THE BIOGEOGRAPHY AND CONSERVATION OF TIDAL MARSH BIRD COMMUNITIES ACROSS A CHANGING LANDSCAPE

By
Maureen D. Correll
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Advisory Committee:

Brian J. Olsen, Associate Professor, School of Biology and Ecology, Co-advisor
Thomas P. Hodgman, Biologist, Maine Department of Inland Fisheries and Wildlife, Co-advisor
Brian J. McGill, Assistant Professor, School of Biology and Ecology
Kate O'Brien, Refuge Biologist, Rachel Carson National Wildlife Refuge, United States Fish and Wildlife Service
Steven S. Sader, Full Professor, School of Forest Resources, The University of Maine

DISSERTATION ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Maureen Correll we affirm that this manuscript is the final and accepted dissertation. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Dr. Brian J. Olsen, Associate Professor Date

Thomas P. Hodgman, M.S., Biologist Date

DEDICATION

This is for my sister.

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CHAPTER 1: INTRODUCTION

1.1 Explaining patterns in biodiversity across changing landscapes

The mechanisms driving patterns in the abundance and distribution of species across landscapes are numerous and confounding. When combined with the difficultly in testing observed large-scale patterns empirically (Shea et al. 2004), they are challenging to disentangle from one another. While we cannot singularly explain the presence or absence of a species on a landscape at a particular point in space and time, ecologists have found evidence for several prevailing drivers of biodiversity across taxa, including the relative amount of primary productivity on the landscape (Loreau et al. 2001), habitat availability and fragmentation (Fahrig 2003), degree and frequency of habitat disturbance (Roxburgh et al. 2004, Balée 2014), disease (Altizer et al. 2003), the evolutionary history of the organisms (Forest et al. 2007), and limiting climate factors such as temperature and precipitation (Thomas et al. 2004, Hampe and Petit 2005, Bellard et al. 2012). These drivers may work additively, synergistically, or antagonistically to drive the patterns in diversity we observe across landscapes (Crain et al. 2008).

1.2 Disturbance regimes and biodiversity

Of the stressors listed above, the frequency, intensity, duration, and time since disturbance of an ecosystem are some of the most intuitive influences on biodiversity, and several theories exist concerning this subset of drivers. The stability-time hypothesis proposed by Sanders (1968) suggests undisturbed communities with adequate sources of water and warm temperatures will exhibit highest levels of diversity. The Intermediate

Disturbance Hypothesis (IDH), a theory developed by Horn (1975) and popularized by Connell (1978) describes maximum species diversity in settings experiencing intermediate levels of habitat disturbance; the highest levels of diversity are found at the intersection of two tradeoff curves produced by opposing life history strategies. A group of hypotheses involving habitat refugia (Haffer 1969, MacArthur 1972, Diamond et al. 1976, Morat et al. 1986, Nores 1999) propose that disturbance events can cause long-term genetic isolation of communities that results in a net increase in species diversity once the disturbance is removed. Finally, the multi-dimensional Dynamic Equilibrium Model (DEM) described by Huston (1979) states that communities left unperturbed over time will develop apex, or late-succession, communities at equilibrium with the resource supply available. In all cases, these hypotheses suggest that disturbance regimes of varying magnitude and frequency can have significant and predictable effects upon biological community assemblage.

Because of the immense variation in the nature of disturbance events across ecosystems and scales, quantification of such occurrences are nearly always context-specific. The frequency and intensity (Gotelli and Colwell 2001, Lindenmayer et al. 2014), landscape context (Krauss et al. 2003, Shriver et al. 2004), spatial and temporal scale (Macarthur and Macarthur 1961, Turner et al. 1989, Whittaker et al. 2001, Hatosy et al. 2013), and level of ecological organization (Leibold et al. 2004, Violle et al. 2012, Dornelas et al. 2014) all influence the effects of disturbance on community structure. It is therefore imperative to clearly identify a setting and explore disturbance across multiple scales specific to that system in any empirical effort to test hypotheses in situ or to provide conservation recommendations for quantifying risk in disturbance scenarios.

1.3 The plight of the habitat specialist

The life history strategy of a set of organisms can influence how that species or community reacts to disturbance to an ecosystem. Generalist and specialist life history strategies represent two extremes along a gradient of habitat use tactics, and are two fundamental concepts in ecology. Both can be explained in the context of the ecological niche first described by Hutchinson (1957) as the set of environmental conditions and requirements of a species to persist across generations. Hutchinson also introduced the concept of the n-dimensional hypervolume, a theoretical, multidimensional space describing the set of all environmental conditions where species persistence is possible, where each axis of variation represents an environmental gradient. “Niche breadth” then quantifies the amount of variability in a species’ use of a particular gradient. Specialism is therefore a relative term, where specialist taxa are those with a smaller niche breadth for a particular, or multiple, environmental gradients compared to more generalist taxa across those same gradients (MacArthur 1972, Julliard et al. 2006).

Given the ongoing fragmentation of global resources through direct and indirect anthropogenic disturbance (Fischer and Lindenmayer 2007), the outlook is not good for specialists globally (Futuyma and Moreno 1988, Devictor et al. 2010). Rising global temperature, sea levels, and altered storm frequency and intensity can all create environmental conditions that fluctuate outside of the constrained niches maintained by specialist species. As a result, specialists have been referred to as the “great losers of past and current global changes” (Devictor et al. 2010), and specialism is now considered one of the dominant factors determining extinction of species (Dennis et al. 2011).

The plight of the specialist is further complicated because of the lack of a single definition for this term. Theoretical tradeoffs between specialism and generalism are well documented, but these concepts have not been rigorously quantified across taxa (Holt 2009), limiting the real-world application of these concepts towards conservation goals. Degree of specialism may refer to variation across individuals, species, or functional groups (Bolnick et al. 2003, Blonder et al. 2014), or to different forms of adaptation (e.g., diet vs. habitat specialization). Quantification measures for specialism also vary, are often limited to a few species (Devictor et al. 2010), and are usually applied across multiple habitat types (Jonsen and Fahrig 1997, Julliard et al. 2006, Devictor et al. 2008). Defining specialism in the context of a particular habitat or ecosystem, with the end goal of using these findings as conservation mechanisms, is the next logical step in the application of these principles to the current biodiversity conservation crisis.

1.4 Specialist birds in tidal marsh landscapes

Of the different ecosystems found worldwide, disturbance events in tidal marshes are very well documented, specifically along the coasts of North America and Western Europe (Adam 2002, Shriver et al. 2004, Sillman 2009). The Laurentide ice sheet (North America) and Devensian glaciation (Western Europe) reached their apex at the Last Glacial Maximum (LGM) ~20,000 ya, removing all biota from temperate latitudes in North America and Europe for several millennia and initiating primary succession upon retreat. More recently, sea-level rise driven by the massive increase in greenhouse gas generation at the advent of the Industrial Revolution shows noticeable effects in tidal marshes (Morris et al. 2002a), with predicted decreases in marsh area up to 1.5%

annually along the Atlantic coast of North America (Greenberg et al. 2006c). Extreme storm events such as Hurricane Katrina, Irene, and Sandy also have potential to permanently alter coastal marsh structure within the span of only one or two days (Scavia et al. 2002, Arkema et al. 2013). Finally, tidal inundation by incoming tides create daily disturbances in the form of flooding and salinization of lower elevation areas, severely limiting the utility of this habitat type to a few of species (Shriver et al. 2004, Isacch et al. 2006b), despite high rates of primary productivity in this ecosystem (Bertness et al. 2008).

In addition to changing environmental stressors, local and direct anthropogenic modifications of marshes have had noticeable effects on the global marsh landscape. Humans have developed coastal marshes for centuries due to the significant ecosystem services they provide, specifically in the form of highly productive areas for agricultural use and open, easy access to the sea. This influx of infrastructure and use has led to a massive loss in tidal marsh area globally. Additionally, recent regional management plans have led to widespread ditching of marshes to remove standing water supporting breeding mosquito populations. Mosquito ditching in marshes of North America has caused removal of peat from the affected marsh, and a net increase the amount of marsh affected by tidal inundation within days (Crain et al. 2009). Further, the application of Open Marsh Water Management (OMWM), a series of pools and ditches created to support fish populations that feed on mosquito larvae, where standing water exists (Sillman 2009). These pools and ditches alter marsh hydrology and persist in the marsh for decades. Tidal restrictions in the form of road crossings over tidal channels can have considerable effects on marsh vegetation even within a single growing season that lower sediment supply, reduce soil salinity, and prevent drainage of upriver marshes (Portnoy 1999). Restrictions also reduce marsh accretion, or vertical growth, over years and decades (Anisfeld et al. 1999, Gedan et al. 2009) and are often not reversible with restoration (Portnoy and Giblin 1997a, Elphick et al. 2015).

Of the tidal marshes occurring globally, those located along the northeastern United States between Maine and Virginia are some of the most-studied and most-modified coastal wetland systems (Gedan et al. 2009). North American tidal marshes are also a hotspot of accelerated sea-level rise, experiencing roughly twice the global average (Sallenger et al. 2012) with even higher rates in the past five years (Goddard et al. 2015). At the same time, North American tidal marshes support the a known suite of avian habitat specialists that breed almost exclusively within tidal marshes between Maine and Virginia (Cornell Lab of Ornithology 2015). Tidal marsh specialist birds including the clapper rail (*Rallus crepitans*), willet (*Tringa semipalmata*), Nelson's sparrow (*Ammodramus nelsonii subvirgatus*), saltmarsh sparrow (*Ammodramus caudacutus*), and seaside sparrow (*Ammodramus maritimus*), rely on high-marsh habitat (Shriver and Hodgman 2010) that differs from low marsh in its elevation, salinity, and frequency of inundation (Bertness and Ellison 1987, Ewanchuk and Bertness 2004) and is likely the most vulnerable tidal marsh vegetation community to increasing sea levels (Donnelly and Bertness 2001).

The specialist avifaunal community generally and the saltmarsh sparrow specifically are potential metrics of biotic response to marsh disturbance due to their strong ties with habitat quality in this ecosystem. The vast majority of specialist birds breeding in tidal marsh do so within inches of the ground; these ground-nesting animals are therefore very sensitive to changes in flood regime, rates of marsh sedimentation and accretion, vegetation community composition, and water chemistry. As a result, the saltmarsh sparrow, the species exhibiting the most extreme habitat endemism to northeastern coastal marshes, is currently recognized by the North American Bird Conservation Initiative (Rosenberg et al. 2014), the International Union for Conservation of Nature (IUCN 2012), and multiple state agencies as a species of conservation concern, and is considered a prime candidate for listing on the US Endangered Species List (USFWS 1979).

My dissertation examines the tidal marsh bird community across scales of space, time, ecological organization, and life history to A) evaluate the impacts of different types of disturbance on tidal marshes and B) provide findings and management recommendations for long-term maintenance and conservation of coastal marsh ecosystems, specifically as they pertain to salt-marsh specialist birds. This document is divided into five chapters. In Chapter 1 I provide an introduction to ecological disturbance in tidal marsh ecosystems and how they may affect bird communities that use these landscapes as habitat. In Chapter 2 I generate population trends in the five species specialized to tidal marsh for breeding habitat using a compiled database of historical marshbird records. I also explore multiple potential drivers for population trends at the species and specialist community level in the form of tidal restrictions, ditching, sea-level rise, and extreme storm events. In Chapter 3 I expand upon the patterns we observe in Chapter 2 to develop a novel index to quantify life history strategies in tidal marsh birds across a gradient of tidal marsh specialization. I then explore the relationship between this metric and several measures of species persistence in tidal marshes. In Chapter 4 I examine the effects of habitat disturbance on the tidal marsh community, and test several well-known but under-tested hypotheses in disturbance ecology using traditional community metrics in conjunction with our novel specialism index. Finally, in Chapter 5 I respond to applied research needs identified in Chapter 4 to develop a method for repeat quantification of high-marsh patch area using remote sensing methods accessible to tidal marsh managers. I hope the research and findings we present here not only contribute towards understanding of the dominant mechanisms driving biodiversity patterns on our planet, but also help inform and highlight conservation priorities within tidal marshes in the context of changing regional and global landscapes.

CHAPTER 2: TIDAL RESTRCTION DRIVES SPECIALIST AVIFAUNAL COLLAPSE IN COASTAL MARSHES

2.1 Abstract

Coastal marshes present an ideal setting to explore multiple anthropogenic stressors simultaneously acting upon an ecosystem. As one of the world's most productive ecosystems, these marshes have been heavily used by humans, resulting in outright ecosystem loss as well as road crossings, ditches, and a number of indirect impacts such as sea-level rise and extreme storm events. It is unclear, however, how impacts of compound stressors affect the sustainability of organismal populations and communities reliant upon this ecosystem. In the northeastern United States, five avian species breed almost exclusively in tidal marshes, making these habitat specialists potentially vulnerable to marsh degradation and loss as a result of anthropogenic change. We used an 18-year marsh-bird database to generate population trends for these specialist species across three spatial scales, and explored possible drivers of change at a species and community level. We found the specialist community showed negative trends in tidally restricted marshes, but was stable in unrestricted marshes across the time period examined. We also found population declines in three of the five specialist species, although species-specific drivers varied. We posit that restriction accelerates degradation of tidal marsh resilience to ubiquitous sea-level rise by limiting sediment supply necessary for marsh accretion, resulting in specialist habitat loss in tidally restricted marshes. We predict collapse of the global population of saltmarsh sparrows (*Ammodramus caudacutus*) within the next 50 years, followed by other specialist species,

and suggest conservation and mitigation actions to support sustainability of tidal marshes in both the short and long term.

2.2 Introduction

A central goal of sustainability science is to understand and reduce human impacts on ecosystems. Ecosystems are affected by anthropogenic stressors at various scales, from the local impacts of habitat loss and resource exploitation to the global effects of climate change. While substantial literature quantifies the independent effects of climate change and other impacts on biodiversity (Hughes et al. 2003, Mora et al. 2007, Liu et al. 2007, Gedan et al. 2009, Côté and Darling 2010, Bellard et al. 2012), less work explores multiple stressors simultaneously, and even fewer studies explicitly rank drivers of ecosystem change or prioritize management strategies at different scales (Benning et al. 2002, Didham et al. 2007). Drivers of change can be additive, synergistic, or antagonistic depending on the setting and stressors in question (Crain et al. 2008, Hof et al. 2011, Mantyka-pringle et al. 2012). Stressors on any ecosystem also may be local, regional, or global in origin, further complicating efforts to draw conclusions about their combined effects (Brown et al. 2013). Understanding the relative importance of different landscape changes is key to developing strategies to achieve sustainability at desired scales (Halpern et al. 2008, Brown et al. 2013). Most studies of multiple stressors come from marine and aquatic systems (e.g 14–16), but coastal wetlands are affected by processes borne from both terrestrial and aquatic sources (Harley et al. 2006), presenting an ideal setting for further study.

Figure 2.1. Examples of direct tidal marsh modifications by humans. A) tidally restricted marsh (white arrows show individual restrictions), B) ditched marsh, and C) marsh treated with Open Marsh Water Management (OMWM).

Coastal marshes experience a suite of stressors ranging from local to global scales. Due to the significant ecosystem services they provide (Costanza et al. 1997), this ecosystem has been used heavily by humans. They have been structurally modified through the installation of local human infrastructure that span tidal marsh channels (e.g. roads, dykes), limiting tidal flow upriver of the restriction (Fig 2.1a). Regional management plans have led to both the widespread ditching of marshes to remove standing water supporting breeding mosquito populations (Fig 2.1b), and the application of Open Marsh Water Management (OMWM, Fig 2.1c), a series of pools and ditches created to support fish populations that feed on mosquito larvae, where standing water exists (Sillman 2009). These pools and ditches alter marsh hydrology and persist in the marsh for decades. Changes in the frequency of extreme storm events at even larger scales are altering tidal patterns of inundation (Day et al. 2008), the rates of erosion of marsh edges, and the movement and loss of barrier islands and beaches. Tidal marshes are also altered globally by sea-level rise; vegetative change and loss driven by sea-level rise has been recorded in coastal marshes worldwide (Australia: 21, North America: 22, Western Europe: 23).

There is good reason to suspect that these threats to the long-term sustainability of tidal marshes play out at different timescales. For instance, tidal restrictions can have considerable effects on marsh vegetation even within a single growing season that lower sediment supply, reduce soil salinity, and drainage of upriver marshes (Portnoy 1999). Tidal restrictions also reduce marsh accretion, or vertical growth, over years and decades (Anisfeld et al. 1999, Gedan et al. 2009) and are often not reversible with restoration (Portnoy and Giblin 1997a, Elphick et al. 2015). Ditching causes removal of peat from the affected marsh, and a net increase the amount of marsh affected by tidal inundation within days (Crain et al. 2009). Likewise, extreme storm events can permanently alter coastal marsh systems within days but cause changes that persist for decades. Recent examples in North America all have shown both short-term (within days, 29) and long-term (multi-year, 30) effects on coastal wetland systems. Sea-level rise is also changing the sediment supply, water salinity, and total area of coastal wetlands (Clark 1986, Pont et al. 2002, Yáñez-Arancibia et al. 2013) at different rates around the globe, effects that are similar to the consequences of more local human impacts on tidal marshes but that play out over longer timescales (Williams and Watford 1996, Isacch et al. 2004, Sillman 2009).

Tidal marshes of the northeastern United States are some of the most-studied and most-modified coastal wetland systems in the world (Gedan et al. 2009). North American tidal marshes are also a hotspot of accelerated sea-level rise, experiencing roughly twice the global average (Sallenger et al. 2012) with even higher rates in the past five years (Goddard et al. 2015). At the same time, North American tidal marshes support a suite of avian habitat specialists that breed almost exclusively within tidal marshes between Maine and Virginia (Cornell Lab of Ornithology 2015). Several of these specialists, particularly the saltmarsh sparrow, rely on high-marsh habitat in the northeastern United States (Shriver and Hodgman 2010) that differs from low marsh in its elevation, salinity, and frequency of inundation (Bertness and Ellison 1987, Ewanchuk and Bertness 2004) and is likely the most vulnerable tidal marsh vegetation community to increasing sea levels (Donnelly and Bertness 2001). Thus, the specialist avifaunal community represents an appropriate metric of biotic response to multiple anthropogenic stressors in these marshes.

In this paper we combined 14 datasets of bird surveys in US coastal marshes from Maine to Virginia, spanning 18 years, and over 170,000 individual observations to explore the effects of multiple ecosystem stressors on the specialist bird community in this region (Fig 2.2). This area includes the entire breeding range for the saltmarsh sparrow and substantial portions of the range of the Acadian Nelson's sparrow (*A. nelsoni subvirgatus*), seaside sparrow (*A. maritimus*), eastern willet (*Tringa semipalmata semipalmata*), and clapper rail (*Rallus crepitans*). Different groups collected data in various subregions from 1994 to 2012, including region-wide surveys in 2011 and 2012 by the authors. We fit a set of hierarchical models to produce the first estimates of population trends for these species at the local (US National Wildlife Refuge), subregional (New England), and regional (Maine-Virginia) scales. To investigate potential drivers of these trends, we quantified ditching, OMWM, tidal restriction, rate of sea-level rise, and extreme flooding risk at each survey point. We used model comparison (Table 2.1) with a holdout dataset to explore the relative effects of these modifications on marsh community resilience at a decadal timescale.

Table 2.1. Candidate models for regional drivers model comparison. The symbol “×” indicates both the main and interactive effect of the terms were included in the model. All parameters listed for the null model were included in all models, but only listed once to aid in clarity when describing the other candidates. Bolded terms indicate variables designated as random effects.

ID	candidate model	ΔAIC	weight
DRS	scale(year)×scale(ditching) + scale(year)×restriction + scale(year)×scale(slt)	0*	0.45
RS	scale(year)×restriction + scale(year)×scale(slt)	0.6	0.35
global	scale(year)×scale(ditching) + scale(year)×restriction + scale(year)×scale(exceedance) + scale(year)×scale(slt)	3.3	0.09
RSE	scale(year)×restriction + scale(year)×scale(exceedance) + scale(year)×scale(slt)	3.8	0.07
R	scale(year)×restriction	6.5	0.02
DR	scale(year)×scale(ditching) + scale(year)×restriction	6.5	0.02
RE	scale(year)×restriction + scale(year)×scale(exceedance)	9.4	0
DRE	scale(year)×scale(ditching) + scale(year)×restriction + scale(year)×scale(exceedance)	9.5	0
DS	scale(year)×scale(ditching) + scale(year)×scale(slt)	38.7	0
D	scale(year)×scale(ditching)	38.9	0
null	scale(log(patch area)) + scale(log(distance upriver)) + scale(year) **+ # visits + tidal gauge/PSU + species**	39.3	0
S	scale(year)×scale(slt)	39.5	0
DSE	scale(year)×scale(ditching) + scale(year)×scale(exceedance) + scale(year)×scale(slt)	41.6	0
DE	scale(year)×scale(ditching) scale(year)×scale(exceedance)	41.9	0
E	scale(year)×scale(exceedance)	42.1	0
SE	scale(year)×scale(exceedance) + scale(year)×scale(slt)	42.2	0

*The AIC value for the top model was 38335.37

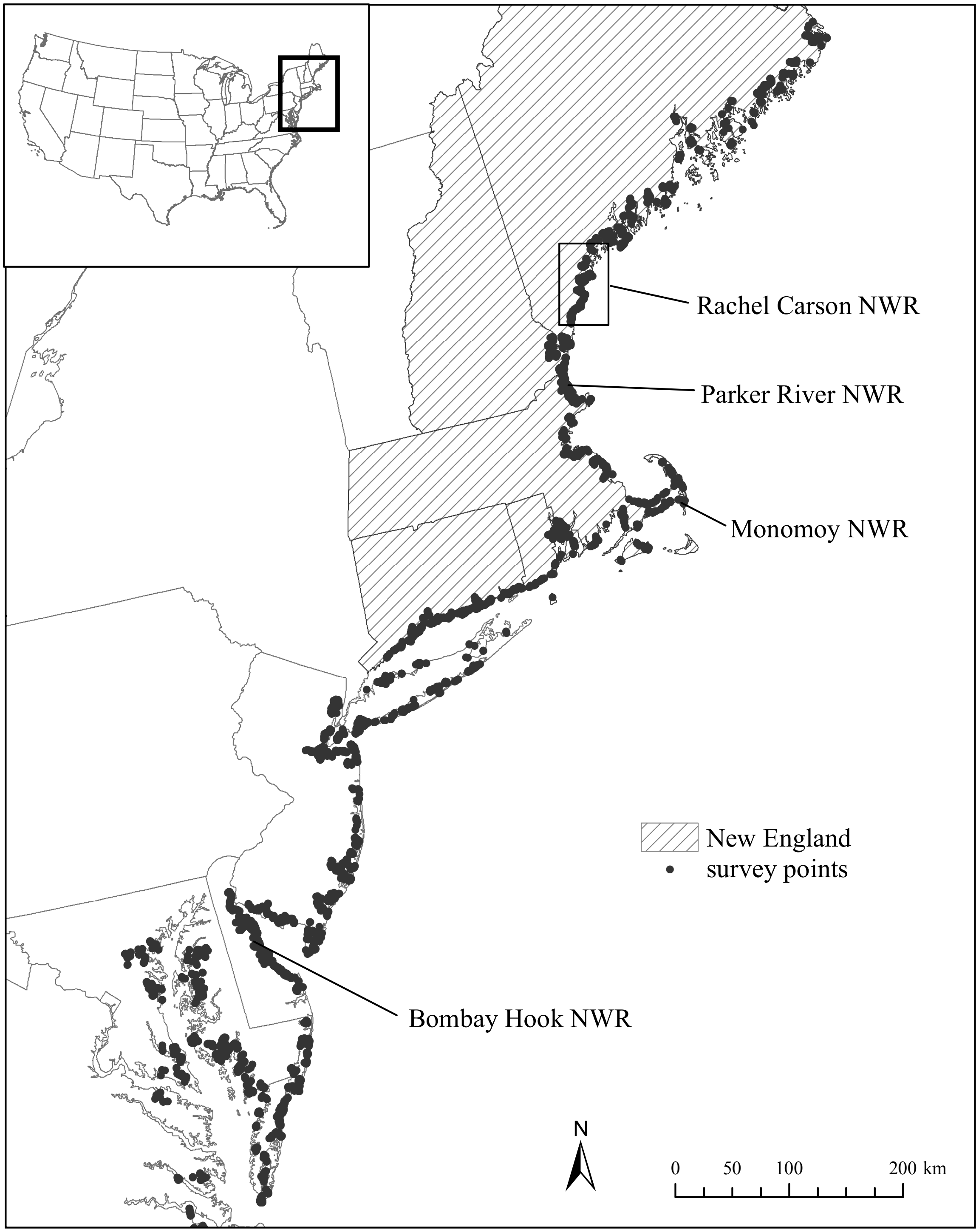

Figure 2.2. Map of survey sites. Map shows locations of spatial subunits used in population analyses including US National Wildlife Refuges, New England, and the entire study region (Maine to Virginia).

2.3 Materials and Methods

2.3.1 Data collection

We combined 13 databases of historical point counts conducted in tidal marshes across the region, spanning observations from 1994 – 2012. The largest historical surveys were conducted by the Maine Department of Inland Fisheries and Wildlife (MDIFW) and WGS from 1998 – 2000 (Shriver et al. 2004) in tidal marshes between Maine and Connecticut (i.e., New England). Rachel Carson National Wildlife Refuge (NWR), Parker River NWR, Monomoy NWR, Bombay Hook NWR, and the Smithsonian Institution all provided local datasets of annually surveyed marshes that spanned at least eight years (Fig 2.2). Massachusetts Audubon, New Hampshire Audubon, New Jersey Audubon, and the New Jersey Meadowlands Commission contributed additional historical data at smaller scales.

We combined data from these historical survey points (n = 3006) with contemporary bird surveys we conducted during the summers of 2011-12 in tidal marshes from Maine to Virginia (n = 1770, Fig 2.2). We selected survey sites based on a two-stage cluster sampling scheme for secretive-marshbird surveys suggested by Johnson et al. (Johnson et al. 2009) and implemented by Wiest et al. (Wiest et al. 2015). For a subset of the contemporary points we revisited locations from historical surveys during contemporary data collection (n = 457). An in-depth description of our contemporary survey site selection is included in SI Results.

We used the sampling scheme from our contemporary surveys to collect spatially stratified data on past marsh modification across the survey region. We assessed number of tidal restrictions, ditching, and OMWM within 50 and 100 m radii around each survey point (n = 3,065) using Google Earth imagery (Google Core Team 2013). As an index for degree of ditching, we recorded the number of ditches that intersected crosshairs centered on survey points within the two radii. We counted all tidal restrictions downriver of each survey point, considering any human structure crossing a tidal river to be a restriction.

We used data from the US NOAA's Center for Operational Oceanographic Products and Services (67) to identify local sea-level rise trends and 1% exceedance values as a proxy for spatially explicit flooding risk across the region following Wiest et al. (Wiest et al. 2015). Both metrics are 30-year averages of measurements from monitoring buoys along the coast. We used data from the closest NOAA gauge station unless the geomorphological and bathymetric properties of the marsh in question differed markedly from that around the nearest gauge (Wiest 2015).

2.3.2 Statistical analyses

We modeled change in populations of clapper rail, willet, and Nelson's, saltmarsh, and seaside sparrows using generalized fixed-effect (GLM) and mixed-effect (GLMM) models in a likelihood framework in Program R (R Core Team 2014). In all analyses we used survey points that overlapped the Estuarine Intertidal Emergent Wetland layer of the National Wetlands Inventory (NWI) that had data from a passive 5-minute observation period during the breeding season (April 15 – August 15 overall, with shifting, narrower ranges by latitude to correct for local phenology). We used observations within a 50-m radius of each survey point recorded between sunrise and 1100 h, when birds are most active. Analyses used data only from within the published breeding range for each species (Cornell Lab of Ornithology 2015). See SI Results for additional detail.

For each species we modeled trends at three spatial scales: local (US National Wildlife Refuge), New England, and the entire surveyed region. At the refuge scale, we modeled maximum count per year at the point level with a Poisson distribution using the *glmer* function within the “lme4” package (Bates et al. 2014). We specified refuge-specific GLMMs using our knowledge of the spatial extent and survey point locations at each refuge. All refuge models possessed a random effect for survey point identity, to account for repeated visits. For refuges with a variable number of visits to survey points per year (Rachel Carson and Parker River NWRs), we also included number of visits as a random effect. For Rachel Carson NWR, where the surveys spanned many independent marsh patches across multiple watersheds, we also included log-transformed patch area as a fixed effect.

We modeled trends differently for the New England and regional estimates due to heterogeneity in the spatial and temporal scale of the historical data. The MDIFW/WGS dataset collected across New England between 1998 and 2000 makes up over half of our historical database records. For New England analyses, we used a “time step” dummy variable in place of year, with an “early” time step that included data from 1998 - 2000, and a “late” time step that included counts conducted in 2011 - 2012. For the complete regional estimates, we considered time (year) as a continuous variable and included data across the entire period examined (1998 – 2012). For both of these analyses, we modeled the sum of all counts within a patch of tidal marsh by year, patch area (log transformed), number of points visited within a patch each year (log transformed), and total visits to each patch per year (log transformed) as fixed effects using a negative binomial distribution and the *glm.nb* function within the “MASS” package (Venables and Ripley

2002). We defined habitat patches using the NWI layer following Wiest et al. (Wiest et al. 2015).

To identify trends in the populations of each species over the time frames at each spatial scale, we used Akaike's Information Criterion (AIC) to compare the fully specified models to a model with the time variable removed. We considered time to have an important effect on abundance when the model including "time" improved model fit by a $\Delta\text{AIC} \geq 2.0$ and the outputs from the training, holdout, and full model outputs agreed. We calculated 95% confidence intervals for all parameter estimates using the Wald approximation function. We calculated compound, $(\text{final value / start value})^{1/\text{number of years}}$ population change per year for all species showing positive or negative population trends, using model estimates for the first and last year included in each analysis.

We explored potential drivers of change in each species individually and as a community group across the entire survey region in a fixed set of model comparisons (Table 1). We modeled maximum count per year, summing across species, at each survey point (Poisson distribution) using a GLMM as a function of year and the interactions (and associated main effects) between year and degree of ditching, whether or not a point was tidally restricted, local sea-level trend, and the 1% exceedance value. We included four additional covariates in all models to account for sources of variation in count that were unrelated to our question of interest. We included patch area (log transformed) and distance upriver (log transformed) to account for the direct effects of these characteristics as well as to control for correlations between them and the marsh stressors. We included visits per point per year (log transformed) as a random variable to account for effort and the identity of our primary grid cell for point selection (40 km^2 hexagon grid, see SI

Results) identity nested within NOAA gauge as a random variable to account for spatial within local areas. In the full specialist community model, we added species as a random variable. We used model averaging considering shrinkage (Burnham and Anderson 2002) to produce parameter estimates and confidence intervals across all candidate models, scaling all continuous variables to allow *post hoc* direct comparison of parameter estimates. When we observed a significant interaction between year and degree of marsh modification, we compared versions of the top model grouping restriction *post hoc* as a binary (unrestricted vs. restricted), three groups (no restrictions, 1-4 restrictions, and >4 restrictions), and six groups (no restrictions, 1 restriction, 2 restrictions, 3 restrictions, 4 restrictions, >4 restrictions).

To further assess model fit and confirm influence of our parameter estimates for all of the above models, we (A) confirmed a dispersion ratio (Pearson residuals compared to degrees of freedom) between 0.5 and 2.5, (B) confirmed acceptable model fit using Q-Q plots of the random effect residuals, (C) withheld a randomly selected 30% of our data to assess model accuracy for the New England and region-wide analyses of the five species, and (D) conducted a sensitivity analysis (community model only) where we analyzed an additional 31 datasets that systematically excluded each historical dataset, species, a randomly selected 10% of the data (repeated 10 times), latitude quintile, and outliers from the model input (points experiencing >5 tidal restrictions, points <38.5° latitude) from the model input.

2.4 Results

2.4.1 Anthropogenic marsh modification

We detected ditching within 100 m of the survey point at 35.1% of points, with the highest concentrations in the states of Connecticut (74.5%) and Massachusetts (60.3%). Tidal restrictions occurred downriver of 42.6% of survey points across the region. Both ditching and tidal restrictions were spread evenly across the region (Table A.1). We found OMWM treatments at only 4.8% of survey locations across the entire region, with the highest rates concentrated in Delaware (12.7% of points), Maryland (12.0%), and New Jersey (12.8%). Due to this spatial clumping and lower historical sampling in these states, we removed OMWM treatment as a potential driver of change in further analyses. Thirty-year sea-level trends from National Oceanic and Atmospheric Administration (NOAA) tidal gauges varied from 1.76 to 5.48 mm/year across our study area, while 1% exceedance values (a proxy for extreme flooding risk) ranged from 0.96 to 2.74 m.

2.32 Population trends and drivers of change

We found a -2.4% compound annual trend in the specialist community from 1998 - 2012 (Table 2.2, Fig 2.3a). In our model selection for regional drivers, the top model included negative interactive effects between year and tidal restriction, year and sea-level trend, and year and ditching, with the tidal restriction interaction possessing the largest parameter estimate after scaling. Trends were stable at survey points with no tidal restrictions and decreased with the number of tidal restrictions, with noteworthy differences between trends at survey points with 1-4 tidal restrictions versus those with >4 tidal restrictions (Fig 2.3b). Tidal restriction parameter estimates were similar across

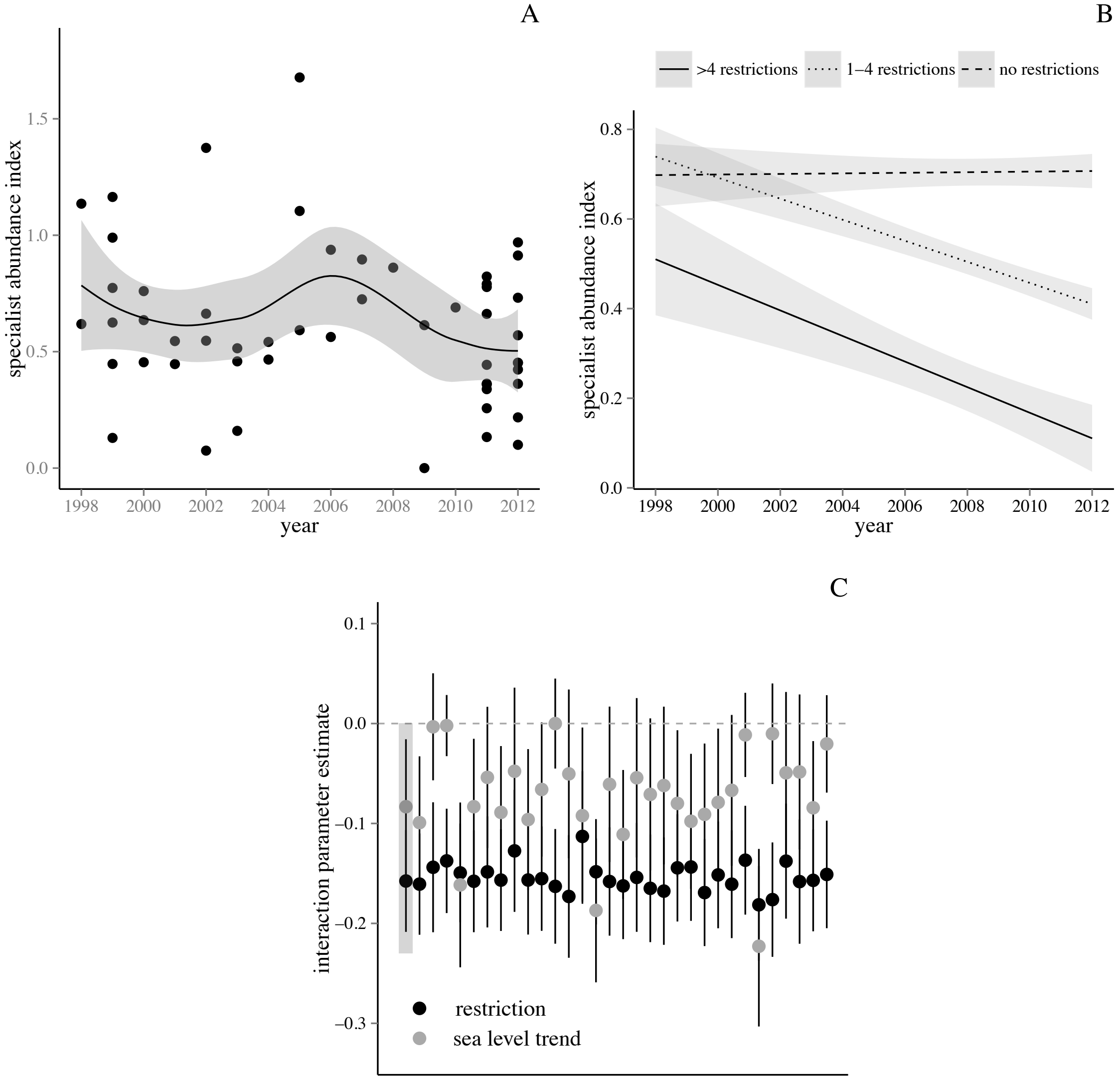

Figure 2.3. Trends for the specialist avifaunal community in tidal marshes from Maine to Virginia. A) LOESS regression (sep = 0.75), with each point showing average point count by state. Seven data points were excluded for visualization purposes only; trends reported include all data points. B) GLM model output grouped by degree of tidal restriction. C) Model-averaged parameter estimates for the interaction between time (year) and either the number of tidal restrictions downriver from a marsh (black) or the 30-year average sea-level rise trend measured by nearby buoy data (grey). Each pair of estimates (n=31) represents a different subset of our complete dataset to test the stability of the parameter estimates. Error bars shows 95% confidence intervals. Parameter estimates from the full dataset are outlined in grey.

Table 2.2. Top model parameter estimates and AIC values. Estimates include 95% confidence intervals for drivers of population change in the clapper rail, willet, Nelson’s sparrow, saltmarsh sparrow, seaside sparrow, and across all specialist species.

species group	**trend estimate**	**year effect**	**n**	**ditching x year interaction**	**restriction x year interaction**	**sea level rise x year interaction**	**1% exceedance x year interaction**	**n**
specialist community	-2.40%	-0.12 (-0.19, -0.04)	4936	-0.01 (-0.04, 0.01)	-0.16 (-0.21, -0.11)	-0.08 (-0.15, -0.02)	0 (-0.01, 0.01)	17812
clapper rail	-4.60%	-0.34 (-0.61, -0.06)	586	0.06 (-0.13, 0.25)	0.02 (-0.25, 0.3)	0.02 (-0.14, 0.19)	-0.17 (-0.45, 0.1)	2161
willet	no trend	0.13 (-0.01, 0.27)	1550	-0.04 (-0.09, 0.01)	0 (-0.11, 0.1)	-0.24 (-0.34, -0.14)	0 (-0.02, 0.02)	5501
Nelson's sparrow	-4.20%	-0.21 (-0.33, -0.08)	608	0.04 (-0.03, 0.12)	0 (-0.11, 0.1)	0.02 (-0.03, 0.06)	0 (-0.03, 0.03)	2393
saltmarsh sparrow	-9.00%	-0.43 (-0.56, -0.31)	1383	0 (-0.01, 0.01)	-0.24 (-0.34, -0.15)	0.03 (-0.09, 0.16)	0.06 (0, 0.11)	5180
seaside sparrow	no trend	0.05 (-0.21, 0.3)	809	0 (-0.04, 0.04)	0.33 (-0.02, 0.68)	0.04 (-0.14, 0.23)	-0.11 (-0.29, 0.08)	2577

our training, holdout, and full models (Fig A.1). Our sensitivity analysis with 31 cross-validation models (Fig 2.3c, Table A.2) showed ditching present in 25 of the top models (80%) with parameter 95% confidence intervals that did not overlap zero in 13 (42%). Sea-level rise was present in 30 of the 31 top models (97%) and significant in 25 (80%). Tidal restriction was included and significant in all of the 31 top models. Although tidal restriction was a strong driving factor of the decline in the saltmarsh sparrow (see below, Fig 2.4c), the community trend remained with this species removed from the dataset (Table A.2).

We observed negative region-wide population trends in three of the five specialist species (Table 2.2, Table A.3). While two of these declining species (clapper rail, Nelson's sparrow) exhibited varying trends (i.e. positive, negative, or stable) at smaller spatial scales, the saltmarsh sparrow experienced decline on every scale examined, and showed the most extreme declines of any species both in New England (-12.0% compound change annually) and across the entire northeast (-9.0%, 45b). When exploring potential drivers of these trends we found interactions between anthropogenic stressors and year in four of the five species (Table 2.2), but the patterns between the majority of these disturbances and population trends were not linear (e.g., the greatest or lowest trends occurred at intermediate levels of disturbance) with the exception of tidal restriction in the saltmarsh sparrow, which showed steeper declines in restricted versus unrestricted marshes (Fig 2.4c).

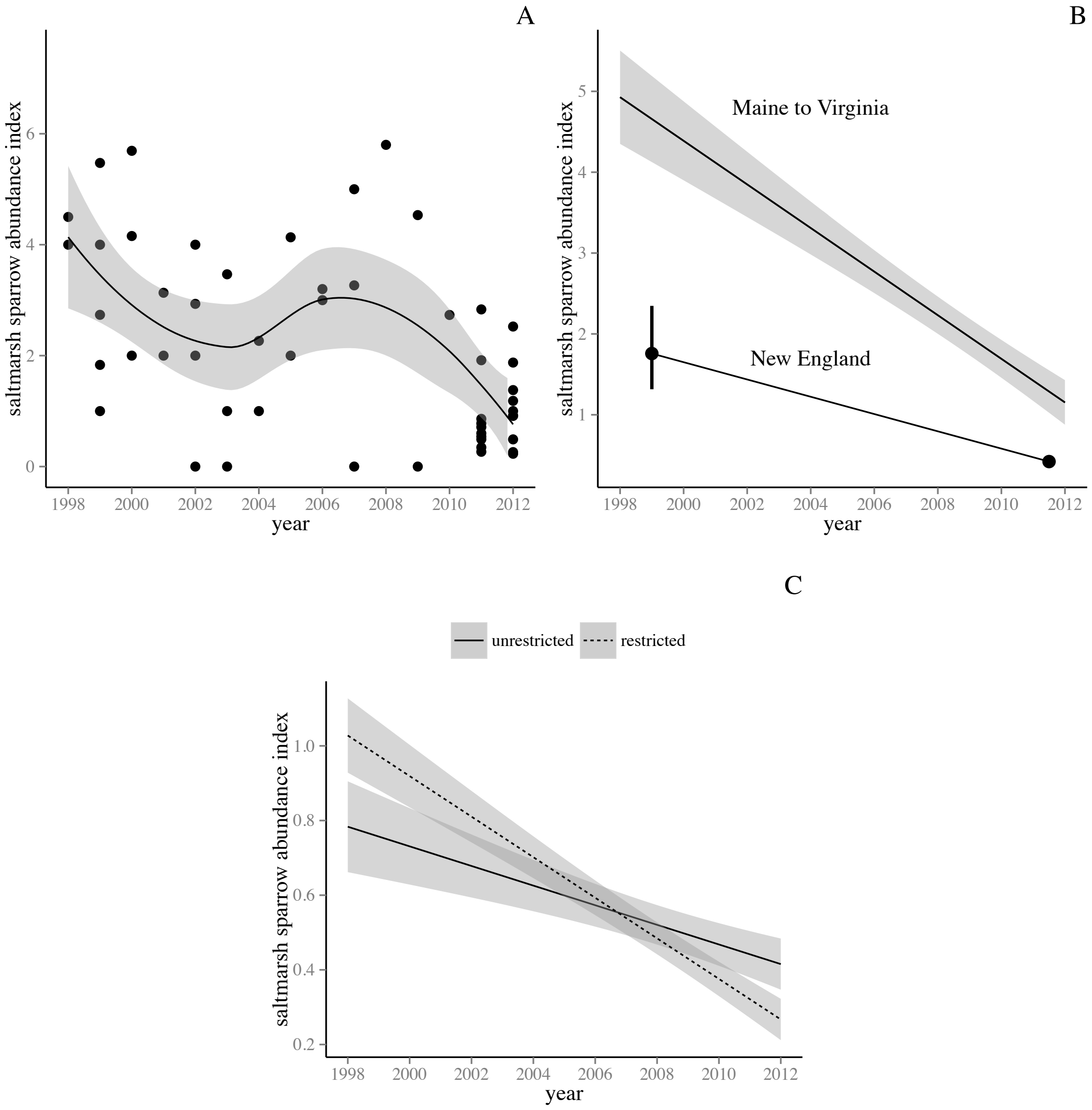

Figure 2.4. Population trends for the saltmarsh sparrow 1998 – 2012. A) LOESS regression (sep = 0.75), with each point showing average patch count by state and year, B) GLM model output at the New England and regional scales, and C) with and without tidal restrictions across the northeastern US. Error shading shows 95% confidence intervals. Seven data points were excluded for visualization purposes only; trends reported include all data points.

2.5 Discussion

2.5.1 Tidal restrictions as drivers of community change

Ecosystems experience multiple anthropogenic stressors at different scales, which can act additively, synergistically, or antagonistically depending on the system and timescale in question. In the tidal marshes of the northeastern US, tidal restriction appears to be a dominant driver of decline both in individual species (saltmarsh sparrow, 4b) and in the specialist avifaunal community on the decadal timescale examined (Fig 2.3). Contrary to expectation (Gedan et al. 2009), tidal restrictions explained steeper population declines than did variation in sea-level rise (Fig 2.3c, Table A.2). Tidal marsh specialists as a group maintained their populations in marshes with no road crossings, but declined in tidally restricted locations, with the most reduced populations in marshes with greater than four downstream restrictions (Fig 2.3). While saltmarsh sparrows exhibited declines at all sites, they showed steeper decline at sites affected by any amount of tidal restriction (Fig 4b). Based on our sensitivity analyses, whether or not a survey point was tidally restricted was consistently a stronger predictor of population change than sea-level rise, and much less variable as a predictor across subsets of our data (Fig 2.3c, Table A.2). In an era of anticipated climate-driven change at landscape scales, this conclusion provides a robust addition to recent literature highlighting non-climate-related stressors as dominant drivers of shorter-term ecosystem change (García-Valdés et al. 2015, Hamilton et al. 2015, Struebig et al. 2015). Further study is necessary to determine if tidal restrictions erode marsh resilience to sea-level rise or whether these restrictions alone cause the changes we report here.

The changes we see in the bird community likely reflect changes to the ecosystem as a whole. Anthropogenic modification of marshes directly affects soil chemistry and sediment supply to coastal wetlands (Portnoy and Giblin 1997a, 1997b), which in turn affect plant communities (Warren and Niering 1993). Globally, humans reduce sediment supply to coastal estuarine systems by a billion metric tons per year (Syvitski et al. 2005), limiting accretion of organic and inorganic material in coastal marshes. Accretion, driven both by sediment input and accumulation of dead vegetative material as peat, is the primary mechanism available to coastal marshes to keep pace with local and regional sea-level rise (Day et al. 1997, Pont et al. 2002). Our results show that the best predictor of bird population change during a period of rising sea-levels globally was not the degree of this stressor itself, but the presence of a secondary anthropogenic driver, tidal restriction. The limitation of tidal flow onto the marsh surface may slow accretion through reduced sediment supply and cause changes in marsh elevation on a timescale shorter than sea-level rise would alone. In short, our findings consistent with the hypothesis that tidal restrictions erode ecological community resiliency to sea level rise.

2.5.2 A conservation strategy for tidal marshes of the northeast

Our findings indicate the collapse of the specialist bird community and the rapid, short-term decline of the global breeding population of saltmarsh sparrows (Fig 2.4a, b). This species is experiencing a roughly 9% annual population decline regionally which is confirmed at smaller spatial scales (54, and this study). Based on a global population estimate of ~60,000 individuals in 2012 (Wiest 2015), and assuming a constant rate of decline, the saltmarsh sparrow population will be reduced to ~6,000 individuals in 25 years, and ~500 individuals in 50 years, demonstrating a high risk of extinction this century. Therefore, we suggest an immediate, detailed review of this species under the US Endangered Species Act (USFWS 1973). Because populations of all specialist tidal marsh species are ultimately affected by marsh elevation relative to maximum tide heights – and the consequent effects on habitat change and nest failure due to flooding – it is likely that the short-term fate of the saltmarsh sparrow is a good indicator of the long-term fate of the entire saltmarsh specialist community. Thus, we predict that species that currently show mixed or stable trends will exhibit more severe declines if rates of sea-level rise accelerates as predicted (IPCC 2013).

Identifying recommendations to prevent further decline of the specialist avian community, however, is difficult because tidal restrictions have been shown to both assist (Diquinzio et al. 2002, Culp 2012) and hinder (30, and this study) specialist birds, especially the saltmarsh sparrow. At an annual timescale, it appears that tidal restrictions can provide refugia, albeit temporary, for breeding birds by dampening extremes of spring lunar tides. Studies at the center of its range report that flooding is the greatest risk to saltmarsh sparrow fecundity (Greenberg et al. 2006a, Bayard and Elphick 2011); in Maine marshes, both nest success (Culp 2012) and seasonal fecundity (Ruskin 2015) are greater in restricted than in unrestricted segments of the same watersheds. In the longer term, however, it appears that there are steeper rates of specialist decline at these same types of sites (Fig 2.3b and 2.4c). Preventing the long-term effects of tidal restriction on high marshes appears necessary to sustain tidal marsh bird populations. The stressor is clearly widespread; nearly half of our randomly selected survey points occur upriver of a restriction. Simply restoring tidal flow, however, does not always restore high marsh and does not provide habitat for high-marsh birds (Elphick et al. 2015). It is clear that removing tidal restrictions from these marshes is not a full solution to the problem.

An alternate option for restoring sediment supply and accretion rates to restricted marshes is upriver dam removal. There is growing evidence globally that dam removal can supply previously sediment-starved systems with ample material to restore some ecosystem function (Chen et al. 2008) and has the potential to restore biodiversity (Asia: 59, South America: 60, South America: 61). The recent removal of two large dams on the Elwha River in northwestern North America demonstrates the large-scale return of sediment to riverine and coastal systems following dam removal (East et al. 2015, Gelfenbaum et al. 2015). Dam removal, however, can also act as an additional stressor to an ecosystem (Bednarek 2001, Poff and Hart 2002), and, in the case of tidal marshes, restoration actions often do not result in the return of full ecosystem function (Diquinzio et al. 2002, Mossman et al. 2012, Elphick et al. 2015). It is therefore important to restore sediment supply to marshes soon to preserve what ecosystem resilience still remains.

2.5.3 Conclusions

While sea-level rise is ubiquitous in tidal marshes globally and is predicted to result in 45% additional loss of emergent tidal wetland by 2100 (Craft et al. 2009), tidal restrictions have been a more consistent and dominant driver of change in the bird community in northeastern tidal marshes over the decadal time scale of our analyses. The bird community in unrestricted marshes appears relatively resilient to recent changes in sea-level rise, while tidally restricted marshes are being degraded to the point of specialist community collapse. In an era of heightened awareness of climate change and its impacts on ecosystems worldwide, our findings act as a warning to not ignore other, local stressors, even in systems that are expected to be dramatically impacted by regional influences such as climate change.

CHAPTER 3: A NOVEL INDEX OF SPECIALIZATION EXPLAINS AVIAN PERSISTENCE IN TIDAL MARSHES

3.1 Abstract

Habitat specialists are declining at alarming rates worldwide, driving the biodiversity loss of the earth's next mass extinction. Specialist organisms maintain a more compact functional niche than their generalist counterparts, and clear tradeoffs exist between these contrasting life history strategies that present conservation challenges to specialist taxa. There is little work, however, explicitly quantifying "specialization"; such information is necessary for the development of conservation strategies. In this paper, we test whether habitat specialization explains the persistence of breeding bird populations in the disturbed tidal-marsh landscape of the northeastern United States. We use the North American Breeding Bird Survey (BBS) together with contemporary marsh bird surveys to develop a Marsh Specialization Index (MSI) for 106 bird species that regularly use tidal marshes during the breeding season. We produce several metrics of species persistence (probability of occupancy, abundance, total biomass supported, and estimates of 14-year population trends) and compare them to MSI values in one of the first community-scale demonstrations of specialist loss in disturbed landscapes. Our results confirm that specialism has short-term benefits but long-term consequences for persistence of tidal marsh birds, results that are generalizable across many changing landscapes. We then use this robust support of niche theory to recommend MSI as a tool in identifying species of conservation concern in disturbed and rapidly changing landscapes.

3.2 Introduction

Generalist and specialist life history strategies are fundamental concepts in ecology, and can be explained most efficiently through the lens of the ecological niche. In the sense first described by Hutchinson (1957), the ecological niche can be described as the set of environmental conditions and requirements of a species to persist across generations. Hutchinson also introduced the concept of the n-dimensional hypervolume, a theoretical, multidimensional space describing the set of all environmental conditions where species persistence is possible, where each axis of variation represents an environmental gradient. “Niche breadth” then quantifies the amount of variability in a species’ use of a particular gradient. Specialism thereby becomes a relative term, where specialist taxa are those with a smaller niche breadth for a particular, or multiple, environmental gradients compared to more generalist taxa across those same gradients (MacArthur 1972, Julliard et al. 2006).

In a world comprised of finite resources, why do generalist species exist? The generalist, while able to use a wide breadth of resources, cannot exploit any one resource as effectively as their specialist counterparts (Levins 1968, MacArthur 1972) due to evolutionary tradeoffs inherent in adapting to multiple strategies. In a static environment comprised of undifferentiated resources, natural selection should faithfully favor the path of the specialist, whose competitive advantage benefits species persistence in homogenous landscapes (Levins 1968, Kawecki 1994). However, there are known consequences to being a specialist. Specialists do not exploit novel resources well, and while they are at a competitive advantage at the center of their most specialized niche axis, they are at a distinct disadvantage outside of this zone to both other specialists and to generalists. As a result of landscape heterogeneity, specialists thus exhibit smaller range sizes, population numbers, and more limited dispersal capabilities (Gaston et al. 1997, Colles et al. 2009) than generalists in the same landscape (Wilson and Yoshimura 1994, Devictor et al. 2008). Environmental setting is therefore integral to determining the fate of generalist versus specialist species; highly homogenous and unchanging landscapes favor specialists, while highly heterogeneous, fluctuating landscapes favor the persistence of more generalist species (Levins 1968, Devictor et al. 2008).

Given the current mass extinction crisis (Wilson 1985) and fragmentation of global resources through direct and indirect anthropogenic effects (Fischer and Lindenmayer 2007), the outlook is dire for specialists globally (Futuyma and Moreno 1988, Devictor et al. 2010). Rising global temperature, sea levels, and altered storm frequency and intensity can all create environmental conditions that fluctuate outside of the constrained niches maintained by specialist species. The fragmentation and degradation of habitat across the globe may further decrease the persistence of specialist species into the future. As a result, specialists have been referred to as the “great losers of past and current global changes” (Devictor et al. 2010), and specialism is now considered one of the dominant factors determining extinction of species (Dennis et al. 2011).

While theoretical tradeoffs between specialism and generalism are well documented, these concepts have not been rigorously quantified across taxa (Holt 2009), limiting the real-world application of these concepts towards conservation goals. Degree of specialism may refer to variation across individuals, species, or functional groups (Bolnick et al. 2003, Blonder et al. 2014), or to different forms of adaptation (e.g., diet vs. habitat specialization). Quantification measures for specialism also vary, are often limited to a few species (Devictor et al. 2010), and are usually applied across multiple habitat types (Jonsen and Fahrig 1997, Julliard et al. 2006, Devictor et al. 2008). Defining specialism in the context of a particular habitat or ecosystem, with the end goal of using these findings as conservation mechanisms, is the next logical step in the application of these principles to the current biodiversity conservation crisis.

We explore the persistence of tidal marsh bird species in the northeastern U.S. as a test of the costs of specialism in disturbed landscapes as predicted by niche theory. These marshes have been used and modified heavily by humans since European colonization for agriculture, mosquito abatement, and ready access to the ocean (Gedan et al. 2009). Tidal marshes also have been degraded by a variety of direct structural modifications, including the installation of roads and other human infrastructure, systematic ditching, and freshwater influx from runoff from impervious surfaces (Bertness et al. 2002, Silliman and Bertness 2004). Further, tidal marshes are being altered by sea-level rise; marshes across the northeastern U.S. experience rates of sea-level rise higher than the global average, with even higher rates recorded within the past five years (Sallenger et al. 2012). The degradation of these habitats make them well suited to test hypotheses about specialist and generalist persistence, and the ecosystem services tidal marshes provide to coastal communities (Shepard et al. 2011) make the answers to these questions particularly important for conservation planning.

In this paper we define a measure of specialization to tidal marsh, the Marsh Specialization Index (MSI) for the 106 most commonly detected tidal-marsh-bird species. This index is akin to the Species Specialism Index (SSI) developed by Julliard et al (2006, 2008) but quantifies specialism relative to a single habitat type. The development of this index is intended both to advance the standardized quantification of habitat specialization and as a tool for identifying species of conservation concern. To accomplish these objectives, we test for tradeoffs across a gradient of specialism between success within the habitat (occupancy, abundance, and biomass) and persistence in the face of habitat change (14-year population trends) using a historical database of tidal marsh bird records created by Correll et al. (in review). Further, we assess the use of MSI as a potential rapid assessment tool for the conservation status of tidal marsh species relative to other identification mechanisms currently in use by regional and global conservation ecologists.

3.3 Methods

3.3.1 Field data collection

We used a historical database of point counts conducted in tidal marshes from Maine to Virginia, spanning observations from 1998 – 2012 following Correll et al. (in review). We combined data from these historical survey points (n = 1550) with contemporary bird surveys conducted during the summers of 2011-12 over the same region (n = 1770 survey locations, Fig B.1). The contemporary surveys employed a Generalized, Random, Tesselated, Stratified sampling scheme as described in Wiest et al. (2015). When possible, we revisited locations from historical surveys during contemporary data collection (n = 457). The resulting database contains records of birds observed using tidal marsh during a passive 5-minute point count, conducted between sunrise and 1100 h between April 1 and August 1 of the survey year. The vast majority of historical data have records for both 50 m and 100 m radii (2782 points), however due to differing distance sampling methodologies a small number of observations were limited to 100m (n =93) distance bands. See Appendix B.1 for additional detail on field data collection.

3.3.2 Marsh Specialization Index (MSI)

We identified the most commonly detected species by scree plot (n = 106) in northeastern U.S. tidal marshes during the last year of our survey database (2012). To quantify tidal marsh specialization for these 106 species, we then compared relative abundance estimates from 2012 as measured by the North American Breeding Bird Survey (BBS, Sauer et al. 2015) to those measured in tidal marshes during 2012 by our surveys. The BBS is a long-running, continental monitoring program comprised of three-minute point counts within a 400 m detection radius conducted along a series of predetermined, roadside survey routes. For each species, we summed count data across all BBS routes where the route center-point was within 100 km of the coast across our survey region. We corrected for effort by dividing this sum by the number of routes (n = 170) and number of count stops on each route (n = 50). Likewise, we summed our contemporary count data from tidal marshes for each species, using detections recorded during the first three minutes of each survey at an unlimited detection radius at each survey point. Again, we corrected for effort by dividing the sum of all birds counted by the number of total visits across all point counts in 2012.

To produce our index of specialization for each species, we divided tidal marsh relative abundance by the sum of tidal marsh and terrestrial (BBS) relative abundance. This produces an index for each species quantifying its degree of habitat specialization to tidal marsh, with values ranging from 0 (extreme generalist) to 1 (extreme tidal-marsh specialist). We refer to this as the Marsh Specialization Index (MSI). This index assumes equal detection probability for each species across habitats, and equates 400 m radius counts (BBS data) with unlimited radius counts (tidal marsh data). These detection distances are likely equivalent, as detection and identification of birds to species >400 m from an observer is extremely rare (Emlen 1971).

3.3.3 Species metrics

We selected a subset of species to examine relationships between MSI and either taxon success in tidal marshes (occupancy, abundance, and biomass) or taxon persistence in tidal marshes (14-year population trends). The subset of species used for these analyses were those that 1) used northeastern tidal marshes during their breeding season, 2) occurred with enough evenness and regularity across our study area to withstand a robust trend analysis, and 3) had MSI values of > 0.5. We also excluded beach- and platform-nesting species from this analysis, because their abundance in tidal marshes is likely tied to proximity of adequate breeding habitat, not quality of the tidal marsh habitat that they were using when detected.

We modeled probability of occupancy and abundance using N-mixture models (Royle 2004) in a likelihood framework using the package unmarked (Fiske and Chandler 2011) in Program R (R Core Team 2015). We used contemporary data collected by the authors from Maine to Virginia in 2012 to produce these estimates. We used the function "occu" to estimate mean probability of occupancy and "pcount" to estimate mean probability of occupancy and abundance across all surveyed points. We used observation-level covariates of Julian day, time of day, and tidal stage to account for differences in detection probability across visits. For each species we only included survey sites within the published breeding range for each species (Cornell Lab of Ornithology 2015). We calculated confidence intervals for these estimates using the Wald approximation function.

We recorded average adult biomass for each species using Cornell Lab of Ornithology's estimates for each species (2015), using the mean when multiple mass estimates were given for a species (i.e., across sexes or subspecies). For Nelson's sparrow (*Ammodramus nelsoni*) and saltmarsh sparrow (*A. caudacutus*), we used estimates from Ruskin (2015) from recent work on these two species along the Atlantic coast. We then took the product of the average biomass and the point abundance estimate for each species to produce a value for average biomass supported.

We modeled population change from 1998 – 2012 in 22 marsh-bird species using generalized fixed-effect models (GLM) in a likelihood framework in Program R (R Core Team 2015). In all analyses we only used survey points that overlapped the Estuarine Intertidal Emergent Wetland layer of the National Wetlands Inventory (NWI) and were within the published breeding range for each species (Cornell Lab of Ornithology 2015). We modeled regional population trends for each species following identical model structure and fit assessment as Correll et al. (in review), using 50 m or 100 m distance band detections depending upon the natural history of each species. See Appendix B.2 for additional detail.

We investigated conservation status information for each of the 22 species through review of the Partners in Flight (PIF) Priority Species Pools for the physiographic areas of Northern New England (Area 27: Hodgman and Rosenberg 2000), Southern New England (Area 09: Dettmers and Rosenberg 2000), and the Mid-Atlantic

(Area 44: Watts 1999) which together make up our focal area for this study. Of the 22 species, 13 were assigned PIF prioritization scores in at least one of the physiographic region plans. The PIF prioritization plan (Carter et al. 2000) combines assessments of breeding and non-breeding distributions, relative abundance, and population trends to assign a single conservation score for each species in relation to that physiographic area. When a species was listed and ranked in a priority species pool for more than one physiographic area, we used the mean of the scores across all areas as a combined score for that species.

3.3.4 Specialism and species persistence

We tested for relationships individually between the degree of specialization (MSI) and each of the four metrics of species success and persistence (probability of occupancy, abundance, biomass supported, and population trend) using linear mixed-effect models in a likelihood framework using the package "lme4" (Bates et al. 2014). We also explored the relationship between MSI and the combined PIF score in a similar model framework to compare assessments of conservation need. To meet assumptions of normality, we first log-transformed three of the five dependent variables (probability of occupancy, abundance, and biomass supported). To control for the effects of phylogeny, we included taxonomic family as a random effect in all models. We tested for the effect of specialization by comparing all models to the intercept-only model, and models with ΔAIC ≤ 2.0 were considered equivalent.

To explore the relationship between degree of specialism and biomass supported further, we used linear mixed-effect quantile regressions in a likelihood framework using the lqmm package (Geraci 2014). We compared models with τ ranging from 0.1 to 0.9 in

0.1 increments to models with $\tau = 0.5$ (equivalent to linear regression). We again assessed relative model performance with AIC.

3.4 Results

Across the 106 species, MSI values ranged from 0.01 (tufted titmouse, *Baeolophus bicolor*) to 1.00 (saltmarsh sparrow, *Ammodramus caudacutus*, among others, see Table B.1) with a mean of 0.62 ± 0.39. We identified 22 species that fit species selection criteria (Fig 3.1). Probability of occupancy point estimates ranged from 0.02 (0.01, 0.03) for the alder flycatcher (*Empidonax alnorum,* Table 3.1) to 0.70 (0.68, 0.72) for the red-winged blackbird (*Agelaius phoeniceus*). Point abundance estimates for each of the selected species ranged from 0.3 (0.01, 6.4) individuals for the alder flycatcher to 19.97 (18.25, 21.85) individuals for the red-winged blackbird. The mean biomass supported at each survey point ranged from 3.99 (0.18, 86.43) g for the alder flycatcher to 1,592.76 g (1,246.42 , 2,035.34) for the clapper rail. Trend parameter estimates ranged from -0.43 (-0.56, -0.31) individuals per year (saltmarsh sparrow) to 0.61 (0.47, 0.75) individuals per year (yellow warbler, *Setophaga petechia*).

We found no relationship between MSI value and either point abundance (Table 3.2, Fig. 3.2a) or occupancy (Table 3.2, Fig 3.2b). We found a positive linear relationship

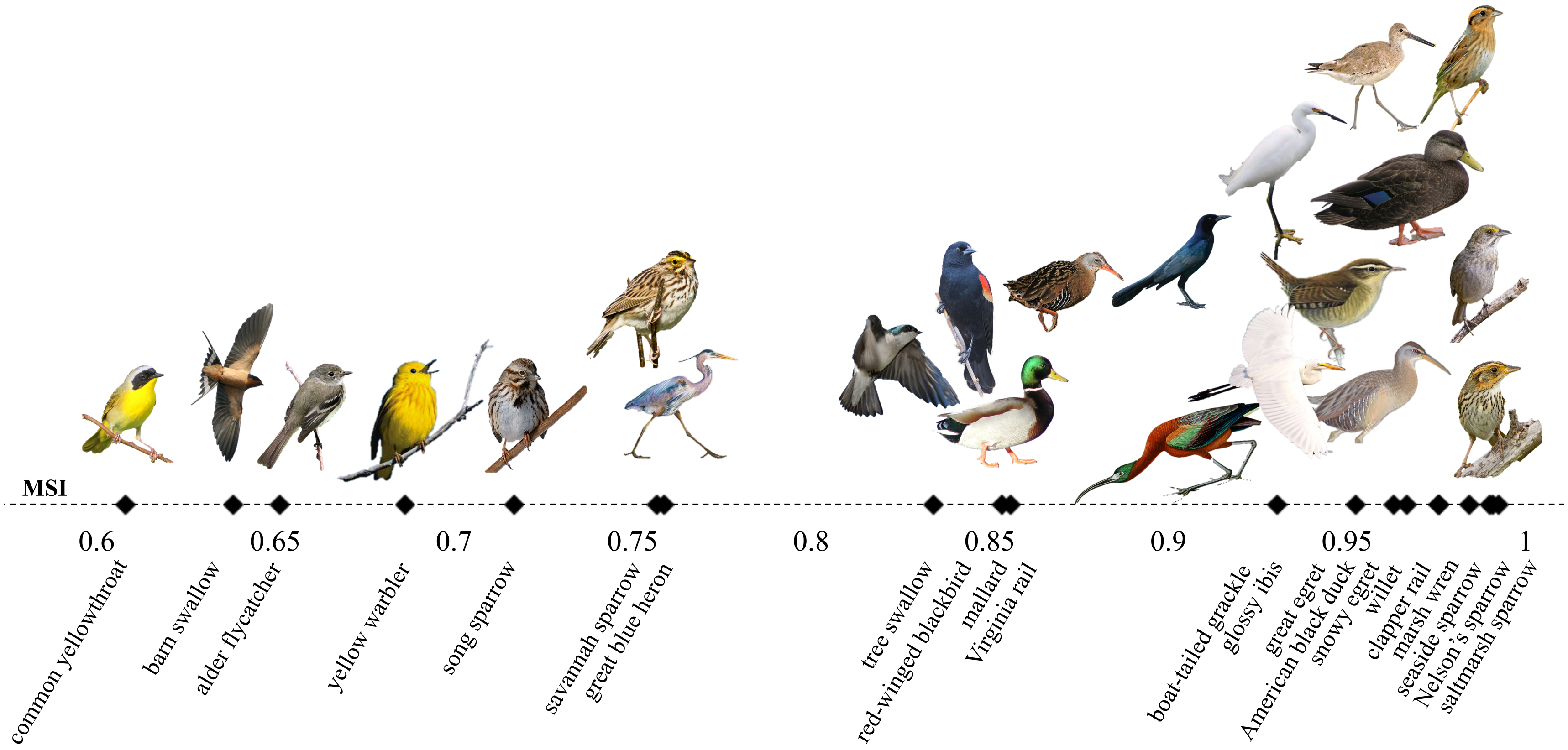

Figure 3.1. Sliding scale of tidal marsh specialization represented through a Marsh Specialization Index (MSI), a quotient of the amount of tidal marsh detections vs. total species detections in a combined database of North American Breeding Bird Survey (BBS) records and tidal marsh bird surveys conducted in 2012.

Table 3.1. Species persistence metrics and Marsh Specialization Indices (MSI). Table shows metrics for 22 bird species occurring in tidal marsh between Maine and Virginia (for the remaining 84 species calculated see Appendix 4).

common name	family	individual biomass (g)	MSI	point abundance	probability of occupancy	trend	biomass supported (g)
Saltmarsh Sparrow	Emberizidae	19.7	1.00	4.25 (3.24, 5.58)	0.22 (0.2, 0.25)	-0.43 (-0.56, -0.31)	83.8 (63.89 ,109.91)
Nelson's Sparrow	Emberizidae	17.3	1.00	1.93 (1.16, 3.2)	0.09 (0.08, 0.1)	-0.21 (-0.33, -0.08)	33.36 (20.1 ,55.37)
Seaside Sparrow	Emberizidae	24.2	0.99	6.13 (4.95, 7.58)	0.28 (0.26, 0.3)	0.05 (-0.21, 0.3)	148.26 (119.89 ,183.34)
Marsh Wren	Troglodytidae	12.2	0.99	5.78 (4.46, 7.49)	0.26 (0.24, 0.29)	-0.07 (-0.33, 0.17)	70.5 (54.41 ,91.35)
Clapper Rail	Rallidae	280	0.99	5.69 (4.45, 7.27)	0.26 (0.24, 0.28)	-0.34 (-0.61, -0.06)	1592.76 (1246.42 ,2035.34)
Willet	Scolopacidae	237.2	0.98	5.93 (5.08, 6.91)	0.36 (0.33, 0.38)	0.13 (-0.01, 0.27)	1405.77 (1206.14 ,1638.43)
Snowy Egret	Ardeidae	369	0.98	1.45 (1.18, 1.79)	0.22 (0.18, 0.27)	-0.11 (-0.25, 0.02)	534.69 (433.87 ,658.92)
American Black Duck	Anatidae	1203.5	0.98	0.76 (0.43, 1.35)	0.06 (0.04, 0.08)	0.04 (-0.21, 0.29)	916.73 (519.08 ,1618.99)
Great Egret	Ardeidae	473.5	0.97	1.77 (1.41, 2.21)	0.24 (0.21, 0.27)	0.26 (0.12, 0.41)	836.14 (667.9 ,1046.75)
Virginia Rail	Rallidae	82.5	0.96	0.54 (0.09, 3.38)	0.03 (0.02, 0.05)	0.23 (-0.32, 0.88)	44.78 (7.2 ,278.44)
Boat-tailed Grackle	Icteridae	152.6	0.95	1.43 (1.06, 1.93)	0.1 (0.09, 0.12)	-0.21 (-0.68, 0.25)	218.48 (162.1 ,294.46)
Glossy Ibis	Threskiornithidae	650	0.93	1.25 (0.9, 1.73)	0.08 (0.07, 0.11)	0.49 (0.22, 0.76)	812.65 (586.41 ,1126.19)
Red-winged Blackbird	Icteridae	54	0.86	19.97 (18.25, 21.85)	0.7 (0.68, 0.72)	0.34 (0.27, 0.41)	1078.48 (985.58 ,1180.13)
Mallard	Anatidae	1150	0.85	0.89 (0.7, 1.13)	0.13 (0.11, 0.16)	0.39 (0.19, 0.59)	1022.59 (805.35 ,1298.42)
Tree Swallow	Hirundinidae	19.5	0.83	4.36 (3.73, 5.09)	0.33 (0.3, 0.36)	0.02 (-0.11, 0.15)	84.96 (72.75 ,99.21)
Great Blue Heron	Ardeidae	212.4	0.76	1.57 (0.84, 2.93)	0.17 (0.09, 0.28)	-0.09 (-0.25, 0.06)	334.13 (179.4 ,622.29)
Savannah Sparrow	Emberizidae	19.9	0.76	0.72 (0.25, 2.07)	0.04 (0.03, 0.05)	0.02 (-0.27, 0.31)	14.4 (5.03 ,41.25)
Song Sparrow	Emberizidae	24.2	0.72	4.21 (2.76, 6.41)	0.49 (0.46, 0.51)	0.1 (0.03, 0.18)	101.78 (66.77 ,155.15)
Yellow Warbler	Parulidae	9.8	0.69	4.26 (2.46, 7.4)	0.2 (0.18, 0.22)	0.61 (0.47, 0.75)	41.77 (24.06 ,72.53)
Barn Swallow	Hirundinidae	18.7	0.65	7.46 (6.52, 8.54)	0.43 (0.41, 0.46)	0.24 (0.13, 0.34)	139.53 (121.87 ,159.74)
Alder Flycatcher	Tyrannidae	13.5	0.64	0.3 (0.01, 6.4)	0.02 (0.01, 0.03)	0.35 (-0.13, 0.92)	3.99 (0.18 ,86.43)
Common Yellowthroat	Parulidae	10.1	0.61	7.45 (4.66, 11.92)	0.37 (0.34, 0.39)	0.38 (0.29, 0.47)	75.29 (47.06 ,120.44)

Table 3.2. Model results comparing specialization to species persistence. Table of model results comparing metrics of species success and persistence in tidal marshes to Marsh Specialization Index (MSI) using Linear Mixed-effects Model (LMM) and Linear Quantile Mixed-effect Models (LQMM).

metric	**model type**	**MSI β estimate (CI)**	**Δ AIC**	**marginal R^2**
abundance	LMM	0.00 (-1.57, 1.56)	-0.64	0.00
occupancy	LMM	-0.03 (-1.57, 1.56)	-0.79	0.00
biomass supported	LMM	2.37 (0.4, 4.34)	4.41	0.21
biomass supported	LQMM	2.92 (1.2, 4.64)	5.25	NA
trend	LMM	-0.94 (-1.69, -0.19)	3.32	0.22
PIF score	LMM	25.5 (6.52, 44.49)	10.04	0.34

between MSI and biomass supported (Fig 3.2c, dotted line), and a negative linear relationship with trend parameter estimate (Fig 3.2d) with negative trends on average when MSI ≥ 0.93. MSI and PIF score were also positively correlated (Fig 3.3). We found improved fit explaining biomass supported with quantile regression and $\tau \geq 0.8$ (Fig 3.2c, dashed line). Model fit was not improved for population trend by varying τ from 0.5.

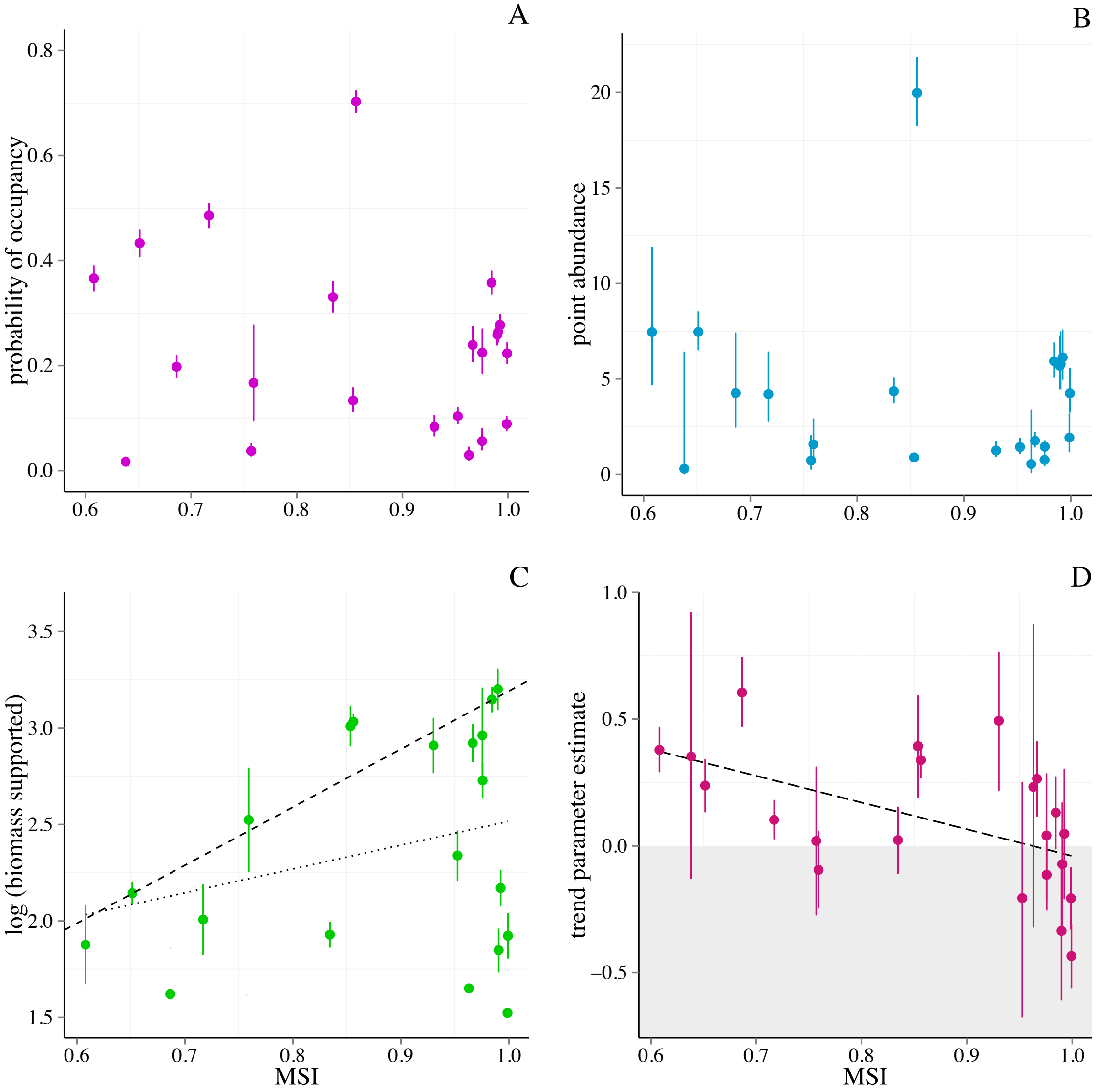

Figure 3.2. Linear mixed-effect model results comparing Marsh Specialism Index (MSI) for 22 tidal marsh-bird species with A) probability of occupancy, B) abundance, C) mean biomass supported (dotted line indicates τ = 0.5, dashed line indicates τ = 0.8), and D) populations trends (grey shading indicates negative parameter space) for all species. Error bars indicate 95% CIs.

3.5 Discussion

3.5.1 Specialism and avian persistence in tidal marshes

Tradeoffs exist between specialist and generalist life history strategies. One result of these tradeoffs is that specialists are predicted to reach higher densities within their preferred niches (Dennis et al. 2011), but habitat generalists are predicted to outperform specialists when these landscapes are disturbed. In our study of tidal marsh birds in the northeastern United States, we found that the consequences and benefits of specialism followed this pattern, as predicted by niche theory. In our analyses, the biomass supported at a survey point for a given species was positively constrained by MSI value, but population trend was negatively correlated with MSI (Fig. 3.2). Controlling for taxonomic family, tidal marshes supported more biomass of specialized species than of their generalist counterparts. More specialized species, however, were also less likely to persist over time. When we examined this pattern across each avian family individually, we found that species with higher MSI values had more negative population trends in five (Anatidae, Rallidae, Hirundinidae, Emberizidae, and Icteridae) of the seven avian families examined (not Ardeidae or Parulidae, Figure B.2), suggesting that no one family was driving the larger pattern. In the short-term or in stable ecosystems, we expect that specialism benefits species competitive ability, but ultimately specialism contributes to population decline if ecosystems are disturbed or change rapidly.

These findings quantitatively support the dark future predicted for habitat specialists: the higher the degree of specialism, the higher the risk of extinction. Taken as a stand-alone case study of the tradeoffs of specialism, our findings are a robust, community-scale addition to a largely single-species collection of literature quantifying the declines of specialists world-wide (Clavel et al. 2011). These findings also suggest that MSI could serve as a rapid-assessment tool for identifying species of concern in specific habitat types.

The species with the highest MSI value in our study, the saltmarsh sparrow, experienced the most severe population trend of all species we examined, and occupies a very limited global breeding range completely within our study region (Cornell Lab of Ornithology 2015, Wiest 2015). These marshes are at high risk to further degradatiobriann (Greenberg et al. 2006b). Extinction within the century is predicted for this species using several different population metrics (Correll et al. in review, Field et al. in review), and it is the highest listed priority species in all three of the PIF physiographic areas in its breeding range. The saltmarsh sparrow is also recognized by the North American Bird Conservation Initiative (Rosenberg et al. 2014), the International Union for Conservation of Nature (IUCN 2013), and multiple state agencies as a species of conservation concern. The saltmarsh sparrow, however, is one of the most studied tidal marsh birds in the northeast; similarly rich demographic information does not exist for many of the other 105 species assigned MSI values in this paper. Using MSI allowed us to identify this specific as a high conservation priority with much less *a priori* information than those used by past conservation lists.

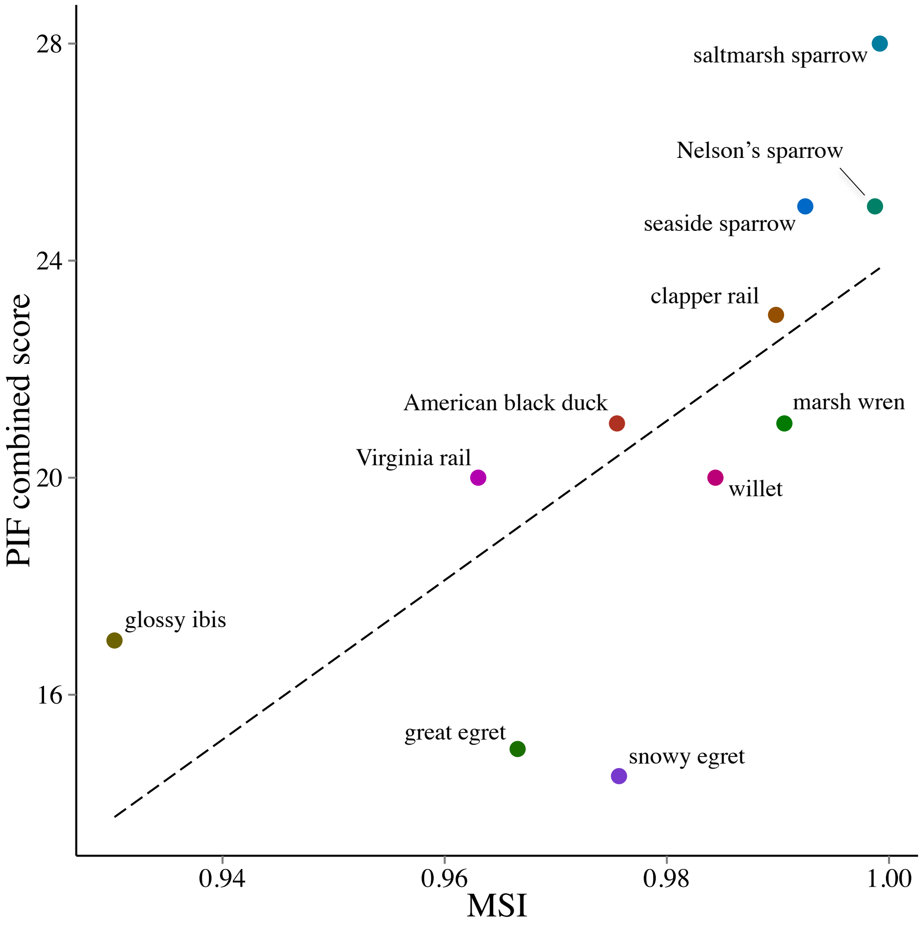

Figure 3.3. Linear mixed-effects model results comparing Partners in Flight (PIF) prioritization scores for 13 tidal marsh bird species plotted to Marsh Specialism Index (MSI).

We found that PIF prioritization score, one of the cornerstone methods for assessing conservation priorities of North American birds, was positively related to MSI value (Fig 3.3). The more specialized a bird was to tidal marsh, the higher it was prioritized using the PIF assessment method. Further, 11 of the 12 species with an MSI value ≥ 0.93 (the range of MSI values where our estimated population trend is negative) were already listed in the priority species pool (warranting particular conservation concern) for at least one PIF area. The MSI, therefore, could act as a rapid-assessment metric with which to identify species of conservation concern without the need to produce data- and effort-intensive occupancy, abundance, or trend estimates for each species. The only requirement is adequate survey data both within the habitat of interest and the broader landscape that includes many other habitat types. Given those constraints, it has potential for quantifying specialization and therefore conservation risk on suites of species across taxa on similar landscape-scale databases (e.g. western hemisphere plants - Enquist and Boyle 2012).

Aside from the quantitative comparison with PIF scores discussed above, our analysis also largely agrees with a recent regional review of marsh birds (Hodgman et al. 2015) with elevated conservation status in the 10 coastal states falling in our study area (Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia). The exceptions, however, are illustrative. After excluding beach- or platform-nesting birds, 22 out of our top 23 species ranked by MSI were identified as focal species of concern from these other sources as well. The one remaining species ranked highly by our MSI was the boat-tailed grackle (*Quiscalus major*: MSI = 0.95). This species is not listed in any PIF priority species pools, was not included in the tidal marsh review, nor is it routinely considered to be part of the suite of northeastern tidal-marsh species (Shriver et al. 2004). Our calculated trend parameter estimate for this species was negative at -0.21 (-0.68, 0.25), indicating potential for regional population decline and further validates the high MSI ranking. The MSI identified a potential species of concern previously overlooked in all of the more traditional conservation planning efforts.

It is important to note that our MSI values may be indicative of marsh or coastal area use generally rather than tidal marsh use specifically. For example, the marsh wren

(*Cistothorus palustris*), which uses freshwater, brackish, and saltwater marshes during the breeding season (Kroodsma and Verner 2014), received a higher MSI value than the willet (*Tringa semipalmata*) and clapper rail (*Rallus crepitans*), both ordinarily understood to be tidal-marsh specialist species (Shriver et al. 2004, Wiest et al. 2015). We believe this is because BBS surveys do not cover coastal or freshwater wetland habitats effectively (Sauer et al. 2015). As the accuracy of our approach relies on how thoroughly the reference survey (BBS in this case) samples all potential habitats, any species that uses habitat that is not well represented will be assigned a more specialist-biased MSI value.

Very rare species could also be assigned biased MSI values if their rarity led to sampling errors across habitats that do not reflect their true distribution. For example, the black rail is a known tidal marsh specialist whose range overlaps much of our study area, but is detected in very low numbers (Wiest 2015), restricting robust analysis of their population status. Black rail was in fact so rarely detected during both tidal marsh and BBS surveys it evaded assignment of an MSI value completely despite its near-exclusive use of tidal marshes on the Atlantic coast. We controlled for these biases in our analysis by removing beach-nesting species (which are also not adequately sampled by the BBS), species undergoing migration during the survey window (which can have either a rarity or temporal bias in sampling), and species that were not adequately common to estimate population trend robustly. We suggest the future use of MSI values in conjunction with knowledge of both the natural history of each species and the strengths and weaknesses of the surveys used to calculate it in order to identify potential outliers in this approach.

3.5.2 Conclusions

In an era of accelerated global change, specialist decline is predicted by niche theory. We find that degree of specialism increases short-term success (total biomass supported) and long-term extinction risk (negative population trends) among the tidal-marsh birds of the northeastern United States, confirming these predictions in this community. We use these findings both to illustrate a quantitative way to test these theoretical concepts at the community level and as an illustration of a rapid-assessment tool for identifying species at risk when other, more labor-intensive assessment methods are not possible. When used in conjunction with traditional species assessments, MSI and similar indices will be useful for developing conservation plans to limit the further degradation of global biodiversity.

CHAPTER 4: A PLEISTOCENE DISTURBANCE EVENT DRIVES PATTERNS IN COMMUNITY STRUCTURE IN COASTAL MARSH BIRDS: EMPIRICAL SUPPORT FOR THE INTERMEDIATE DISTURBANCE HYPOTHESIS

4.1 Abstract

Of the many hypotheses that attempt to explain the distribution of global biodiversity, many involve the effects of disturbance. While the term “disturbance” maintains several definitions in ecology, variance in disturbances across space and time have been documented and defined well enough in some landscapes to compare their effects on the biotic community. Tidal marshes of the United States experience disturbance at a wide range of spatial and temporal scales, and disturbance events in these ecosystems are well documented, making this system ideal to compare relative effects of these stressors across scales and to shed light on several competing disturbance theories that have not often been tested empirically. We explored community structure in tidal marsh birds using both traditional (richness, evenness, abundance, and biomass) and novel (Community Habitat Specialism Index, or CHSI) diversity indices to show that disturbance at a millennial timescale in the form of glacial advance and retreat explains present-day patterns in avian community structure. Richness, abundance, and biomass all peaked at the location of the Last Glacial Maximum, while specialization increased steadily from the north to the south across the range. These patterns are consistent with the hypothesis that tradeoffs between competition by marsh specialists and colonization by generalist taxa drive maximum diversity in the center of our study area and provide robust support for the Intermediate Disturbance Hypothesis (IDH). These drivers of

community structure differ from those reported previously at the species level, showing that biological scale is also important for understanding the impacts of disturbance across landscapes.

4.2 Introduction

Biodiversity can be driven by a variety of mechanisms across taxa, including the relative amount of photosynthetic activity on the landscape (e.g., Loreau et al. 2001), habitat availability and fragmentation (e.g., Fahrig 2003), degree and frequency of habitat disturbance (e.g., Roxburgh et al. 2004, Balée 2014), disease (e.g. Altizer et al. 2003), the evolutionary history of the organisms (e.g., Forest et al. 2007), and limiting climate factors such as temperature and precipitation (e.g., Thomas et al. 2004, Hampe and Petit 2005, Bellard et al. 2012). Due to the extreme complexity with which these mechanisms operate and the difficulty in testing large-scale patterns empirically (Shea et al. 2004), which processes most commonly drive diversity patterns remains an open question in ecology.

Of these factors, disturbance, including its frequency, intensity, and duration, has received wide support as a driver biodiversity patterns, although the suggested mechanisms vary. The stability-time hypothesis suggested by Sanders (1968) suggests undisturbed communities with adequate water and temperatures will exhibit the highest levels of diversity. A group of hypotheses that involve habitat refugia (Haffer 1969, MacArthur 1972, Diamond et al. 1976, Morat et al. 1986, Nores 1999), predict that diversity will be greatest where long-term disturbance periodicity has altered genetic isolation of communities and increased species diversity through allopatric speciation.

The multi-dimensional Dynamic Equilibrium Model (DEM) described by Huston (1979) states that communities left unperturbed over time will develop apex, or late-succession, communities at equilibrium with the resource supply available. Disturbance regimes of varying magnitude and frequency will have different effects upon community structure based on the resource availability of the habitat in question. This theory predicts that highly productive habitats will exhibit high-diversity communities long after disturbance, whereas peaks in diversity occur soon after disturbance in low-productivity systems. Finally, the Intermediate Disturbance Hypothesis (IDH), a theory developed by Horn (1975) and popularized by Connell (1978), describes maximum species diversity in settings experiencing intermediate levels of habitat disturbance. The highest levels of diversity are found at the intersection of two tradeoff curves (Fig 3.1) produced by opposing life history strategies, one prioritizing colonization of newly disturbed habitats (generalism), and the other prioritizing competition for resources in relatively unchanging landscapes (specialism).

In addition to these hypotheses regarding large-scale changes along a gradient of disturbance, there has been wide support for relationships between the specific form of disturbance and resulting diversity. The frequency and intensity of disturbance (Gotelli and Colwell 2001, Lindenmayer et al. 2014), landscape context (Krauss et al. 2003, Shriver et al. 2004), the spatial and temporal scales of disturbance (Macarthur and Macarthur 1961, Turner et al. 1989, Whittaker et al. 2001, Hatosy et al. 2013), and level of ecological organization (Leibold et al. 2004, Violle et al. 2012, Dornelas et al. 2014) all influence the effects of disturbance on community structure. The relative importance of different forms of disturbance across particular systems remains an active area of scientific inquiry.

Tidal marshes are a particularly useful ecosystem in which to explore the degree and form of disturbances and their effects on biota. They experience disturbance at a wide range of spatial and temporal scales, and disturbance events in these ecosystems are well documented, specifically along the coasts of North America and Western Europe (Adam 2002, Shriver et al. 2004, Sillman 2009). At the longest and largest scales, the Laurentide ice sheet (North America) and Devensian glaciation (Western Europe) reached their apex of disturbance of these systems at the Last Glacial Maximum (LGM, Fig 3.2) *circa* 20 kya, removing all wetland biota from the northern extent of marshes in North America and Europe for several millennia and impacting sea-level and the extent of estuaries across southern refugia (Bratton et al. 2002, Greenberg et al. 2006b). More recently,

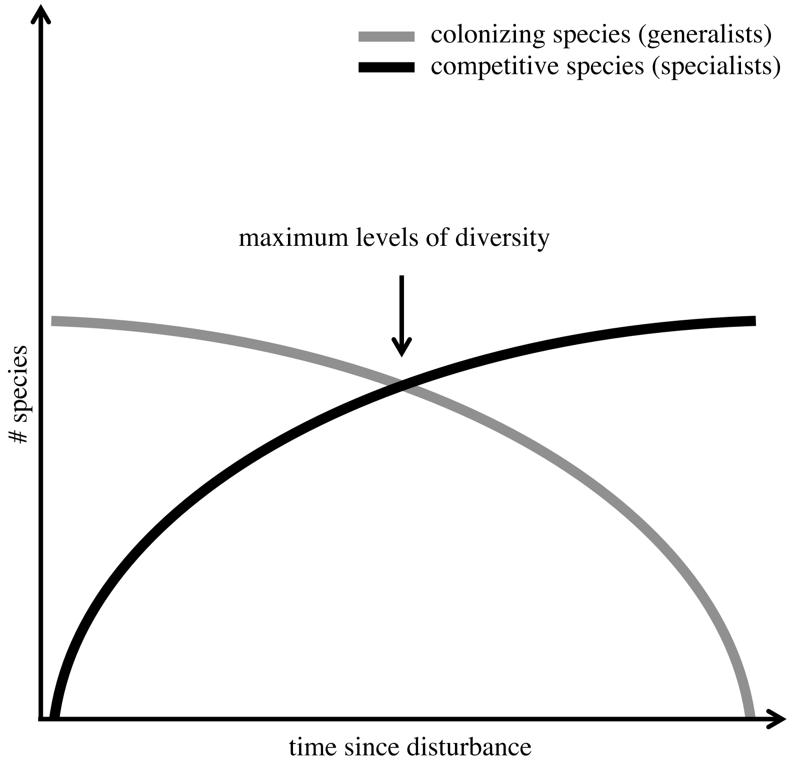

Figure 4.1. Idealized tradeoffs curves of specialism and generalism.

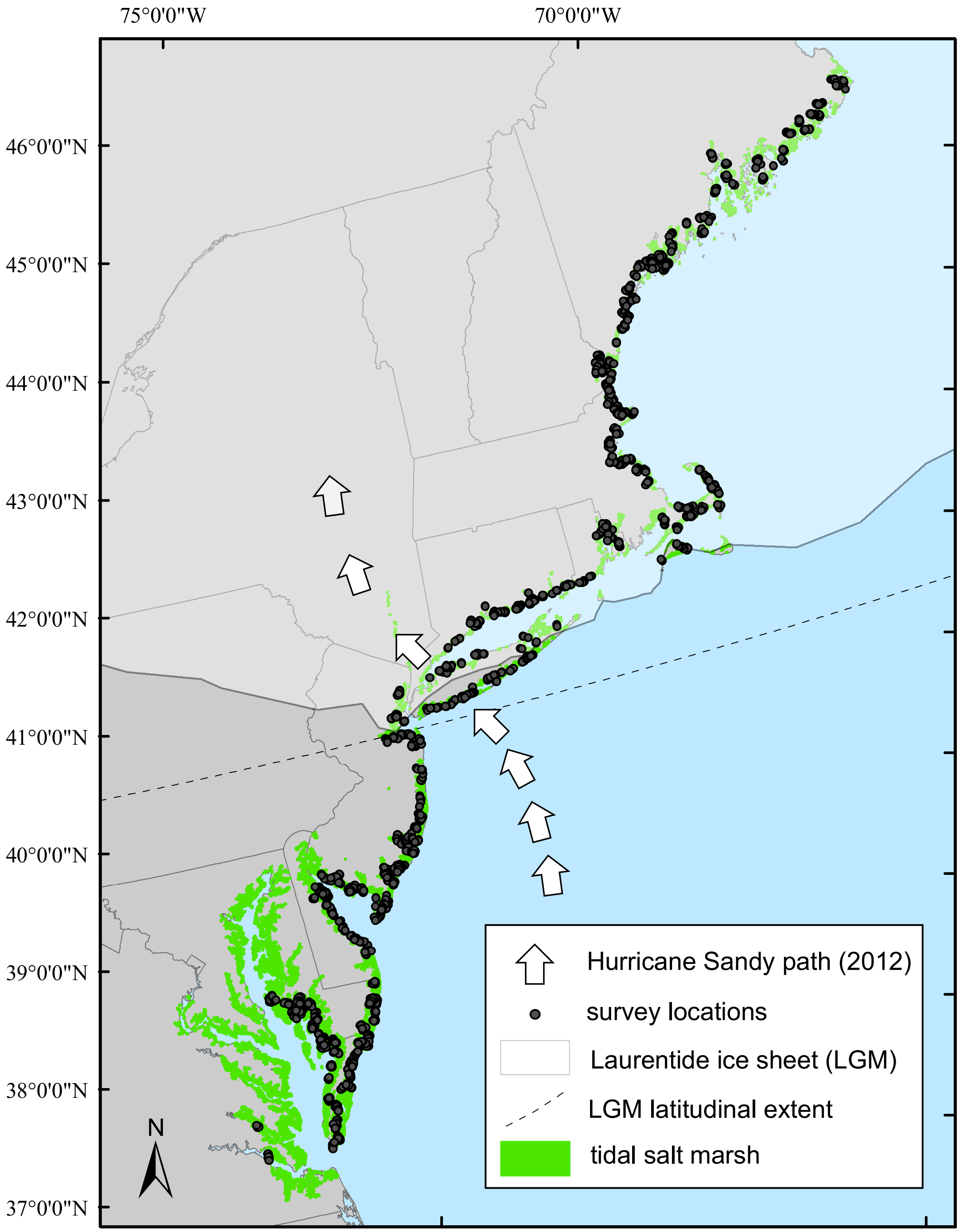

Figure 4.2. Map showing spatial distribution of disturbance events to tidal marshes between Maine and Virginia, USA.

sea-level rise, beginning at the advent of the Industrial Revolution, has disturbed tidal marsh systems on the scale of centuries (Morris et al. 2002a), with current decreases in marsh area up to 1.5% annually along the Atlantic coast of North America (Greenberg et al. 2006c). Marsh patches have simultaneously been fragmented by anthropogenic coastal development (Gedan et al. 2009) along a similar timescale. Locally, over decadal time scales, tidal restriction in the form of road crossings and culverts have reduced rates of marsh accretion (Anisfeld et al. 1999), which have impacted both flora and fauna in restricted marshes (Correll et al. in review, Roman et al. 1984). Extreme storm events, such as hurricanes, have potential to permanently alter coastal marsh structure within the span of only one or two days (Scavia et al. 2002, Arkema et al. 2013). Finally, tidal inundation itself creates daily disturbances in the form of flooding and salinization of lower elevation areas, severely limiting the diversity of the ecosystem (Shriver et al. 2004, Isacch et al. 2006b), despite high rates of primary productivity (Bertness et al. 2008).

In this paper we use a large, contemporary dataset of tidal marsh bird surveys collected between Maine and Virginia, USA to explore potential change in avian community structure due to several types of disturbances affecting this ecosystem. The tidal marsh bird community offers several benefits. Their habitat has easily definable boundaries and open landscapes, making communities easily observable compared to other habitat types. This is also one of the few communities where specialism to this particular habitat type has previously been quantified across the vast majority of species observed (Correll et al. in review), which allows us to test the stability-time, refugial, DEM, and intermediate disturbance hypotheses directly. We calculated traditional community diversity metrics (i.e., rarefied richness, evenness, total individuals, and total biomass supported) to quantify avian community structure in these marshes. Additionally, we quantified community specialism to tidal marsh using a weighted mean of the Marsh Specialization Index (MSI) for each species (Correll et al. in review) to develop a novel Community Habitat Specialism Index (CHSI). We examined these metrics across several potential disturbance scenarios in tidal marshes: time since glaciation, change in patch area, degree of tidal restriction, and degree of an extreme storm surge using Hurricane Sandy as a case study. Our comparisons allow us to empirically test theories with long-standing influence in disturbance ecology and shed light on the driving forces behind patterns in biodiversity at sub-continental scales.

4.3 Methods

4.3.1 Field data

We conducted point-count surveys to record the presence and abundance of marsh birds during the summers of 2011-2014 in tidal marshes from Maine to Virginia (n = 1319, Fig 4.2). We selected survey sites based on a two-stage cluster sampling scheme for secretive-marshbird surveys developed by Johnson et al. (2009) and implemented by Wiest et al. (in review). To select the first cluster of Primary Sampling Units (PSUs), we overlaid a 40 km^2 North American hexagon grid over National Wetlands Inventory (NWI) Estuarine Intertidal Emergent Wetland polygons (E2EM, USFWS 1979) from Maine to Virginia to identify our sampling extent. We then selected PSUs along the coast using a Generalized Random Tessellated Stratified (GRTS) sampling scheme, stratified by subregion (n=9) and chosen using a combination of watershed boundaries and large geographic features (e.g. Cape Cod, Long Island, etc.). We used the “spsurvey” package (Kincaid and Olsen 2012) in Program R (R Core Team 2014) to carry out our sampling scheme.

Within each PSU, we selected and visited up to 10 secondary sampling units (SSUs) using GRTS equal probability sampling design, stratifying by PSU. When historical survey sites were located within the sampling PSU (n = 457), we prioritized these historical locations over visitation of the randomly selected SSUs for uses unrelated to this study. In this article, we refer to all historical survey points and SSUs collectively as “survey points”. We conducted bird surveys at each survey point between April 15 and July 31 of each survey year from 2011-2014, with narrower survey windows within each subregion that were adjusted to account for differences in migration phenology along the coastline (Fig C.1). Our point-count surveys implemented a modified version of the National Marshbird Monitoring Protocol (Conway 2009) involving a five-minute passive survey period during which the distance to each bird detection was estimated as one of three distance bands (<50 m, 50-100 m, and >100 m). Birds were only recorded if they were observed using tidal marsh habitat, including the periodically flooded immediate upland terrestrial border. For our analyses here, we only use observations recorded within 50 m of the observer for our analyses following Wiest (2015).

4.3.2 Quantifying disturbance

We defined and measured glacial extent of the Laurentide ice sheet using a spatial layer developed by S. Birkel (in prep). For North American coastal ecosystems this ice sheet reached its maximum extent at 40.5 degrees latitude, roughly the center of our study area between Maine and Virginia. Since the North American coast in this region is oriented roughly north-south and this large-scale glaciation operated across the same gradient (Boulton et al. 1985), we used latitude in decimal degrees (North American Datum 1983) as a space-for-time substitution to measure time since glaciation along the coast.

We defined and measured habitat patches using methods developed in Wiest et al. (in review). We defined habitat patches by isolating wetlands delineated by the NWI E2EM layer and creating a 50 m buffer around all delineated patches. If a buffered marsh intersected with the border of any other buffered marshes, we considered them the same habitat patch for tidal marsh birds, based on local home range sizes (Shriver and Hodgman 2010) maintained by the saltmarsh sparrow (*Ammodramus caudacutus*), an aquatic passerine endemic to tidal marshes of the northeastern United States. Because there are currently no spatially explicit estimates of change in tidal marsh patch area across the past century (the time period where patch area has likely changed the most), we also substituted variation in this habitat characteristic across space for variation in this characteristic across time (e.g., Olson 1958, Chapin et al. 1994) to explore potential effects of patch area change on the tidal marsh bird community.

To quantify the degree of tidal restriction at each survey point, we counted the number of tidal restrictions downriver of each survey location visited (n = 1319) using Google Earth imagery (Google Core Team 2013). We considered any human structure crossing a tidal river (e.g., road crossing, culvert) to be a restriction following methods from Correll et al (in review). These counts generated an integer value along a continuous gradient of tidal restriction for each survey point, and allow us to measure potential effects on the marsh bird community due to this type of local and direct anthropogenic disturbance.

We quantified storm event intensity using data collected by the United States Geological Survey coastal gauges deployed along the coastline to record storm surge from Hurricane Sandy (McCallum et al. 2013). Each measurement represents peak storm tide experienced between October 29 and 30, 2012. We then assigned the storm intensity value of the closest survey gauge to each survey point, allowing us to quantify degree of extreme flooding along our study area during Hurricane Sandy.

4.3.3 Community metrics

We created two databases from the data above. One database ("4-year") included the mean count of each bird species detected at each survey point averaged across all visits to that point. We then calculated Pielou's evenness index (Pielou 1966), total number of individuals (N), and total biomass supported for each survey point using this averaged count data. To produce a measure of species richness independent of the number of individuals detected, we calculated rarefied richness for each survey point (Gotelli and Colwell 2001). As rarefied richness measures can only be calculated using integer values, we summed the number of species occurring across all visits and years at each survey point and then rarefied these numbers using a threshold of the median of all summed counts plus one standard deviation (final threshold = 102 individuals). We recorded average adult biomass for each species following Correll et al (in review) using the Cornell Lab of Ornithology's (2015) estimates for each species. We took the mean mass value when multiple mass estimates were given across sexes or subspecies. For Nelson's sparrow (*Ammodramus nelsoni*) and saltmarsh sparrow (*A. caudacutus*), we used estimates from Ruskin (2015) from recent work on these two species along the

Atlantic coast. We then took a weighted sum of biomass at each survey point by summing the products of biomass estimates and the mean count for each species across all visits and years, producing an index of total bird biomass supported for each survey point.

The second database ("before/after") averaged counts of all bird species detected across visits in 2011 – 2012 (before Hurricane Sandy) and 2013 – 2014 (after Hurricane Sandy). We then calculated the change in Pielou's evenness index, total number of individuals (N), and total biomass supported for each survey point between these two time periods. We also calculated the change in rarefied richness after first estimating richness for each time step using identical methods to those described for the 4-year database above.

4.3.4 Community Habitat Specialization Index (CHSI)

We identified the most commonly detected species by scree plot (n = 106) in northeastern U.S. tidal marshes following methods used by Correll et al (in review). To quantify tidal marsh specialization for these 106 species, we compared relative abundance estimates from 2012 as measured by the North American Breeding Bird Survey (BBS, Sauer et al. 2015) to those measured in tidal marshes during 2012 by our surveys. We used survey data from 2012 because surveys for this year occurred before Hurricane Sandy but after the pilot year of our data collection (2011), where data collection protocol differed slightly (forest edge birds were counted in addition to species using the marsh) from the following years (2012 – 2014).

The BBS is a North American bird-monitoring program comprised of three-minute point counts within a 400 m detection radius of the observer conducted along a series of roadside survey routes (Sauer et al. 2015). For each species, we summed count data across all BBS routes where the center-point of the route was within 100 km of the coastline within our survey sampling extent. We corrected for effort by dividing this sum by the number of routes (n = 170) and number of count stops on each route (n = 50). We also summed our tidal marsh count data for each species, using detections recorded during only the first three minutes of each survey at an unlimited detection radius at each survey point. We corrected for effort by dividing the sum of all birds counted by the number of total visits across all point counts in 2012.

To produce an index of specialization for each species, we divided tidal marsh relative abundance by the sum of tidal marsh and terrestrial (BBS) relative abundance. This produces a Marsh Specialization Index (MSI) for each species that quantifies relative habitat specialization to tidal marsh, with values ranging from 0 (extreme generalist) to 1 (extreme tidal-marsh specialist). This index assumes equal detection probability for each species across habitats, and equates 400 m radius counts (BBS data) with unlimited radius counts (tidal marsh data). These detection distances are likely equivalent given the demonstrated inability of human observers to accurately detect species at long distances (Emlen 1971).

To produce an index of specialization at the community level for each survey point, we took a weighted average of community specialism using the MSI value for each species detected at the point divided by the average number of individuals of that species detected at the point over all visits. This produced a Community Habitat Specialism Index (CHSI) quantifying the average degree of tidal marsh specialism of an individual at the survey point in question.

4.3.5 Statistical analysis

All statistical analyses were completed using Program R (R Core Team 2015). To satisfy assumptions of normality in our community metrics, we transformed values using logit (evenness) and natural log (N, total biomass) transformations. To explore patterns in rarefied richness, evenness, N, total biomass, and CHSI across disturbance scenarios, we compared a set of candidate linear regressions (“lm” function) in base R using adjusted R^2. Additionally, we compared our identified top models with equivalent models including quadratic and logarithmic terms.

We then explored the combined patterns in community structure across different disturbance scenarios through redundancy analysis (RDA) using the “rda” function in the “vegan” package (Oksanen et al. 2015). This is a multivariate analysis technique involving simultaneous constrained ordination of multiple continuous community metrics (rarefied richness, evenness, N, and total biomass) and continuous explanatory variables (patch area, time since glaciation, degree of tidal restriction, and storm surge). We conducted two RDAs. To explore the impact of glaciation, patch area, and restrictions on community metrics, we modeled our 4-year database of community metrics as dependent variables and tidal restrictions, patch size, and latitude as explanatory variables. We also included a quadratic term for our glaciation metric in this RDA due to the strong quadratic relationship exhibited between this disturbance variable and community metrics in our univariate models. To explore the impact of storm surge on community metrics, we modeled our before/after database of community metrics as dependent variables and degree of storm surge as an explanatory variable in a separate RDA. In both RDAs we included distance from the coastline for each survey point to account for differences in community structure due to this landscape characteristic. We compared relative strengths of explanatory variables by scaling the variables and including them in a set of candidate models containing subsets of the explanatory variables and comparing adjusted R^2 values of models with and without the explanatory variable included.

4.4 Results

4.4.1 Community metrics

Rarefied richness values ranged from 1.00 to 27.13 ($\mu \pm SE = 10.09 \pm 0.11$), Pielou's evenness values ranged from 0.04 to 1.00 ($\mu = 0.86 \pm 0.01$), N ranged from 0.45 to 124.86 individuals ($\mu = 12.03 \pm 0.26$), and total biomass ranged from 8.49 to 103,352.8 g ($\mu = 3622.06 \pm 202.15$).

Univariate regressions exploring time since glaciation exhibited strong quadratic relationships in three of the four traditional community metrics (rarefied richness, N, and biomass). The most variance was explained in rarefied richness ($R^2 = 0.22$, Fig 4.3a), followed by N ($R^2 = 0.19$, Fig 4.3c), and total biomass ($R^2 = 0.08$, Fig 4.3d). Inflection points for the rarefied richness, N, and total biomass quadratic curves occurred at 40.05, 39.97, and 40.01 degrees north latitude, respectively, values all within 0.5 decimal degrees of the LGM ice sheet extent.

Our univariate regressions showed weak linear relationships between each community metric and patch area (Fig 4.4). Patch area explained little variance in rarefied richness ($R^2 = 0.01$), evenness ($R^2 = 0.05$, Fig 4.4b), N ($R^2 = 0.03$, Fig 4.4c), and total biomass ($R^2 = 0.02$, Fig 4.4d). Additionally, we found a strong positive relationship between patch area and latitude ($R^2 = 0.33$, Fig C.3). Univariate regressions between our metrics and restrictions showed no relationship between this disturbance and community structure in tidal marshes.

Our 4-year RDA including time since glaciation, patch area, and degree of restriction resulted in an adjusted R^2 of 0.22 (Table 4.1, Fig 4.5). Time since glaciation was responsible for the bulk of variance explained by the full model (partial $R^2 = 0.20$). Patch area had a low partial R^2 of 0.02, and the inclusion of restrictions actually lowered the variance explained in the model (-0.001). Our before/after RDA exploring the influence of storm surge from Hurricane Sandy on change in our community metrics explained almost no variance in our dataset (adjusted $R^2 < 0.001$).

4.3.2 Community Habitat Specialism Index

Community Habitat Specialism Index values ranged from 0.02 to 1.00 ($\mu \pm SE = 0.69 \pm 0.01$). The linear regression of CHSI with the highest adjusted R^2 value included both time since glaciation and patch area ($R^2 = 0.12$). This model was not improved with the inclusion of tidal restriction ($R^2 = 0.12$). Overall (Table 4.2) there was a positive quadratic relationship between patch area and CHSI ($R^2 = 0.11$, Fig 4.6a) and a negative quadratic relationship between time since glaciation and CHSI ($R^2 = 0.11$, Fig 4.6b). These polynomial relationships explained more variance than linear models ($R^2 = 0.08$ and 0.10, respectively). There was no relationship between delta CHSI and storm surge ($R^2 < 0.01$).

Table 4.1. Adjusted R^2 in eight redundancy analyses (RDA) exploring large-scale patterns in community structure in tidal marsh birds between Maine and Virginia. Potential explanatory variables include linear and quadratic latitude (decimal degrees), number of tidal restrictions affecting the survey point, and marsh patch area (ha). All metrics were scaled prior to analyses to allow comparison of relative influence between predictors.

unit of summarization	RDA explanatory variables	Adjusted R2
μ (2011 - 2014)	upriver + patch area + restriction + latitude + latitude2	0.219
μ (2011 - 2014)	upriver + patch area + latitude + latitude2	0.218
μ (2011 - 2014)	upriver + restriction + latitude + latitude2	0.202
μ (2011 - 2014)	upriver + restriction + patch area	0.010
μ (2011 - 2014)	upriver + latitude + latitude2	0.200
μ (2011 - 2014)	upriver + patch area	0.008
μ (2011 - 2014)	upriver + restriction	0.003
μ (2011 - 2014)	upriver	0.003
Δ (before/after Sandy)	storm surge + latitude + upriver	<0.001

Table 4.2. Adjusted R^2 in regressions exploring large-scale patterns in Community habitat Specialism Index (CHSI) in tidal marsh birds between Maine and Virginia. All models include logit-transformed CHSI metrics and scaled landscape metrics to allow for comparison between drivers.

model	Adjusted R^2
linear models	
CHSI ~ restriction + patch.area + latitude + upriver	0.12
CHSI ~ patch.area + latitude + upriver	0.12
CHSI ~ restriction + latitude + upriver	0.11
CHSI ~ latitude + upriver	0.1
CHSI ~ restriction + patch.area + upriver	0.08
CHSI ~ patch.area + upriver	0.08
CHSI ~ restriction + upriver	0.02
CHSI ~ upriver	<0.001
linear models with a quadratic term	
CHSI ~ latitude + latitude^2+ upriver	0.11
CHSI ~ patch.area + patch area^2 + upriver	0.11

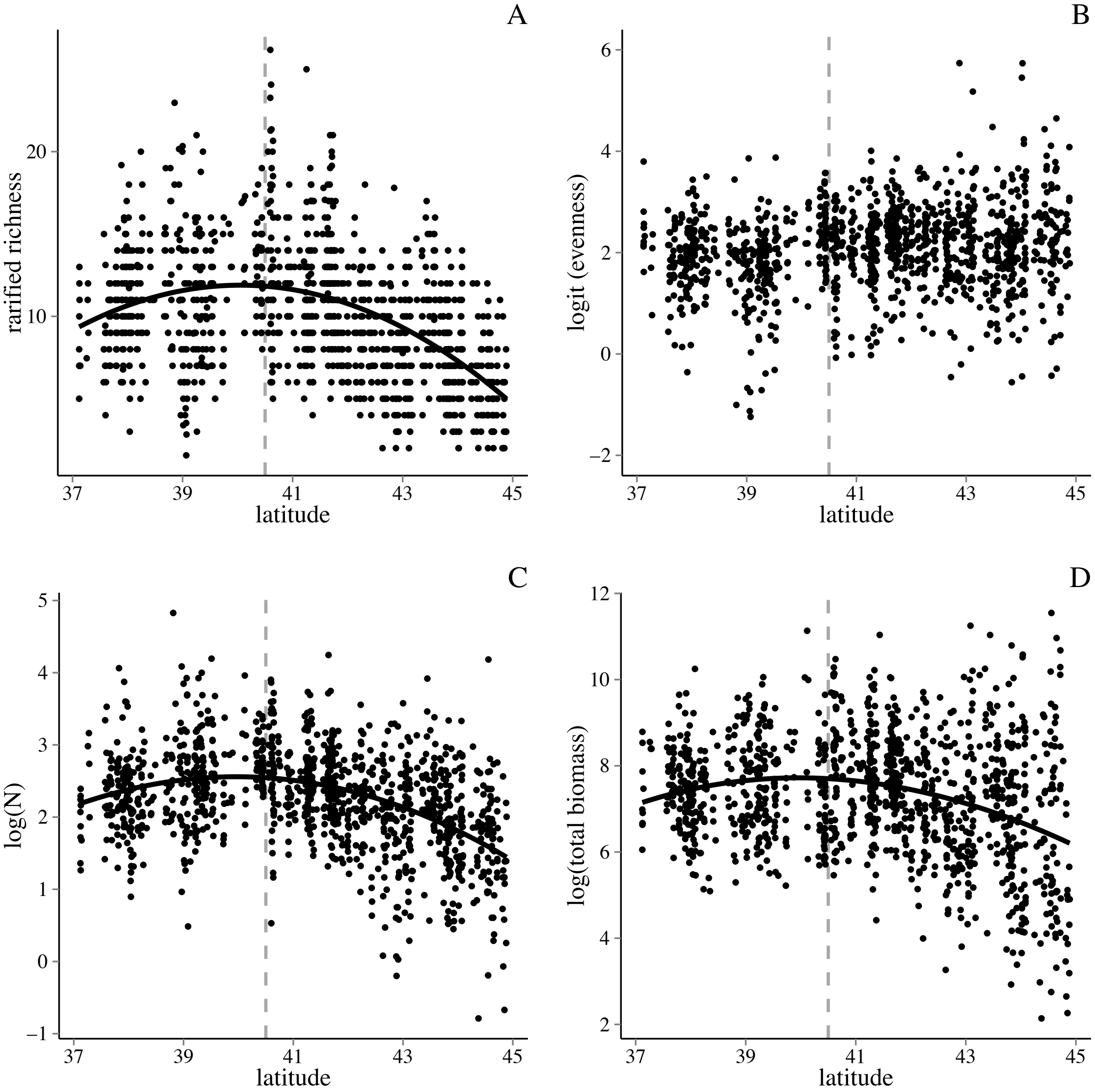

Figure 4.3. Results of linear regressions with a quadratic term comparing A) rarefied richness, B) Pielou's evenness index, C) total abundance N, and D) total biomass supported for the tidal marsh bird community from Maine to Virginia, USA across a latitudinal gradient. A dashed grey line indicates the maximum latitudinal extent of glaciation during the Last Glacial Maximum.

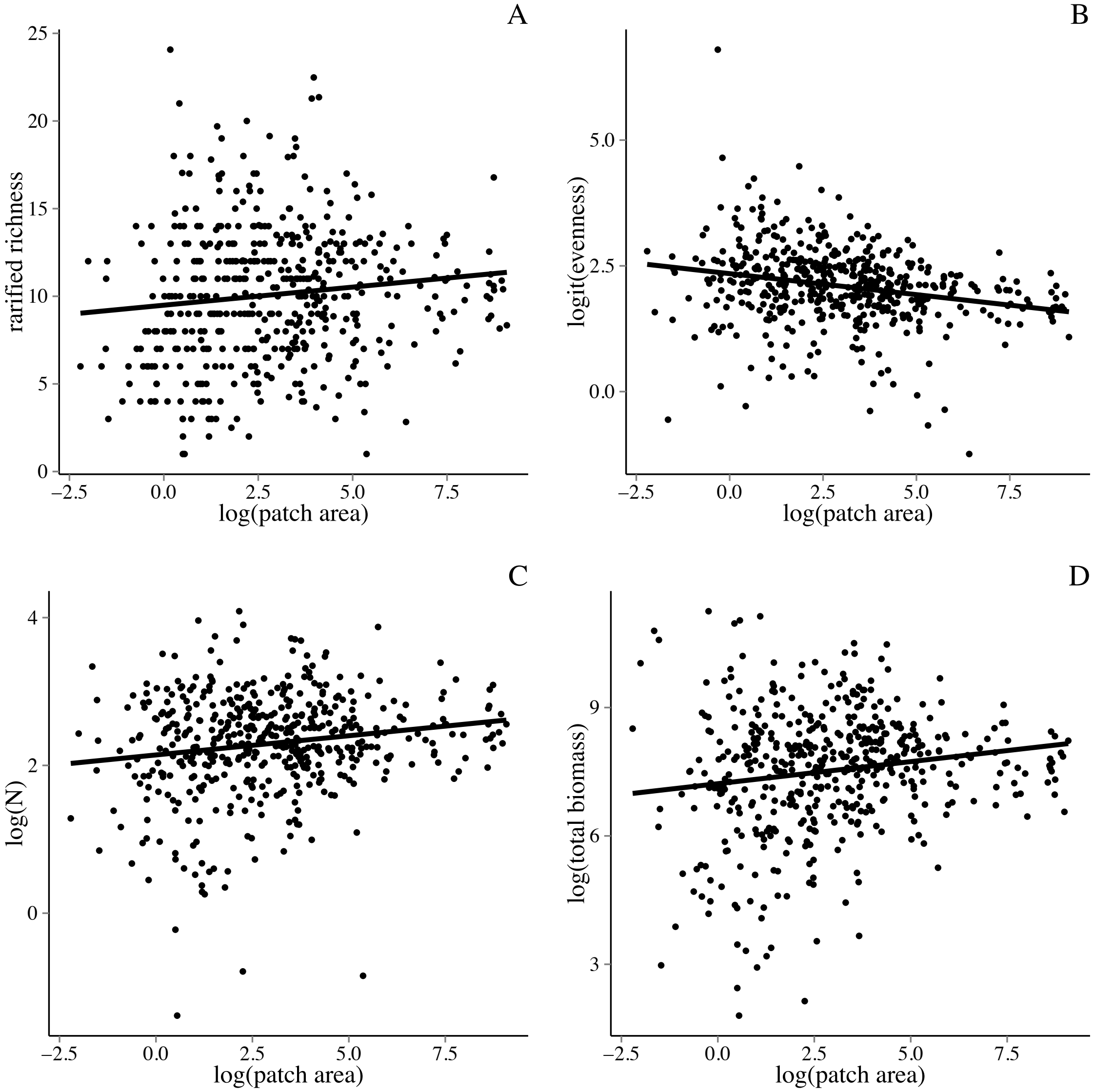

Figure 4.4. Results of linear regressions with a quadratic term comparing A) rarefied richness, B) Pielou's evenness index, C) total abundance N, and D) total biomass supported of the tidal marsh bird community from Maine to Virginia, USA by patch area (ha).

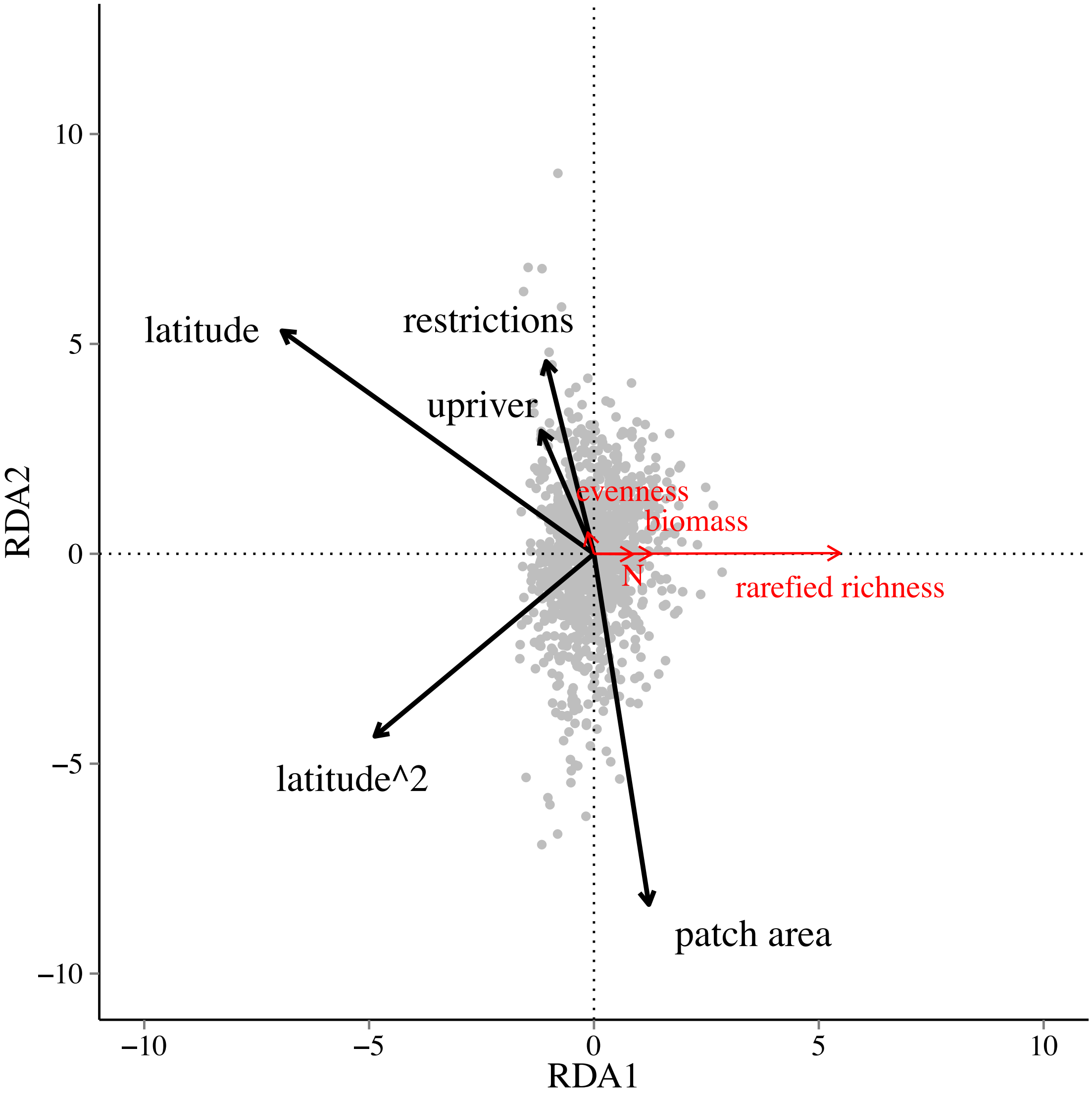

Figure 4.5. Results of redundancy analysis (RDA) of scaled rarefied richness, Pielou evenness, total abundance (N), and total biomass supported for the tidal marsh bird community between Maine and Virginia, USA, explained by disturbance scenario. Black lines represent biplot values for each explanatory variable, increased by one order of magnitude each to clarify direction and relative strengths.

4.5 Discussion

4.5.1 Empirical support for the Intermediate Disturbance Hypothesis

Disturbance regimes often drive variation in the abundance and distribution of species across landscapes. In the case of tidal marsh birds of the northeastern United States, we found that disturbance by glacial advance and retreat explains the most variation in community structure when compared to marsh stressors operating at shorter time scales (Fig 4.2), including variation in marsh area (occurring over centuries), tidal restriction (occurring over decades), and an extreme storm event (occurring over a matter of days). Time since glaciation predicts maximum diversity as measured by rarefied richness (Fig 4.4a), number of individuals (Fig 4.4c), and total biomass (Fig 4.4d), with the strongest trend apparent in richness. There are also clear relationships between time since glaciation and CHSI (Fig 4.6b), with the highest levels of specialism shown in southern latitudes and the lowest levels of specialism exhibited in the most recently glaciated latitudes.

These observed patterns provide robust support for the evolutionary and ecological mechanisms described by the Intermediate Disturbance Hypothesis (IDH). The quadratic distribution we see in our community diversity metrics closely mirrors the idealized relationship between disturbance and diversity shown in Connell's 1978 seminal paper, with colonists and specialist populations combining to produce maximum diversity numbers in areas where an intermediate period of time has passed since the disturbance in question occurred. We observed maximum diversity near 40 degrees latitude in three of the four community metrics measured. This apex of biodiversity occurs at the latitude coincident with the terminal moraine of the Laurentide ice sheet, which marks the maximum extent of glaciation at the LGM at 40.5 degrees north latitude (Figs 4.2 and 4.4).

These patterns and their inflection points are consistent within the theoretical context of the IDH. The Laurentide ice sheet, after reaching its largest extent at the Last Glacial Maximum, created a wake of graduated disturbance during retreat spanning thousands of years that has led to differential community membership among taxa with different degrees of specialism. Glaciated coastal areas were denuded of their bird communities, and current diversity represents the slow process of colonization over the last few millennia. Colonization could have occurred primarily via two routes: from southern glacial refugia with taxa already specialized to the particular challenges of tidal marshes and from upland habitats where generalist taxa expanded their niche into the locally novel, unoccupied habitat. The slow withdrawal of the ice sheet gave marshes located closest to the LGM several extra millennia relative to their northern counterparts to attract colonizing species from both sources and to drive the evolution of specialism in taxa. Conversely, marshes existing south of the ice sheet's LGM extent remained unglaciated during the last ice age (Rampino and Sanders 1980, Fletcher et al. 1990), maintaining specialist marsh bird populations in nearby refugia such as ancient, now-drowned estuaries and fringing tidal river marshes (Greenberg et al. 2006c). Wetland-adapted birds existing in these alternate habitats then colonized the newly formed marshes quickly and were able to competitively exclude more generalist species from using coastal marshes as habitat. These patterns in colonization and competitive exclusion are consistent with the maximized diversity numbers at the LGM extent, where we would expect colonization from both pathways to occur, and the lower diversity

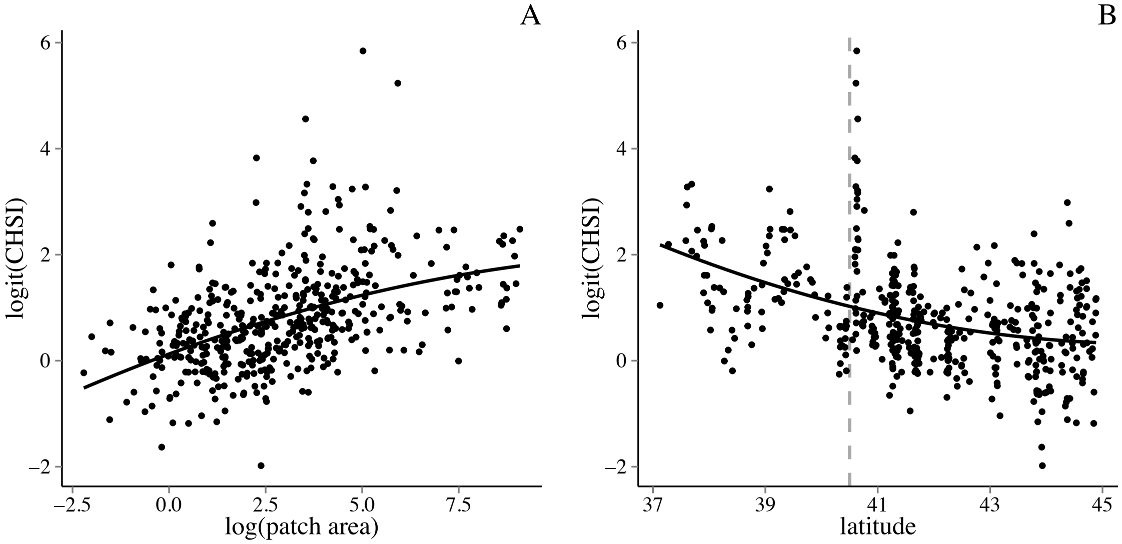

Figure 4.6. Results of linear regressions with a quadratic term showing a Community habitat Specialism Index (CHSI) of the tidal marsh bird community from Maine to Virginia, USA modeled A) by increasing patch area and B) across a latitudinal gradient. A dashed grey line indicates the maximum latitudinal extent of glaciation during the Last Glacial Maximum.

occurring to the north, where colonization was mainly by generalists, and to the south, where colonization would be primarily by specialists.

The case for the IDH in this system is strengthened by patterns of CHSI across the region, which reflect the two predicted patterns of colonization across a gradient of disturbance under the IDH scenario. While diversity peaks at the LGM, CHSI exhibits a nearly linear negative relationship (Fig 4.6b) with time since glaciation: the closer marshes are to southern refugia, the higher the specialism index. We posit that degree of competitive exclusion is likely indicated by higher CHSI values, given the ability of specialists to outcompete relative generalists for resources (Wilson and Yoshimura 1994, Dennis et al. 2011). Further, lower CHSI values should indicate a concentration of generalist taxa known to have actively colonized this tidal system since the LGM (Greenberg et al. 2006). Locations with the highest diversity are thus those areas where we would expect intermediate levels of colonization from specialist and generalist pathways. Intermediate CHSI values could indicate either mixes of generalist (e.g., song sparrow, red-winged blackbird) and specialist (e.g., seaside sparrow, saltmarsh sparrow, clapper rail) taxa or the inclusion of taxa with intermediate levels of specialism (e.g., Virginia rail, swamp sparrow). This lack of generalists to the south is not consistent with the stability-time, refugia, or DEM hypotheses, but is easily explained with the IDH. It is important to note that time since glaciation varies across latitude, which is perhaps the most well-examined and studied of ecological gradients for many other reasons (Pianka 1966, MacArthur 1972, Stevens 1989, Hawkins et al. 2003, Hampe and Petit 2005). Major biological properties, such as primary productivity, species diversity, range size, body size, and pigmentation, and numerous abiotic variables, such as precipitation and temperature, covary with latitude. However, nearly all of these latitudinal covariates predict linear relationships with latitude, and although these properties almost certainly contribute to variance in our dataset, none explain the convex trend across latitude apparent in the majority of our diversity metrics. The diversity of tidal marshes would therefore be difficult to explain using any single diversity hypothesis that invokes these linear patterns.

4.5.2 Secondary drivers of community structure

The species-area relationship of increasing diversity with patch area that we demonstrate in our system is well recorded in the literature (e.g. MacArthur 1972, Bates et al. 1998, Mantyka-pringle et al. 2012). However, this pattern is relatively weak in our data when compared to time since glaciation. We hypothesize this is largely due to the quadratic, not linear, relationship we find with diversity metrics and time since deglaciation, which is measured using latitude. Patch area is linearly correlated with latitude ($R^2 = 0.32$), and would therefore explain little variation along a strongly quadratic trend. Additional study is needed in this area to clarify regional relationships between marsh bird diversity and spatial characteristics of marsh habitat.

Interestingly, the extreme storm event of Hurricane Sandy explained almost no variance in our before/after dataset. A similar analysis done at the species level for both birds and plants (CRF, unpublished data) produced similar results, showing no change in specialist species presence or abundance before and after the storm. The lack of compelling patterns across this particular disturbance scenario adds weight to the description of tidal marshes as one of the more resilient ecosystems occurring globally (Wigand et al. 2015). Perhaps this resilience is due to selection provided by the daily disturbance of incoming and outgoing tides endured by this ecosystem. An additional extreme storm surge lasting only 1-2 days may not be enough to permanently shift biotic communities in one direction or the other.

While Hurricane Sandy did not drive change either at the species or community level, tidal restrictions have been previously shown to be the driving factor of species decline in the specialist marsh bird community in the tidal marshes we examine in this paper (Correll et al. in review). However, our findings at the community level show no noteworthy variation in diversity explained by degree of tidal restriction, demonstrating a stark contrast between drivers across the scale of ecological organization in this system. Changes at the species level in this ecosystem appear to be influenced by disturbances at time scales on the order of decades, while drivers of community diversity are strongest across millennia due to interactions between ecology and evolution.

4.5.3 Conclusions

The IDH invoked in this study has also been theorized to explain patterns in Amazonian bird diversity (Haffer 1969, Colinvaux 1987, Nores 2000) as well as in other taxa and regions (Townsend et al. 1997, Yamanoi et al. 2000, Roxburgh et al. 2004, Shea et al. 2004). However, the IDH has recently received scrutiny for its generality as an ecological principle (Fox 2013a, 2013b, Sheil and Burslem 2013) and for the difficulty in validating the evolutionary mechanisms empirically (Sheil and Burslem 2003, Fox 2013a). Our work provides empirical support both for the patterns produced by the IDH as well as the evolutionary and ecological mechanisms upon which those patterns are based. This study is the first to confirm diversity patterns consistent with the IDH with a quantitative metric of community specialism, and creates an analytical framework with which to confirm or refute criticisms of this theory and others in the literature. Further, the drivers we identify at the community level do not match single-species drivers of population change (Correll et al. in review), showing that the effects of disturbance on diversity are dependent on biological, temporal, and spatial scale. We hope the methods we present here create an analytical pathway for quantification of life history strategies to further support or refute the IDH and other theories in species diversity patterns.

CHAPTER 5: PREDICTING TIDAL MARSH COMMUNITIES VIA REMOTE SENSING: A POTENTIAL TOOL FOR ADAPTIVE COASTAL CONSERVATION

5.1 Abstract

The distribution of high- and low-marsh communities within a tidal wetland can change quickly due to both natural and anthropogenic stressors. These communities along the coast of the northeastern United States support both regional and global biodiversity through the maintenance of habitat for a number of vertebrate species obligate to tidal marsh, including the saltmarsh sparrow (*Ammodramus caudacutus).* This bird's global breeding range falls entirely between coastal Maine and Virginia. To date there has been no effort to develop a tool for managers to repeatedly quantify high-marsh habitat across the region at a rate relevant to the potential rapid change in these communities. We present a series of analyses to quantify high-marsh areas using Landsat Thematic Mapper (TM) imagery and validate the approach against ground-truthed measurements. Our top-performing model exceeded our *a priori* goal of 70% overall accuracy, although within-class accuracies for high marsh did not. We also explored classification at smaller scales and LiDAR elevation data as a supplement to spectral reflectance along a portion of our study area. We recommend use of higher-resolution imagery, fine-scale tidal covariates, and elevation data in the classification of high-marsh in future regional efforts.

5.2 Introduction

5.2.1 Tidal marsh ecosystems

Coastal marshes provide significant ecosystem services to human populations locally, regionally, and nationally. They act as a physical barrier between marine and terrestrial ecosystems, provide areas of high primary productivity, improve water quality in bays, and estuaries and provide critical nutrients to marine foodwebs (Bertness et al. 2002, Bridgham et al. 2006, Craft et al. 2009). Further, tidal marshes protect biodiversity by providing critical habitat to marine and estuarine fish, crustacean populations, and various migratory birds (Boesch and Turner 1984, Master 1992, Brown et al. 2002). Marshes along the Atlantic coast of the United States support the highest number of tidal-marsh specialist vertebrates described worldwide (Greenberg et al. 2006b). The saltmarsh sparrow in particular is fully obligate to tidal marshes between Virginia to Maine during the breeding season (Greenlaw and Rising 1994).

Terrestrial species that breed in tidal marshes such as the saltmarsh sparrow rely heavily on higher-elevation areas within the marsh (Greenlaw and Rising 1994, Shriver and Hodgman 2010). These “high-marsh” areas differ from “low-marsh” in elevation, salinity, and frequency of inundation (Bertness and Ellison 1987, Pennings and Callaway 1992, Ewanchuk and Bertness 2004). In eastern North America, tall-form *Spartina alterniflora* occupies low-marsh areas exclusively, whereas high marsh communities host a more complex suite of plant species (Nixon and Oviatt 1973, Bertness 1991, Ewanchuk and Bertness 2004). Short-form *S. alterniflora* as well as *S. patens*, *Distichlis spicata*, and *Juncus gerardii* characterize high-marsh zones, while additional species such as *Salicornia* spp., *Glaux maritima*, and *Solidago sempervirens* populate the high marsh to a lesser degree (Emery et al. 2001). Standing water in the form of pools and pannes occur in mid-elevation marsh and have their own suite of marsh plant species (Miller and Egler 1950, Ewanchuk and Bertness 2004). *Typha spp.* and *Phragmites australis* border marshes with significant freshwater input from the surrounding upland areas.

High- and low-marsh zonation has the potential to shift rapidly, sometimes on a sub-decal timescale (Bertness and Ellison 1987, Donnelly and Bertness 2001, Van der Wal et al. 2008), often driven by climate-related stressors such as sea-level rise (SLR) and extreme storm events (Morris et al. 2002; Kirwan et al. 2010). When high-marsh migration is limited by the upland landscape and sea-level rise is encroaching on the seaward side, some high-marsh zones experience a pinching effect with net losses over time that are more extensive than those in the low marsh (Donnelly and Bertness 2001, Smith 2009), however this phenomenon is not ubiquitous to all marshes (Kirwan and Guntenspergen 2010, Wilson et al. 2014). The future of high-marsh habitat in the northeast and mid-Atlantic therefore remains uncertain (Chu-Agor et al. 2011).

The saltmarsh sparrow's dependence on this ephemeral habitat has driven elevated conservation concern for this species by the International Union for Conservation of Nature (IUCN) Red List, Partners in Flight, and every coastal state government included in our study area (IUCN 2012, Partners in Flight Science Committee 2012, USGS 2012). The ability to 1) identify areas of high marsh and 2) re-assess this information on a biologically significant timescale is integral to the adaptive management of coastal wetlands (Klemas 2011), particularly in the northeastern United States to monitor habitat for the saltmarsh sparrow and other high-marsh specialist species.

5.2.2 Remote sensing of tidal marshes

Remote sensing methods through classification of hyper-spectral imagery work well to detect differences in soil moisture, vegetative cover, and water content in earth surface features, and offers an economical alternative to extensive field studies (Bannari et al. 1995, Leyequien et al. 2007, Meiman et al. 2012). Because high- and low-marsh areas vary both in vegetation community composition and soil moisture content, these zones are potentially detectible using TM satellite imagery, which records both visible and infrared wavelengths of radiation (Belluco et al. 2006, Yang 2009). Infrared reflectance (0.76 – 2.35 um) is especially important in discerning between vegetation types and differences in soil moisture (Jin and Sader 2005, Pettorelli et al. 2005), particularly in tidal wetlands (Klemas 2011). Several studies have previously demonstrated distinct spectral differences between dominant vegetation species within tidal marshes (Zhang and Ustin 1997, Gilmore et al. 2008), and TM imagery has previously been used as a tool to predict tidal marsh communities both in smaller regions within the northeastern United States (Gilmore et al. 2008, Hoover et al. 2010, Meiman et al. 2012) and elsewhere (Isacch et al. 2006a, Liu et al. 2010). As of yet, however, there is no easily repeatable assessment of high- and low-marsh zonation across the range of the saltmarsh sparrow accessible to managers, and it is unclear whether the methods of smaller studies will scale up to a user-friendly classification tool for this larger region.

In this study we compare 2 classic remote sensing techniques using Landsat TM imagery to develop an affordable tool capable of repeated classification of high-marsh zones in tidal marshes in the northeastern United States with a minimum overall accuracy of 70%. We also explore classification within single Landsat scenes and explore the use of Light Detection and Ranging (LiDAR) elevation datasets in a small case study to suggest future improvements to our tool. All methods and datasets involved in our study are freely available to the public, and we limited our analyses to tools available through ArcGIS, a commonly-used GIS in federal, state, and private conservation organizations, or simple Program R code, which is freely available to the public. Our manuscript provides code in Program R to complete analyses described which are not available through the ArcGIS interface.

5.3 Methods

5.3.1 Study area

Our study area includes all coastal, tidal marsh as delineated by the National Wetland Inventory (NWI, USFWS 1979) estuarine emergent wetland (E2EM) layer occurring between Maine and Virginia (Fig 5.1). This area approximates Bird Conservation Region 30 (BCR30) as delineated by the North American Bird Conservation Initiative, but includes coastline above the northern border of BCR30 to cover the entire range of the saltmarsh sparrow (BCR30+). We separated BCR30+ into sub-regions based on watershed and differences in vegetation greening phenology along the coast.

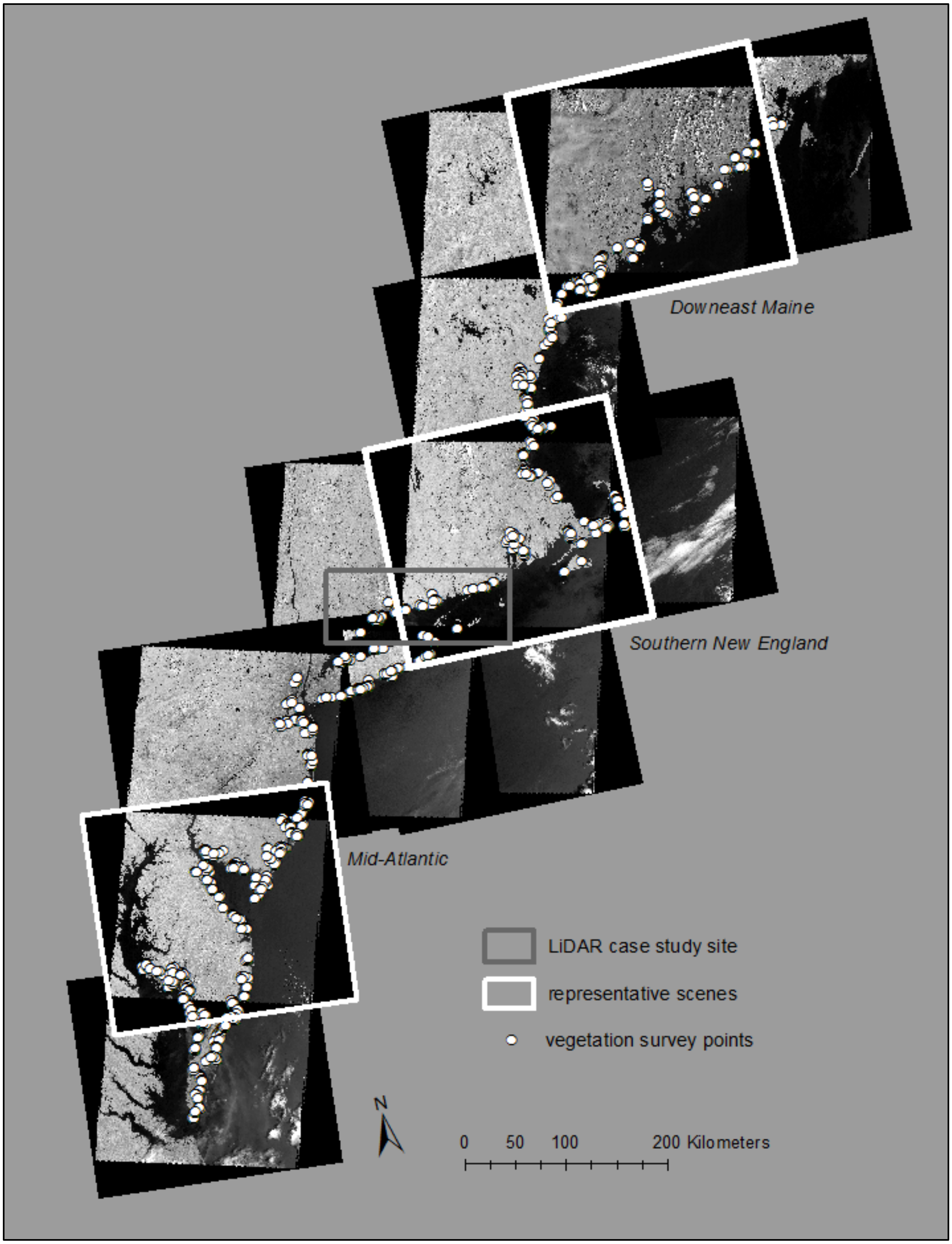

Figure 5.1. Experimental setup. Landsat scenes are shown along the coast; survey points are shown in white dots, representative scenes for reduced area analyses are outlined in white, LiDAR case study site outlined in gray.

5.3.2 Vegetation data collection

We obtained ground-truthed data for high- and low-marsh vegetation communities from surveys conducted by the Saltmarsh Habitat and Avian Research Program (SHARP, http://www.tidalmarshbirds.org) in 2011 and 2012. We selected survey sites based on a two-stage cluster sampling scheme for waterbird surveys outlined by Johnson et al. (2009). To select Primary Sampling Units (PSUs), we overlaid the Environmental Protection Agency's (EPA) 40 km^2 hexagon grid over the NWI E2EM polygons within BCR30+ to create our sampling universe. We then selected PSUs using a Generalized Random Tessellated Stratified (GRTS) sampling scheme stratified by sub-region (n=8) using the "spsurvey" package (Kincaid and Olsen 2012) in Program R (R Core Team 2014). Within each PSU, we visited up to 10 secondary sampling units (SSUs) using the GRTS sampling design. When historical bird survey sites were located within a PSU, we substituted these locations for SSUs. We refer to all historical survey points and SSUs as "survey points."

We conducted vegetation surveys at each survey point between June and August of each year using a protocol modified from Neckles and Gutenspergen (2010). We categorized marsh communities into nine types: High Marsh, Low Marsh, Pools/Pannes/Creeks, Open Water, Upland, Salt Marsh Terrestrial Border, Brackish Terrestrial Border, Invasives, and Wrack. We assigned each community to quartiles (i.e., <25%, 25-49%, 50-75%, >75%) of the survey area based on ocular cover assessment within a 50 m radius of each survey point.

5.3.3 Imagery selection and preprocessing

We used 11 scenes of TM imagery with a resolution of 30 X 30 m collected by the Landsat 5 satellite (USGS Global Visualization Viewer: http://www.glovis.gov). We compared scenes with minimal cloud cover taken between June and August of 2011 to SHARP vegetation survey data collected in 2012. We used 2011 imagery because Landsat 5 was offline during the summer of 2012, and the scan-line corrector of Landsat 7 was malfunctioning over the same period. We used 2012 vegetation survey data due to our increased confidence in technician training from that season, although the difference in cover classes between the two years was negligible (μ= 0.01, 95% CI ±0.1). When a survey point was not visited in 2012, we used vegetation data from 2011.

We conducted all image preprocessing in ArcGIS 10.1. We first assessed the geographic accuracy of our scenes. Each of the 11 scenes that we used were rated “1T” by NASA, indicating a georeference accuracy of roughly 30 meters (USGS 2013a). We selected 10 ground control points within each of 3 representative scenes (14033, 12031, and 11029) based on visible bridge intersections and compared them with highly accurate (~1m) USGS 1:24,000 quadrangle maps (USGS 2013b). Our georeferencing yielded similar results to the stated “1T” classification by NASA (33.1 m mean difference) in Landsat vs. USGS map points. Based on these findings we made no further efforts to georeference scenes.

We then isolated scene pixels within our study area. We created composite band ArcGIS GRID rasters of Landsat scene bands 1-5 and 7, omitting the thermal band. We then extracted Landsat scene pixels that fell within the NWI marsh layer for BCR30+ and within the National Oceanographic and Atmospheric Administration’s (NOAA) coarse salinity zonation for seawater and mixing water zones (NOAA 1999). This produced rasters of tidal marsh within BCR30+ occurring in saltwater areas.

We corrected for clouds in our imagery by choosing scenes with minimal cloud cover and removing the existing cloud layer from the scenes we selected. We identified cloud pixels using isodata clustering (McCullough et al. 2013), then removed the cloud classes from the rasters. We deemed cloud shadow to be negligible for this analysis because of the relatively minimal presence of cloud shadow within our area of interest (< 0.5% of all marsh pixels used).

Finally, we corrected for differences in atmospheric condition, vegetation phenology, and time since large precipitation events between scenes by using Z-scores. Z-scores normalized values to the standard deviation and mean from each scene and band and allowed the comparison of relative instead of raw values across scenes. We calculated Z-scores for each pixel within each scene and mosaicked them together, taking mean values when pixels overlapped between scenes. We also calculated local tidal information (time since high tide, days since astronomical high tide, and Julian date) for each scene using NOAA tidal predictions (NOAA 2011) closest to the centroid of each scene to help eliminate noise in spectral reflectance values due to scene.

5.3.4 Imagery classification – data inputs

We attempted classification using both high-marsh quartiles and binary high-marsh/non-high marsh classification schemes. Within these classification schemes we compared Classification And Regression Trees (CART) and traditional Maximum-Likelihood (ML) supervised classification techniques, using our vegetation survey data to train and validate the models as appropriate. Both ML and CART methods have been used extensively in classification and comparison of TM spectral values in northeastern wetlands at smaller scales (Friedl and Brodley 1997, Belluco et al. 2006, Rokitnicki-Wojcik et al. 2011, Richards 2013) and in other marshes worldwide (Ozesmi and Bauer 2002, Liu et al. 2010).

We used normalized (Z-score) band values, Normalized Difference Moisture Index (NDMI) values (Jin and Sader 2005), and Principal Component Analysis values as the inputs for our models. We included Principal Component (PC) values as these have been previously shown to further normalize remote sensing data (Pangaribuan 1996, Richards 2013), especially with collinear datasets such as spectral bands. We calculated PC values using the normalized band rasters as inputs. We included all PCs with an eigenvalue over 1.0 (PCs 1-3 in Program R) in our classification efforts when PC values were used. Previously, NDMI values have been used to detect vegetation communities in the northeast (Jin and Sader 2005), and preliminary data exploration revealed a significant negative relationship between NDMI values and high-marsh zonation (OLS regression, $p = 1.12e-4$) while we found no significant relationship with other vegetation indices such as the Normalized Difference Vegetation Index (NDVI). For these reasons we included NDMI as an additional input in our models. We calculated NDMI values ((Band 4 - Band 5)/(Band 4 + Band 5)) from the normalized band rasters.

5.3.5 Imagery classification – analysis, classification, and ground validation

5.3.5.1 Regional analysis

We attempted 2 types of classifications: quartile (0-24% high marsh, 25-49% high marsh, 50-74% high marsh, and 75-100% high marsh) and binary, which combined all of the non-high marsh categories from our vegetation surveys into a single class, “non-high marsh". We compared methods, classification schemes, and covariates using the combinations listed in 5.1 and 5.2.

For our ML binary classification models, we used supervised classification (Congalton 1991) based on logistic (binary) and multinomial (quartile) regression, which use model inputs (normalized band, PC, and NDMI) to predict between several output "states" (e.g. high marsh and non-high marsh). Because CART analysis maintains no assumptions and allows for highly collinear variables, we combined normalized band, PC, and NDMI values for our CART analysis. We then used the R package "rpart" (Therneau et al. 2013) to create classification trees for our raster values. We used the threshold values from these trees to create conditional rasters in ArcGIS.

We developed and assessed our models iteratively. Initially we tested all models without tidal covariates (Tests 1-4, 6). Based on the relatively low performance of these models, we added tidal covariates to the global models for both the ML and CART methods (Tests 5 and 7). It was clear from our first iteration of models that NDMI was not a useful predictor of high marsh (see Results); thus, we did not include NDMI values in our second iteration of classifications.

We trained all models on the pixels included in 50 m buffers around each training survey point to match our field protocols (Fig 5.2). Because field technicians recorded marsh cover for the entire survey circle, we did not have ground-based assessments of high marsh cover at the 30 m resolution of our spectral data. Thus, we used only the survey points that had been assessed by ground observers as either >75% high marsh cover or < 25% high marsh cover as training data. We reserved one third of these points prior to training as validation data (n= 304 for binary, n=504 for quartile).

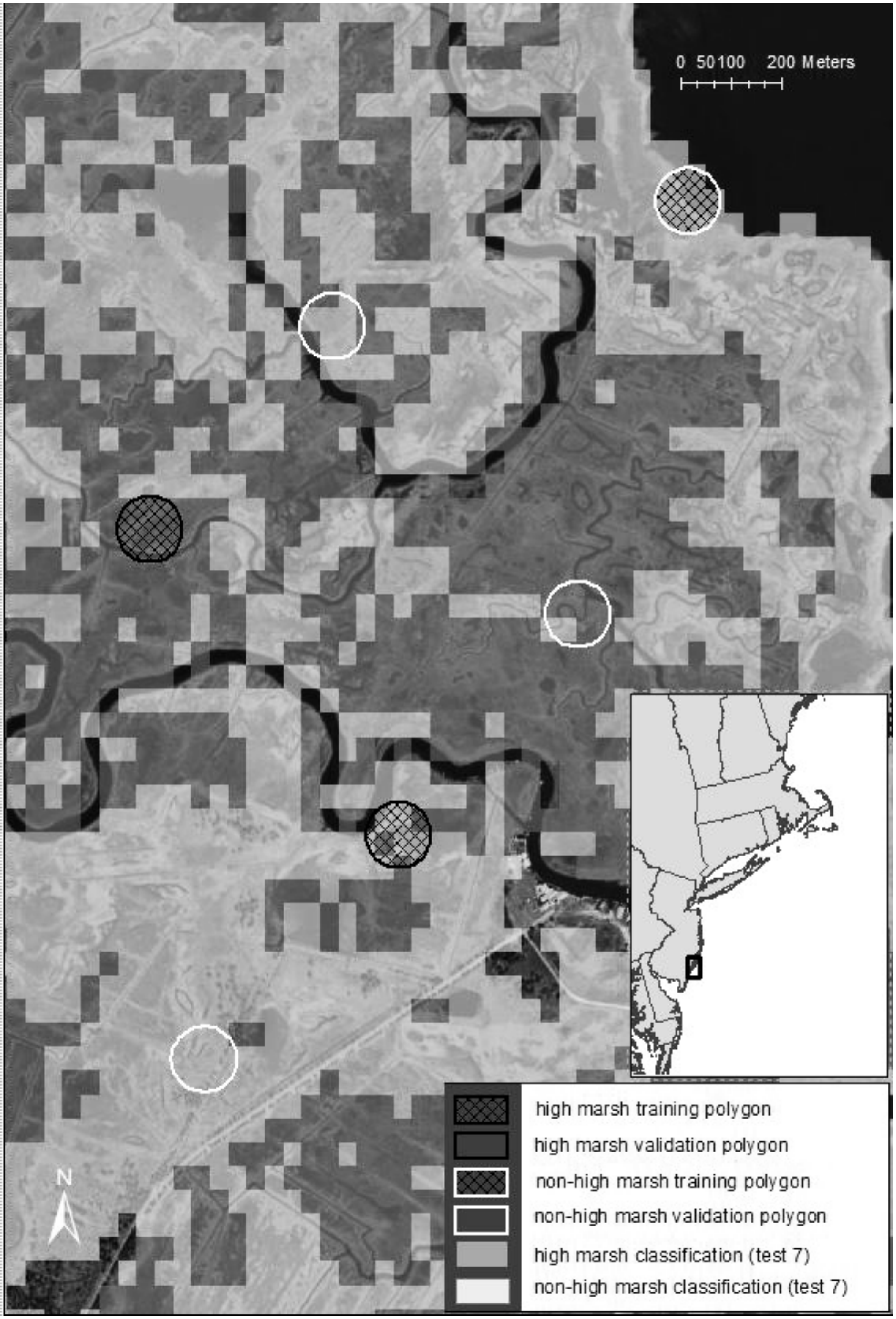

Figure 5.2. Visualization of best-performing model (test 7) over aerial photography of the southern New Jersey coast (Bing maps 2013). Training (hatched) and validation (hollow) polygons are shown for both high (black outline) and non-high (white outline) marsh.

5.3.5.2 Model validation and error estimation

We validated our models at vegetation survey points we withheld from our training dataset. Because of the higher resolution of our spectral data compared to our ground-based assessments, our classifications had a mismatch in scale to our validation data (see Fig 5.2). To address this discrepancy in scale during validation, we used Monte-Carlo weighted averages to assign a single classification to each validation survey circle. We generated 100 random points within each validation circle and extracted the predicted values of the classified raster to these points. In the binary data, if >75% of these points were classified as high marsh by the candidate model, the entire survey location was classified as high marsh. For our quartile models, we took the mean of classified values from the randomly generated points, and rounded these values to the nearest quartile. We were then able to compare these values to the observed community type collected by technicians in the field at the same 50-m radius scale.

To compare the performance of our models, we produced confusion/error matrices (Congalton 1991) for each classification. From these matrices we calculated user's (assessment of false positives) and producer's (assessment of false negatives) accuracy for individual classes (Congalton 1991; Janssen and van der Wel 1994, Appendices B and C). We also calculated un-weighted kappa statistics (κ) for our binary classifications (Congalton and Mead 1983, Stehman 1997) and linear weighted κ (Cohen 1968) appropriate for accuracy assessment of ordered classes for our quartile classifications. We also report adjusted κ (κ') by the maximum κ possible for each classification (Mertens et al. 2003).

To explore sources of error once our classifications were complete, we plotted the absolute value of differences between predicted and observed values at our validation points and used universal kriging on our top four classification models to estimate classification error across BCR30+. Further, we randomly generated points in our training and validation polygons in band 3, the top CART threshold value for spectral bands from our top performing model, and plotted these values by region to explore sources of error in high-marsh vs. non-high marsh.

In addition to our regional analyses, we assessed error independently for three Landsat scenes spread across the region (Fig 5.1) to explore spatial heterogeneity in accuracy. For this analysis we used the best performing model that did not include tidal covariates, since tidal covariates had a single value per scene.

5.3.5.3 Incorporating elevation data

Many smaller-scale classifications of tidal marshes include an elevation data later in their community classifications (Sadro et al. 2007, Yang 2009, Hladik and Alber 2012, Hladik et al. 2013). To explore the use of elevation data on a small scale, we compared the performance of our best non-tidal covariate model to the same model including LiDAR imagery along the Connecticut coastline (Fig 5.1, gray box). We used 10 x 10 m LiDAR data for our analyses with 15 cm vertical accuracy, which we mosaicked and clipped using similar preprocessing methods to our Landsat data. We predicted high marsh and non-high marsh using a combination of Landsat imagery and LiDAR data. We produced error matrices and calculated user’s and producer’s accuracy, κ, and κ’ to assess classification accuracy.

5.4 Results

5.4.1 Regional analyses

Depending on the accuracy assessment used, we had 2 top-performing models, both in binary classification of marsh communities (Table 5.1). Our efforts at predicting a gradient of high marsh cover using quartiles only produced accuracies within the realm of chance agreement (Table 5.2). We therefore limit further discussion of classifications to our binary classifications.

Of all classifications attempted, we reached the highest overall accuracy using conditional rasters produced from threshold values in our binary CART analysis that incorporated tidal covariates (Test 7). This classification had an overall accuracy of 71%, with high marsh accuracies of 61.5% (user's) and 38.1% (producer's). The non-high marsh accuracies were higher at 73.5% (user's) and 87.8% (producer's). When examining κ and κ' values, the top-performing model was Test 5 (κ =0.2953, κ' = 0.4322) using binary ML classification using z-score band values, PCs, and tidal covariates (Table 5.1). Test 5 user's and producer's accuracies showed a similar pattern to Test 7 where most of the map accuracy stemmed from the correct classification of non-high marsh. Simply put, the classifications with the highest overall accuracy were very good at identifying areas that were not high marsh, but not very good at identifying high-marsh areas. Table 5.1 and 5.2 show results from our regional analyses, and Appendices B and C show error matrices for all tests evaluated.

Across all classifications there was a clear trend for higher overall accuracies in identifying non high-marsh areas, with the exception of Test 3 (NDMI classification). Test 3 was highly biased towards identification of high marsh on the ground, classifying

Table 5.1. User’s, producer’s, and overall accuracies as well as κ, and κ’ for binary classification schemes within tidal marshes from Maine to Virginia, USA.

Method	Raster Inputs	Test ID	HM User's Accuracy	HM Producer’s Accuracy	NHM User's Accuracy	NHM Producer's Accuracy	**Overall Accuracy**	**κ**	**κ'**
ML	TM bands	Test 1	0.513	0.581	0.762	0.709	**0.664**	**0.2807**	**0.3114**
	PCA	Test 2	0.459	0.59	0.746	0.633	**0.618**	**0.2095**	**0.2633**
	NDMI	Test 3	0.346	0.99	0.667	0.01	**0.349**	**0.0004**	**0.0381**
	TM bands, PCA, NDMI	Test 4	0.531	0.486	0.74	0.774	**0.674**	**0.2649**	**0.2839**
	TM bands, PCA, tidal covariates	Test 5	0.487	0.714	0.808	0.615	**0.648**	**0.2953**	**0.4322**
CART	TM bands, PCA, NDMI	Test 6	0.365	0.295	0.671	0.737	**0.587**	**0.0334**	**0.0567**
	TM bands, PCA, tidal covariates	Test 7	0.615	0.381	0.735	0.878	**0.71**	**0.2855**	**0.4183**

Table 5.2. User’s, producer’s, and overall accuracies as well as κ, and κ’ for quartile classification schemes within tidal marshes from Maine to Virginia, USA.

			0 - 25% High Marsh		25 - 50% High Marsh		50 - 75% High Marsh		75 - 100% High Marsh				
Method	Raster Inputs	Test ID	User's Accuracy	Producer's Accuracy	User's Accuracy	Producer's Accuracy	User's Accuracy	Producer's Accuracy	User's Accuracy	Producer's Accuracy	**Overall Accuracy**	**κ**	**κ'**
ML	TM bands	Test 8	0.467	0.07	0.224	0.361	0.233	0.462	0.278	0.294	**0.254**	**0.11**	**0.2117**
	PCA	Test 9	0.458	0.111	0.188	0.289	0.225	0.368	0.231	0.304	**0.238**	**0.0773**	**0.1361**
	NDMI	Test 10	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	TM bands, PCA, NDMI	Test 11	0.286	0.01	0.22	0.32	0.207	0.434	0.21	0.382	**0.234**	**0.0107**	**0.289**
CART	TM bands, PCA, NDMI	Test 12	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

the majority of pixels as high marsh. This resulted in a very high producer's accuracy (99.0%) but very low accuracy overall (34.9%). For this reason, we dropped NDMI as a data input during the second iteration of binary classifications that included tidal covariates (Tests 5 and 7).

We display the continuous kriged surfaces of error for our top four regional classifications (Tests 1, 4, 5, and 7) in Figure 5.3. The main image in Figure 5.3 shows the spatial arrangement of error in Test 7, our top-performing model. There are three hotspots of classification error along the coast, including the coasts of Long Island, New Jersey, and the Delmarva Peninsula. These hotspots are present in three of the four error interpolations. Error hotspots in Casco and Narragansett Bays were present in multiple tests, but not in our best model. The insets in Figure 5.3 show variation in error for Casco Bay in the top four models, which lessens with overall model accuracy. Full-color kriged surfaces from our top four classifications are in Figs D.1 – D.

5.4.2 Scene-specific analyses

We repeated our classification efforts within three representative scenes chosen from our original 11 (Fig 5.1). Scene 11029 (hereafter "Downeast Maine Scene") covers the coast of Downeast Maine; scene 12031 (hereafter "Southern New England Scene") covers parts of the Massachusetts, Rhode Island, and Connecticut coastlines; and scene 14033 (hereafter "Mid-Atlantic Scene") covers southern New Jersey and the northern Delmarva peninsula. We report a summary of our findings from these efforts in Table 5.3 and full sets of error matrices in Appendix D.1.

Overall accuracies did not increase significantly when we repeated our analyses by scene. The Downeast Maine scene had a high overall accuracy of 83.3%, however the

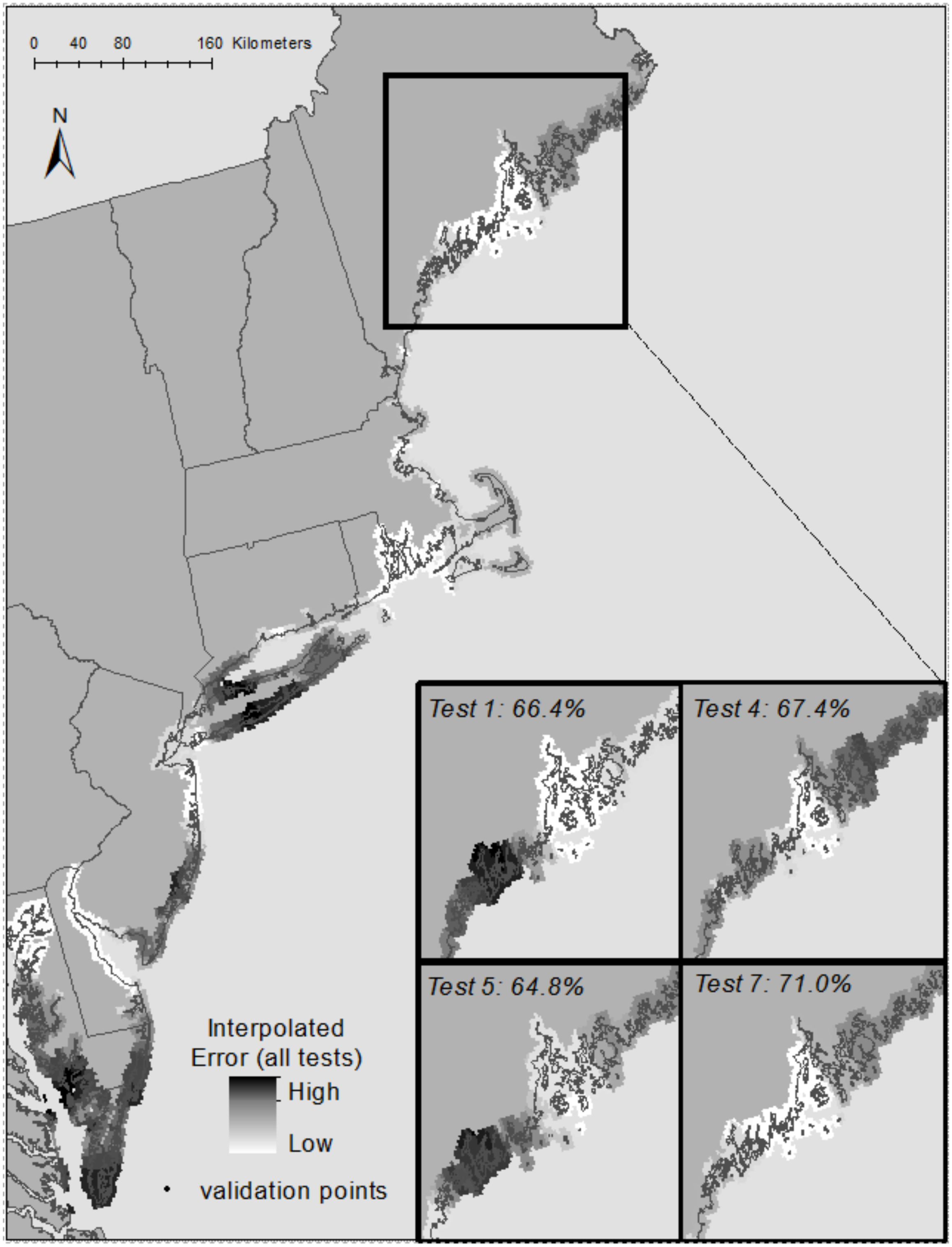

Fig. 5.3. Error rates of predicted vs. observed values in Test 7 using basic kriging of predicted and observed value differences for validation points in Test 4 (Maximum Likelihood Supervised classification using normalized band values, PC values, and NDMI): color ramp shows concentrations of error rates across BCR30+.

proportion of classification accuracy captured in the non-high and high-marsh accuracies (Table 5.3) remained similar to our regional results. We interpreted this scene’s accuracy assessment with caution since the results were produced from a low number of points during training (n=11) and validation (n = 4). Downeast Maine marshes are characteristically small in area; this combined with the size of our survey radius and the size of the marshes surveyed make it comparatively rare to have survey points that are >75% high marsh.

Our case study involving LiDAR data met with limited success. Models only converged on the LiDAR-only classification (overall = 62.5%, high marsh user’s/producers = 33.0%/100%, non-high marsh user’s/producers = 100%/53.8%, κ = 0.304, κ’ = 1, error matrix in Appendix D.3). There were notably small amounts of high marsh training (n = 2) and validation (n = 3) data points, which probably contributed to skewed estimates of error, indicated by the κ’ of 1 despite several misclassified pixels in our dataset.

5.5 Discussion

5.5.1 A successful model for predicting non-high marsh

Our best-performing regional models were Tests 5 and 7, with Test 7 attaining an accuracy of 71.0%, which exceeded our 70% *a priori* goal. Both of these top models incorporate normalized band values, PC values, and tidal covariates. A closer look reveals that much of the accuracy is in the classification of non-high marsh along the coast. User’s accuracies for high marsh across binary classification range from 34.6% to 61.5%; producer’s accuracies have a similar range between 38.1% and 59.0% (excluding

NDMI, see *Results*). A map with this type of accuracy distribution is good for identifying non-high marsh areas, but not for identifying high marsh.

When we examined classification schemes at a smaller scale, we found little improvement over our regional models, although this may be due to small samples sizes. Scene-specific classification returned slightly higher overall accuracies ranging from 61.5% - 83.3%, although both user's (36.4% - 61.5%) and producer's (25.0% - 59.3%) high marsh accuracies exhibited a pattern similar to our regional classification efforts. The number of training and validation polygons for high marsh was low in all of our single scenes due to the low availability of points with >75% high-marsh cover (Table 5.4). The regional sampling scheme used by SHARP was not designed specifically for the delineation of high- and non-high-marsh vegetation communities, resulting in many mixed-community survey points. A repeated effort for the regional classification of high-marsh areas should include a stratified sampling scheme to delineate enough high and non-high marsh polygons along the coast.

The methods we used to collect training and validation data also introduced error to this analysis. We collected plant community data in quartile bins; this method, while inclusive of the constraints necessitated by SHARP's greater sampling scheme, introduces a potential of 25% error into the ground-truthed data. Future efforts in marsh classification should include training polygons of exclusively high-, low-, and mixed-marsh zones, or attempt to develop a continuous scale of marsh elevation. This would eliminate both the low sample size for scene-specific classification efforts as well as lessen the window of error associated with our training signatures.

Table 5.3. User’s, producer’s, and overall accuracies as well as κ, and κ’ for binary classification schemes within tidal marshes in three Landsat scenes.

Scene	Scene Name	HM User's Accuracy	HM Producer's Accuracy	NHM User's Accuracy	NHM Producer's Accuracy	**Overall Accuracy**	**κ**	**κ'**
11029	Downeast Maine	0.5	0.25	0.864	0.95	**0.833**	**0.25**	**0.4**
12031	Southern New England	0.364	0.333	0.714	0.741	**0.615**	**0.0758**	**0.08**
14033	Mid-Atlantic	0.615	0.593	0.804	0.818	**0.744**	**0.4147**	**0.4266**

Table 5.4. Sample sizes for training and validation polygons in regional and scene-specific analyses.

Scene	Scene Name	HM Training	HM Validation	NHM Training	NHM Validation
11029	Downeast Maine	11	4	35	20
12031	Southern New England	13	12	46	27
14033	Mid-Atlantic	55	27	93	55
BCR 30+	-	211	105	383	205

Finally, as seen in Figure 5.3, we identified several error hotspots (white) in our top classification efforts along the coast of Casco Bay, Long Island, New Jersey's southern coast, and the Delmarva peninsula. We speculate that these hotspots may be due either to regional differences in spectral signatures (e.g., plant community differences or within-scene tidal heterogeneity) or to observer error. Several hotspots of error are the same across multiple classification schemes; it may be that observers in the Casco Bay, Long Island shore, New Jersey south shore, and Delmarva were not as efficient at assessing high- and low-marsh areas as in other areas.

5.5.2 The importance of tidal covariates and elevation in prediction of high marsh

We believe that fine-scale differences in tide within scenes are one of the main sources of error and misclassification in the efforts presented here. Known noise exists in our dataset from differences in tidal inundation between scenes. We attempted to address this by 1) normalizing band values using Z-scores to facilitate direct comparison among scenes, 2) conducting scene-specific analyses that should account for some tidal variation in our regional classifications, and 3) including local tidal covariates in a subset of our models, which resulted in the production of our 2 top classifications. In our top CART classification (Test 7), Julian date was the highest ranked threshold value, and astronomical high tide was also included in threshold covariates. Time since high tide was not selected a threshold, suggesting not enough variation was captured within all scenes to make up for the amount of variation ignored by assigning one time since high tide value to a 170 km X 185 km area, the approximate dimensions of one Landsat scene. Tidal heights and timing can vary between marshes located in close proximity to one another due to location of the marsh relative to the coast, local bathymetry and hydrology, and artificial structures inhibiting tidal flow (Bertness 2007, Davidson-Arnott 2010). Tidal amplitude is known to vary along portions of our study area, specifically in the Chesapeake Bay and Long Island Sound (NOAA 2011).

Many of the cover types included in our non-high marsh bin (low marsh, open water, or mudflat, upland) would be classified as the same non-high marsh category during either high or low tide; the same is not true for high-marsh areas. High-marsh vegetation flooded at high tide would likely be similar in reflectance values to low marsh or open water, which would change the pixel's binary classification to non-high marsh. Similarly, high marsh at low tide may resemble upland or salt marsh terrestrial border, which would also change a pixel's classification to non-high marsh. These increased misclassifications due to tide in high marsh likely contributed to the lower user's and producer's accuracies in this community type.

We hypothesize that the breadth of local tidal inundation must be described on a smaller scale to accurately discriminate between non-high and high marsh areas. Data retrieval from tide gauges or the use of tidal predictions will be integral to any repeat effort. Similarly, regional elevation data will help further discriminate tidal regime within delineated wetland boundaries; for example, reflectance values characteristic of *S. alterniflora* with a higher elevation value would more likely be classified as high marsh; without this elevation information, we would need to rely on tide information alone to help discriminate between community types with the same reflectance value. Elevation datasets are regularly used to classify marsh plant communities at smaller scales (Klemas 2011, Hladik and Alber 2012, Hladik et al. 2013). The combination of hyperspectral imagery and LiDAR elevation datasets into is a growing practice in salt marsh vegetation mapping (Artigas and Yang 2005, Yang 2009, Collin et al. 2010), although the presence of high-resolution elevation data limits the application of this method in some instances. Further, work combining LiDAR and hyperspectral imagery into a single vegetation index was effective at predicting tidal marsh plant communities in the Gulf of St. Lawrence, Canada (Collin et al. 2010, 2012).

5.5.3 Future directions and conservation implications

In the midst of developing this tool we interacted with many scientists and managers managing tidal marshes across our study region. Through these interactions we detected a clear need for a comprehensive high/low marsh spatial layer for the northeast, separate from the development of a tool capable of easily, economically, and repeatedly classifying specific marshes (the primary goal of our study). In light of Hurricane Sandy, accelerating SLR, and other landscape-scale stressors in the northeast, there is a pressing need for the development of a spatial data layer specific to marsh community for analyses and planning at the regional scale. We suggest the timely development of such a layer using imagery and analytical tools using the modifications listed below.

Increasing the resolution of imagery is likely to increase classification accuracy. The National Agricultural Imagery Program (NAIP) collects 1 X 1 m resolution data across the conterminous United States at visible and some infrared wavelengths (0.70 - 0.94 um). A regional effort using recent NAIP imagery including these values could be a significant step towards a low-cost, regional classification of marsh zonation along the Atlantic coast. Additionally, the privately-owned SPOT and Quickbird programs both produce TM imagery available at 2.5, 5, 10, and 20 m resolution with a larger breadth of wavelengths recorded in their infrared bands.

Delineating a large number of community-specific polygons to use for training and validation will further reduce error. It is imperative that a delineation effort include 1) the use of high-accuracy GPS equipment to reduced unit-based error, 2) a sampling scheme stratified by phenology and species differences across the region, and 3) community-specific delineation (high marsh, low marsh, and mixed) to eliminate reflectance noise in the training and validation datasets. Any repeated effort for tidal marsh characterization should also use the updated coastal NWI as delineation specific to 2007 and now available through the USFWS.

LiDAR and other fine-scale elevation data remain a promising addition to spectral imagery in the classification of coastal wetlands and other regional efforts (Brock and Purkis 2009). Limited validation and training data prevented a robust test with our dataset, however we recommend use of elevation data in further classification efforts in conjunction with hyperspectral imagery. Coastal LiDAR has been flown for much of the northeast U.S. from Maine to Virginia, however a *regional, post-processed* data layer does not yet exist. In our conversations with marsh managers we detected a distinct need for such a layer in the northeast along with a high/low marsh layer for use in remote sensing studies as well as in regional-scale vegetation, marsh migration, and habitat simulation models, including that of the saltmarsh sparrow. Until such a dataset is produced, the National Elevation Dataset (NED) created and maintained by the USGS maintains a 10 m resolution (1/3 arc-second) and 3 m resolution (1/9 arc-second) layer for the northeastern US.

Finally, we suggest the application of more computationally intensive classification techniques to develop a high/low marsh layer for the northeast. Support

Vector Machines (SVMs) are based on Bayes' rule of probability and are a recent addition to more traditional remote sensing techniques (Mountrakis et al. 2011), however they have performed well in small-scale studies of salt marshes (Wilson et al. 2004, Timm and McGarigal 2012) and can outperform other methods especially when sample sizes are small (Sanchez-Hernandez et al. 2007). Artificial Neural Networks (ANN) have been used in remote sensing of tidal marshes on both the Pacific and Atlantic coasts (Morris et al. 2005, Adam et al. 2009) and offer another computationally-intensive alternative to the simpler approaches presented in our analyses. Finally, fuzzy logic approaches have been used to classify salt marshes in the US (Xie et al. 2008, Adam et al. 2009) and present a probabilistic classification alternative to the deterministic methods used in our study.

From the multi-scale analyses presented here we conclude that the development of a user-friendly, regional tool to repeatedly identify high-marsh areas in BCR30+ may be possible, but should not be attempted using the methods presented and Landsat imagery alone. We support the use of our best-performing model in identifying non-high marsh within previously delineated tidal wetland areas such as the NWI. Perhaps most importantly, we urge the development of a comprehensive high/low marsh layer for the northeast using advanced remote sensing techniques and resources as well as a post-processed LiDAR dataset for the east coast for use in coastal research and conservation. We suggest areas for improvement in future efforts including use of higher-resolution tidal covariates and TM imagery, inclusion of community-specific training polygons using a stratified sampling scheme, inclusion of high-resolution elevation data such as LiDAR, and the use of more robust, computationally intensive classification methods to increase accuracy. We hope the analyses and discussion presented here provide insight toward development of these tools and data layers to facilitate preservation of tidal marsh ecosystems in the Northeastern United States and organisms that depend upon them such as the saltmarsh sparrow.

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APPENDIX A: SUPPLEMENTAL INFORMATION FOR CHAPTER 2

Table A.1. Quantification of past marsh management practices by US state in two buffer sizes around survey points, stratified from Maine to Virginia.

	ditching		**Open Water Marsh Management (OMWM)**		**downriver tidal restriction**	
state	% locations affected (50m)	% locations affected (100m)	% locations affected (50m)	% locations affected (100m)	% locations affected	**total locations**
Maine	9.43	13.52	0.00	0.00	58.18	318
New Hampshire	41.94	50.00	0.00	0.00	67.74	62
Massachusetts	60.31	66.54	0.00	0.00	44.36	257
Rhode Island	33.33	46.30	0.00	0.00	72.22	54
Connecticut	66.33	74.49	0.00	0.00	47.96	98
New York	55.38	64.62	0.77	0.77	43.85	130
New Jersey	40.86	49.14	9.14	12.86	49.14	350
Delaware	38.24	49.02	6.86	12.75	28.43	102
Maryland	38.39	47.32	6.25	12.05	27.68	224
Virginia	0.47	0.47	0.00	0.00	11.16	215
total	**35.08**	**41.77**	**2.98**	**4.75**	**42.60**	**1810**

Table A.2. Sensitivity analysis of drivers of community change in five avifaunal specialists in US coastal marshes. Each row represents a modified analysis with a subset of the data removed, to evaluate whether conclusions are robust to data inclusion decisions.

model	**ditching main effect β (CI)**	**ditching interactive effect β (CI)**	**restriction main effect β (CI)**	**restriction interactive effect β (CI)**	**sea level rise main effect β (CI)**	**sea level rise interactive effect β (CI)**
full model	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.01)	0.05 (-0.02, 0.12)	-0.16 (-0.21, -0.11)	-0.25 (-0.66, 0.16)	-0.08 (-0.15, -0.02)
no BD	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.01)	0.04 (-0.03, 0.11)	-0.16 (-0.21, -0.11)	-0.04 (-0.41, 0.33)	-0.1 (-0.17, -0.03)
no RP	-0.01 (-0.04, 0.03)	0 (-0.02, 0.03)	0.32 (0.23, 0.41)	-0.14 (-0.21, -0.08)	-0.34 (-0.85, 0.17)	0 (-0.06, 0.05)
no SH	0.01 (-0.02, 0.03)	0 (-0.02, 0.02)	0.1 (0.02, 0.17)	-0.14 (-0.19, -0.09)	-0.07 (-0.39, 0.26)	0 (-0.03, 0.03)
no BH	0.01 (-0.02, 0.03)	-0.01 (-0.03, 0.02)	0.04 (-0.03, 0.11)	-0.15 (-0.2, -0.1)	-0.26 (-0.69, 0.17)	-0.16 (-0.24, -0.08)
no RR	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.01)	0.05 (-0.02, 0.12)	-0.16 (-0.21, -0.11)	-0.23 (-0.63, 0.16)	-0.08 (-0.15, -0.02)
no HO	0 (-0.01, 0.01)	0 (-0.02, 0.01)	0.01 (-0.06, 0.08)	-0.15 (-0.2, -0.09)	-0.22 (-0.64, 0.2)	-0.05 (-0.12, 0.02)
no MO	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.01)	0.05 (-0.02, 0.12)	-0.16 (-0.21, -0.11)	-0.26 (-0.67, 0.15)	-0.09 (-0.16, -0.02)
no RC	0.02 (-0.01, 0.05)	-0.03 (-0.06, 0.01)	-0.1 (-0.2, -0.01)	-0.13 (-0.19, -0.07)	-0.1 (-0.46, 0.26)	-0.05 (-0.13, 0.04)
no PR	0.02 (-0.01, 0.05)	-0.03 (-0.05, 0)	0.05 (-0.02, 0.12)	-0.16 (-0.21, -0.1)	-0.25 (-0.66, 0.16)	-0.1 (-0.17, -0.03)
no CLRA	0.01 (-0.02, 0.03)	-0.02 (-0.05, 0.01)	0.08 (0.01, 0.15)	-0.16 (-0.21, -0.1)	-0.41 (-0.88, 0.07)	-0.07 (-0.13, 0)
no WILL	0 (-0.02, 0.02)	0 (-0.02, 0.01)	0.24 (0.15, 0.32)	-0.16 (-0.22, -0.11)	-0.16 (-0.62, 0.31)	0 (-0.05, 0.04)
no NESP	0 (-0.02, 0.02)	-0.01 (-0.04, 0.02)	-0.13 (-0.21, -0.05)	-0.17 (-0.23, -0.11)	-0.03 (-0.42, 0.37)	-0.05 (-0.13, 0.03)
no SALS	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.02)	-0.07 (-0.15, 0.01)	-0.11 (-0.18, -0.05)	-0.02 (-0.36, 0.33)	-0.09 (-0.18, 0)
no SESP	0.01 (-0.02, 0.04)	-0.01 (-0.04, 0.02)	0.1 (0.03, 0.17)	-0.15 (-0.2, -0.1)	-0.33 (-0.79, 0.12)	-0.19 (-0.26, -0.11)
90% data, rep 1	0 (-0.01, 0.01)	0 (-0.01, 0.01)	0.01 (-0.06, 0.08)	-0.16 (-0.21, -0.1)	-0.21 (-0.62, 0.2)	-0.06 (-0.14, 0.02)
90% data, rep 2	0.01 (-0.02, 0.04)	-0.02 (-0.05, 0.01)	0.06 (-0.02, 0.13)	-0.16 (-0.22, -0.11)	-0.25 (-0.64, 0.15)	-0.11 (-0.18, -0.05)
90% data, rep 3	0.03 (0, 0.07)	-0.02 (-0.05, 0)	0.07 (0, 0.14)	-0.15 (-0.21, -0.1)	-0.17 (-0.56, 0.21)	-0.05 (-0.13, 0.03)
90% data, rep 4	0 (-0.02, 0.03)	-0.01 (-0.04, 0.02)	0.05 (-0.02, 0.12)	-0.16 (-0.22, -0.11)	-0.23 (-0.65, 0.18)	-0.07 (-0.15, 0.01)
90% data, rep 5	0 (-0.02, 0.03)	-0.01 (-0.03, 0.02)	0.06 (-0.01, 0.13)	-0.17 (-0.22, -0.11)	-0.2 (-0.6, 0.2)	-0.06 (-0.14, 0.02)
90% data, rep 6	0 (-0.02, 0.02)	-0.01 (-0.04, 0.02)	0.06 (-0.02, 0.13)	-0.14 (-0.2, -0.09)	-0.22 (-0.61, 0.17)	-0.08 (-0.15, -0.01)
90% data, rep 7	0.01 (-0.02, 0.05)	-0.01 (-0.04, 0.01)	0.02 (-0.05, 0.09)	-0.14 (-0.2, -0.09)	-0.26 (-0.67, 0.16)	-0.1 (-0.17, -0.03)
90% data, rep 8	0 (-0.02, 0.02)	-0.01 (-0.04, 0.02)	0.05 (-0.02, 0.12)	-0.17 (-0.22, -0.12)	-0.24 (-0.64, 0.16)	-0.09 (-0.16, -0.02)
90% data, rep 9	0.01 (-0.02, 0.03)	-0.01 (-0.03, 0.02)	0.08 (0, 0.15)	-0.15 (-0.2, -0.1)	-0.25 (-0.65, 0.15)	-0.08 (-0.15, -0.01)
90% data, rep 10	0.01 (-0.02, 0.03)	-0.03 (-0.06, 0)	0.02 (-0.05, 0.09)	-0.16 (-0.21, -0.11)	-0.27 (-0.7, 0.15)	-0.07 (-0.14, 0.01)

Table A.2 (continued)

model	ditching main effect β (CI)	ditching interactive effect β (CI)	restriction main effect β (CI)	restriction interactive effect β (CI)	sea level rise main effect β (CI)	sea level rise interactive effect β (CI)
latitude no Q1	0.02 (-0.02, 0.07)	-0.01 (-0.03, 0.01)	0.13 (0.06, 0.2)	-0.14 (-0.19, -0.08)	-0.09 (-0.47, 0.28)	-0.01 (-0.05, 0.03)
latitude no Q2	0 (-0.02, 0.02)	-0.01 (-0.03, 0.02)	0.14 (0.06, 0.21)	-0.18 (-0.24, -0.13)	-0.11 (-0.5, 0.29)	-0.22 (-0.3, -0.14)
latitude no Q3	0 (-0.02, 0.02)	0 (-0.02, 0.01)	0.06 (-0.01, 0.13)	-0.18 (-0.23, -0.12)	-0.08 (-0.41, 0.26)	-0.01 (-0.06, 0.04)
latitude no Q4	0.01 (-0.02, 0.04)	-0.02 (-0.05, 0.01)	0.02 (-0.07, 0.1)	-0.14 (-0.2, -0.08)	-0.13 (-0.51, 0.25)	-0.05 (-0.13, 0.03)
latitude no Q5	0 (-0.02, 0.01)	0 (-0.02, 0.01)	-0.14 (-0.22, -0.06)	-0.16 (-0.22, -0.1)	-0.2 (-0.66, 0.26)	-0.05 (-0.13, 0.03)
<5 restrictions	0.01 (-0.02, 0.03)	-0.01 (-0.04, 0.01)	0.05 (-0.02, 0.12)	-0.16 (-0.21, -0.11)	-0.27 (-0.67, 0.14)	-0.08 (-0.15, -0.02)
latitude >38.5°	0.03 (-0.02, 0.07)	-0.01 (-0.03, 0.01)	0.1 (0.03, 0.17)	-0.15 (-0.2, -0.1)	-0.34 (-0.97, 0.28)	-0.02 (-0.07, 0.03)

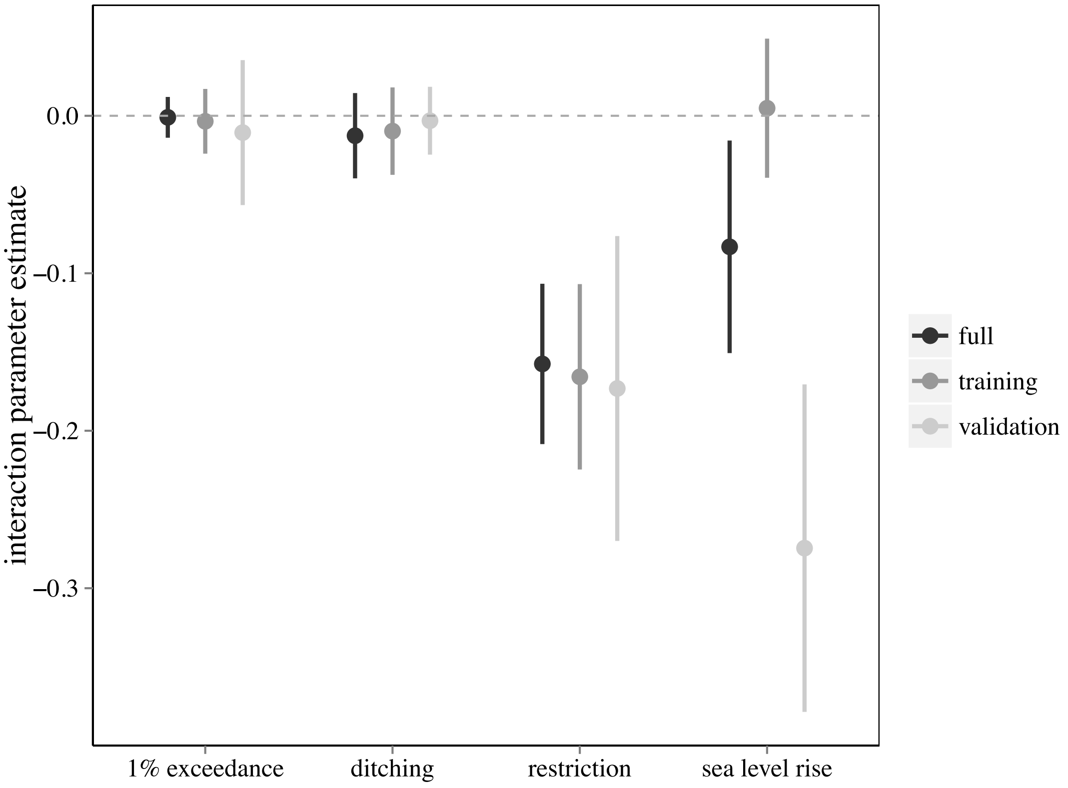
Dataset acronyms:
BD –contributed by Bill Deluca and the Smithsonian (2002 – 2003)
RP – contemporary dataset collected by the authors (2011 – 2012)
SH – contributed by WGS (1998 – 2000)
BH – contributed by Bombay Hook NWR (1994 – 2007)
RR – contributed by New Jersey Audubon (2006)
HO – contributed by MDIFW (1997 – 2000)
MO – contributed by Monomoy NWR (2005 – 2012)
RC – contributed by Rachel Carson NWR (2000 – 2012)
PR – contributed by Parker River NWR (2000 – 2012)
Q1 – first group of latitude, divided by quintile
Q2 – second group of latitude, divided by quintile
Q3 – third group of latitude, divided by quintile
Q4 – fourth group of latitude, divided by quintile
Q5 – fifth group of latitude, divided by quintile

Species acronyms:
CLRA – clapper rail WILL – willet NESP – Nelson’s sparrow SALS – saltmarsh sparrow SESP – seaside sparrow

Table A.3. Beta coefficients, confidence intervals, and Δ AIC values for population change analyses of five tidal-marsh specialist birds at three spatial scales in the northeastern US. Beta coefficients are reported for the time variable term in each model. Δ AIC values indicate difference between AIC values of models including a term for year and one with the time term removed.

		clapper rail		*willet*		*Nelson's sparrow*		*saltmarsh sparrow*		*seaside sparrow*	
spatial scale	**refuge**	**β (95% CI)**	**Δ AIC**	**β (95% CI)**	**Δ AIC**	**β (95% CI)**	**Δ AIC**	**β (95% CI)**	**Δ AIC**	**β (95% CI)**	**Δ AIC**
United States National Wildlife Refuge (NWR)	**Rachel Carson NWR** (2000 - 2012)	.	.	0.25 (0.12, 0.39)	11.40	0.15 (0.02, 0.28)	2.40	-0.19 (-0.33, -0.05)	4.30	.	.
	Parker River NWR (2000 - 2012)	.	.	0.03 (-0.11, 0.15)	-1.92	.	.	-0.22 (-0.32, -0.11)	12.65	.	.
	Monomoy NWR (2005 - 2012)	.	.	0.24 (0.04, 0.43)	3.91	.	.	-0.12 (-0.3, 0.05)	-0.12	.	.
	Bombay Hook NWR (1994 - 2007)	-0.8 (-0.97, -0.64)	97.79	-0.55 (-0.64, -0.45)	135.20	.	.	-0.4 (-0.67, -0.14)	7.25	-0.14 (-0.19, -0.08)	20.30
New England	.	-0.38 (-1.29, 0.53)	-1.31	0.09 (-0.3, 0.46)	0.65	-0.67 (-1.09, -0.26)	8.28	-1.22 (-1.57, -0.89)	49.68	0.23 (-0.5, 0.95)	-1.62
Maine to Virginia	.	-0.34 (-0.61, -0.06)	3.79	0.13 (-0.01, 0.27)	1.25	-0.21 (-0.33, -0.08)	8.84	-0.43 (-0.56, -0.31)	44.08	0.05 (-0.21, 0.3)	-1.86

Figure A.1. Training, validation, and full dataset parameter estimates for community-level models exploring regional drivers of population change for the tidal-marsh specialist community.



A.1: Saltmarsh Habitat and Avian Research Program survey site selection and methods

A.1.1 Contemporary survey site selection

To select the first cluster of Primary Sampling Units (PSUs), we overlaid a 40 km^2 North American hexagon grid over National Wetlands Inventory (NWI) Estuarine Intertidal Emergent Wetland polygons (USFWS 1979) occurring on the Maine to Virginia coastline to identify our sampling universe. We then selected PSUs along the coast using a Generalized Random Tessellated Stratified (GRTS) sampling scheme stratified by subregion (n=9) chosen using a combination of watershed boundaries and large geographic features (e.g. Cape Cod, Long Island, etc) using the "spsurvey" package (Kincaid and Olsen 2012) in Program R (R Core Team 2014). Within each PSU, we selected and visited up to 10 secondary sampling units (SSUs) using GRTS equal probability sampling design, stratifying by PSU. When historical survey sites were located within the sampling PSU, we substituted these historical locations for SSUs. In this article, we refer to all historical survey points and SSUs as "survey points". We conducted bird surveys at each survey point between April and July of each survey year at 1780 points between 2011 and 2012 using a modified version of the National Marshbird Monitoring Protocol (Wiest et al. 2015).

A.1.2 Addressing detection probability in modeled abundance indices

Addressing detection probability is an integral step in population modeling (Reed 1996, Nichols et al. 2000, Farnsworth et al. 2005). Given the nature of our historical database, explicitly estimating detection probability for each species was not possible because we lacked a universal measure of detection probability across our compiled datasets. We therefore reduced the likelihood of differences in detection probability by A) using only data only collected between sunrise and 11 AM (when birds are most active) and between April 15 and August 15, B) using maximum count by species at each survey point each year as a response variable to maximize detections within year, and C) including number of visits as a covariate in all models. This model framework has been used previously to model bird population in tidal marsh systems (Shriver et al. 2004).

A.1.3 Dataset limitations

It is important to note that the results and conclusions in this paper are driven more by data from the northern states (Maine to Connecticut) than southern (New York to Virginia); most of our historical observations collected before 2011 are from New England states (n = 2189) versus those in the Mid-Atlantic (n=431). This could amplify patterns observed in the north and underplay or overlook existing patterns occurring in the south; the results and discussion in this paper should be considered in light of this unbalanced setup.

A.2: Individual National Wildlife Refuge results

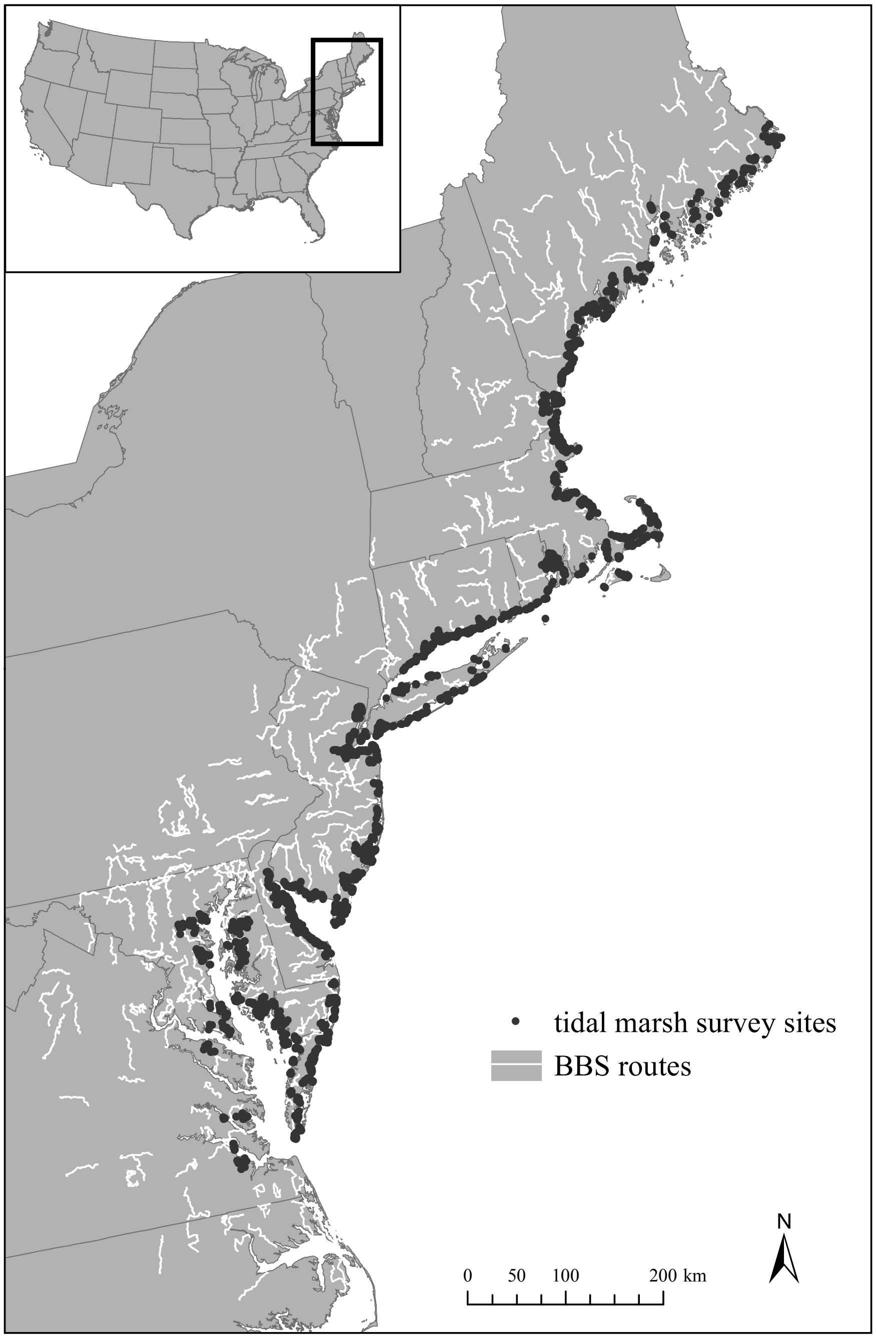
Our scalar trend analyses allowed us to examine trends at local scales within protected areas along the coastline at Rachel Carson, Parker River, Monomoy, and Bombay Hook National Wildlife Refuges (NWRs) that differ in the amount of tidal restriction and physical barriers characterizing each marsh complex. We found refuge-specific patterns in species trends. Monomoy exhibited no negative trends in the species surveyed, while Bombay Hook exhibited negative trends in all species examined; Rachel Carson and Parker River NWRs fell in between these two extremes. Abundance indices were over an order of magnitude higher at Parker River and Monomoy NWRs than at Rachel Carson and Bombay Hook NWRs, or when compared to regional estimates.

Monomoy NWR is unique in northeast refuges in that it is one of the few open barrier beach systems from Maine to Virginia. This refuge is comprised of a 15km sandy beach spit, which is often (but not always) connected to the mainland, and is devoid both of tidal restrictions and ditching. Conversely, Rachel Carson NWR protects a long but thin tract of bordering marsh along the Maine coast, constrained by forests and human coastal infrastructure on the western side of the refuge. Parker River NWR contains both a barrier beach (Plum Island) and open marsh system, but has a paved road directly through the center of the refuge, which separates the beach from the marsh and limits the ability of the sand beach to break and reform. This, in turn, limits sediment passage into the marsh on the leeward side of the road. Bombay Hook includes significant waterfowl impoundments throughout the refuge, limiting both sediment and water exchange within much of the property.

The relative success of Parker River and Monomoy NWRs at maintaining larger numbers of tidal marsh bird populations is due to their geomorphological and human impact conditions. Both refuges are semi-open beach systems, however Monomoy stands out as a completely ephemeral landscape where sediment supply is abundant, and as a result maintains the marsh systems as well as the specialist species that use them. Conversely, Bombay Hook's many impoundments may exacerbate marsh loss caused by sea-level rise through immobilization of existing marshes, driving the steeper declines in tidal marsh specialists that we observed at this refuge. The relative rate of sea-level rise is higher in the Mid-Atlantic than it is in New England, which may also explain much of the challenges to more southern systems. A ready sediment supply is likely even more important for maintaining high marsh habitats and the organisms they support.

APPENDIX B: SUPPLEMENTAL INFORMATION FOR CHAPTER 3

Figure B.1. Map of survey sites from Maine to Virginia, USA. Black dots represent survey sites at which data were collected for a historical marsh bird database 1998 – 2012, including a region-wide survey by the authors in 2012. White lines show BBS routes within 100 km of the US coastline between the US states of Maine and Virginia.



B.1. Additional methods: field data collection

We selected survey sites based on a two-stage cluster sampling scheme for secretive marshbird surveys suggested by Johnson et al. (2009) and implemented by Wiest et al. (2015). For a subset of points we revisited locations from historical surveys during contemporary data collection (n = 457). To select the first cluster of Primary Sampling Units (PSUs), we overlaid a 40 km^2 North American hexagon grid over National Wetlands Inventory (NWI) Estuarine Intertidal Emergent Wetland polygons (USFWS 1979) occurring on the Maine to Virginia coastline to identify our sampling universe. We then selected PSUs along the coast using a Generalized Random Tessellated Stratified (GRTS) sampling scheme stratified by subregion (n=9) chosen using a combination of watershed boundaries and large geographic features (e.g. Cape Cod, Long Island, etc.) using the "spsurvey" package (Kincaid and Olsen 2012) in Program R (R Core Team 2014). Within each PSU, we selected and visited up to 10 secondary sampling units (SSUs) using GRTS equal probability sampling design, stratifying by PSU. When historical survey sites were located within the sampling PSU, we substituted these historical locations for SSUs. In this article, we refer to all historical survey points and SSUs as "survey points". We conducted bird surveys at each survey point between April and July of each survey year at 1780 points between 2011 and 2012 using a modified version of the National Marshbird Monitoring Protocol (Wiest et al. 2015).

B.2. Additional methods: 14-year trends

We combined 13 databases of historical point counts conducted in tidal marshes across the region, spanning observations from 1994 – 2012. The largest historical surveys were conducted by the Maine Department of Inland Fisheries and Wildlife (MDIFW) and WGS from 1998 – 2000 (Shriver et al. 2004) in tidal marshes between Maine and Connecticut (i.e., New England). Rachel Carson National Wildlife Refuge (NWR), Parker River NWR, Monomoy NWR, Bombay Hook NWR, and the Smithsonian Institution all provided local datasets of annually surveyed marshes that spanned at least eight years. Massachusetts Audubon, New Hampshire Audubon, New Jersey Audubon, and the New Jersey Meadowlands Commission contributed additional historical data at smaller scales. We then combined data from these historical survey points (n = 3006) with our contemporary bird surveys to produce a full trend database.

We used the sum of counts within a patch of tidal marsh by year, patch area (log transformed), sum of points visited within a patch each year (log transformed), and total visits to each patch per year (log transformed) as fixed effects using a negative binomial distribution and the *glm.nb* function within the "MASS" package (Venables and Ripley 2002). We defined habitat patches using the NWI layer following Wiest et al. (2015). To assess model fit and confirm influence of our parameter estimates for all of the above models, we (A) confirmed a dispersion ratio (Pearson residuals compared to degrees of freedom) between 0.5 and 2.5, (B) confirmed acceptable model fit using Q-Q plots of the random effect residuals, (C) withheld 30% of our data as a holdout dataset to assess model accuracy.

The results and conclusions in this paper are driven more by data from the northern states (Maine to Connecticut) than southern (New York to Virginia); most of our historical observations collected before 2011 are from New England states (n = 2189) versus those in the Mid-Atlantic (n=431). This could amplify patterns observed in the north and underplay or overlook existing patterns occurring in the south; the results and discussion in this paper should be considered in light of this unbalanced setup.

Table B.1. Common name, family name, and Marsh Specialization Index (MSI) value (an ndex of habitat specialization to tidal marsh between 0 and 1, with specialization increasing with MI value) of the top 106 most commonly detected species in tidal marshes between Maine and Virginia.

common name	family	MSI
American Avocet	Recurvirostridae	1.00
Black-bellied Plover	Charadriidae	1.00
Atlantic Brant	Anatidae	1.00
Dunlin	Scolopacidae	1.00
Gull-billed Tern	Sternidae	1.00
Greater Yellowlegs	Scolopacidae	1.00
Least Sandpiper	Scolopacidae	1.00
Lesser Yellowlegs	Scolopacidae	1.00
Red-breasted Merganser	Anatidae	1.00
Red Knot	Scolopacidae	1.00
Ruddy Turnstone	Charadriidae	1.00
Sanderling	Scolopacidae	1.00
Short-billed Dowitcher	Scolopacidae	1.00
Semipalmated Plover	Charadriidae	1.00
Semipalmated Sandpiper	Scolopacidae	1.00
Spotted Sandpiper	Scolopacidae	1.00
Tricolored Heron	Ardeidae	1.00
White Ibis	Threskiornithidae	1.00
Whimbrel	Scolopacidae	1.00
Yellow-crowned Night-Heron	Ardeidae	1.00
Saltmarsh Sparrow	Emberizidae	1.00
Nelson's Sparrow	Emberizidae	1.00
American Oystercatcher	Haematopodidae	1.00
Least Tern	Sternidae	0.99
Seaside Sparrow	Emberizidae	0.99
Marsh Wren	Troglodytidae	0.99
Common Tern	Sternidae	0.99
Clapper Rail	Rallidae	0.99
Willet	Scolopacidae	0.98
Black Skimmer	Rynchopidae	0.98
Snowy Egret	Ardeidae	0.98
American Black Duck	Anatidae	0.98
Forster's Tern	Sternidae	0.97
Great Egret	Ardeidae	0.97
Virginia Rail	Rallidae	0.96
Little Blue Heron	Ardeidae	0.96
Mute Swan	Anatidae	0.96

Table B.1 (continued)

common name	family	MSI
Boat-tailed Grackle	Icteridae	0.95
Great Black-backed Gull	Laridae	0.95
Black-crowned Night-Heron	Ardeidae	0.95
Double-crested Cormorant	Phalacrocoracidae	0.94
Herring Gull	Laridae	0.93
Glossy Ibis	Threskiornithidae	0.93
Osprey	Pandionidae	0.91
Laughing Gull	Laridae	0.89
Least Bittern	Threskiornithidae	0.87
Common Eider	Anatidae	0.86
Red-winged Blackbird	Icteridae	0.86
Mallard	Anatidae	0.85
Black-necked Stilt	Recurvirostridae	0.85
Ring-billed Gull	Laridae	0.85
Tree Swallow	Hirundinidae	0.83
Swamp Sparrow	Emberizidae	0.83
Great Blue Heron	Ardeidae	0.76
Savannah Sparrow	Emberizidae	0.76
Bald Eagle	Accipitridae	0.74
Canada Goose	Anatidae	0.73
Song Sparrow	Emberizidae	0.72
Yellow Warbler	Parulidae	0.69
Willow Flycatcher	Tyrannidae	0.68
Belted Kingfisher	Cerylidae	0.66
Barn Swallow	Hirundinidae	0.65
Alder Flycatcher	Tyrannidae	0.64
Green Heron	Ardeidae	0.62
Common Yellowthroat	Parulidae	0.61
Bank Swallow	Hirundinidae	0.48
Bobolink	Icteridae	0.46
Northern Rough-winged Swallow	Hirundinidae	0.45
Red-tailed Hawk	Accipitridae	0.40
Dark-eyed Junco	Emberizidae	0.40
Eastern Kingbird	Tyrannidae	0.36
Killdeer	Charadriidae	0.33
Fish Crow	Corvidae	0.30
Purple Martin	Hirundinidae	0.29
Common Grackle	Icteridae	0.25
American Goldfinch	Fringillidae	0.23
European Starling	Sturnidae	0.21

Table B.1 (continued)

common name	family	MSI
Eastern Meadowlark	Icteridae	0.21
Cliff Swallow	Hirundinidae	0.18
Orchard Oriole	Icteridae	0.18
Brown-headed Cowbird	Icteridae	0.16
American Crow	Corvidae	0.15
Gray Catbird	Mimidae	0.11
House Wren	Troglodytidae	0.10
Chimney Swift	Apodidae	0.10
House Finch	Fringillidae	0.09
House Sparrow	Passeridae	0.09
Northern Mockingbird	Mimidae	0.09
Eastern Phoebe	Tyrannidae	0.09
Northern Flicker	Picidae	0.08
Blue Grosbeak	Cardinalidae	0.07
Mourning Dove	Columbidae	0.07
Northern Parula	Parulidae	0.07
Eastern Towhee	Emberizidae	0.06
Baltimore Oriole	Icteridae	0.05
Cedar Waxwing	Bombycillidae	0.05
Carolina Wren	Troglodytidae	0.05
Black-capped Chickadee	Paridae	0.05
Blue Jay	Corvidae	0.04
Northern Cardinal	Cardinalidae	0.04
Turkey Vulture	Cathartidae	0.04
American Robin	Turdidae	0.04
Eastern Wood-Pewee	Tyrannidae	0.03
Indigo Bunting	Cardinalidae	0.02
Chipping Sparrow	Emberizidae	0.01
Tufted Titmouse	Paridae	0.01

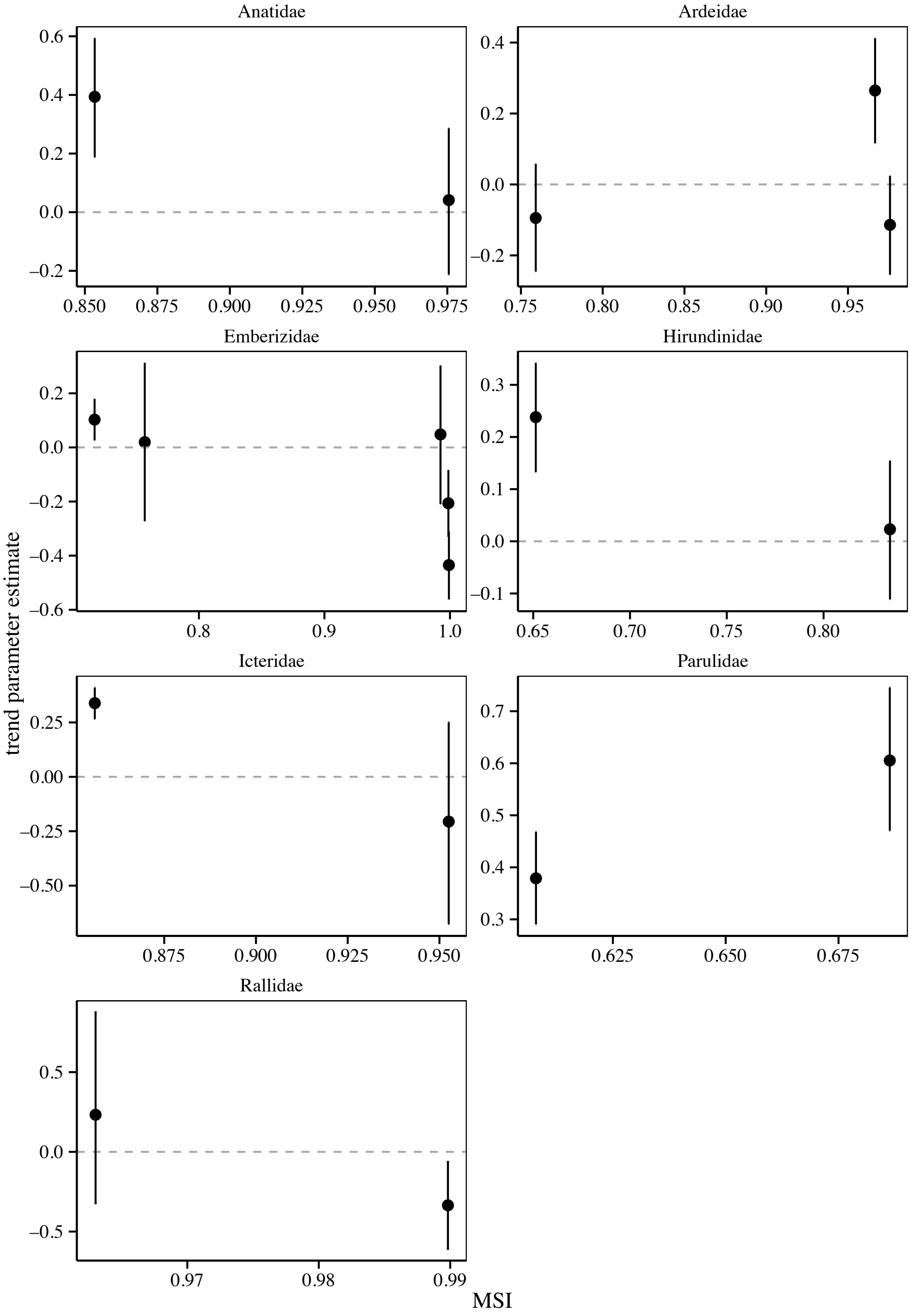


Figure B.2. Trend estimates for 22 tidal marsh bird species plotted by Marsh Specialization Index (MSI) value, grouped by family. Error bars indicate 95% CI around each trend estimate.

APPENDIX C: SUPPLEMENTAL INFORMATION FOR CHAPTER 4

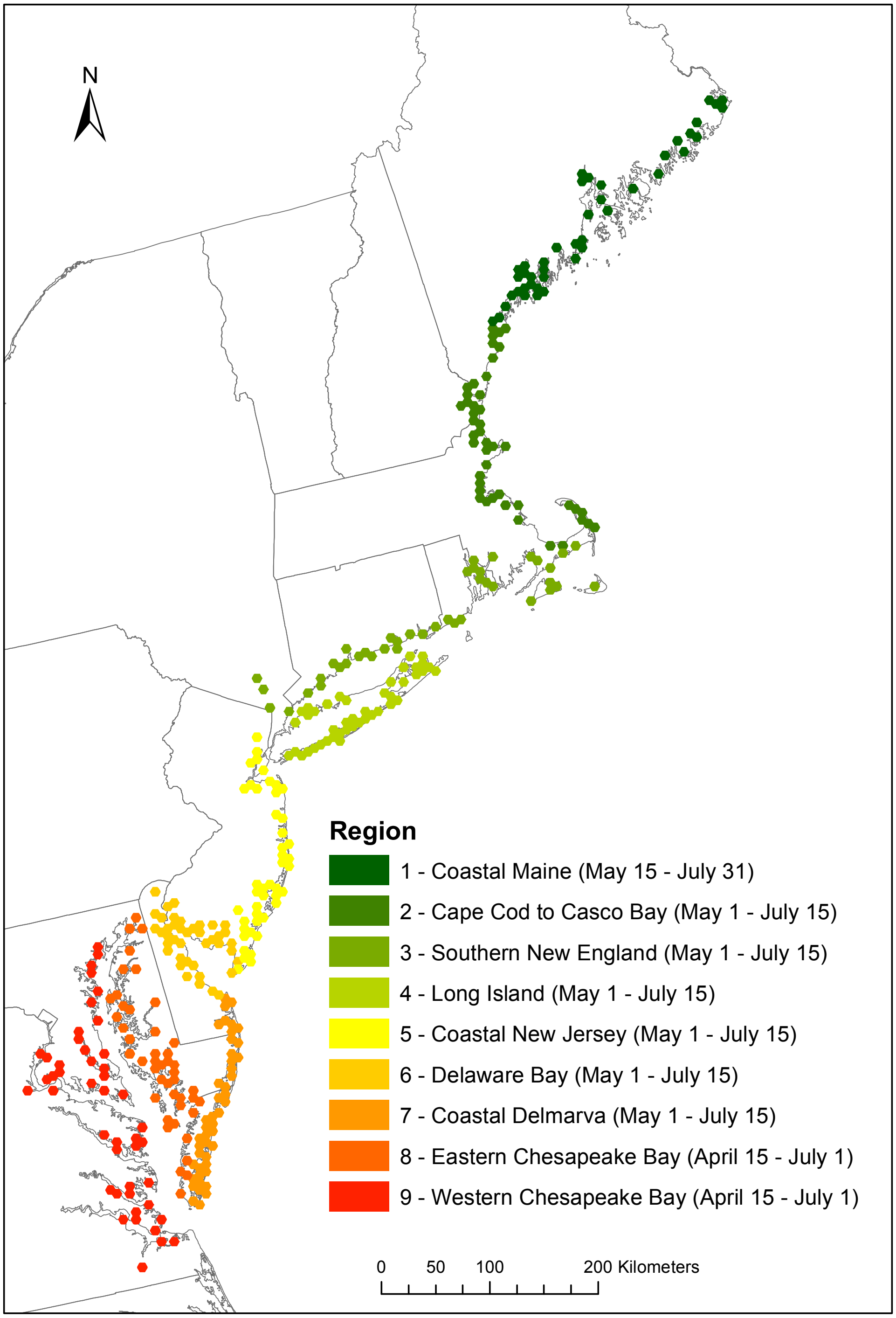


Figure C.1. Primary Sampling Units surveyed 2011 – 2014, labeled by biological subregion. Each subregion indicated the survey window used by observers for tidal marsh bird surveys.

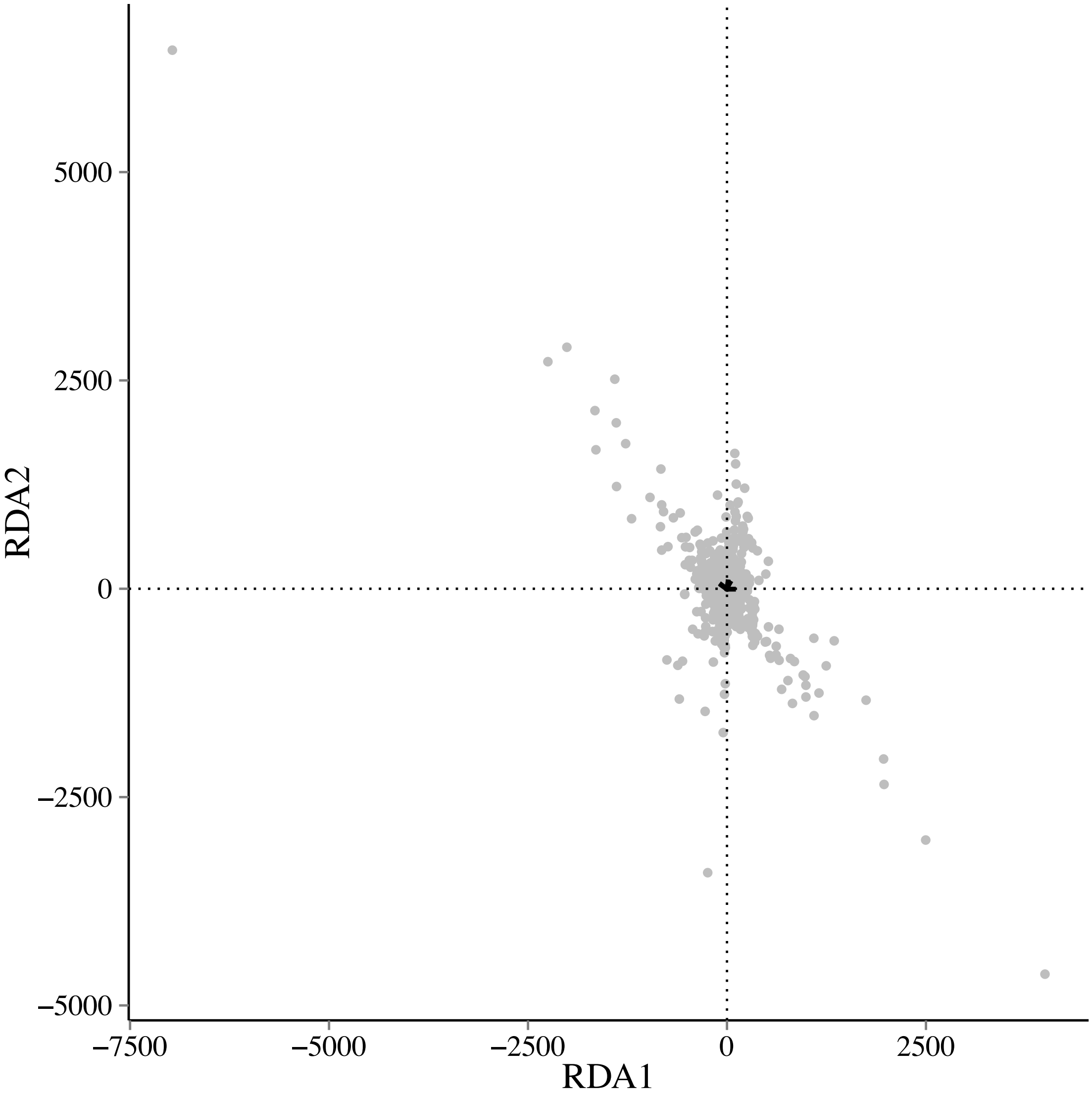


Figure C.2. Results of a redundancy analysis modeling change in rarefied richness, evenness, total number of individuals (N), and total biomass supported before (2011 – 2012) and after (2013 – 2014) Hurricane Sandy by degree of storm surge experienced during the hurricane (Adjusted R^2 = <0.001).

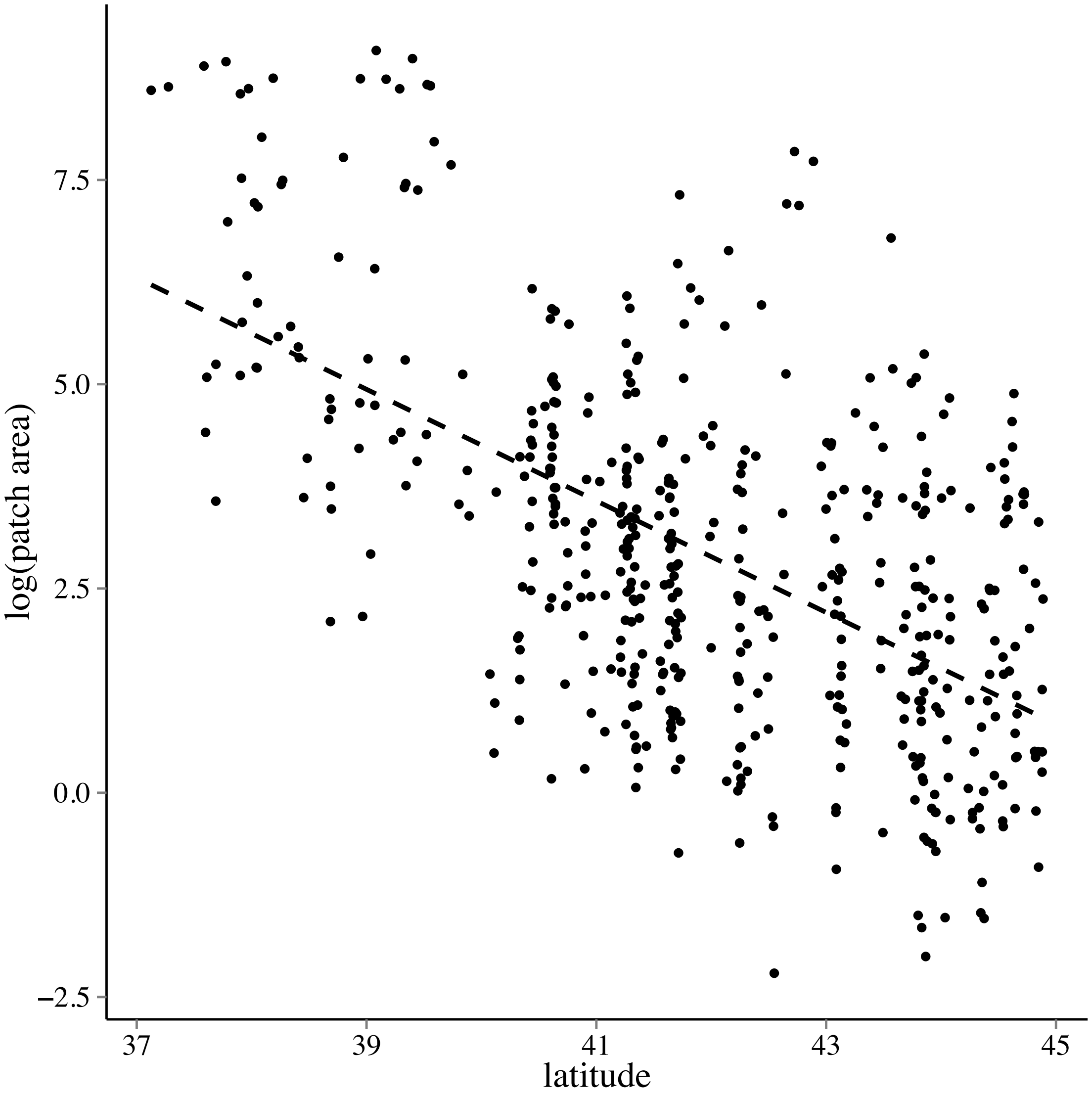


Figure C.3. Linear regression (dashed line) showing a positive relationship between latitude and patch area in tidal marshes between Maine and Virginia (adjusted $R^2 = 0.33$).

Appendix C.1: Landscape context and biodiversity

Landscape context is another important driver of diversity numbers globally (Shriver et al. 2004, McKinney 2008), often resulting in higher diversity numbers at intermediate levels of development (Blair 1999, Grimm et al. 2008). Urban development and density along the Atlantic coast peaks around New York City, which occurs in the middle of our survey area, and an influx of urban generalist species from this latitude could create the peak in diversity we see in our dataset. In this scenario, however, we would also expect to see a convex trend in CHSI around this area, with specialism values higher to both the north and the south of this concentration point of urbanization. Our strong linear trends in CHSI (Fig 4.6b) make it unlikely that urbanization is the central driver of diversity in this system. Urbanization, however, may instead explain the slight bowing of the linear CHSI trend around the middle of our study area; a local influx of generalist birds successful in urban environments would dampen an otherwise linear specialism trend, which is exactly what we observe in the slightly concave CHSI trend across latitude.

APPENDIX D: SUPPLEMENTAL INFORMATION FOR CHAPTER 5

D.1 – Regional Error Matrices for binary data classification

Below are error matrices assessing prediction error across all methods tested. The following terms are used within each matrix:

HM – High Marsh

NHM – Non-High Marsh

User's – Assesses false positives within the predicted layer

Producer's – Assesses false negatives within the predicted layer

Overall – Assesses inclusive accuracy for the predicted area

Test 1 - ML normalized band values

		observed		
		HM	NHM	Total
predicted	HM	61	58	119
	NHM	44	141	185
	Total	105	199	**304**

overall	**0.664**
HM user's	0.513
HM producer's	0.581
NHM user's	0.762
NHM producer's	0.709

Test 2 - ML PCA values

		observed		
		HM	NHM	Total
predicted	HM	62	73	135
	NHM	43	126	169
	Total	105	199	**304**

overall	**0.618**
HM user's	0.459
HM producer's	0.590
NHM user's	0.746
NHM producer's	0.633

Test 3 - ML NDMI values

		observed		
		HM	NHM	Total
predicted	HM	104	197	301
	NHM	1	2	3
	Total	105	199	**304**

overall	**0.349**
HM user's	0.346
HM producer's	0.990
NHM user's	0.667
NHM producer's	0.010

Test 4 - ML normalized band values, PCA values, NDMI

observed

predicted

	HM	NHM	Total
HM	51	45	96
NHM	54	154	208
Total	105	199	**304**

overall	**0.674**
HM user's	0.531
HM producer's	0.486
NHM user's	0.740
NHM producer's	0.774

Test 5 - ML normalized band values, PCA values, tidal covariates

observed

predicted

	HM	NHM	Total
HM	75	79	154
NHM	30	126	156
Total	105	205	310

overall	**0.648**
HM user's	0.487
HM producer's	0.714
NHM user's	0.808
NHM producer's	0.615

Test 6 - CART normalized band values, PCA values, NDMI values

observed

predicted

	HM	NHM	Total
HM	31	54	85
NHM	74	151	225
Total	105	205	310

overall	**0.587**
HM user's	0.365
HM producer's	0.295
NHM user's	0.671
NHM producer's	0.737

Test 7 - CART normalized band values, PCA values, tidal covariates

observed

predicted

	HM	NHM	Total
HM	40	25	65
NHM	65	180	245
Total	105	205	310

overall	**0.710**
HM user's	0.615
HM producer's	0.381
NHM user's	0.735
NHM producer's	0.878

D.2. Regional Error matrices for quartile classifications

Below are error matrices assessing prediction error across all methods tested using binned quartile data (0-25% HM, 25-50% HM, 50-75% HM, and 75-100% HM). While these results are not examined directly in the manuscript, the findings are important in that they show a finer-scale classification using these methods and data was not fruitful. Similar terms are used as in Appendix D.1.

Test 8 - ML normalized band values
(Quartile)

		observed				
		1	2	3	4	Total
predicted	1	14	5	7	4	30
	2	82	35	19	20	156
	3	70	43	49	48	210
	4	33	14	31	30	108
	Total	199	97	106	102	504

overall	**0.254**
0-25% HM user's	0.467
0-25% HM producer's	0.070
25-50% HM user's	0.224
25-50% HM producer's	0.361
50-75% HM user's	0.233
50-75% HM producer's	0.462
75-100% HM user's	0.278
75-100% HM producer's	0.294

Test 9 - ML PCA values
(Quartile)

		observed				
		1	2	3	4	Total
predicted	1	22	7	10	9	48
	2	77	28	22	22	149
	3	57	37	39	40	173
	4	43	25	35	31	134
	Total	199	97	106	102	504

overall	**0.238**
0-25% HM user's	0.458
0-25% HM producer's	0.111
25-50% HM user's	0.188
25-50% HM producer's	0.289
50-75% HM user's	0.225
50-75% HM producer's	0.368
75-100% HM user's	0.231
75-100% HM producer's	0.304

Test 10 - ML NDMI values
(Quartile)

Prediction did not converge on classes 1 or 4; analysis dropped

Test 11 - ML normalized band values, PCA values, NDMI values
(Quartile)

		1	2	3	4	Total
predicted	1	2	0	3	2	7
	2	78	31	14	18	141
	3	84	49	46	43	222
	4	35	17	43	39	134
	Total	199	97	106	102	504

overall	**0.234**
0-25% HM user's	0.286
0-25% HM producer's	0.010
25-50% HM user's	0.220
25-50% HM producer's	0.320
50-75% HM user's	0.207
50-75% HM producer's	0.434
75-100% HM user's	0.291
75-100% HM producer's	0.382

Test 12 – CART normalized band values, PCA values, NDMI values
(Quartile)

Prediction did not converge on class 3; analysis dropped

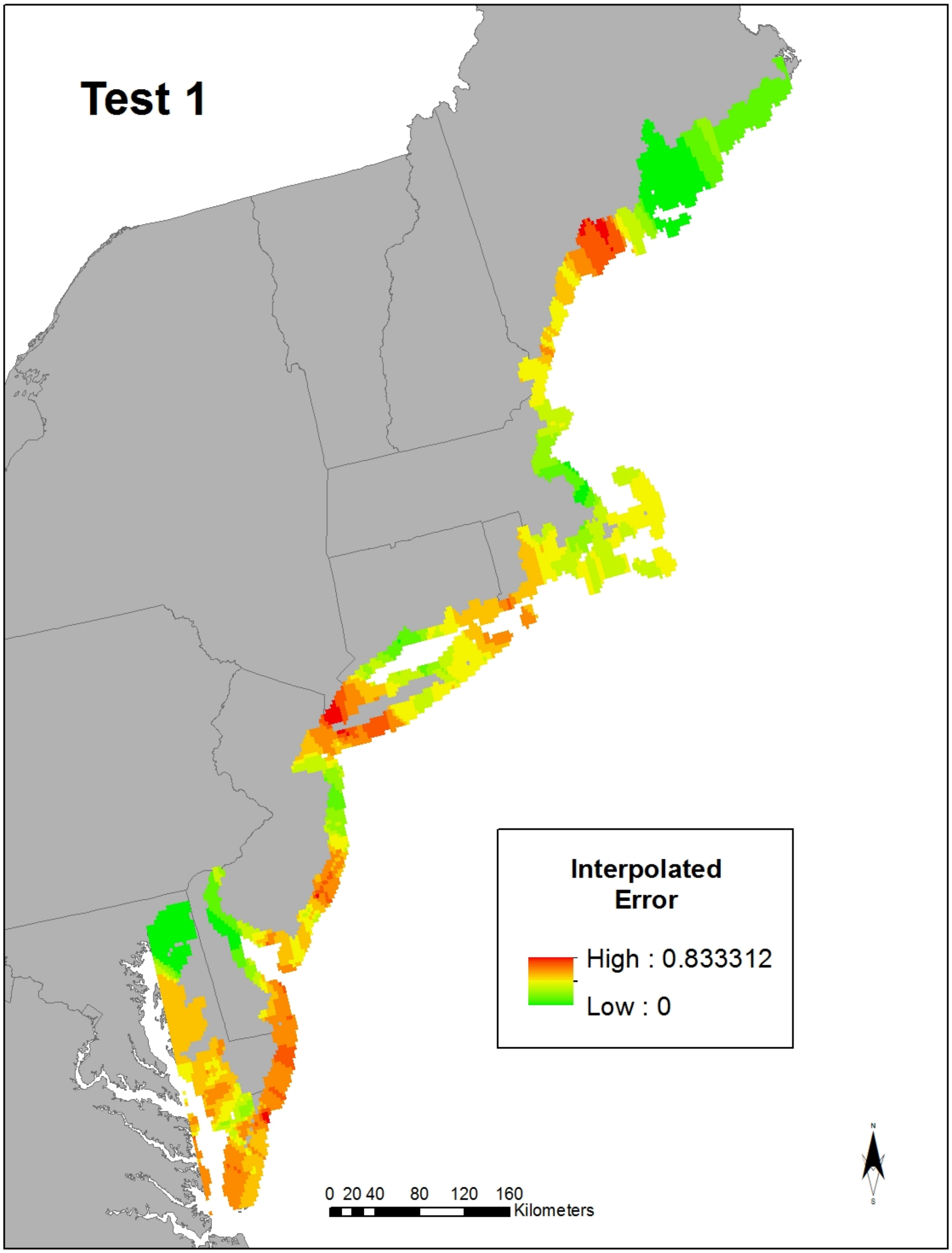


Figure D.1. Kriged interpolation of error rates for Test 1 (Maximum Likelihood methods using normalized bands).

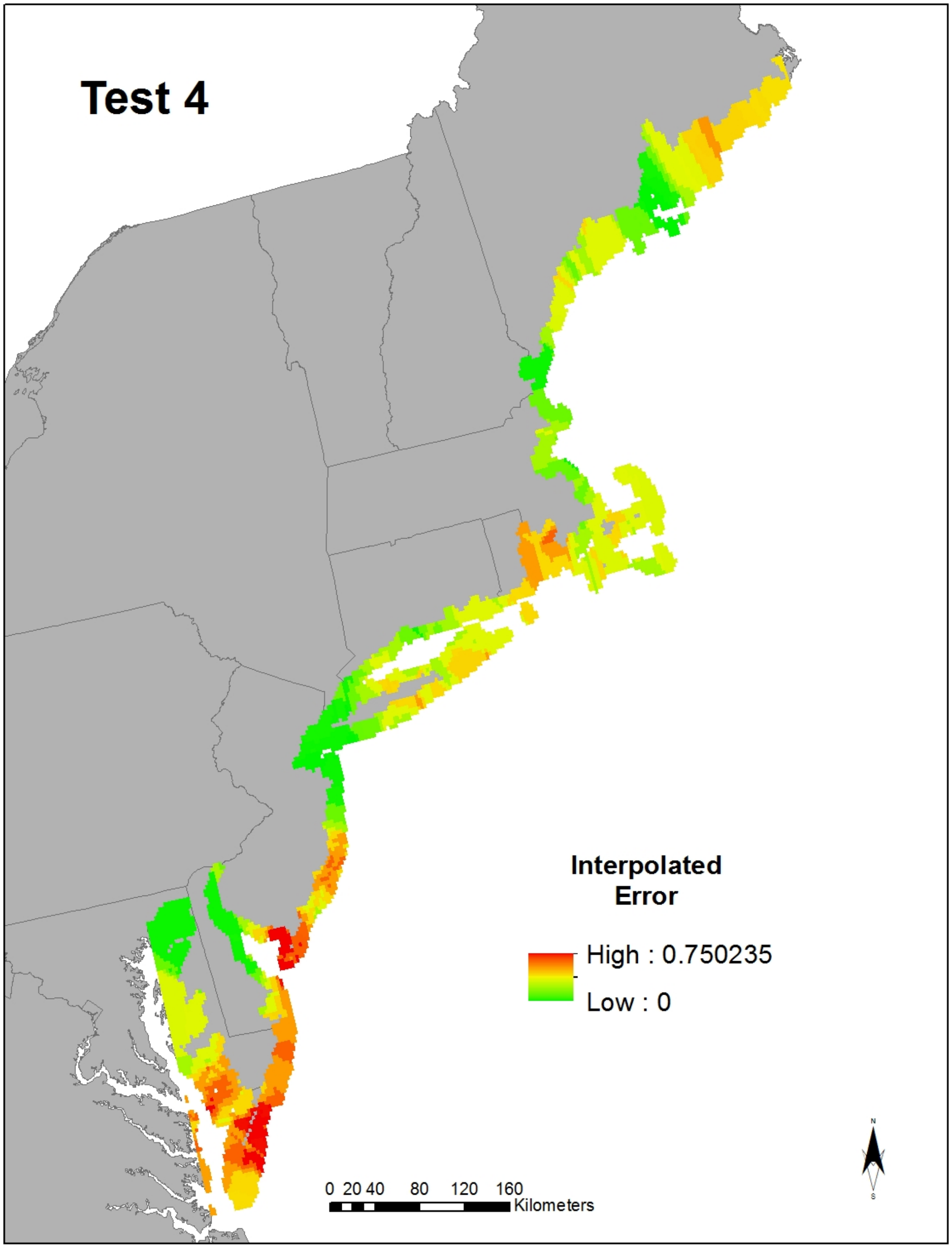


Figure D.2 Kriged interpolation of error rates for Test 4 (Maximum Likelihood methods using normalized bands, PCA values, and NDMI values).

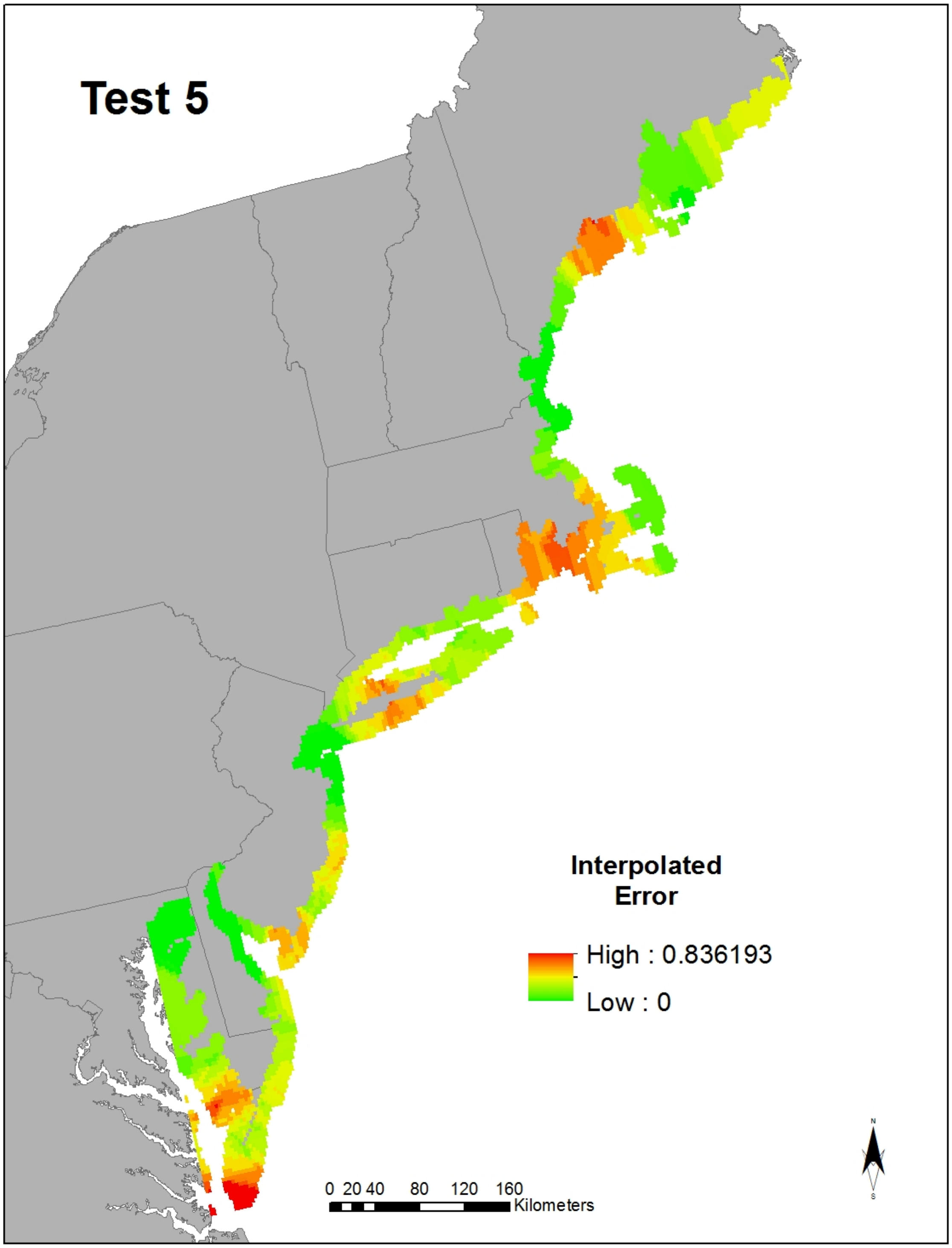


Figure D.3 Kriged interpolation of error rates for Test 5 (Maximum Likelihood methods using normalized bands, PCA values, and tidal covariates).

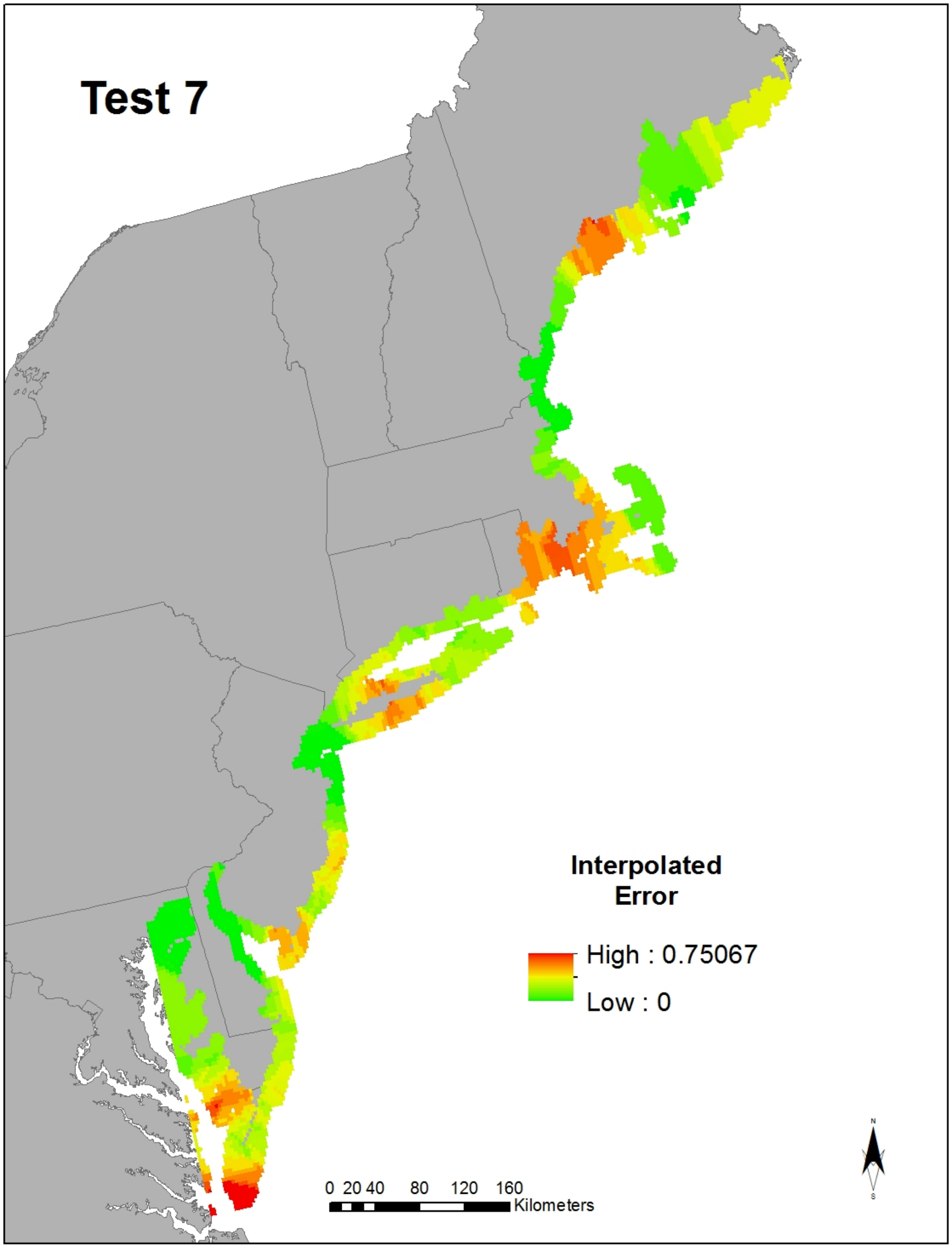


Figure D.4 Kriged interpolation of error rates for Test 7 (CART methods using normalized bands, PCA values, and tidal covariates).

Appendix D.3 – Reduced Area Error Matrices

Below are matrices assessing prediction error across all reduced-area analyses. All classifications are Binary ML. The following terms are used within each matrix:

HM – High Marsh

NHM – Not High Marsh

User's – User's accuracy assesses false positives within the predicted layer

Producer's – Producer's accuracy assess false negatives within the predicted layer

Overall – overall accuracy divides the total of correctly predicted pixels by the total number of pixels in each scene.

Single Scene – 11029 (Downeast Maine)

observed

predicted

	HM	NHM	Total
HM	1	1	2
NHM	3	19	22
Total	4	20	24

overall	**0.833**
HM user's	0.500
HM producer's	0.250
NHM user's	0.864
NHM producer's	0.950

Single Scene – 12031 (Southern New England)

observed

predicted

	HM	NHM	Total
HM	4	7	11
NHM	8	20	28
Total	12	27	39

overall	**0.615**
HM user's	0.364
HM producer's	0.333
NHM user's	0.714
NHM producer's	0.741

Single Scene – 14033 (Mid-Atlantic)

observed

predicted

	HM	NHM	Total
HM	16	10	26
NHM	11	45	56
Total	27	55	82

overall	**0.744**
HM user's	0.615
HM producer's	0.593
NHM user's	0.804
NHM producer's	0.818

CT coast – normalized band values, PCA values, NDMI values

Prediction did not converge on class 1; analysis dropped

CT coast – normalized band values, PCA values, NDMI values, LiDAR

Prediction did not converge on class 1; analysis dropped

CT coast – LiDAR only

observed

predicted

	HM	NHM	Total
HM	3	6	9
NHM	0	7	7
Total	3	13	16

overall	**0.625**
HM user's	0.333
HM producer's	1.000
NHM user's	1.000
NHM producer's	0.538

BIOGRAPHY OF THE AUTHOR

Maureen “Mo” Deborah Correll was born and raised in Conway, Massachusetts, the capital of the universe. She attended high school at Deerfield Academy, participating in drama club with roles such as “lady in a box” and “parent #2” and heading up the senior class prank committee. After graduation from Deerfield in 1999 she attended the College of William and Mary in Williamsburg, VA where she joined the Swaddle lab and videotaped the mating behavior of zebra finches in the name of science. After earning her B.S. in 2003, Mo travelled to South Africa to work as a wildlife technician collecting elephant excreta out of a Land Rover, and had a baby elephant named after her. After she exhausted her meager earnings from this job in a blur of international travel, Mo took a high-roller position as a food safety inspector in Fairfax County, VA, where she successfully protected Virginia residents from food-borne illness while maintaining a permanent residence in a friend’s laundry room. Mo eventually learned food safety was not for her, and in 2004 began a 6-year string of wildlife technician work, driving sleighs on the side during the winters for extra cash. Mo maintained “residences” in California, Utah, Alaska, Panama, Australia, Washington, Massachusetts, and Costa Rica before she tired of living out of her car, and became set on attending graduate school. After completing the best phone interview of her life, she was offered and accepted a position as a Master’s student at the University of Maine, co-advised by Brian Olsen and Tom Hodgman. After her first field season in 2011, Mo bullied her advisors into taking her on as a doctoral student. Mo is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from the University of Maine in December 2015.