolation all explained some variation in family richness of macroinvertebrates, but certain covariates better characterized this variation (Table 2.1). In general, depth (size), rate of depth drying (temporal isolation), and average distance to all wetlands (spatial isolation) best explained variation in family richness, given that the most-supported models included at least one or some additive combination of these variables (Table 2.1). However, some of these covariates had confidence intervals that overlapped zero. In addition, the null model was among the competing models (Table 2.1), suggesting that our measured covariates did not explain substantial variation in richness.

Rate of depth drying (temporal isolation) was especially important and was included in 9 of the 12 competing models (Table 2.1). As we predicted, family richness decreased with temporal isolation; all estimates were consistent in direction and magnitude (range of estimated coefficients for the rate of depth drying: -0.95 to -0.72, Table 2.1), and confidence intervals generally did not overlap zero.

Although all of the size variables (depth, area, and overall change in area) were included in at least one competing model, we found consistent evidence that depth best explained variation in family richness; all but one of the models with depth were among the competing models (Table 2.1). Further, competing models that included other size covariates (overall change in area or area) also included the rate of depth drying (temporal isolation), which is a different way to characterize depth. As we predicted, family richness increased in wetlands with deeper water, larger area, and low overall change in area, although size-based covariates often were uninformative, with confidence intervals that overlapped zero (Table 2.1).

The average distance to all wetlands better explained variation in family richness than the distance to the nearest wetland (Table 2.1). We predicted that spatially isolated wetlands would have lower family richness due to decreased colonization, but instead found some evidence that family richness increased (range of estimated coefficients for average distance to neighboring wetlands: 0.005 to 0.008, distance to the nearest wetland: 0.003, Table 2.1); confidence intervals again overlapped zero.

Community Composition

Principal Component Analysis. Most of the variation (>99%) in the relative abundance of life history strategies was explained by three principal components, which explained 47%, 29%, and 23% of the variation respectively. Principal component 1 (PC1) largely described variation in the relative abundance of the drought tolerators (r = 0.95) and wet layers (r = -0.91) (Appendix Figure 2.1). Specifically, the relative abundance of drought tolerators increased and wet layers decreased with higher values of PC1. Larger values of principal component 2 (PC2) primarily were associated with decreased abundance of the dry layers (r = -0.99), whereas higher values of principal component 3 (PC3) mainly were associated with increased relative abundance of active dispersers (r = 0.91). In the subsequent analyses, we refer to each PC by the dominant life history strategy represented; PC1 is referred to as drought tolerators and wet layers, PC2 as dry layers, and PC3 as active dispersers.

Drought Tolerators and Wet Layers. During the exploratory step, we found the overall change in depth, the overall change in area, area, and depth were included in the most-supported models to characterize the relationship between wetland size and the drought tolerators and wet layers (Appendix Table 2.4). Both distance metrics were included in well-supported models to describe spatial isolation, whereas the rate of depth drying was the only variable included to characterize temporal isolation (Appendix Table 2.4). We retained overall change in depth, the overall change in area, area, depth, distance to the nearest wetland, the average distance to all wetlands, and the rate of depth drying for inclusion in models focused on drought tolerators and wet layers (PC1) in the inferential step.

During the inferential step, we found the rate of depth drying (temporal isolation) best characterized variation in the relative abundance of drought tolerators and wet layers (PC1); all competing models included rate of depth drying (Table 2.2). Based on the best-supported model, abundance of drought tolerators and wet layers depended on an interaction between rate of depth drying and the distance to the nearest wetland. When wetlands had a close neighboring wetland (90 m away, representing the 25th percentile in our data), the relative abundance of drought tolerators increased and wet layers decreased in wetlands with faster rates of depth drying (Figure 2.2). For wetlands that were more spatially isolated (neighboring wetland 190 m away, representing the 75th percentile in our data), the relative abundance of drought tolerators and wet layers changed little with different rates of depth drying (Figure 2.2). In additive models, wetlands that dried faster (higher rate of depth drying) had more drought tolerators and fewer wet layers (Table 2.2). The importance of size and spatial isolation for these life history strategies was less clear, given that these covariates often were uninformative (Arnold 2010, Table 2.2).

Dry Layers. During the exploratory step, area, depth, overall change in area, and overall change in depth were among the most-supported models to describe the relationship between size and dry layers (Appendix Table 2.5). Both distance metrics were included in well-supported models to characterize spatial isolation. We found that rate of depth drying, rate of area drying, and the additive combination of the rate of depth drying and rate of area drying helped to characterize temporal isolation. We retained these eight individual variables and the additive combination for the inferential step.

During the inferential step, variation in the relative abundance of dry layers (PC2) was best characterized by spatial isolation (Table 2.3); most of the competing models included either distance to the nearest wetland or average distance to all wetlands. Distance to nearest neighbor, average distance to all wetlands, and combinations of these with covariates for size were among the competing models, as was the null model (Table 2.3), suggesting that additional factors were needed to fully understand variation in abundance of dry layers. Based on the best-supported model, abundance of dry layers again depended on an interaction between rate of depth drying and the distance to the nearest wetland, although there was some uncertainty in the estimated effects. At wetlands with a close neighboring wetland (90 m), the relative abundance of dry layers changed little with different rates of depth drying (Figure 2.3). However, the relationship changed for more spatially isolated wetlands (distance to neighboring wetland 132 m away); the relative abundance of dry layers decreased in wetlands with faster rates of depth drying (Figure

2.3). The covariates for size and temporal isolation often were uninformative (Arnold 2010, Table 2.3).

Active Dispersers. During the exploratory step, we found that area, depth, overall change in area, overall change in depth, the additive combinations of area with the overall change in depth, and area with the overall change in area helped to characterize the relationship between active dispersers and size (Appendix Table 2.6). Distance to the nearest wetland best characterized spatial isolation and the rate of depth drying best described temporal isolation. We retained these six individual variables and the two additive combinations for the inferential step.

During the inferential step, spatial and temporal isolation best characterized variation in the relative abundance of active dispersers (Table 2.4). Combinations of distance to the nearest wetland (spatial isolation) and rate of depth drying (temporal isolation) were included in all competing models (Table 2.4). Based on the best-supported model, the relative abundance of active dispersers again depended on the interaction of distance to nearest wetland with rate of depth drying. The relative abundance of active dispersers always increased with the rate of depth drying, regardless of the increased distance to the nearest wetlands (Figure 2.4). However, the magnitude of this relationship was the largest when the wetland was spatially isolated (far from the nearest wetland neighbor). The importance of wetland size for active dispersers was less clear, given that these covariates often were uninformative (Arnold 2010, Table 2.4).

Discussion

Adding a temporal dimension to the IBT framework captured important dynamics in wetlands for aquatic macroinvertebrates. Temporally isolated wetlands (as measured by the rate of depth drying) had fewer families, consistent with our predictions and with Ebert and Balko

(1980). We also found that water depth explained more variation in family richness than area. Other studies echo this pattern: water depth structures communities of wetland macroinvertebrates (Zimmer et al 2000, Gleason and Rooney 2018, Tarr et al. 2004, Hall et al. 2004). IBT predicts increased richness with island area because of the relationship with habitat heterogeneity (MacArthur and Wilson 1967). In wetlands similar in size to those in this study, water depth also creates more habitat heterogeneity (Baber et al. 2004). Wetlands with deeper water are less likely to dry, potentially also resulting in lower extinction rates that lead to higher richness (Baber et al. 2004). Although we did find that family richness of aquatic macroinvertebrates increased with wetland area, the relationship was not especially strong. Some researchers have documented increases in richness with area (Brooks and Colburn 2012, Moraes et al. 2014), although Hall et al. (2004) found a decrease and Swartz et al. (2019) found no effect. Wetland area may be a poor predictor of richness, given that size can change rapidly due to seasonal drying (Batzer et al. 2013, Angler and Alvarez-Cobelas 2005, Hall et al. 2004).

Contrary to our predictions, family richness increased with both measures of spatial isolation, but the relationships were not especially strong (confidence intervals overlapped zero). We observed more variation in family richness for wetlands with close neighbors (90m), such that the uncertainty associated with these patterns may reflect unexplained variation. Swartz et al. (2019) studied several types of wetlands (created, impacted, and reference) near our study sites in the GYE and found no relationship between taxonomic richness and spatial isolation (characterized based on the distance to the nearest natural wetland). Similarly, Moraes et al. (2014) found spatial isolation did not structure macroinvertebrate richness in temporary wetlands in southern Brazil. The absence of observed patterns in these studies and our weak relationship between richness and spatial isolation may suggest that wetlands are not truly isolated in space (Leibowitz 2003). Although effectiveness of invertebrate dispersal changes based on the distance between sites (Incagnone et al. 2015), dispersal ability, and thus sensitivity to insularity, also varies among taxa (Itescu 2019) and within families (Incagnone et al. 2015). For most species of Culicidae, adults disperse < 5 km, whereas others move < 1 km (Service 1997). Adults in some species of Odonata complete very long-distance migrations (e.g., from India to North Africa) and other species exhibit high territoriality, leading to low dispersal **(**May 2013). In addition, some macroinvertebrates spend time living in terrestrial environments at different life stages (Leigh et al. 2016), increasing the ability to colonize different wetlands. Although IBT is an appealing framework to study the insularity of wetlands as discrete units in space, the surrounding matrix may be more permeable than observed with true islands (Itescu 2019) with some macroinvertebrates having both aquatic and terrestrial life stages (Wiggins et al. 1980). As such, the relationship between richness of aquatic macroinvertebrates and spatial isolation of wetlands may be more complicated and nuanced than we originally hypothesized.

We expected to see changes in relative abundance of the different life history strategies for drying as a function of wetland size, spatial isolation, and temporal isolation. Although we documented little change in the relative abundance of the different life history strategies based on wetland size (area and depth), spatial and temporal isolation did explain variation in abundance of the different groups, mostly following our predicted patterns. We focused on responses to drying when defining our functional groups of interest; abundance of these groups may be less driven by size-related mechanisms (e.g., habitat heterogeneity, visibility). The rate of drying provides an important cue for physiological changes, as slower drying can allow species to make the necessary metabolic shifts to avoid or tolerate desiccation (Strachan et al. 2015).

The interaction between the distance to the nearest wetland (spatial isolation) and the rate of depth drying (temporal isolation) consistently explained the most variation in abundance of all groups. We developed our predictions in part based on Gleason and Rooney (2018), who studied the same life history strategies. They found wet layers and dispersers were more sensitive to wetland permanence (hydroperiod, temporal isolation), with shorter hydroperiods constraining their abundance, whereas the abundance of drought tolerators and dry layers did not change with hydroperiod, due to their adaptations for drying (Gleason and Rooney 2018). In contrast, we found drought tolerators were less sensitive to temporal isolation – and hence more abundant in faster drying wetlands – whereas abundance of wet layers decreased with drying, and dry layers and dispersers changed based on the combined influences of temporal and spatial isolation. Understanding whether these differences stem from regional variation, variability inherent to wetland systems (Batzer et al. 2013), or other factors entirely, remains an important information gap.

We focused our work on characterizing macroinvertebrate communities in wetlands as a function of several factors, but additional information would further enhance our insights. Patterns of community composition change over time (Bohonak and Jenkins 2003, Tarr et al. 2004), emphasizing the importance of the timing and frequency of data collection. Wet layers and drought tolerators are fast colonizers, whereas dry layers and migrators tend to colonize later in the season (Wiggins et al. 1980). Given that a third of our wetlands dried before the final sampling effort, our results may better represent colonization patterns during the early and midseason. Later in the summer, distances between wetlands continue to increase as wetlands dry (Leibowitz 2003). In 2018, when we collected these data, the total annual accumulated snow water equivalent was 5,383 cm, compared to the 37-year average (1980-2017) total annual accumulate snow water equivalent of 5,085 cm based on Base Camp SNOTEL site data (3km east of GTNP boundary). Sampling more frequently throughout the summer and over many years would capture multiple colonization or dormancy events (Buoro and Carlson 2014), as well as other important patterns of temporal variation.

We used a few basic measurements (area and depth) to estimate drying (temporal isolation), but adding more hydrological characteristics would allow for a more nuanced analysis. Hydroperiod also can characterize temporal isolation, with higher macroinvertebrate richness generally associated with longer periods of wetland inundation (Baber et al. 2004, Duffy et al. 1999, Gleason and Rooney 2018). Yet measuring hydroperiod is difficult (Lee et al. 2015) and many studies instead rely on hydroperiod categories (e.g., seasonal, permanent, Batzer et al. 2013). Originally, we tried to do the same, but found that some wetlands categorized as permanent (based on the NWI) dried before others categorized as seasonal wetlands. Instead, we found that estimating temporal isolation based on rates of drying was a more reasonable approximation; the wetlands that dried completely had the fastest rates of drying (for both area and depth) and these rates explained variation in life history strategies. Climate change is shifting wetland hydrological regimes, such that older wetland classifications may no longer match current conditions (Matthews et al. 2016). Quantifying the duration of inundation and dry phases, frequency of inundation and drying, and other details of the hydrological regime will provide better estimates of drying.

Although we focused on grouping species based on specific strategies for persistence in the face of wetland drying, we recognize there is substantial variation within the categories and within taxa (Strachan et al. 2015). For example, some drought tolerators can persist for decades (e.g., 15-20 years for Anostraca, Chironomidae) or centuries (e.g., ≥200 years for Copepoda), whereas others only can disperse across short temporal distances (e.g., 17 days for Hirudinea, Strachen et al. 2015). In addition, the same species may use multiple strategies, sometimes during different life history stages, and rely on other water sources in addition to wetlands (Strachen et al. 2015). Characterizing species-specific, and even stage-specific, responses would provide additional insights into the diverse strategies to mitigate the challenges associated with wetland drying.

Wetland vegetation, much like the dynamic hydrology, supports and drives biodiversity through many mechanisms (Mitsch and Gosslink 2015); adding vegetation variables to analyses could reveal additional insights. Swartz et al. (2019) found canopy cover was the most important driver of community composition in wetlands near GTNP. These wetlands were human created with relatively new vegetation (Swartz et al. 2019), whereas we focused on protected wetlands with well-established vegetation. Characterizing the relationship between vegetation and biodiversity in the wetlands we studied would provide an important contrast. Given that wetland vegetation also is sensitive to water depth (Zimmer et al. 2000), separating the influences of hydroperiod and vegetation could be difficult (Gleason and Rooney 2018).

Aquatic organisms that live in wetlands at high latitudes and elevations are especially vulnerable to shifts in snowpack, snowmelt, and evaporation rates resulting from changes in climate, given concomitant changes in wetland inundation and drying (Lund et al. 2016). Even though aquatic macroinvertebrates possess adaptations for withstanding dry periods, shifts in climate patterns will test the threshold of tolerance for many species (Strachan et al. 2015, Stubbington et al. 2016). Although the wetlands in our study are protected from many anthropogenic influences, they still are susceptible to increased drying from climate change (Ray et al. 2019). Taxa that occur in places without the protections of a national park (or similar designation) are subject to many additional threats that alter size, spatial, and temporal isolation of wetlands. For example, fragmentation from human development and agriculture exacerbate climate-induced changes to wetlands (Hall et al. 2004). The wetlands in our study provide essential reference points for how macroinvertebrates in the Northern Rockies are affected by climate change, without substantial additional stresses of draining, tilling, and other activities. Wetland drying is a complicated disturbance that is necessary to support some unique taxa, while operating as a threat to others. Understanding the nuanced relationship between wetland drying and biodiversity can help us better protect these diverse ecosystems from the inevitable shifts triggered by climate change.

Table 2.1. Estimates and 95% confidence intervals for coefficients in competing models (ΔAICc ≤ 4) from the inferential step explaining variation in family richness of aquatic macroinvertebrates in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). Models with multiple terms are additive unless listed with a * **in bold**.

Size	Spatial Isolation	Temporal Isolation	Estimated Coefficients and 95% CIs			
			Size	Spatial Isolation	Temporal Isolation	Interaction
Depth		Rate of depth drying	0.12 (-0.44 to 0.68)		-0.90 (-1.71 to -0.12)	
		Rate of depth drying			-0.95 (-1.73 to -0.18)	
Depth	AvgDist	Rate of depth drying	0.1 (-0.46 to 0.65)	0.005 (-0.004 to 0.014)	-0.72 (-1.58 to -0.12)	
	AvgDist	Rate of depth drying		0.005 (-0.004 to 0.014)	-0.74 (-1.59 to -0.09)	
Depth	AvgDist		0.025 (-0.004 to 0.05)	0.008 (-0.00 to 0.02)		
Depth	Dist to Neighbor	Rate of depth drying	0.024 (-0.004 to 0.052)	0.003 (-0.005 to 0.011)	-0.85 (-1.65 to -0.072)	
	Dist to Neighbor	Rate of depth drying		0.003 (-0.005 to 0.011)	-0.84 (-1.66 to -0.04)	
	AvgDist			0.008 (0.000 to 0.017)		
Depth*		**Rate of depth drying**	0.04 (-0.04 to 0.13)		-0.74 (-1.94 to 0.46)	-0.004 (-0.03 to 0.02)
Area		Rate of depth drying	0.12 (-0.44 to 0.68)		-0.90 (-1.71 to -0.12)	

Table 2.1 Continued

Overall change in area		Rate of depth drying	-0.63 (-5.64 to 4.33)		-0.90 (-1.75 to -0.07)
Depth			0.03 (0.00 to 0.06)		

Table 2.2. Estimates (and 95% confidence intervals) for coefficients in competing models (ΔAICc ≤ 4) from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically drought tolerators and wet layers (as measured by principal component 1) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). Models with multiple terms are additive unless listed with a * **in bold**.

Size	Spatial Isolation	Temporal Isolation	Estimated Coefficients and 95% CIs			
			Size	Spatial Isolation	Temporal Isolation	Interaction
	Dist to Neighbor*	**Rate of depth drying**		0.007 (0.001 to 0.014)	0.85 (0.4 to 1.31)	-0.004 (-0.008 to -0.001)
		Rate of depth drying			0.37 (0.08 to 0.66)	
Overall change in area		Rate of depth drying	-0.68 (-2.5 to 0.67)		0.41 (0.11 to 0.72)	
	AvgDist	Rate of depth drying		0.001 (-0.002 to 0.004)	0.42 (0.10 to 0.73)	
Area		Rate of depth drying	0.06 (-0.14 to 0.26)		0.39 (0.09 to 0.69)	
Overall change in depth		Rate of depth drying	0.07 (-1.67 to 1.8)		0.37 (0.07 to 0.66)	

Table 2.2 Continued

Depth		Rate of depth drying	0.000 (-0.01 to 0.01)		0.37 (0.08 to 0.66)	
	Dist to Neighbor	Rate of depth drying		0.000 (-0.003 to 0.003)	0.37 (0.06 to 0.67)	

Table 2.3. Estimates (and 95% confidence intervals) for coefficients in competing models (ΔAICc ≤ 4) from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically dry layers (as measured by principal component 2) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). Models with multiple terms are additive unless listed with a * **in bold**.

Size	Spatial Isolation	Temporal Isolation	Estimated Coefficients and 95% CIs			
			Size	Spatial Isolation	Temporal Isolation	Interaction
	Dist to Neighbor*	**Rate of depth drying**		0.007 (0.003 to 0.011)	0.26 (-0.04 to 0.56)	-0.003 (-0.005 to -0.001)
	Dist to Neighbor			0.002 (0.0002 to 0.004)		
	AvgDist			0.002 (0.0006 to 0.004)		
Area	Dist to Neighbor		0.001 (-0.008 to 0.01)	0.002 (0.0001 to 0.004)		
Null						
	Dist to Neighbor	Rate of depth drying		0.002 (-0.0001 to 0.004)	-0.05 (-0.026 to 0.159)	
Overall change in area	AvgDist		0.43 (-0.75 to 1.59)	0.002 (0.0002 to 0.004)		

Table 2.3 Continued

Area	AvgDist		0.002 (-0.007 to 0.01)	0.002 (0.0001 to 0.004)	
Depth	Dist to Neighbor		0.001 (-0.008 to 0.01)	0.002 (0.0001 to 0.004)	
Overall change in area	Dist to Neighbor		0.09 (-1.09 to 1.27)	0.002 (0.0001 to 0.004)	
Overall change in depth	Dist to Neighbor		0.04 (-1.16 to 1.23)	0.002 (0.0002 to 0.004)	
Overall change in depth	AvgDist		0.33 (-0.91 to 1.54)	0.002 (0.0002 to 0.004)	
Depth	AvgDist		0.002 (-0.007 to 0.011)	0.002 (0.0001 to 0.004)	
	AvgDist	Rate of depth drying		0.002 (-0.0003 to 0.004)	-0.02 (-0.25 to 0.20)
		Rate of depth drying			-0.11 (-0.34 to 0.11)

Table 2.4. Estimates (and 95% confidence intervals) for coefficients in competing models (ΔAICc ≤ 4) from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically of active dispersers (as measured by principal component 3) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). Models with multiple terms are additive unless listed with a * **in bold**.

Size	Spatial Isolation	Temporal Isolation	Estimated Coefficients and 95% CIs			
			Size	Spatial Isolation	Temporal Isolation	Interaction
	Dist to Neighbor*	**Rate of depth drying**		-0.002	-0.06	0.003

Table 2.4 Continued

				(-0.01 to 0.002)	(-0.35 to 0.22)	(0.001 to 0.22)
	Dist to Neighbor	Rate of depth drying		0.003 (0.000 to 0.004	0.23 (0.04 to 0.42)	
Area	Dist to Neighbor	Rate of depth drying	-0.12 (-0.27 to 0.03)	0.003 (0.001 to 0.005)	0.20 (0.01 to 0.39)	

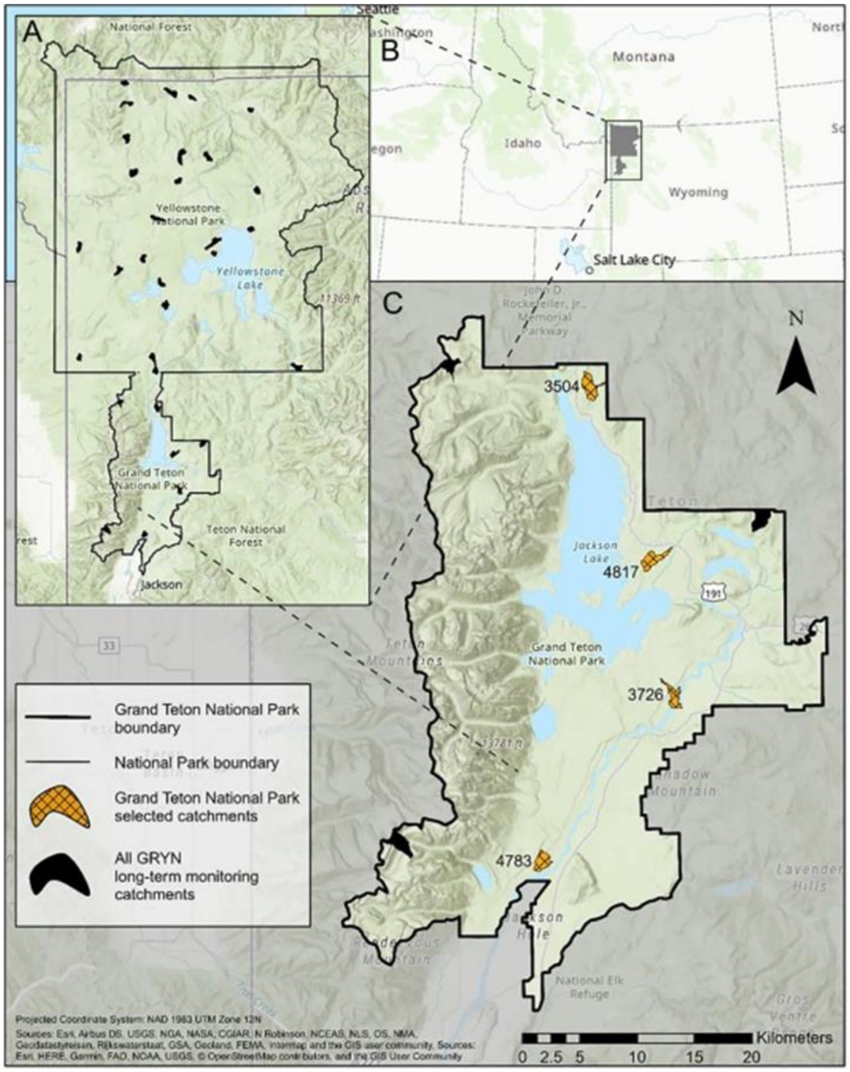

Figure 2.1. A) The Greater Yellowstone Inventory and Monitoring Network completes long-term wetland monitoring at catchments (in black) throughout the B) Greater Yellowstone Area including C) seven catchments in GNTP, Wyoming, USA. We sampled wetlands in four of these catchments (yellow crosshatch labeled by catchment number), summer 2018 (Levandowski et al. 2021 courtesy of Jana Cram, NPS).

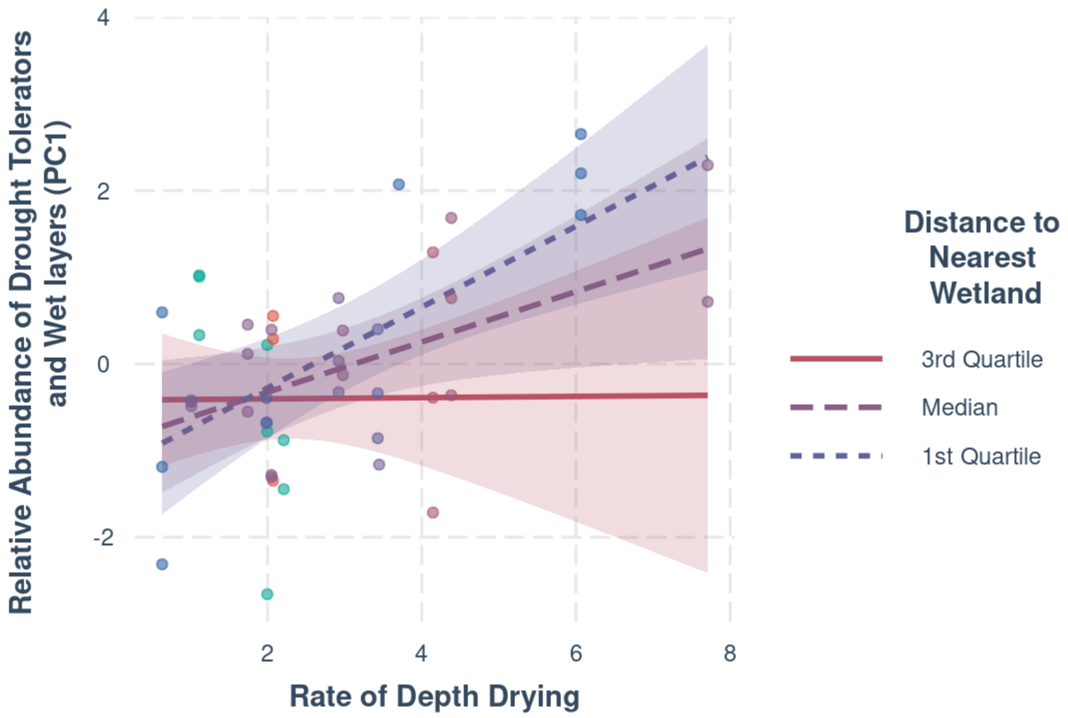

Figure 2.2. Predicted changes in relative abundance of drought tolerators and wet layers (as measured by principal component 1) as a function of the interaction between the rate of depth drying and distance to the nearest wetland, based on the top model (Table 2.2), summer 2018, GTNP, Wyoming. We plotted PC1, where a low score represents high abundance of drought tolerators and low abundance of wet layers. The rate of depth drying is estimated by the average daily percent change in depth, with larger values representing faster drying. We predicted changes in drought tolerators and wet layers for wetlands with nearest neighbors at distances representing the 1st (90 m), 2nd (132 m), and 3rd (190 m) quartiles.

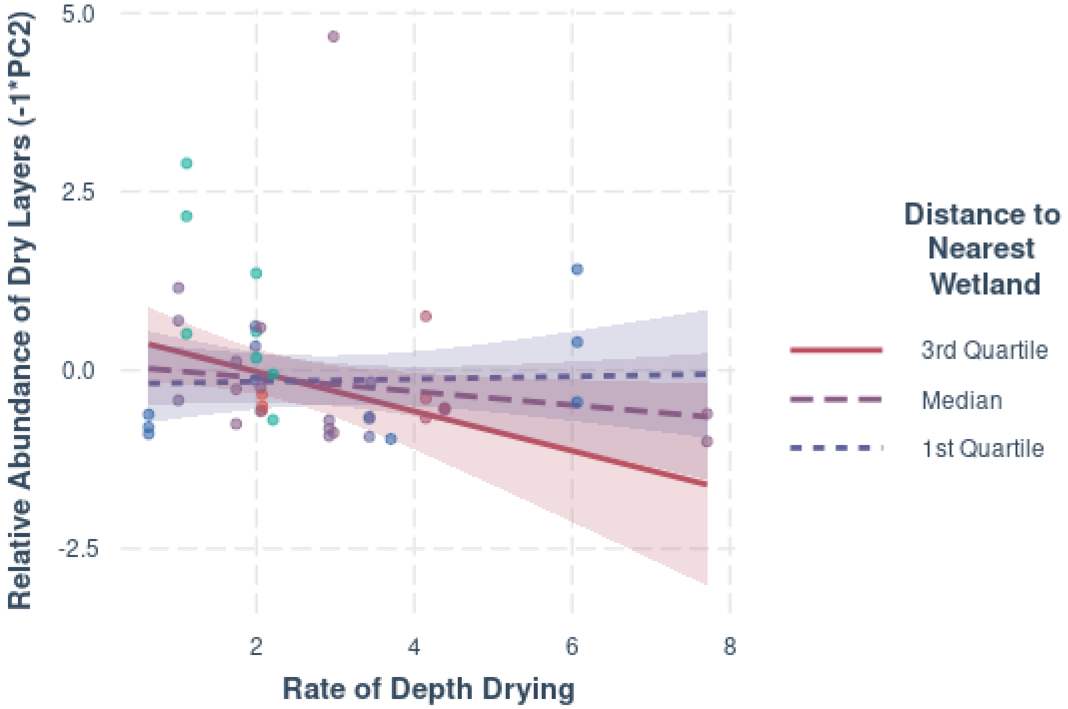

Figure 2.3: Predicted changes in relative abundance of dry layers (as measured by principal component 2) as a function of the interaction between the rate of depth drying and distance to the nearest wetland, based on the top model (Table 2.3), summer 2018, GTNP, Wyoming. We plotted the inverse of PC2, where a low score represents low abundance of dry layer. The rate of depth drying is estimated by the average daily percent change in depth, with larger values representing faster drying. We predicted changes in dry layers for wetlands with nearest neighbors at distances representing the 1st (90 m), 2nd (132 m), and 3rd (190 m) quartiles.

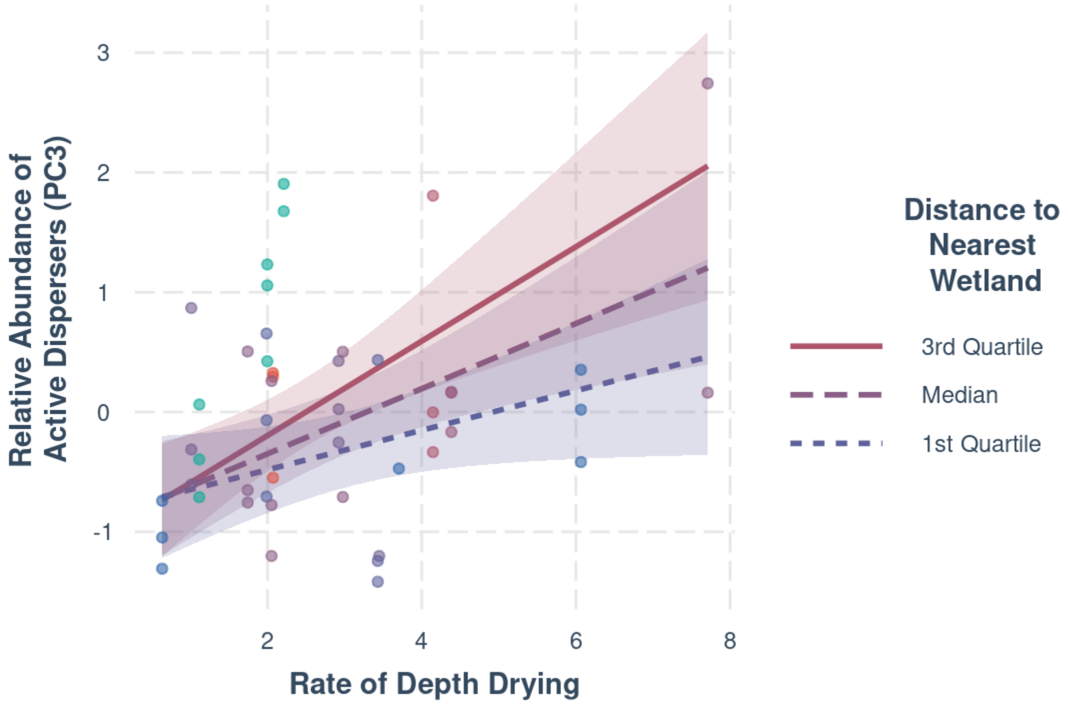

Figure 2.4: Predicted changes in relative abundance of active dispersers (as measured by principal component 3) as a function of the interaction between the rate of depth drying and distance to the nearest wetland, based on the top model (Table 2.4), summer 2018, GTNP, Wyoming. We plotted PC3, where a low score represents low abundance of active dispersers. The rate of depth drying is estimated by the average daily percent change in depth, with larger values representing faster drying. We predicted changes in active dispersers for wetlands with nearest neighbors at distances representing the 1st (90 m), 2nd (132 m), and 3rd (190 m) quartiles.

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CHAPTER THREE

MULTI-METHOD BIODIVERSITY ASSESSMENTS FROM WETLANDS IN GRAND TETON NATIONAL PARK

Contribution of Authors and Co-Authors

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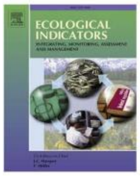

Multi-method biodiversity assessments from wetlands in Grand Teton National Park

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ABSTRACT

A cost-efficient approach to long-term monitoring is to focus on one species or group of organisms as indicators of ecological condition. Through the use of autonomous monitoring technologies, monitoring programs can efficiently expand the biological community surveyed and inferences made. Amphibians have been monitored in Yellowstone and Grand Teton national parks by the Greater Yellowstone Inventory and Monitoring Network (GRYN) since 2006, yet other taxa dependent on wetlands have not been systematically studied. Our main aim was to explore what additional insights we could gain about wetland biodiversity by combining GRYN's amphibian surveys with multiple autonomous technologies. We deployed wildlife cameras and acoustic recorders (for audible and ultrasonic sounds) at 4 permanent wetlands in Grand Teton National Park, WY during early and late summer 2017 and used descriptive metrics to summarize our findings. During GRYN's surveys, 3 of 4 native amphibians were detected. With autonomous monitoring tools, we also documented avian and mammalian communities and detected changes in the degree of activity over the summer. Combining multiple, complementary technologies with field-based surveys provides a more comprehensive picture of wetland biodiversity and enhances insights about ecological condition and change.

1. Introduction

Freshwater wetlands cover <8% of the Earth's land surface, yet they provide numerous ecosystem services, as well as habitat for diverse plants and animals (Keddy et al., 2009). Arguably, wetlands are keystone ecosystems because their area is disproportional to their influence on landscape processes (Calhoun et al., 2017). More than half of the wetland area in the conterminous United States has been lost due to conversion and changes in climate and land use, with some estimates as high as 87% (Davidson, 2014). Wetlands are even threatened within protected areas like Grand Teton National Park (GTNP) and Yellowstone National Park (YNP), where lower precipitation and higher temperatures have been linked to wetland desiccation (Ray et al., 2019). Understanding the ecological consequences of wetland changes requires tools that can provide a large-scale, long-term, and comprehensive picture.

Indicator species often are used for biodiversity monitoring, given limited resources (reviewed in Caro, 2010), yet some indicators may not capture ecosystem complexity (Hilty and Merenlender, 2000). For example, amphibian richness has been used as a proxy for other taxa in montane wetlands (Sergio and Pedrini, 2007), but the importance of wetlands to other animals, such as terrestrial and volant mammals, often is less understood (Kingsford et al., 2016, Mas et al., 2021). Combining autonomous monitoring technologies with field-based surveys provides an opportunity to expand the indicators monitored, providing a more holistic assessment (Boullhesen et al., 2021, Pimm et al., 2015) of wetland biodiversity.

The Greater Yellowstone Inventory and Monitoring Network (GRYN) of the National Park Service (NPS) conducts long-term monitoring of wetlands and amphibians in YNP and GTNP. GRYN visits 31 catchments (Fig. 1A), sampling over 300 wetlands annually since 2006 (Gould et al., 2012). Other taxa disproportionately use wetlands for elements of their life cycle, but have not been studied systematically in these biodiverse areas. Our main aim was to explore what additional insights we could gain about wetland biodiversity by combining GRYN's amphibian surveys with data from autonomous monitoring technologies. We focused

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on wetlands in GTNP and used descriptive metrics to summarize our findings.

2. Materials and methods

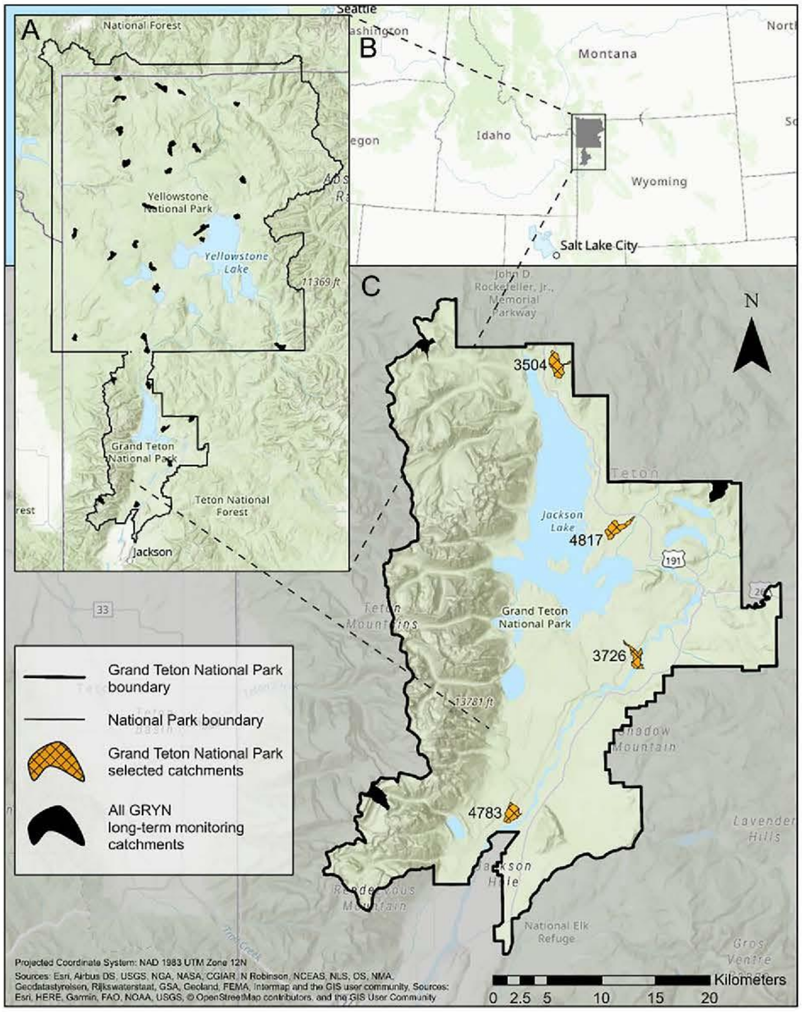
2.1. Study area

GTNP is located in western Wyoming (Fig. 1B). Approximately 10% of the park is covered by surface water, with all waters draining into the Snake River. Terraces rising above the floodplain, primarily covered by sagebrush (*Artemisia* spp.) and grasses, are occasionally interrupted by glacial moraines and buttes. The forests consist of lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*) and aspen at lower elevations, with Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*), and subalpine fir (*Abies lasiocarpa*) at higher elevations.

Wetlands across GTNP are the fullest from mid-June to early July and begin drying in late August (Ray et al. 2019). Average temperature is −3.6° C in January and 25.3° C in July, with most snowfall from November and April. GTNP is home to 4 native amphibians: boreal chorus frog (*Pseudacris maculata*), Columbia spotted frog (*Rana luteiventris*), western tiger salamander (*Ambystoma mavortium*), and western toad (*Anaxyrus boreas*), and 1 nonnative amphibian: American bullfrog (*Lithobates catesbeianus*); these species are the focus of GRYN's wetland monitoring. Surveys also document presence of reptiles (mainly terrestrial gartersnake, *Thamnophis elegans*).

2.2. General methods

We selected 1 permanent wetland in 4 of the 7 catchments in GTNP visited annually by GRYN (Fig. 1C); these 4 catchments represent a north–south gradient. Wetland permanence was classified based on the USFWS National Wetland Inventory and data collected by GRYN (see Brice et al., *this issue*). These 4 wetlands are characterized as lakes, ponds, or wet meadows with 50–75% cover of sedges, rushes, and grasses. GRYN completed visual encounter surveys for amphibians following Bennetts et al. (2013). We deployed wildlife cameras and acoustic recorders (1 of each per wetland) in early and late summer 2017 (details in Table 1) to document wetland use by other taxa. These exploratory efforts were part of a larger project, such that we were limited by available personnel and sets of identical sampling equipment. Although we sampled relatively few wetlands, our goal was to explore the utility of expanding to a larger sample in the future.



Projected Coordinate System: NAD 1983 UTM Zone 12N

Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community, Sources: Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

Fig. 1. A) Catchments (in black) sampled by the Greater Yellowstone Inventory and Monitoring Network (GRYN) in Yellowstone and Grand Teton national parks, which are B) located in Montana and Wyoming. Each catchment is comprised of multiple wetlands. C) We selected and sampled 1 permanent wetland in 4 of the 7 catchments in Grant Teton National Park, Wyoming (sampled catchments are numbered and in gold, others are in black), summer 2017 (Table 1). Map courtesy of Jana Cram, GRYN.

Table 1
Taxonomic richness at 4 permanent wetlands (identified by catchment and wetland number) sampled in summer 2017, Grand Teton National Park, Wyoming (Fig. 1C). The Greater Yellowstone Inventory and Monitoring Network completed visual encounter surveys for amphibians in late June and July. We deployed and co-located cameras and ultrasonic recorders in early and late summer; we also sampled audible acoustics (Fig. 2). Wetland 3504-1 was sampled July 2–8 (early)/Aug 20–25 (late), 3726-3 was sampled June 23–29/Aug 12–18, 4783-68 was sampled June 24–30/Aug 25-Sept 1, and 4817-12 was sampled July 1–7/Aug 25-Sept 3. Due to equipment anomalies, no ultrasonic data were collected at 2 wetlands during late summer. Area is based on GPS track data collected while walking the wetted perimeter of each site; we did not record an area for 4783-68 in early summer.

Wetland	Elevation (m)	Wetted Area (m^2)		Amphibian Richness	Camera Richness (mammals)		Camera Richness (birds)		Bat Richness	
		Early	Late		Early	Late	Early	Late	Early	Late
3504-1	2299	2271	980	2	0	1	0	0	8	8
3726-3	2034	891	412	2*	0	0	0	0	5	5
4783-68	1961	–	774	0	1	1	1	0	6	–
4817-12	2081	4998	4739	2	0	0	0	1	2	–

* Terrestrial gartersnake also was observed.

2.3. Wildlife cameras

We used infrared cameras (Stealth Cam PX18CMO, GSM Outdoors, Irving, TX), which were motion-triggered, but in operation 24 hours/day. Wildlife cameras were attached to aluminum conduit (~1.5 m high), pointed at the wetland and positioned to capture as much of the wetted area as possible, with the same orientation during both sampling periods. The visible proportion of the wetland varied; no wetlands were completely in view (wetted edge to wetted edge) in early summer and only 1 was in late summer. We applied a 30-second delay to the trigger to minimize incidental photos. All images were processed by the senior author, who had extensive experience sampling wildlife in this area. To account for equipment malfunctions and standardize effort, we tallied the number of species captured in images during the first 4 days of each sampling period.

2.4. Audible and ultrasonic acoustics

Audible acoustics were recorded with Song Meters (SM3BAT, firmware version 1.3.1) and acoustic microphones (SMM-A2, Wildlife Acoustics, Inc., Concord, MA) at a sampling rate of 44.1 kHz and gain of 0 dB. Each unit was attached to the same pole as the camera (~1.5 m high). We oriented microphones to minimize sound interference, with the same orientation during both sampling periods. Audible recordings were continuous, starting 30 min before sunrise and ending at sunset, saved as uncompressed .WAV files.

Processing acoustic recordings to identify individual species requires time-intensive effort from experts or algorithms trained for a particular region (e.g., Kahl et al., 2021). As an alternative, we used an index to summarize bioacoustic activity in the audible recordings within the frequency range of calls of most avian species. A variety of acoustic indices have been used to represent biodiversity (Buxton et al., 2018), and we specifically chose the acoustic complexity index (ACI, Pieretti et al., 2011) as it has been shown to describe avian diversity during the dawn chorus. Although other species, like the boreal chorus frog, produce audible signals in this area, our audible recordings and calculation of ACI were only during day time hours, when frogs are typically less vocal. We used custom scripts built in Program R (R Core Team, 2021) to first convert files to calibrated 1-second, 1/3 octave band sound pressure levels (dB $\mathrm{Leq}_{,1s}$) between 12.5 and 8000 Hz (based on Merchant et al., 2015), then calculated ACI in 10-minute intervals (based on Buxton et al., 2018) within 1.6–8 kHz bands to capture the avian community. To standardize effort, we graphed the variation in ACI for each day a wetland was sampled.

We recorded ultrasonic sounds with the same Song Meters, attaching an ultrasonic microphone (SMM-U1, Wildlife Acoustics, Inc.) to the top of the conduit (~2.3 m high), pointed towards the wetland. Ultrasonic recordings were collected from sunset until 30 min before sunrise, using defined trigger settings (TRGWIN 3.0 s, TRGMAX 5.0 s, TRGLVL 12 dB, call duration: 1.5–300 ms). Frequencies were set to capture bats in GTNP (8–192 kHz). We processed ultrasonic sounds with Sonobat 4.2.1 (Arcata, CA), eliminating non-bat and poor-quality recordings with Sonobat Batch Scrubber 5.7, identified species with Western Wyoming classifiers in SonoBatch, and summarized output with SonoVet. Due to equipment anomalies, no data were collected at 2 wetlands in late summer; we sampled other wetlands for 3–7 nights. To standardize effort, we tallied the number of species and total number of calls identified (by species) during the first 3 nights of each sampling period.

3. Results

During visual surveys of these wetlands, GRYN documented 3 of the 4 native amphibians: boreal chorus frog, Columbia spotted frog, and western tiger salamander, along with terrestrial gartersnake (Table 1); they did not detect American bullfrogs. Using cameras and expert review, we increased the biological community sampled through the detection of 4 additional species: elk (*Cervus canadensis*), black bear (*Ursus americanus*), sandhill crane (*Grus canadensis*), and an unidentified bird, with images of animals captured in 3 of 4 wetlands (Table 1). Using ultrasonic recordings and bat identification software, we further increased the biological community sampled, identifying 8 bat species by their calls: big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), and 5 species of *Myotis*, with 2–8 species at each wetland (Tables 1 & 2). The number of identified bat calls varied among wetlands and between early and late summer; the majority of these calls were made by little brown myotis (*Myotis lucifugus*) (73%, Table 2). Using audible acoustic recordings processed with an index of avian diversity (ACI), we quantified variation within and among the wetlands and a decrease in bioacoustic activity in late summer (Fig. 2).

4. Discussion

Using several autonomous monitoring technologies improved our understanding of the ecological community in wetlands and could enhance GRYN's ongoing amphibian monitoring program. GRYN's visual encounter surveys provided a snapshot of wetland biodiversity, namely 3 of 4 amphibians (and 1 reptile). By investing some additional effort, we also documented avian species (via cameras, and a proxy for avian diversity using audible sound) and several mammalian taxa (via cameras, ultrasonic recordings) in the same wetlands. We detected 7 of 10 bat species documented by Keinath (2005) and also recorded California myotis, contributing to an important knowledge gap (Mas et al., 2021).

Autonomous monitoring technologies are non-invasive and can collect data over large temporal and spatial scales, potentially simultaneously (e.g., Blumstein et al., 2011). Deploying wildlife cameras and acoustic recorders required us to return to the sampled wetlands more often (4 times during the summer) than would occur following GRYN's monitoring protocol (1 visit), but we collected data at these sites for a

Table 2
Total number of calls identified for each bat species recorded at 4 permanent wetlands (Fig. 1C) during the early and late summer 2017 (Table 1), Grand Teton National Park, Wyoming; number of calls can be used as a proxy for relative activity. To standardize effort, we summarized only the first 3 days of each sampling period. Due to equipment anomalies, we did not collect ultrasonic data at 2 sites during the late summer (4783-68, 4817-12). We recorded big brown bat (*Eptesicus fuscus*, EPFU), hoary bat (*Lasiurus cinereus*, LACI), silver-haired bat (*Lasionycteris noctivagans*, LANO), California myotis (*Myotis californicus*, MYCA), western small-footed myotis (*Myotis ciliolabrum*, MYCI), long-eared myotis (*Myotis evotis*, MYEV), little brown myotis (*Myotis lucifugus*, MYLU), and long-legged myotis (*Myotis volans*, MYVO). Sonobat classified only a few recorded calls to 2 species (pallid bat, *Antrozous pallidus*, Yuma myotis, *Myotis yumanensis*); we did not include these in the species tally, given the small number of calls and that these species are less likely to be present in GTNP.

Early summer								
Wetland	EPFU	LACI	LANO	MYCA	MYCI	MYEV	MYLU	MYVO
3504-1	1	4	1	1	2	43	644	11
3726-3	4	5	5			1	4	
4783-68	13	58	26			7	67	3
4817-12						1	6	
Late summer								
Wetland	EPFU	LACI	LANO	MYCA	MYCI	MYEV	MYLU	MYVO
3504-1	66	115	320	2	3	47	153	5
3726-3	2	5	32			4	22	

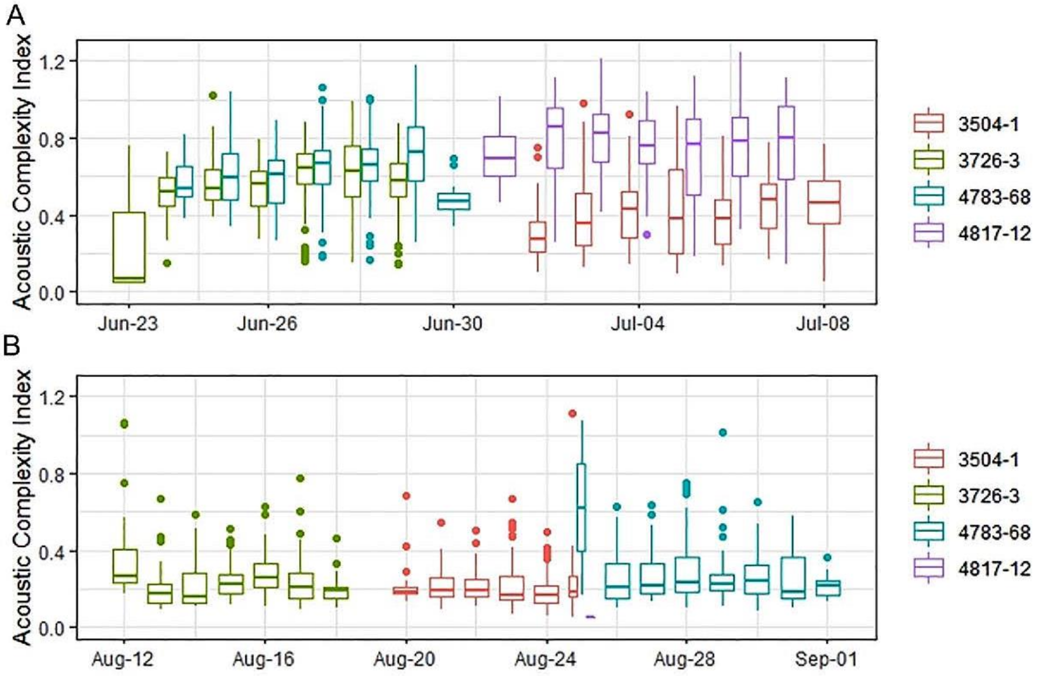


Fig. 2. Daily variation (median [line], first and third quartiles [boxes], 1.5 inter-quartile range [whiskers], and outliers [points]) in the acoustic complexity index (ACI) during **A)** early and **B)** late summer 2017 for 4 permanent wetlands, identified by catchment and wetland number, Grand Teton National Park, Wyoming (Table 1, Fig. 1C). We used ACI to summarize bioacoustic activity of the avian community. Acoustic equipment malfunctioned at wetland 4817-12 (purple) such that sampling occurred for only 1 day during the late summer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

longer time period, which could allow for additional insights. Despite relatively modest sampling effort, we documented changes over the summer in the species using these wetlands and the degree of activity (e.g., Table 2, Fig. 2). We also recorded seasonal changes in wetland size, water depth, and vegetation cover in camera images (Supplementary Information), with a finer temporal resolution than possible with annual site visits. Data from autonomous monitoring technologies also can be used to estimate occupancy or abundance, accounting for imperfect detection (MacKenzie et al., 2002, Marques et al., 2013), and insights can extend beyond the focal species (e.g., anthropogenic noise to study human activity patterns, Pimm et al., 2015). These tools can provide baseline information and be expanded over space and time to address questions related to climate change and other threats.

The ability to collect data without being on-site is an appealing quality of autonomous monitoring technologies, but substantial effort is still required. With current technology, monitored sites must be visited at least twice (once for equipment deployment and again to retrieve equipment) and potentially more often to maintain functionality. In addition, equipment can malfunction and result in data loss. The costs associated with equipment can be high, but more cost-effective models are increasingly available (e.g., Hill et al., 2018). The abundant data collected also require specialized software and extensive effort and expertise to process, store, and archive files. Increasingly, software packages include algorithms that automatically recognize potential detections and identify species (e.g., Sonobat, Kahl et al., 2021). These algorithms help reduce processing time and effort, but are subject to errors and ambiguous results, often still requiring at least some manual verification or appropriate statistical modeling frameworks (e.g., Wright et al., 2020). Regardless of the approach, training is needed to ensure proper use of software and statistical analyses and a clear understanding of limitations.

5. Conclusion

Despite the importance of wetlands, there is a surprising lack of information on the diversity of species using these ecosystems. GRYN's monitoring program is filling that gap for amphibians, and our work demonstrates the utility of autonomous monitoring technologies to increase the breadth of the biological community sampled and document ecological patterns not possible with current survey efforts. No single survey method can detect all taxa or provide all of the insights gained by complementary tools. Decisions about which tools to employ given limited resources lead to inherent tradeoffs (e.g., number of tools versus sample size: breadth versus depth of insights) that must be informed by the specific monitoring objectives and priorities. Ultimately, integrating multiple, complementary methods will result in monitoring plans that are sustainable, in terms of cost and feasibility, and meaningful, in terms of ecological features that can be tracked as conditions change.

CRediT authorship contribution statement

Mary L. Levandowski: Conceptualization, Formal analysis, Investigation, Writing – review & editing, Funding acquisition, Project administration. **Andrea R. Litt:** Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition, Supervision. **Megan F. McKenna:** Formal analysis, Writing – review & editing, Visualization. **Shan Burson:** Formal analysis, Resources, Writing – review & editing. **Kristin L. Legg:** Conceptualization, Resources, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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CHAPTER FOUR

CONCLUSION

Wetlands are disproportionately biodiverse relative to their size and anthropogenic influences, such as climate change, threaten these ecosystems (Gopal 2000). Although climate change has varying effects regionally, warmer and drier conditions are expected in the Greater Yellowstone Area, leading to increases in wetland drying (Ray et al. 2019). In this thesis, we studied biodiversity in wetlands within Grand Teton National Park. Given that this area is protected from many anthropogenic influences, our data may provide important reference information for land management and conservation. We focused on one taxon in depth to connect wetland hydrology with diversity patterns, and we also looked at a wide range of taxa while testing the use of novel survey techniques. In chapter two, we sought to understand how patterns of insularity affect biodiversity of macroinvertebrates. Specifically, we studied the relationship between wetland characteristics that are susceptible to change with drying (e.g., wetland size, spatial isolation, and temporal isolation) and patterns of diversity. Many macroinvertebrates have adaptations to withstand drying, yet we showed that the rate of drying affects not only family richness, but community composition as well. As climate change creates conditions that test species' tolerance thresholds for drying, we are likely to see shifts in the composition of wetland communities (Stubbington et al. 2019).

To better understand how this drying will manifest ecologically, we believe it is necessary to monitor multiple taxa, including vegetation, birds, mammals, and amphibians. In chapter three, we added automated recording units (ARUs) to wetland field surveys and were able to capture images or sounds for several of these taxa, confirming the complementarity of these tools. Our findings support the need for future work using ARUs to look for cross-taxon patterns of diversity in wetlands that are threatened by climate change. Adding ARUs to collect data on many taxa may help us better understand ecological changes to wetlands with increased drying. We can then use this understanding to better protect current wetlands, as well as design created wetlands for restoration.

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APPENDIX A

Appendix Table 2.1. Life history strategies designated for aquatic macroinvertebrate families collected from wetlands, Grand Teton National Park, Wyoming, summer 2018 and included in analysis. We also include the abundance and references used for categorization. **Bold indicates identification to order**. When multiple life history strategies were possible, we picked one strategy per family, based on the most commonly found species in the region. We list the possible strategies and denote the selected classification with *.

Family	Life History Strategy	References
Aeshindae	Active Disperser	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018, Wiggins et al. 1980
Ameletidae	Wet Layer	Merrit et al. 2008
Baetidae	Wet Layer*, Dry Layer	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Belostomatidae	Active Disperser	Merrit et al. 2008, Wiggins et al. 1980
Calanoida	Drought Tolerator	Merrit et al. 2008
Carabidae	Active Disperser	Merrit et al. 2008
Ceratopogonidae	Wet Layer	Merrit et al. 2008, Wiggins et al. 1980
Chaoboridae	Dry Layer*, Active Disperser	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Chironomidae	Wet Layer*, Active Dispersers	Merrit et al. 2008, Wiggins et al. 1980
Chydoridae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Coenagrionidae	Dry Layer	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018
Corixidae	Active Disperser	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Culicidae	Dry Layer	Merrit et al. 2008
Curculionidae	Dry Layer	Merrit et al. 2008, Gleason and Rooney 2018
Daphnidae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Dixidae	Wet Layer	Merrit et al. 2008
Dolichopopdidae	Wet Layer	Merrit et al. 2008
Dytiscidae	Wet Layer	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Elmidae	Active Disperser	Merrit et al. 2008, Gleason and Rooney 2018
Entomobryinae	Drought Tolerator	Merrit et al. 2008, Gleason and Rooney 2018
Ephydridae	Active Disperser	Merrit et al. 2008

Appendix Table 2.1 Continued

Erpobdellidae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001
Gammaridae	Drought Tolerator	Merrit et al. 2008, Wiggins et al. 1980
Gerridae	Active Disperser	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Glossiphoniidae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001,
Gyrinidae	Active Disperser	Merrit et al. 2008, Wiggins et al. 1980
Haliplidae	Wet Layer	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Helophoridae	Active Disperser	Merrit et al. 2008
Hyalellidae	Drought Tolerator	Merrit et al. 2008
Hydrachnidia	Wet Layer	Merrit et al. 2008, Gleason and Rooney 2018
Hydraenidae	Dry Layer	Merrit et al. 2008, Gleason and Rooney 2018
Hydrophilidae	Wet Layer*, Active Dispersers	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Lestidae	Dry Layer	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018, Wiggins et al. 1980
Libellulidae	Dry Layer	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018
Limnephilidae	Dry Layer	Merrit et al. 2008, Gleason and Rooney 2018
Lymnaeidae	Drought Tolerator	Merrit et al. 2008, Wiggins et al. 1980
Mesoveliidae	Active Disperser	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Notonectidae	Active Disperser	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018, Wiggins et al. 1980
Oligochaete	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001, Wiggins et al. 1980
Ostracoda	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018, Wiggins et al. 1980
Physidae	Drought Tolerator	Merrit et al. 2008, Wiggins et al. 1980
Pisidiidae	Drought Tolerator	Merrit et al. 2008
Planorbidae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001, Gleason and Rooney 2018, Wiggins et al. 1980

Appendix Table 2.1 Continued

Psychodidae	Wet Layer	Merrit et al. 2008
Saldidae	Active Disperser	Merrit et al. 2008, Gleason and Rooney 2018, Wiggins et al. 1980
Scritidae	Active Disperser	Merrit et al. 2008
Sididae	Drought Tolerator	Merrit et al. 2008, Battle and Golladay 2001
Stratiomyidae	Wet Layer	Merrit et al. 2008, Wiggins et al. 1980

Appendix Table 2.2. Explanatory variables (with units, and the range, mean and standard deviation) included in models describing family richness and community composition of aquatic macroinvertebrates in wetlands, Grand Teton National Park, Wyoming, summer 2018.

Explanatory Variable	Unit	Range	Mean	Standard Deviation
ln(Area)	m	1.8 to 9.7	6.1	1.9
Depth	cm	5 to 234	48	36
Overall Change in Depth	Proportion of change to max value	0.04 to 1	0.52	0.28
Overall Change in Area	Proportion of change to max value	0.05 to 1	0.69	0.29
Average Distance to All Neighboring Wetlands	m	536 to 1070	696	170
Distance to Nearest Wetland	m	24 to 620	199	174
Rate of Depth Drying	% change/day	0.6 to 7.7	2.8	1.7
Rate of Area Drying	% change/day	0.3 to 10.8	3.5	2.7

Appendix Table 2.3. Results for model selection from the exploratory step explaining variation in family richness of aquatic macroinvertebrates in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). K is the number of parameters in the model.

Model Suite	Covariate	K	AICc	ΔAICc	Weight
Size	Depth	4	253.65	0.00	0.28
	Overall change in area	4	255.21	1.56	0.41

Appendix Table 2.3 Continued

	Area	4	255.63	1.98	0.52
Spatial Isolation	AvgDist	4	252.76	0.00	0.70
	Dist to neighbor	4	254.42	1.65	0.30
Temporal Isolation	Rate of depth drying	4	250.82	0.00	0.72

Appendix Table 2.4. Results for model selection from the exploratory step explaining variation in relative abundance of aquatic macroinvertebrates, specifically drought tolerators and wet layers (as measured by principal component 1) Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). K is the number of parameters in the model.

Model Suite	Covariate	K	AICc	ΔAICc	Weight
Size	Overall change in depth	4	160.50	0.00	0.18
	Overall change in area	4	160.71	0.21	0.17
	Area	4	160.77	0.27	0.16
	Depth	4	160.79	0.29	0.16
Spatial Isolation	Dist to neighbor	4	160.16	0.00	0.55
	AvgDist	4	160.55	0.39	0.45
Temporal Isolation	Rate of depth drying	4	154.90	0.00	0.71

Appendix Table 2.5. Results for model selection from the exploratory step explaining variation in relative abundance of aquatic macroinvertebrates, specifically dry layers (as measured by principal component 2) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). K is the number of parameters in the model.

Appendix Table 2.5 Continued

Model Suite	**Covariate**	**K**	**AICc**	**ΔAICc**	**Weight**
Size	Overall change in area	4	147.21	0.00	0.17
	Depth	4	147.22	0.01	0.17
	Area	4	147.35	0.13	0.16
	Overall change in depth	4	147.39	0.17	0.16
Spatial Isolation	Dist to neighbor	4	142.97	0.00	0.55
	AvgDist	4	143.36	0.39	0.45
Temporal Isolation	Rate of depth drying	4	154.90	0.00	0.71
	Rate of area drying	4	146.30	0.00	0.44
	Rate of depth drying + Rate of area drying	4	147.00	0.70	0.31

Appendix Table 2.6. Results for model selection from the exploratory step explaining variation in relative abundance of aquatic macroinvertebrates, specifically of active dispersers (as measured by principal component 3) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in area, overall change in depth, and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). K is the number of parameters in the model.

Model Suite	Covariate	K	AICc	ΔAICc	Weight
Size	Area	4	131.10	0.00	0.19
	Overall change in area	4	131.48	0.38	0.16
	Overall change in depth	4	131.85	0.75	0.13
	Depth	4	132.16	1.06	0.11
	Area + Overall change in depth	5	132.86	1.76	0.08
	Area + Overall change in area	5	132.90	1.80	0.08
Spatial Isolation	Dist to neighbor	4	130.75	0.00	0.59
Temporal Isolation	Rate of depth drying	4	129.71	0.00	0.82

Appendix Table 2.7. Results for model selection from the inferential step explaining variation in family richness of aquatic macroinvertebrates in wetlands, Grand Teton National Park, Wyoming, 2018. Size covariates included: maximum depth (Depth), overall change in area (ΔArea), and log-transformed area (Area). Spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor). Temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). The Null model includes only an intercept. Models with multiple terms are additive unless listed with a *** in bold**. K is the number of parameters in the model.

Size	Spatial Isolation	Temporal Isolation	K	AICc	ΔAICc	Weight
Depth		Rate of depth drying	5	250.39	0.00	0.15
		Rate of depth drying	4	250.82	0.43	0.12
Depth	AvgDist	Rate of depth drying	6	251.72	1.33	0.08
	AvgDist	Rate of depth drying	5	252.14	1.75	0.06
Depth	AvgDist		5	252.33	1.94	0.06
Depth	Dist to Neighbor	Rate of depth drying	6	252.57	2.18	0.05
	Dist to Neighbor	Rate of depth drying	5	252.70	2.31	0.05
	AvgDist		4	252.76	2.37	0.05
Depth*		**Rate of depth drying**	6	252.85	2.46	0.04
Area		Rate of depth drying	5	253.14	2.75	0.04
ΔArea		Rate of depth drying	5	253.26	2.87	0.04
Depth			4	253.65	3.26	0.03
Null			3	254.00	3.61	0.02
Depth*	**AvgDist**		6	254.37	4.00	0.02
ΔArea	AvgDist		5	254.40	4.01	0.02
	Dist to Neighbor		4	254.42	4.03	0.02
Depth	Dist to Neighbor		5	254.43	4.04	0.02
Area	AvgDist	Rate of depth drying	6	254.65	4.26	0.02

Appendix Table 2.7 Continued

ΔArea	AvgDist	Rate of depth drying	6	254.66	4.27	0.02
	AvgDist*	**Rate of depth drying**	6	254.70	4.31	0.02
Area	AvgDist		5	254.89	4.50	0.02
ΔArea	Dist to Neighbor	Rate of depth drying	6	255.05	4.66	0.01
ΔArea	Dist to Neighbor		5	255.07	4.68	0.01
ΔArea			4	255.21	4.82	0.01
Area	Dist to Neighbor	Rate of depth drying	6	255.29	4.90	0.01
Area*		**Rate of depth drying**	6	255.47	5.08	0.01
Area			4	255.63	5.24	0.01
Area*	**AvgDist**		6	255.87	5.48	0.01
Area	Dist to Neighbor		5	256.68	6.29	0.01

Appendix Table 2.8. Results for model selection from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically drought tolerators and wet layers (as measured by principal component 1) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in depth (ΔDepth), overall change in area (ΔArea**)**, and log-transformed area (Area), spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor), and temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying) The Null model includes only an intercept. Models with multiple terms are additive unless listed with a *** in bold**. K is the number of parameters in the model.

Size	Spatial Isolation	Temporal Isolation	K	AICc	ΔAICc	Weight
	Dist to Neighbor*	**Rate of depth drying**	6	153.92	0.00	0.26
		Rate of depth drying	4	154.90	0.98	0.16
ΔArea		Rate of depth drying	5	156.82	2.90	0.06

Appendix Table 2.8 Continued

	AvgDist	Rate of depth drying	5	156.85	2.94	0.06
Area		Rate of depth drying	5	157.03	3.11	0.06
ΔDepth		Rate of depth drying	5	157.40	3.49	0.05
Depth		Rate of depth drying	5	157.41	3.49	0.05
	Dist to Neighbor	Rate of depth drying	5	157.41	3.49	0.05
Null			3	158.40	4.48	0.03
ΔArea	AvgDist	Rate of depth drying	6	158.78	4.87	0.02
Area	AvgDist	Rate of depth drying	6	159.20	5.28	0.02
ΔArea	Dist to Neighbor	Rate of depth drying	6	159.41	5.49	0.02
ΔDepth	AvgDist	Rate of depth drying	6	159.45	5.54	0.02
Depth	AvgDist	Rate of depth drying	6	159.49	5.57	0.02
Area	Dist to Neighbor	Rate of depth drying	6	159.62	5.70	0.02
ΔDepth *		**Rate of depth drying**	6	160.00	6.09	0.01
ΔDepth	Dist to Neighbor	Rate of depth drying	6	160.04	6.12	0.01
Depth	Dist to Neighbor	Rate of depth drying	6	160.04	6.13	0.01
	Dist to Neighbor		4	160.16	6.24	0.01
ΔDepth			4	160.50	6.59	0.01
	AvgDist		4	160.55	6.64	0.01
ΔArea			4	160.71	6.80	0.01
Area			4	160.77	6.86	0.01
Depth			4	160.79	6.88	0.01
ΔDepth	Dist to Neighbor		5	162.38	8.46	0.00
ΔArea	Dist to Neighbor		5	162.51	8.60	0.00
Area	Dist to Neighbor		5	162.53	8.61	0.00

Appendix Table 2.8 Continued

Depth	Dist to Neighbor		5	162.67	8.75	0.00
ΔDepth	AvgDist		5	162.87	8.95	0.00
ΔDepth *	**Dist to Neighbor**		6	162.88	8.96	0.00
Area	AvgDist		5	163.01	9.10	0.00
ΔArea	AvgDist		5	163.02	9.10	0.00
Depth	AvgDist		5	163.06	9.15	0.00
ΔDepth * ΔArea			6	164.20	10.29	0.00

Appendix Table 2.9. Results for model selection from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically dry layers (as measured by principal component 2) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in depth (ΔDepth), overall change in area (ΔArea), and log-transformed area (Area), spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor), and temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying) and average rate of percent change in area (Rate of area drying). The Null model includes only an intercept. Models with multiple terms are additive unless listed with a * **in bold**. K is the number of parameters in the model.

Size	Spatial Isolation	Temporal Isolation	K	AICc	ΔAICc	Weight
	Dist to Neighbor*	**Rate of depth drying**	6	142.43	0.00	0.16
	Dist to Neighbor		4	142.97	0.54	0.12
	AvgDist		4	143.36	0.93	0.10
Area	Dist to Neighbor		5	143.86	1.44	0.08
Null			3	145.00	2.57	0.04
	Dist to Neighbor	Rate of depth drying	5	145.26	2.84	0.04
ΔArea	AvgDist		5	145.29	2.87	0.04
Area	AvgDist		5	145.33	2.90	0.04
Depth	Dist to Neighbor		5	145.43	3.00	0.04

Appendix Table 2.9 Continued

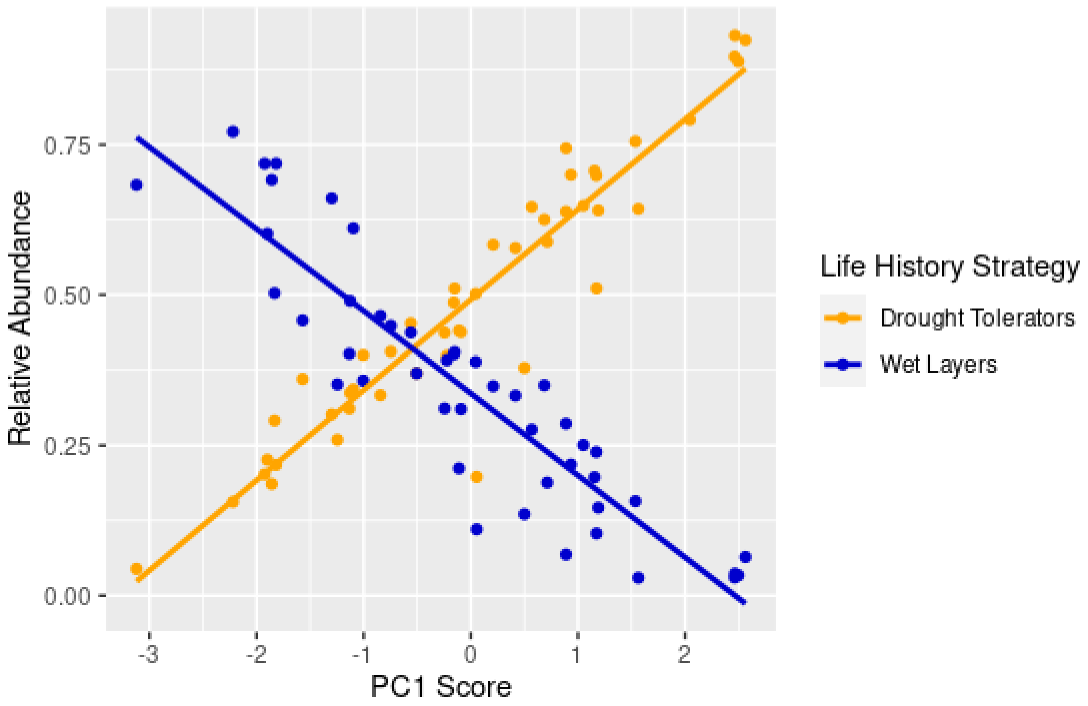
ΔArea	Dist to Neighbor		5	145.46	3.03	0.03
ΔDepth	Dist to Neighbor		5	145.48	3.05	0.03
ΔDepth	AvgDist		5	145.57	3.14	0.03
Depth	AvgDist		5	145.66	3.23	0.03
	AvgDist	Rate of depth drying	5	145.82	3.39	0.03
		Rate of depth drying	4	146.30	3.87	0.02
ΔArea *	**Dist to Neighbor**		6	146.99	4.56	0.02
		Rate of area drying	4	147.00	4.57	0.02
ΔArea			4	147.21	4.79	0.01
Depth			4	147.22	4.79	0.01
		Rate of depth drying, Rate of area drying	5	147.35	4.92	0.01
Area			4	147.35	4.92	0.01
ΔDepth			4	147.39	4.96	0.01
ΔArea	Dist to Neighbor	Rate of depth drying	6	147.72	5.30	0.01
ΔArea		Rate of depth drying	5	147.95	5.53	0.01
Area		Rate of depth drying	5	148.52	6.09	0.01
Depth		Rate of depth drying	5	148.64	6.21	0.01
ΔDepth*Depth			6	148.64	6.22	0.01
ΔDepth		Rate of depth drying	5	148.73	6.30	0.01
Depth		Rate of area drying	5	149.02	6.59	0.01
ΔDepth		Rate of area drying	5	149.41	6.98	0.00
ΔArea		Rate of area drying	5	149.48	7.05	0.00
Area		Rate of area drying	5	149.49	7.06	0.00
ΔArea		Rate of depth drying	6	150.42	7.99	0.00

Appendix Table 2.10. Results for model selection from the inferential step explaining variation in relative abundance of aquatic macroinvertebrates, specifically of active dispersers (as measured by principal component 3) in wetlands, Grand Teton National Park, Wyoming, summer 2018. Size covariates included: maximum depth (Depth), overall change in depth (ΔDepth), overall change in area (ΔArea), and log-transformed area (Area), spatial isolation covariates included: Average distance to all wetlands (AvgDist) and distance to the nearest wetland (Dist to neighbor), and temporal isolation covariates included: Average rate of percent change in depth (Rate of depth drying). The Null model includes only an intercept. Models with multiple terms are additive unless listed with a * **in bold**. K is the number of parameters in the model.

Size	Spatial Isolation	Temporal Isolation	K	AICc	ΔAICc	Weight
	Dist to Neighbor*	**Rate of depth drying**	6	123.66	0.00	0.46
	Dist to Neighbor	Rate of depth drying	5	126.78	3.12	0.10
Area	Dist to Neighbor	Rate of depth drying	6	126.80	3.15	0.10
Area	Dist to Neighbor		5	128.32	4.66	0.05
Area*		**Rate of depth drying**	6	128.47	4.81	0.04
Depth	Dist to Neighbor	Rate of depth drying	6	128.61	4.96	0.04
ΔDepth	Dist to Neighbor	Rate of depth drying	6	128.91	5.25	0.03
ΔArea	Dist to Neighbor	Rate of depth drying	6	129.42	5.76	0.03
	Dist to Neighbor		4	129.71	6.05	0.02
Area*	**Dist to Neighbor**		6	130.28	6.63	0.02
NULL			3	130.35	6.69	0.02
		Rate of depth drying	4	130.75	7.09	0.01
Area			4	131.10	7.44	0.01
ΔDepth	Dist to Neighbor		5	131.14	7.48	0.01
ΔArea	Dist to Neighbor		5	131.29	7.63	0.01

Appendix Table 2.10 Continued

Depth	Dist to Neighbor		5	131.42	7.77	0.01
ΔArea			4	131.48	7.82	0.01
ΔDepth			4	131.85	8.19	0.01
Depth			4	132.16	8.50	0.01
Area		Rate of depth drying	5	132.44	8.78	0.01
ΔDepth		Rate of depth drying	5	132.72	9.07	0.00
Depth		Rate of depth drying	5	132.75	9.09	0.00
ΔArea		Rate of depth drying	5	132.80	9.15	0.00
Area* Depth			6	134.54	10.89	0.00



Appendix Figure 2.1. Relative abundance of drought tolerators (orange) and wet layers (blue) as measured by principal component 1 (PC1) in summer 2018, GTNP, Wyoming. Low values of PC1 were associated with a high abundance of drought tolerators and low abundance of wet layers.