ABSTRACT

Title of Dissertation:	MARINE COMMUNITY ASSEMBLY IN A DYNAMIC ECOTONE
	Cora Ann Johnston, Doctor of Philosophy, 2016
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Species distributions are shifting with climate change. By altering the presence and distribution of biogenic foundation species, climate change effectively modifies habitat. Where biogenic habitats meet, a patchy ecotone landscape forms. The impacts that range shifts and habitat modification have on broader ecological communities will depend in part on how communities assemble in frontier landscapes of patchy habitat. Here, as a case study, I investigate marine fauna community formation and habitat associations along a wetland ecotone in which tropical mangroves invade temperate saltmarsh. When foundation species shift ranges, resulting changes in geographic context and local conditions will affect the contributions of dispersal limitation and species sorting to assembly. By evaluating the presence of community structure – grouping of species – in larval supply and settlers in each pure landscape and into the ecotone, I determine that ecotone marine communities are shaped by habitat-based sorting but not dispersal limitation. Where inhabitant species can access the ecotone, the attributes that inform habitat use and

the scale(s) at which inhabitants distinguish between habitat types within an ecotone should determine the apparency of emerging patches along the range edge, affecting the precision with which inhabitants occupy them. I monitored marine fauna within an experimental array that isolated physical structure from broader habitat patch attributes, revealing that nested scales of habitat sensitivity should result in increasing community divergence as habitat patches expand along the range edge. Finally, habitat associations at settlement may be driven by preference or survival. I determine habitat-specific recruitment patterns of *Callinectes* spp. (Decapoda: Portunidae) crabs in the ecotone and use lab trials to determine that associations are driven by preference for and superior survival in vegetation with branched architecture. Together, these results demonstrate that marine fauna are sensitive to changes in structural attributes and fine-scale emergence of mangrove habitat within marshes, which do not provide equivalent habitat. This work also contributes to our understanding of community formation in a transitional landscape, illuminating the influence of patchy foundation species expansion on community-structuring ecological processes.

MARINE COMMUNITY ASSEMBLY IN A DYNAMIC ECOTONE

by

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Preface

This dissertation contains an overview (Chapter I), three research chapters in manuscript form (Chapters II-IV), and appendices to the chapters, including the findings of an additional study that provides supporting data. A single bibliography is provided at the end for literature cited throughout the dissertation.

Dedication

For the coastal communities, like my home town, whose livelihoods depend on fisheries and who are most at risk from climate change.

"I would rather go without a shirt...through the whole of the Florida swamps in mosquito time than labor as I have...with the pen." – John James Audubon, 1834

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This work could not have been completed without the hospitality and guidance of the staff and scientists at the Smithsonian Marine Station in Fort Pierce. Over a dozen volunteers also contributed to the completion of this work, and I am deeply grateful to each of them. I am also indebted to the public and private landowners who provided access to my research sites: Guana Tolomato Matanzas National Estuarine Research Reserve, Timucuan Ecologial and Historic Preserve, Florida State Parks, Fort Matanzas National Monument, University of Florida's Whitney Lab, the city of St Augustine, Sealove Boatworks, and St Lucie County Parks and Recreation. The completion of my dissertation research was significantly eased by the support of Captain Conrad and the crew at the Pirate Haus. Moreover, I am grateful to E. Dark, D. Langley, A. Lilly, E. Petrou, J. Baird, and the Johnston family for invaluable intellectual, emotional, and logistical support throughout my dissertation research.

The Gruner lab has provided me with a stimulating intellectual home in which to develop as an ecologist. I am very grateful to the members of my lab for help with everything from theory (wipe board discussions and "Mangrove tea") to modeling and coding. I also appreciate the formative input of my dissertation committee, especially I.C. Feller's welcome into the macrosystems project, K. Gedan's guidance in coastal ecology, and D.S. Gruner's steadfast academic and logistical support.

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Chapter 1: Overview

Climate change and interactions shape species distributions

Climate change is altering the basic ecological attributes of natural systems through abiotic and biotic effects (Harley et al. 2006). To stay within their fundamental environmental limits as climate changes, some species must shift their geographic distributions, which can decouple interactions and create novel assemblages (Parmesan and Yohe 2003, Winder and Schindler 2004, Edwards and Richardson 2004, Hobbs et al. 2006, Yang and Rudolf 2010, IPCC 2013, Moritz and Agudo 2013, Vergés et al. 2014, Riley et al. 2014). The velocity of climate change – the rate at which species need to shift ranges in order to keep pace with suitable climate – is predicted to be especially high in regions of low topographic relief, such as coastal plains (Loarie et al. 2009). In those areas, species have to cover long distances in order to attain small changes in climate. Circulating water homogenizes temperature such that the oceanic temperature terrain is less variable than land, necessitating long distance dispersal to adjust to even small changes in temperature (Burrows et al. 2011, Poloczanska et al. 2013). Nonetheless, marine organisms have shown remarkable ability to keep pace with their shifting climate envelopes, with ~80% showing shifts in the direction of changing environmental conditions (Poloczanska et al. 2013).

Beyond climate, biotic interactions also shape species distributions and interface with climate change to shape ecological communities (Lenoir et al. 2010, Zarnetske et al. 2012, Moritz and Agudo 2013). Although species range shifts are profound, with averages estimated at 6.1 to 16.9 km per decade poleward (Parmesan

and Yohe 2003, Chen et al. 2011), they are also nuanced (Lenoir et al. 2010, Pinsky et al. 2013). The accuracy of climate envelope models of species responses to climate change is often diminished by omitting the effects of biotic interactions on species distributions (Lenoir et al. 2010, Zarnetske et al. 2012, Moritz and Agudo 2013). Facilitation is especially important in stressful conditions, such as along range edges where species are likely to meet their fundamental physiological limits (Bruno and Bertness 2001, Bruno et al. 2003, Mair et al. 2014, Sommer et al. 2014). Growth and environmental modification by foundation species can form habitats that facilitate the assembly of entire communities (Bruno and Bertness 2001, Bruno et al. 2003, Silliman et al. 2011). The benefits of biogenic habitats – those produced by organisms (Holbrook et al. 1990, Lohrer et al. 2013) – are so marked that effects of changes in foundation species can surpass the direct abiotic effects of climate change (Gedan and Bertness 2010). Indeed, reduced habitat complexity due to loss or change of foundation species is the clearest impact of climate change on marine systems (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010).

When changing climate modifies the presence and distribution of foundation species, the influences of climate change and habitat modification become intermingled, permeating effects through broader ecological communities (Bruno and Bertness 2001, Harley et al. 2006, Hoegh-Guldberg and Bruno 2010, Vergés et al. 2014). Where the presence of biogenic habitat is required for inhabitant expansion and establishment, redistributions of foundation species may act as biological multipliers of climate change (Zarnetske et al. 2012, Vergés et al. 2014). Even without a net loss of biogenic habitat, differences in foundation species attributes can

alter habitat quality where one habitat-forming species displaces another (Johnston and Lipcius 2012).

Moreover, range expansion forces species into neighboring ecosystems, and when foundation species shift ranges, one habitat essentially invades another (Bruno et al. 2003, Hoegh-Guldberg and Bruno 2010, Osland et al. 2013, Saintilan et al. 2014, Vergés et al. 2014). The merging of ecosystems forms an ecotone. These mixed transitional landscapes are patchy, not abrupt, and often host rich and abundant assemblages (Figure 1.1; Neilson 1993, Kark 2013). The extent to which communities of inhabitants distinguish between and differentially use intermixed habitats along ecotones will determine the form and resolution of communities inhabiting transitional landscapes. Assembly processes, habitat attributes, and species interactions are all likely to influence inhabitants' access to and use of interspersed habitat patches along expanding range edges.

Here, as a case study, I examine how mangrove expansion into saltmarsh alters the marine nearshore habitat landscape and determine how attributes of the ecotone landscape and its component foundation species shape communities of mobile marine fauna along an ecosystem transition zone.

Mangrove intrusion into saltmarsh: expansion, wetland features, and implications for habitat

Globally, between 25 and 40 ° along the tropical-temperate divide, woody mangal forests meet herbaceous marshes (Pomeroy and Weigert 1981, Perry and Mendelssohn 2009), forming a mangrove-marsh ecotone. A shallow climate gradient

exposes these wetlands to remarkably high predicted climate change velocity (0.9 km

per year; Loarie et al. 2009), and mangroves are expanding poleward accordingly

(Osland et al. 2013, Cavanaugh et al. 2014). Limited evidence suggests that mangrove

competition suppresses marsh grasses in the tropics, but cold sensitivity limits

mangrove temperate expansion (Simpson et al. 2013, Cook-Patton et al. 2015). Since

the 1980s, Florida's mangroves have proliferated at their northern limit along the

coast in association with reduced frequency of hard freeze events (Cavanaugh et al.

2014). Of the lower intertidal species in the Atlantic/East Pacific, *Avicennia*

germinans (black mangroves, family: Acanthaceae) are the most cold-tolerant and

form the frontier (Stuart et al. 2007, Williams et al. 2014, Cook-Patton et al. 2015,

Cavanaugh et al. 2015). Tens of kilometers lower in latitude, *Rhizophora mangle* (red

mangroves, family: Rhizophoraceae) emerge in the landscape (Williams et al. 2014).

The spread of mangroves into historically grass-dominated marshes may not change

the extent of wetlands *per se*, but differences in the attributes between these wetland

foundation species have the potential to shape broader ecosystem dynamics and

associated marine communities (Nagelkerken et al. 2008, Barbier et al. 2011, Vergés

et al. 2014).

Both types of coastal wetlands fulfill a variety of comparable functions,

including habitat provisioning, shoreline stabilization, carbon storage, and production

(Gedan et al. 2010, Barbier et al. 2011). In saltmarshes and mangal forests,

production – which can be very high (3900 g C m^{-2} y^{-1}, comparable to tropical

rainforests; Barbier et al. 2011) – is tidally exported into marine systems (marsh:

Odum et al. 1995, Odum 2002; mangrove: Wolanski 1992). Both mangal forests and

saltmarshes are composed of vegetation that emerges from the intertidal, structuring

the coastal fringe. In both wetland types, vegetation follows an elevation zonation

pattern (Lugo and Snedaker 1974). In estuaries of eastern North America, the marsh

fringe is dominated by monoculture stands of *Spartina alterniflora* (smooth

cordgrass, family: Poaceae; hereafter "*Spartina*"); higher in the marsh, succulents and

other forbs emerge (Pennings and Bertness 2001). In mangal forests, *Rhizophora*

establish lowest in the intertidal and then intersperse with *Avicennia* in the mid

intertidal; further upland, *Laguncularia racemosa* (white mangrove, family:

Combretaceae) resides in the high intertidal (Smith 1992). Given their positions

relative to tidal inundation, *Spartina*, *Rhizophora*, and *Avicennia* are the species most

likely to directly affect marine communities and will be the only species further

examined here (Figure 1.2).

Despite the basic similarities of productivity, location, and zonation in mangal

forest and saltmarshes, these wetlands differ in many important attributes, including

structural complexity and the form, timing, and use of their production. Marshes are

shorter statured, non-woody, wind pollinated, and seasonally productive (Adam

1993). *Spartina* senescence in the fall produces a flux of detritus and the buildup of

wrack – a thick straw mat of *Spartina* stems (Pennings and Bertness 2001). Saltmarsh

production has been traced throughout marine food webs; it supports both resident

and transient species, including those that inhabit marsh nurseries before moving

offshore to secondary adult habitat (Deegan et al. 2002, Minello et al. 2003).

Mangroves, though structurally variable across species, are taller, woody,

predominantly insect pollinated, and evergreen, with seasonal fluctuations in biomass

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based primarily in propagule production (Ellison and Farnsworth 2001). They also form aerial roots for stabilization and gas exchange: *Avicennia* produce emergent pencil-like pneumatophores; *Rhizophora* produce overhanging, stilt-like prop roots. There is limited evidence that mangrove production supports marine food webs; instead, adjacent algae and plankton are primary food sources, and mangrove roots settle suspended food particulates and provide surface area for settlement by and foraging on encrusting organisms (Perry 1988, Ellison and Farnsworth 1990, 1992, Newell et al. 1995, Rönnbäck 1999, Sheridan and Hays 2003, Layman 2007, Demopoulos and Smith 2010). Ultimately, there are a suite of differences between mangal forest and saltmarsh attributes that make them unlikely to provide equivalent habitat for marine fauna.

Both types of wetlands are formed by foundation species that mitigate coastal zone physiological stress for resident fauna (Dayton 1972, Bruno and Bertness 2001), but differences in their production and physical features has the potential to broadly impact the habitat quality of alternative wetlands for food- and refuge-seeking inhabitants (Friess et al. 2012). In particular, structural complexity – the variety of elements that form the physical three-dimensional structure of a habitat (Tokeshi and Arakaki 2012, Graham and Nash 2012) – is a driver of differences in habitat quality, such that survival is often highest in the most complex habitat available (e.g., sponge clusters, rocky reefs, and branching macroalgae compared to shell, cobble, or seagrass; Tupper and Boutilier 1995, Scharf et al. 2006, Johnston and Lipcius 2012). Based on their specific attributes, habitat structures may differ in how they mediate species interactions, which can in turn affect refuge effectiveness, habitat quality, and

residency of nursery-seeking species (Robinson and Tully 2000, Halpin 2000, Beck and et al 2001, Heck et al. 2001, 2003, Minello et al. 2003, van Montfrans et al. 2003, Schofield 2003, Pallas et al. 2006, Johnston and Lipcius 2012). Structurally, mangrove and marsh foundation species differ in shoot or root diameter, density, articulation, and woodiness (Appendix 1), each of which may affect refuge dimensions, navigability, and foraging area for inhabitant species.

I hypothesize that mangroves and marshes differ in their habitat quality for marine fauna, due at least in part to differences in their structural forms. Primarily, I expect that the branching architecture of *Spartina* stems and leaves (hereafter "shoots") and *Rhizophora* prop roots provide superior habitat compared to simple *Avicennia* pneumatophores. As such, I expect that the change in intertidal habitat attributes with mangrove expansion into saltmarsh will elicit changes in the composition of mobile marine fauna that use coastal wetlands as habitat (Beck et al. 2001, Dahlgren et al. 2006, Friess et al. 2012, Osland et al. 2013).

Importantly, the shift of mangroves into saltmarshes alters the coastal zone at a series of hierarchical scales. At the coarsest scale, pure – or baseline – mangal forest and saltmarsh are connected by a patchy ecotone, which encompasses kilometers of wetland area. Within these landscapes, distinctive habitats are formed by each vegetation type, including all of their associated attributes. *Rhizophora*, *Avicennia*, and *Spartina* each form habitat patches on the scale of meters to hundreds of meters. *Spartina* habitats occur in the marsh landscape, *Rhizophora* and *Avicennia* habitats occur in mangal forest landscapes, and all three occur within the ecotone. Finally, at the sub-patch scale, each vegetation type provides a unique growth structure; prop

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roots (*Rhizophora*), pneumatophores (*Avicennia*), and shoots (*Spartina*) grow and structure the intertidal zone at the fine spatial grain of centimeters to tens of centimeters – the scale at which marine organisms interact with growth forms. In all further discussion, marsh, mangal, and ecotone refer to landscapes, generic names refer to habitat patches, and growth forms refer to structural features.

Mobile marine fauna: wetland ecotone inhabitants

Within this shifting wetland landscape, I studied nursery-seeking crustaceans – primarily crabs – and other mobile marine fauna that settle in near-shore habitats after a brief free-floating larval stage. Physical processes such as wind, tide, and currents shape their distribution during dispersal as planktonic larvae (Paula et al. 2001, Lee et al. 2004, Pralon et al. 2012, Biermann et al. 2015, Grey et al. 2015), but active habitat associations also shape local patterns of occurrence (Etherington and Eggleston 2000, van Montfrans et al. 2003, Moksnes and Heck 2006, Epifanio and Cohen 2016). Active habitat selection and non-random distribution in the landscape are particularly evident in active swimmers that are sensitive to chemical, acoustic, physical, conspecific, and predator cues (Tupper and Boutilier 1995, Forward et al. 1996, 2001, Diaz et al. 1999, Rodriguez and Epifanio 2000, van Montfrans et al. 2003, Steinberg et al. 2008, Lillis et al. 2013). Mobile marine fauna actively assess their surroundings and can even adjust molting in response to these cues and the availability of preferred substrate. Conspecific, vegetation, and substrate cues promote habitat selection, while predator cues can lead to habitat avoidance (Welch et al. 1997, Moksnes et al. 1997, Forward et al. 2001, Diele and Simith 2007). Many

estuarine species actively select habitat suitable for growth and survival (Halpin 2000, Dahlgren and Eggleston 2000). Mobile marine fauna differentially inhabit co-occurring habitats, creating patchily distributed communities across coastal environments (Heck et al. 2001, Moksnes 2002, van Montfrans et al. 2003, Lindsey et al. 2006, Moksnes and Heck 2006, Johnston and Lipcius 2012). For these species, population growth is predominantly determined during larval and juvenile stages, due in part to predation pressure that can be reduced by effective refuge-use, making close habitat associations both likely and important (Houde and Hoyt 1987, Hsueh et al. 1993, Heck et al. 2001, Moksnes 2002). Juvenile habitat use is driven primarily by mortality avoidance (Halpin 2000, Dahlgren and Eggleston 2000, Johnston and Lipcius 2012), so preference for a specific habitat should reflect its structural complexity and value as a refuge. Along with their close habitat associations and ecological and economic importance (as scavengers and seafood, respectively), the small size (<100 mm) and rapid development of many mobile marine fauna that inhabit wetlands allows me to test both mechanisms and patterns of habitat use over biologically relevant but tractable spatial and temporal scales.

Synthesis and inference

To better understand how communities form at range edges and are likely to change with climate-induced range expansion, we need to better understand the ecological processes that drive community formation and habitat use in patchy landscapes. I use a transitional wetland landscape to determine 1) the relative influences of dispersal and ecological sorting on assembly processes, 2) the scales of

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associations and their correspondence to specific habitat attributes, and 3) the roles of preference and survival in shaping habitat associations where foundation species co-occur. Derived within a shifting ecotone landscape, all three contribute to our understanding of how communities form along habitat range edges and thus are most likely to respond during shifts associated with climate change.

The ability of inhabitants to reach and detect patchy edges will determine the relative influences of basic assembly processes on community formation (Vellend 2010, Yang and Rudolf 2010). With shifts in the distributions of foundation species, changes in geographic occurrence can affect successful dispersal of inhabitants to the range frontier. Local changes in wetland attributes where foundation species intermix can also affect species sorting via habitat preferences or environmental filtering. The composition of the mixed habitat ecotone may also affect the relative importance of secondary dispersal and stochasticity in shaping community composition (Kareiva et al. 1990). For Chapter II, I test the influences of each assembly process by evaluating the presence of community structure – groupings of species – in larval supply and settlers in pure saltmarsh and mangal landscapes and into the ecotone. Investigating the form and origin of communities along range edges can help us understand how species inhabiting shifting frontiers will integrate or displace each other. Clear structure in settled but not larval communities revealed that sufficient dispersal and strong vegetation-based sorting contribute to the formation of distinct mangrove and marsh communities even where patches co-occur within the ecotone.

A growing body of literature indicates that fine scale heterogeneity shapes species responses to climate change (Ashcroft et al. 2009, Lenoir et al. 2010, Moritz

and Agudo 2013). Microclimate improves our understanding of responses to shifting climate (Bennie et al. 2013). Habitat fragmentation – breaking up of the landscape – also limits range shifts in response to climate change (Honnay et al. 2002, Opdam and Wascher 2004, Holyoak and Heath 2016). Where one foundation species expands into another, a fragmented, patchy ecotone landscape occurs (Figure 1.1). The attributes that inform habitat use and the scale(s) at which inhabitants distinguish between habitat types within an ecotone should determine the apparency of emerging patches along the range edge, in turn affecting the precision with which inhabitants occupy them. Habitat recognition and colonization may not occur in vegetation patches smaller than some threshold area, below which cues and/or habitat extent are insufficient to elicit associative response (i.e., the small island effect; Lomolino and Weiser 2001, Fahrig 2013). For Chapter III, I monitored marine fauna within an experimental array that isolates physical structure from broader habitat patch attributes in order to determine 1) the attributes stimulating species associations and 2) the scale(s) of sensitivity to emerging habitat. Mobile marine fauna community composition structured by site, habitat type, and physical structure, indicating that inhabitant communities are sorting finely among habitat patches, even where they co-occur within the ecotone.

Where sorting among patches occurs, differences in habitat associations at settlement may be driven by preference or apparent preference – a difference in abundance caused by habitat-based differences in post-settlement survival. Habitat attributes can shape survival, which provides a measure of relative habitat quality, and often higher quality habitats are actively preferred. For Chapter IV, I determined

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habitat-specific recruitment patterns of a cohort of *Callinectes* spp. (family:

Portunidae) crabs in the ecotone. I then conducted preference and survival trials in the

lab to determine the source of differences and how they relate to vegetation attributes.

Differences in recruitment, preference, and survival demonstrate that mangroves and

saltmarsh differ in habitat quality, based primarily on differences in their structural

complexity. Differences in habitat quality of branching and simple structures

highlights the need to account for shifts between foundation species, not just the loss

of biogenic habitat, when considering the impacts of climate change on marine

systems (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010).

Through this work, I demonstrate that the influences of climate change and

habitat modification become intermingled when changing climate modifies the

presence and distribution of foundation species and the habitats they form. By

determining the relative importance of assembly processes in a shifting landscape

context (Chapter II), the scales and attributes influencing community composition in

patchy landscapes (Chapter III), and the effects of vegetation structure on habitat

quality and use (Chapter IV), this study helps illuminate realistic implications of

foundation species range shifts on community-structuring ecological processes.

FIGURES
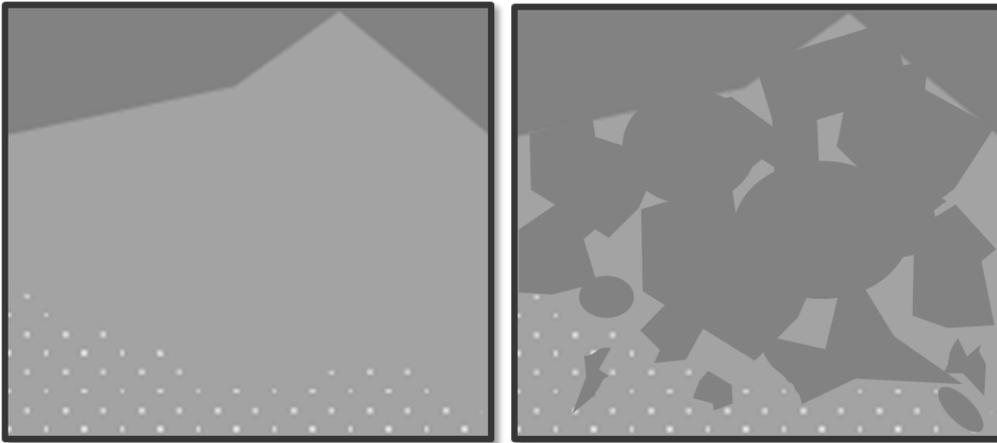
Figure 1.1: Though ecotones are often depicted as abrupt transitions between ecosystems (light and dark grey, left), realistically, they are often patchy transition zones (right). The patchiness of an ecotone may affect how inhabitants (white points) occupy a given habitat type.

Figure 1.2: Mangrove (left) and marsh (right) intertidal vegetation; *Avicennia* produce short, thin pneumatophores (left, foreground), *Rhizophora* produce overhanging, branching prop roots (left, background), and *Spartina* produce tall, leafy shoots (right).

Chapter 2: Species sorting upon settlement shapes community assemblages in an expanding range

Abstract

Climate change is redistributing foundation species, shifting habitats across the landscape. The ability of inhabitant species to track those shifts and the form that frontier communities take will depend on the relative effects of range shifts on assembly processes. I expected changes in foundation species distributions to most markedly influence 1) dispersal via shifts in geographic context and 2) sorting via changes in habitat arrangement and local conditions. Broad dispersal should make expanding habitat more accessible, while local sorting via preference or filtering secures associations within patchy frontier landscapes. Within an ecotone where tropical mangroves are expanding into temperate marshes, I characterized marine decapod crustacean community structure at multiple scales across the landscape. I used comparative surveys of crab planktonic larval supply and settlement to assess dispersal limitation and settler sorting by habitat features in each pure landscape and where they mix along the ecotone. Planktonic supply was unstructured across the landscape, indicating a single regional species pool and minimal dispersal limitation. Clear structure in settled communities revealed that strong vegetation-based sorting contributes to the formation of distinct mangrove and marsh communities even where patches co-occur within the ecotone. Life history and landscape attributes help

explain the results in this study system and can inform our expectations for the progression of frontier communities in other systems.

Key words: assembly, crabs, dispersal, ecotone, habitat-tracking, mangroves, marshes, species pool, species ranges, wetland

Introduction

Ecological communities – suites of species that co-occur in space and time – are assembled through the shared influences of dispersal, neutral processes, and deterministic sorting (Vellend 2010, Weiher et al. 2011). Climate change may influence community formation by stimulating range shifts that alter species distributions (Parmesan and Yohe 2003, Perry et al. 2005, Cheung et al. 2009, Loarie et al. 2009, Chen et al. 2011, Burrows et al. 2011, Moritz and Agudo 2013, Pinsky et al. 2013, Poloczanska et al. 2013). Range shifts have the potential to alter community composition, in part through the likely influences that changes in distribution can have on the relative roles of dispersal and secondary sorting during community formation (Ibáñez et al. 2006, Vellend 2010, Pinsky et al. 2013). Mismatches in organismal responses to changing environments can decouple species co-occurrence and interactions, leading to the formation of novel assemblages (Winder and Schindler 2004, Edwards and Richardson 2004, Hobbs et al. 2009, Yang and Rudolf 2010, Blois et al. 2013, Vergés et al. 2014, Riley et al. 2014). Although responses to climate change are pervasive, their translation into trajectories of community change are less certain (Walther et al. 2002, Baselga and Araújo 2009, Lavergne et al. 2010,

De Senerpont Domis et al. 2013, Gruner et al. 2016). Examining the influences of dispersal and sorting on assembly at a range edge can help us understand the form and origin of frontier communities, in turn clarifying expected trajectories of community change.

The effects of species redistribution scale up to entire communities when foundation species – those that facilitate whole communities by modifying the environment – shift ranges (Bruno and Bertness 2001, Hobbs et al. 2006, 2009). Shifts in foundation species with climate change can affect community composition through two distinct routes. First, foundation species emergence in a new range alters the geographic context and spatial extent of available habitat for dependent species. Differences in geography shape community formation by affecting propagule supply by increasing dispersal limitation by distance (Hubbell 2008, Ricklefs 2008). Second, the replacement of one foundation species by another can lead to change in local environmental conditions and habitat attributes. Foundation species mediate abiotic stress and species interactions, so changes in local conditions with the distribution of their biogenic habitats across a landscape can affect the strength of environmental filtering and deterministic sorting (hereafter "sorting") on inhabitant assemblages (Harms et al. 2000, Bruno and Bertness 2001, Phillips et al. 2003, Gedan and Bertness 2010, Beaudrot et al. 2013). Thus, dispersal and sorting should be the processes most influencing frontier communities (Vellend 2010). Together, changes that affect these processes will shape community dynamics within the expanding landscape (hereafter "frontier"), determining frontier community composition and the

rate at which shifts in foundation species elicit change in the broader community of associated species.

Worldwide, coastal wetlands along soft-bottom substrates are characterized by woody mangroves in the tropics and subtropics and by herbaceous saltmarshes in temperate zones (Spalding 2010, Friess et al. 2012). As climate change relieves abiotic constraints along their poleward limit, mangroves are expanding into saltmarshes along a patchy ecotone (Perry and Mendelssohn 2009, Osland et al. 2013, Saintilan et al. 2014, Cavanaugh et al. 2014). Mangroves and marshes fulfill a variety of comparable functions, including shoreline stabilization, carbon storage, and primary production (Feller et al. 2010, Gedan et al. 2010, Barbier et al. 2011). However, their foundation species differ markedly in structural attributes, such that local conversion of marsh to mangroves is likely to change wetland habitats for associated marine communities (Nagelkerken et al. 2008, Vergés et al. 2014).

Within this mangrove-marsh complex, I studied nursery-seeking decapod crustaceans (hereafter "crabs") to evaluate community structure, defined here as distinguishable patterns of species occurrence, as a function of this transitional ecotone landscape. After a brief planktonic larval stage, these species settle in coastal habitats that enhance their juvenile growth and survival (Beck and et al 2001, Moksnes 2002, van Montfrans et al. 2003, Moksnes and Heck 2006, Dahlgren et al. 2006, Epifanio and Cohen 2016). For species that disperse primarily as propagules (e.g., eggs, seeds, spores), propagule distribution is a good indicator of dispersal potential and range limits (Underwood and Fairweather 1989, Harms et al. 2000, Kinlan and Gaines 2003, Wahle 2003, Lockwood et al. 2005, Cowen and Sponaugle

2009). Likewise, patterns of successful propagule establishment (e.g., larval

settlement and molting, seed sprouting) are an emergent property of resource

preferences, habitat associations (i.e., recognition, *sensu lato*), and environmental

filtering (Weber and Epifanio 1996, Forward et al. 1996, 2001, Harms et al. 2000,

Phillips et al. 2003, O'Connor and Judge 2004, Stanley et al. 2010, Beaudrot et al.

2013). I sampled crabs from plankton and estuarine vegetation as measures of

propagule supply and establishment, respectively, and characterized community

structure in each to infer the influences of dispersal and sorting on community

formation in the shifting mangrove-marsh landscape along the Atlantic Coast of

Florida (Figure 2.1A; Moksnes and Wennhage 2001, Paula et al. 2006, Pan et al.

2010).

Limited evidence suggests that separate assemblages of marine invertebrates

inhabit mangroves and saltmarshes, with mangroves hosting slightly richer

communities (Bloomfield and Gillanders 2005). Thus, I expected mangrove

expansion to elicit a shift in the crab community along the ecotone. With the spread of

mangroves into marshes, the form that frontier communities of crabs will take

depends on the influences that changing context and habitat attributes have on

dispersal and settlement (Figure 2.1B; Pallas et al. 2006). If inhabitant assembly at the

range edge is limited by dispersal, then distinctive community structure should arise

within supply samples, suggesting separate species pools by landscape (Harrison and

Cornell 2008, Ricklefs 2008, Carstensen et al. 2013, Fukami 2015). Using plankton

tows, I tested for breaks in larval supply composition that indicate partitioning of

species pools, defined as all species present in an area with the potential to establish,

and likely dispersal limitation (Harrison and Cornell 2008). When supply is undifferentiated, patterns of settled community composition indicate the influences of neutral assembly and deterministic sorting (Vellend 2010). Using crabs collected from settlement traps, I tested for differences in established community composition between landscape types and among habitats. Breaks in settled community composition indicate deterministic sorting via preference or filtering; a lack of community structure may indicate neutral influences but is indistinguishable from unexplained sorting associated with missing predictors (Vellend 2010). Finally, structure in supply (regional species pool) and established (local species pool) communities would indicate that mixed influences of foundation species change on geographic context and the local environment both are contributing to the formation of novel ecotone communities. I tested community composition by landscape type (mangal forest, marsh, ecotone) and tested a habitat by context interaction to determine the form of frontier communities given the combined influences of all assembly processes. By evaluating species supply and establishment across a transitional landscape at the range edge, I determine the relative importance of dispersal and sorting in shaping a frontier community, helping to illuminate the realistic implications of climate-driven habitat modification on community-structuring ecological processes.

Methods

To evaluate the relative influences of dispersal and sorting on shaping community formation along an expanding range limit, I characterized community composition 1)

of decapod crustacean larval supply captured by plankton net in inlets and 2) of recruits on passive hogs-hair collectors (hereafter "traps") placed in vegetation patches directly adjacent to inlets. In 2013 and 2014, supply and settlement samples were collected biweekly from late April through early June during peak crab recruitment along the coast of central Florida (K. Hill, S. Reed, J. Dineen, *unpublished data*). The study spanned eight sites, a subset of which were sampled each year. Each sampling event included five sites (Figure 2.1A) and was conducted over ≤72 hours to minimize temporal variation (Eggleston and Armstrong 1995). All sampling was conducted in or adjacent to inlets to help control for spatial and environmental variation on arrival and settlement within the estuary (Etherington and Eggleston 2000, Paula et al. 2001, Pallas et al. 2006, Pralon et al. 2012). The 2013 survey covered the maximum study extent (395km, from 27-30°), spanning ecotone and adjacent mangal forest and marsh landscapes. In 2014, I decreased the study extent to focus on the region north of Cape Canaveral and refined the grain by adding two sites to the prior three within that range (Figure 2.1A) to better resolve ecotone and marsh community structure. The two-year survey ultimately included every major inlet (n=8) on the east coast of Florida between Stuart (27.20°) and Jacksonville (30.51°).

Supply

To capture the most spatially consistent and temporally concentrated samples of the arriving species pool (i.e., larval supply; Boehlert and Mundy 1988; Johnson, Allen, and Fylling 2005), I deployed a conical <500 μm plankton net outfitted with a flow meter (General Oceanics 2030R) from a dock in the inlet (i.e., deep water

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openings into estuaries or shallow coastal zones) at each site during rising night tides. Two to three sites were sampled per night, following the natural latitudinal progression of the rising tide. I sampled an average of 10 m^3±2.3SE of water with each deployment. Sampling duration varied with date, tide, and wind conditions. The net was rinsed with fresh water between sites. In order to assess the community of competent settlers, all plankton samples were sieved and only crabs retained in a 710 μm sieve – predominantly megalopae and first instar juveniles – were kept for analysis (Lipcius et al. 1990, Pan et al. 2010). Sieved samples were preserved in 95% molecular grade ethanol until individuals were identified and counted under a dissecting scope (Bullard 2003, Johnson et al. 2005).

Settlement

To survey settling crabs, I used passive settlement traps of 32 x 33 cm of hogs-hair mesh, curled into a cylinder and deployed within natural vegetation (van Montfrans et al. 1990, Eggleston and Armstrong 1995, Pan et al. 2010). Crabs collected on mesh traps are considered settled and therefore part of the assembling community of wetland inhabitants (Moksnes and Wennhage 2001). Although there are concerns of settlement bias on artificial traps compared to natural substrate, such concerns are documented only in open water or on unvegetated substrate, where traps may stimulate unrepresentative, high recruitment (Paula et al. 2006, Reinsel et al. 2015). Traps in this study were always deployed within vegetation. Specifically, I deployed traps within wetland vegetation along main waterways directly adjacent to (<3 km from) each inlet.

In 2013, some settlement traps were affixed to PVC pipe within the vegetation and some were affixed directly to the vegetation. Settlement was similar across these arrangements, so samples are pooled during analysis. Ten traps were deployed per site (n=5 sites; entire range, Figure 2.1A). Within each site, replicate traps were distributed according to the approximate prevalence of each vegetation type at each site. In 2014, all traps were affixed directly to vegetation, and four traps were deployed per vegetation type per site (n=5 sites, all north of Cape Canaveral), such that the total number of traps per site varied from four in marsh with only *Spartina* to twelve in the ecotone with all three vegetation types – *Rhizophora*, *Avicennia*, and *Spartina*. Traps were initially deployed one week before the study commenced. To maximize inundation, traps were sampled during daylight high tide within 48 hours after corresponding collections from plankton tows. During sampling, the mesh was freed and quickly transferred into a sealable bag along with any accompanying water and detritus. Each trap was outfitted with a clean mesh cover. Tidal inundation varied with weather, so occasional traps that were not submerged upon retrieval were excluded from analysis. At the lab, each collected mesh cover was soaked in fresh water, rinsed vigorously, and inspected for remaining invertebrates (van Montfrans et al. 1990). The extracted samples were rinsed through a 500 μm sieve, from which retained invertebrates were placed in 95% molecular grade ethanol. Less than 1 mL of Rose Bengal stain was added to each preserved sample to improve fauna detection. As needed, samples were first coarse sorted by two independent observers to separate crabs from detritus, then recovered individuals were identified and counted under a

dissecting scope (resources as above). Crabs greater than 3 mm carapace width were noted and excluded from community data, as they are unlikely to be new settlers.

Analysis

Only small juveniles and megalopae (i.e., competent settlers; Moksnes and Wennhage 2001) were included from each sample type. For analysis, developmental stages were pooled into one record of abundance per species per sample. Analyses were conducted on the highest level of taxonomic certainty, predominantly genus or family. Given variation in tow volume and trap recovery, I developed individual-based rarefaction curves for each site and sampling type to verify adequate community characterization as curve saturation in all groups before proceeding with analyses. All analyses were conducted within the program R version 3.2.3 (R Core Team 2015). For permutational multivariate analysis of variance (PERMANOVA) and visualization, species occurrence data were standardized within a sample. Plankton tow samples were also standardized by the volume of the tow. Dispersion was evaluated with the betadisper function in the vegan package in R (Dixon 2003). Dispersion was comparable across groups in planktonic larval supply, so data were analyzed with PERMANOVA using the adonis function with Bray-Curtis dissimilarity measures in the vegan package in R (Anderson 2001). Dispersion was more variable for settled communities, so I conducted generalized linear mixed effects models (GLMM) on species abundances using the glmer function in the lme4 package in R (Bates et al. 2015). Where dispersion was even among settlement traps, I also conducted PERMANOVA. Results were consistent across analysis methods, so I report only GLMM results here. Community composition was modeled relative to

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predictors landscape (mangal forest, marsh, and ecotone) and habitat type

(*Rhizophora, Avicennia, Spartina*). Context was also used to specify whether habitats

occurred in pure landscapes or the mixed ecotone. Within GLMMs, I used the random

effect model structure "(1+predictor|species)" to model random slopes for changes in

community composition driven by species-specific responses (Bolker et al. 2009,

Johnson 2014). All models also included the predictor as a fixed effect to account for

overall differences in abundance. Model performance was optimized with the

"bobyqa" control function to adjust for over-conservatism in model convergence in

later versions of lme4 (K. Edwards, *personal communication*). Diagnostics and model

selection follow (Bolker et al. 2009); specifically, the significance and explanatory

contribution of each predictor was determined from Likelihood Ratio Tests and

changes in small sample size-corrected information criterion scores (AICc) between

full and simplified models; terms that elicit greater score changes (ΔAICc) have more

explanatory power. I also used the r.squaredGLMM function in the MuMIn package

to calculate pseudo-R^2 values that represent the absolute value of goodness-of-fit for

each model (Nakagawa and Schielzeth 2013, Johnson 2014, Barton 2015); marginal

R^2_{GLMM} indicates the amount of total variation explained by the fixed effects, while

conditional R^2_{GLMM} indicates the combined explanatory power of fixed and random

effects. The explanatory power of fixed effects was often very low, so here I do not

report marginal R^2_{GLMM} in cases where it fell below 0.01; in those instances fixed

effects were negligible, so conditional R^2_{GLMM} effectively measured random effects.

Species contributing to significant groupings were identified by plotting modeled

species-specific responses to each predictor (Appendix 2). Results are visualized with non-metric multidimensional scaling (nMDS) ordination.

Results

Supply

There was a small but significant difference in larval supply composition between years from plankton tows at sites sampled in both 2013 and 2014 (PERMANOVA, df=1, R^2=0.09, p=0.038). Nonetheless, results of individual tests were comparable when each year was analyzed separately. Also, combining data across years balances sampling coverage (resulting in 12 samples from mangrove landscape and 15 from marsh). Thus, for simplicity, I present the results of analysis on combined years. Ultimately, I collected 47 plankton samples from which I characterized 44,771 individuals across 25 identified taxa; 17,193 individuals were shrimp; 27,578 were brachyuran crabs and kin – mostly in families Ocypodidae and Panopeidae. The composition of planktonic larval supply was not different between mangal forest and marsh landscapes (df=1, R^2=0.04, p=0.36). Moreover, no significant structure emerged in supply community composition in any year: composition did not differ significantly among sites (df=5, R^2=0.11, p=0.39), marsh, ecotone, or mangal forest landscapes (df=1, R^2=0.02, p=0.52), or position relative to Cape Canaveral – a hypothesized barrier to dispersal (df=1, R^2=0.04, p=0.12).

Settlement

Crabs were present on a higher proportion of settlement traps in *Rhizophora* (mean±SE: 0.63±0.06) compared to *Avicennia* vegetation (0.39±0.05; binomial logit-

link GLM, df=282, p=0.007); trap occupancy in *Spartina* was intermediate

(0.51±0.05). The uneven incidence of empty traps across vegetation types caused

unbalanced sampling each year; there was no significant effect of year on settled crab

community composition, so I combined data across years to re-balance sampling

effort. Ultimately, I successfully recovered 142 settlement samples from which I

collected 1659 individuals across 16 identified taxa. Most crabs were in families

Panopeidae, Ocypodidae, and Sesarmidae. Only nine individuals were shrimp

(suborder: Dendrobranchiata).

I expected mangrove expansion to elicit a shift in the crab community along

the ecotone, but this expectation implicitly assumes that crab communities differ in

mangal forests and marshes. I evaluated this assumption by comparing settlement by

habitat type in baseline marsh and mangrove landscapes at each end of the ecotone

(Figure 2.1). The settled community differed significantly between pure mangal forest

and marsh landscapes outside the ecotone (likelihood ratio χ^2=656.99, df=5,

P<0.0001, conditional R^2_{GLMM}=0.46 [marginal R^2_{GLMM}=0.085]; Table 2.1; Figure

A2.2A, Appendix 2). The differences were even more distinctive by vegetation type,

such that marsh and mangal forest host distinct communties, and within mangroves,

Avicennia and *Rhizophora* host distinct communities (χ^2=722.41, df=9, P<0.0001,

conditional R^2_{GLMM}=0.52 [marginal R^2_{GLMM}=0.0999], Figure 2.2B). Settled

communities were distinctive across all landscape types (marsh vs. ecotone vs.

mangal forest, χ^2=852.09, df=9, P<0.0001, conditional R^2_{GLMM}=0.40 [marginal

R^2_{GLMM}=0.072], Figure 2.3A), and settled crab communities were distinctive by

habitat type even where all three co-occur in the ecotone landscape (χ^2=31.86, df=9,

P<0.0001, conditional R^2_{GLMM}=0.36, Figure 2.3B). There was a significant habitat by context (pure or mixed landscape) interaction, with weaker differentiation by habitat in the ecotone than in baseline landscapes, suggesting that though communities are distinctive by habitat type in the ecotone, they are not equivalent to the communities found in each vegetation within their pure baseline conditions (χ^2=89.57, df=25, P<0.0001, conditional R^2_{GLMM}=0.39, Figure 2.4).

Discussion

Sparse prior comparisons found that mangroves and marshes host different marine invertebrate assemblages; thus, I expected that mangroves and marshes along the Atlantic Coast of Florida would host distinct crab communities, such that foundation species range shifts should stimulate broader community changes (Bloomfield and Gillanders 2005). Indeed, settled communities of crabs differed between baseline mangrove and marsh landscapes where they occur north and south of the ecotone. Along the mangrove-marsh transition zone, I found minimal evidence for dispersal limitation, with a predominantly unified species pool available to all habitat types across the study range. Among settled communities, there was a strong signature of local, habitat-based clustering. Structure, i.e., distinguishable patterns of composition, in the settled community was clear even within the ecotone. Settled communities differed between mixed and baseline landscapes and by habitat type within each. Together, these patterns indicate that the crab community in the ecotone is responding to mangrove expansion in real time. The life history and landscape

attributes of the system help explain the contributions of dispersal and sorting to community assembly along the ecotone.

Primary processes: Dispersal and supply

Dispersal is generally broad in marine species due to planktonic larval dispersal (Kinlan and Gaines 2003, Pelc et al. 2009). I found that the distribution of estuarine crab larvae indicates dispersal sufficient to keep pace with mangrove expansion, which is matching one of the highest known predicted velocities of climate change (0.9 km per decade; Loarie et al. 2009). No break in larval supply from plankton tows was apparent between mangal forest and marsh landscapes, suggesting that a single species pool of crabs spans the Atlantic Coast of Florida, including mangal forest, ecotone, and marsh landscapes. Although low power (n=40 plankton tows) could contribute to the lack of significant pattern, species richness reached an asymptote at all sites in all years, suggesting that sampling was sufficient to characterize and compare supply composition. Capes are expected to present the most likely barrier to coastal dispersal, but no signature of a divide at Cape Canaveral was apparent in my results. Likewise, in a meta-analysis, Pelc et al. (2009) found no phylogeographic structure among planktonic dispersers along the Atlantic Coast of Florida, despite the convergence of the Florida Current and the South Atlantic Bight at Cape Canaveral. Thus, the mangrove-marsh transition zone is accessible to the full suite of species that occur in both mangrove and marsh landscapes, indicating no evidence for dispersal limitation on community assembly along the frontier.

Secondary processes: Sorting and stochasticity

After passive planktonic dispersal, recruiting crabs actively select habitat based on acoustic, chemical, and physical cues from substrate, conspecifics, and predators (van Montfrans et al. 1990, 2003, Tupper and Boutilier 1995, 1997, Forward et al. 1996, 2001, Diaz et al. 1999, 2001, Rodriguez and Epifanio 2000, Moksnes 2002, Lee et al. 2004, Steinberg et al. 2008, Lillis et al. 2013). I characterized only competent settlers (i.e., megalopae and early juveniles) from the plankton, and examined assembled (settled) communities directly adjacent to inlets. Therefore, presence in my supply samples from plankton tows indicates arrival in the local community (i.e., successful dispersal; Moksnes and Wennhage 2001). As such, structure across landscapes or habitats that arises in the settled community (traps) but not in supply (tows) is indicative of sorting processes during establishment. I found distinctive community structure between mangrove and marsh landscapes and between individual vegetation types where they occur in baseline landscapes. This settled community structure indicates small-scale responses to habitat attributes (e.g., chemical cues, physical structure) and/or environmental filtering (Kohn and Leviten 1976, Gratwicke and Speight 2005, Dixson et al. 2014, Epifanio and Cohen 2016). Apparent habitat associations may be driven by selection in the form of behavioral preference (active habitat selection) and/or differential survival upon settlement (passive environmental filtering; Dixson et al. 2014).

Assembled communities also differed by habitat type within the ecotone, indicating that mangrove and marsh vegetation shapes the inhabitant community even where habitats co-occur in patches along the frontier. Such distinctions reveal that

even small patches of emerging mangrove are sufficient to elicit a response in assembling crab communities. Community structure by vegetation type in the ecotone also indicates that sorting is formative at the mangrove range edge, overriding unified dispersal and species pools (Sommer et al. 2014).

Community composition variability in the ecotone is somewhat higher than in baseline ranges, as is expected in a transitional landscape where multiple communities converge (Munguia et al. 2011). In baseline mangrove and marsh landscapes, regional sorting of the crab community is attributable to recruitment during natal dispersal (Moksnes 2002), because distances between landscapes are too great for effective redistribution during secondary (post-settlement) dispersal. However, the decrease in community resolution within the ecotone may indicate that the decreasing extent of habitat due to patchy vegetation expansion along the mangrove frontier may increase the influence of short-range secondary dispersal (Holyoak et al 2005). Such dispersal may blend communities between patch types, leading to lower community resolution by habitat type in the ecotone. Additionally, increasing patchiness due to the mixing of habitats along the frontier may increase ecological stochasticity and neutral processes if habitat-associated communities are made smaller and, thus, subject to stochastic events in a patchy landscape (Vellend 2010, Weiher et al. 2011).

Many assembly studies have found clear signatures of sorting (Phillips et al. 2003, Freestone and Osman 2011, Beaudrot et al. 2013, Osman 2015), but the study of assembly processes in organisms that become sessile upon establishment (e.g. plants, encrusting epifauna) may overemphasize the relative importance of sorting

during settlement (Phillips et al. 2003, Vellend 2010, Weiher et al. 2011, Beaudrot et al. 2013). Ongoing secondary dispersal – added to stochasticity – in a patchy landscape could lead to a less distinct division of community composition by habitat type in the frontier landscape (Holyoak et al. 2005, Vellend 2010). The crab community in this study combines plant-like propagule-controlled primary dispersal with localized secondary dispersal, providing a glimpse into the influence of secondary mobility in patchy landscapes on the prevalence of sorting (Vellend 2010, Weiher et al. 2011). I found that even with some secondary mobility, sorting upon settlement was still evident, lending support to the prevailing processes identified in studies of sessile organism assembly (Phillips et al. 2003, Freestone and Osman 2011, Beaudrot et al. 2013, Osman 2015). These dynamics need to be further examined for later life stages and in groups with other dispersal life histories, as there are likely to be thresholds in the spatial relationship between patchiness and dispersal (Jenkins et al. 2007).

Further considerations for characterizing frontier communities

Together, the lack of dispersal limitation and appearance of vegetation associations suggest that the composition of crab communities will shift as mangrove associates successfully accompany their habitat's expansion. It is noteworthy that within my study the marsh landscape and *Spartina* habitat therein contained species generally considered mangrove associates (e.g. *Goniopsis cruentata*, personal observation; *Aratus pisonii*, Riley et al. 2014). The broad dispersal of crabs has made their habitat tracking efficient, with some even overshooting the mangrove frontier.

For example, *Aratus pisonii* occurs 60 km north of the leading mangrove (Riley et al.

2014). Thus, my baseline marsh conditions do not represent "pure" baseline marsh

communities such that community differentiation and associated species expansion

should be interpreted liberally. Remarkably, I nonetheless detected a split in the

community between ecotone and marsh landscapes, which may come from the loss of

mangrove growth forms in the landscape. Future research should expand surveys

farther north, as a secondary split in the marsh crab community likely exists where

mangrove species no longer spill over from the ecotone. More broadly, where

dispersal is not limiting, similar generalized habitat associations and novel

interactions may become more common as patchy landscapes increase the influences

of stochasticity and local dispersal on frontier communities otherwise shaped by

habitat-specific species sorting.

Conclusion

As the ranges of habitat-forming species shift, the relative roles of

community-shaping processes on species arrival and community formation will shape

successful habitat tracking (Vellend 2010, Weiher et al. 2011). Where supply is

equivalent but establishment is strongly structured, the frontier inhabitant community

should change synchronously with foundation species shifts due to the presence of

associated inhabitants within newly emerging habitat patches. However, climate

change is expected to reduce the distance and duration of larval dispersal, thus marine

communities may track their shifting foundation species less effectively with

increasing climate change (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010).

With limited dispersal, broader community change may be undetectable or lag behind the expanding foundation species such that a broader community shift is not immediately apparent along the range frontier. Furthermore, if limited dispersal by geographic distance creates separate regional species pools, then foundation species expansion may elicit little change in local inhabitant community formation. In those conditions, the effect of local changes in habitat quality will need to be considered for inhabitants of the recipient system (see Chapter IV). As many species shift geographic ranges in response to climate change, it becomes pertinent to investigate how communities assemble in habitats out of context, because altering the influence of a single assembly process can affect the trajectory of ecological communities (Hobbs et al. 2006, 2009, Urban et al. 2013, Singer et al. 2016).

TABLES

Table 2.1: Model results for settled crab community composition. All models were superior to simplified versions, in which the random effect of the predictor was removed; ΔAICc indicates the difference between full and simplified models. Fixed effects were negligibly small across models; thus, the conditional R^2_{GLMM}, which measures fixed + random effects, essentially indicates the explanatory power of the random effect, which here models changes in community composition due to species-specific responses to each predictor. For each model, "data = baseline" indicates communities modeled in pure mangal forest or marsh landscapes; "data = ecotone" indicates communities modeled in the ecotone landscape; "data = all" indicates communities that were modeled across the entire suite of landscape types.

| Test	Model	DF	Likelihood ratio χ^2	ΔAICc	Conditional R^2_{GLMM}
Do communities differ between baseline marsh and mangal landscapes?	Abundance ~ Landscape + (1+ Landscape|Species), Data = baseline	5	659.99	653	0.46
Do communities differ by vegetation type within baseline landscapes?	Abundance ~ Habitat Type + (1+ Habitat Type | Species), Data = baseline	9	722.41	713	0.52
Do communities differ by landscape type?	Abundance ~ Landscape + (1+ Landscape|Species), Data = all	9	852.09	842	0.40
Do communities differ by vegetation type within the ecotone?	Abundance ~ Habitat Type + (1+ Habitat Type|Species), Data = ecotone	9	31.86	22	0.36
Do community differences by habitat type depend on landscape context?	Abundance ~ Habitat Type + Context + (1+ Habitat * Context|Species), Data = all	25	89.57	67	0.39

FIGURES

A)
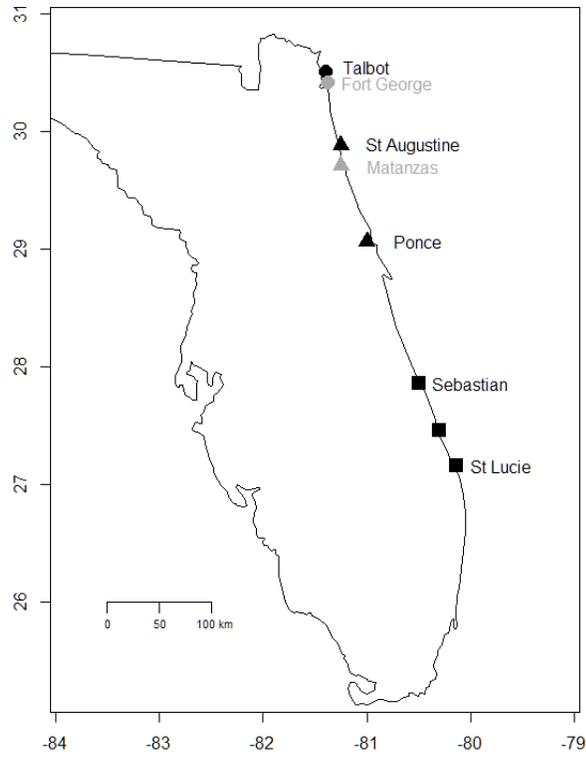
B)
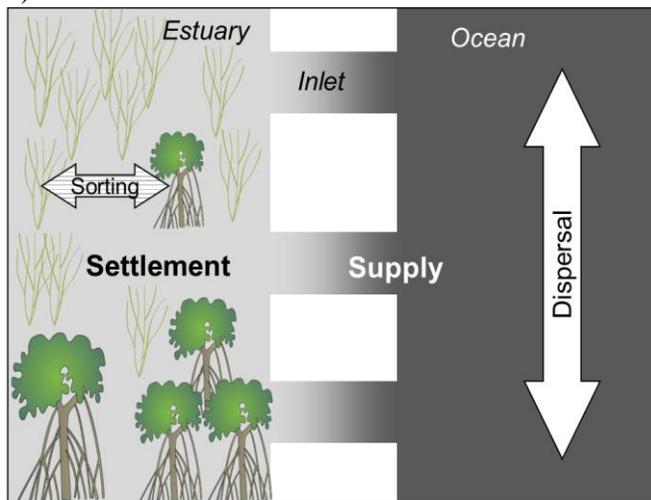
Figure 2.1: Supply and settlement surveys spanned four degrees of latitude along the Atlantic Coast of Florida (A). Symbols indicate study sites (each is an inlet): sites in black were sampled in 2013; sites in grey were added in 2014 in place of the three sites in the mangal landscape. Squares correspond to mangal forest landscape, triangles to ecotone, and circles to marsh. Larval supply was collected at every site. Settlement was characterized at the subset of named sites. (B) Theoretical representation of assembly processes (in arrows) most likely to affect community composition at the range edge and sampling (in **bold**) relative to coastal features (in *italics*). Neutral and stochastic processes can only be inferred from a reduction in or lack of sorting.

A)

B)
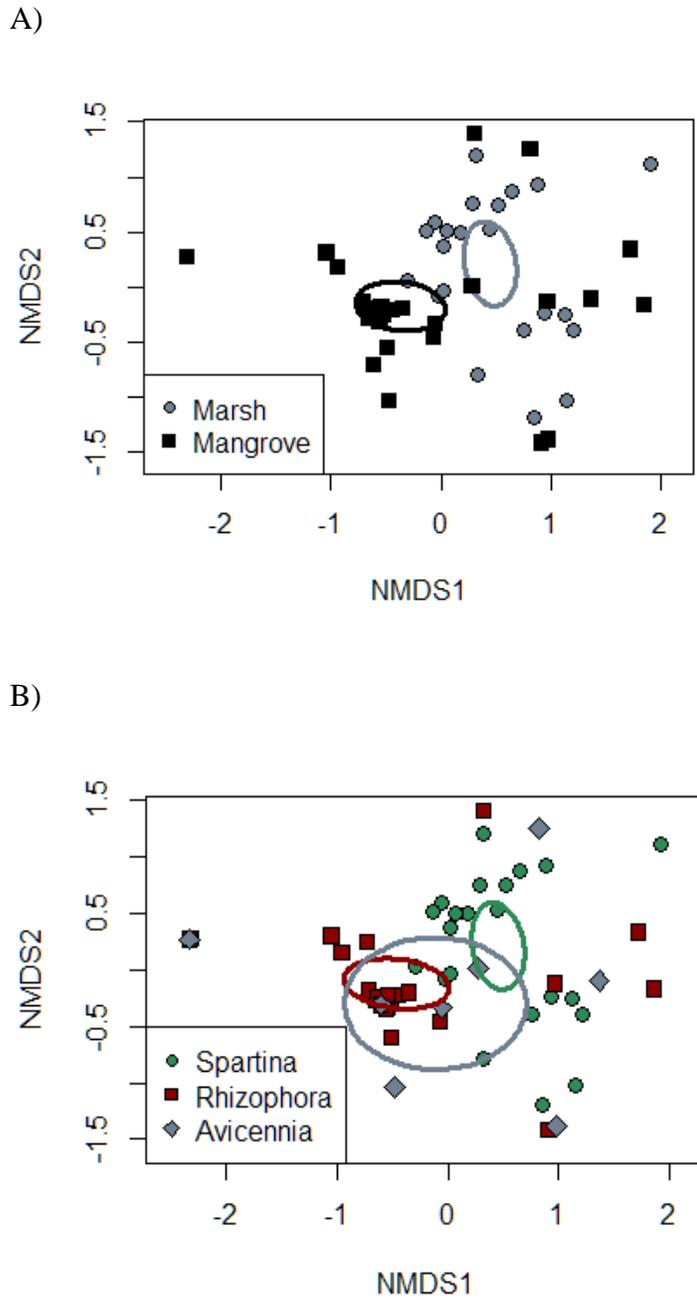
Figure 2.2: Settled communities differed significantly between A) marsh and mangal forest landscapes (north and south of the ecotone, respectively; nMDS stress=0.1) and B) *Rhizophora*, *Spartina*, and *Avicennia* habitat types (stress=0.1) where they occur in pure stands outside the ecotone. Plotted ellipses delineate 95% SE of the centroid.

A)

B)
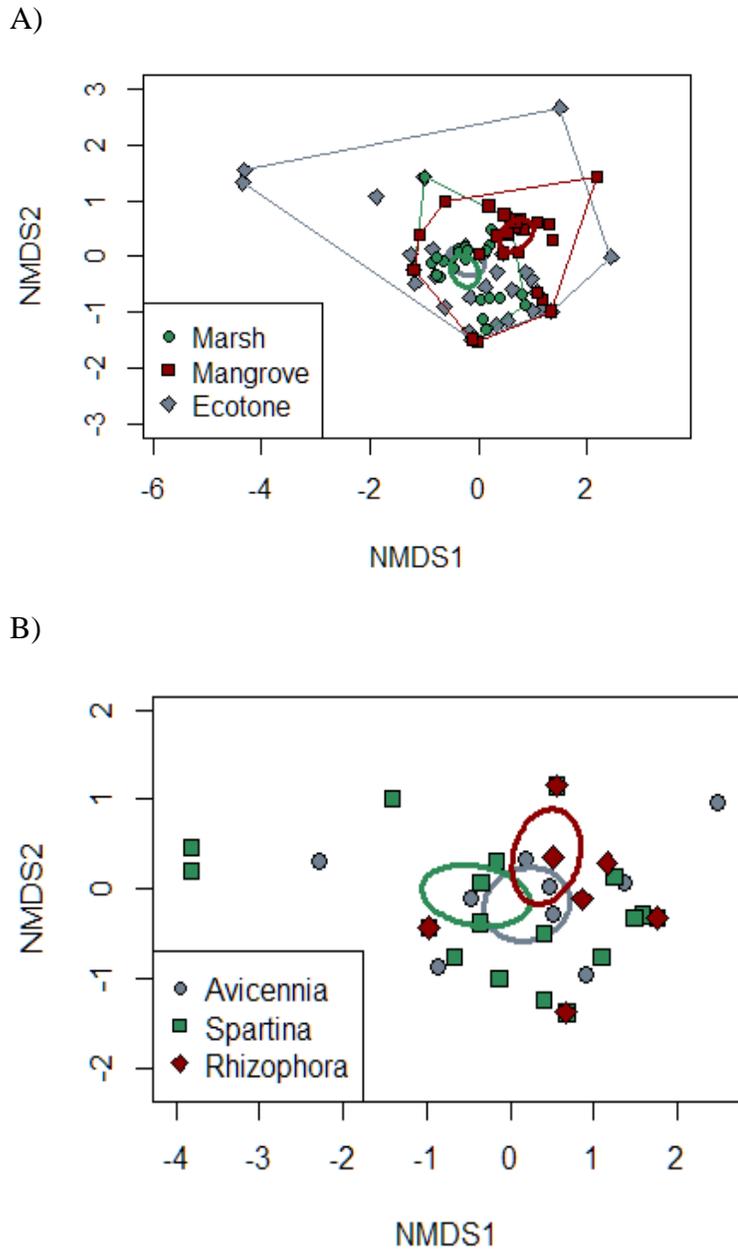
Figure 2.3: Settled communities differed significantly A) across all landscape types (stress=0.08). Ellipses delineate 95% SE of the centroid; fine lines delineate hulls to highlight differences in community dispersion. Settled communities were also distinct by B) habitat type in the mixed ecotone (stress=0.04; an outlier containing a single *Limulus* was removed for visualization); ellipses delineate 95% SE of the centroid.
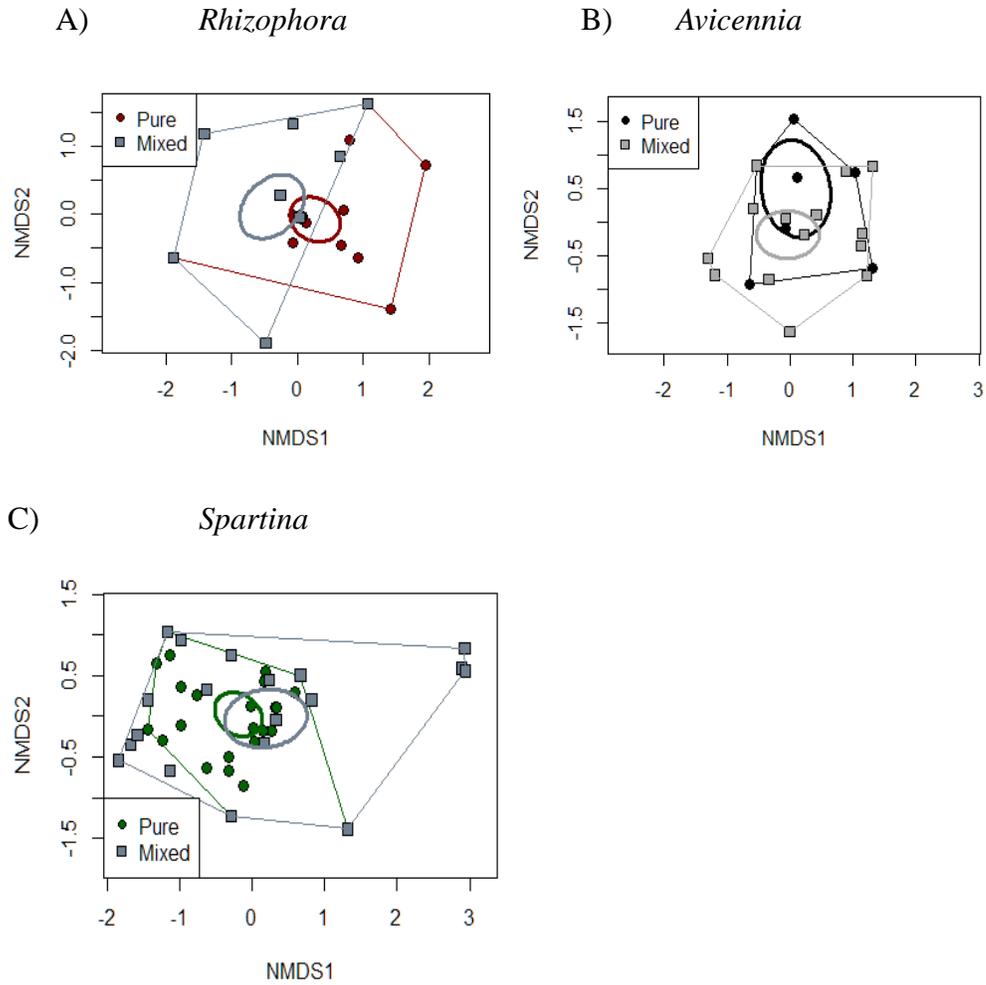
Figure 2.4: Settled communities were distinct by vegetation type, but within a vegetation type, communities differed by landscape (pure or mixed): A) *Rhizophora* (stress=0.03), B) *Avicennia* (stress=0.06; two outliers containing only a singleton each were removed for visualization), C) *Spartina* (stress=0.07). Ellipses delineate 95% SE of the centroid; fine lines delineate hulls to highlight differences in community dispersion.

Chapter 3: Habitat attributes and fine-scale sorting shape community composition among ecotone habitat patches

Abstract

  The impacts of range shifts on broader ecological communities will depend in part on how communities assemble in frontier landscapes of patchy habitat. Where foundation species meet, they form a patchy ecotone of habitats. As climate change shifts the distribution of foundation species, the patchiness of these ecotones will affect local structuring of community responses to climate change. The habitat cues used and scale(s) at which patches are distinguished will determine the precision with which inhabitants associate with habitat along range edges. In this study, I used a manipulative landscape-scale field experiment to evaluate marine community sorting in a mangrove-marsh ecotone. By deploying vegetation mimics on retrievable panels, I isolated macrofauna responses to physical structure and compared them to sorting at the broader patch scale, which accounted for all other habitat attributes, including production, shading, and chemical cues. Mobile marine fauna community composition was partitioned by site, habitat type, and physical structure, with differentiation detectable across nested scales from kilometers to centimeters. Fine and multi-scale responses to mangrove and marsh vegetation and their physical attributes indicate that inhabitant communities are sorting among habitat patches, even where they co-occur within the ecotone. As such, the marine macrofauna community is expected to closely track the emergence of mangrove vegetation as it shifts geographically with climate change.

Key words: climate change, ecotone, fragmentation, habitat patch, species sorting, structural complexity

Introduction

Climate change is shifting species distributions (Parmesan and Yohe 2003, Chen et al. 2011). Species responses to broader climate trends are shaped by habitat patchiness from local fragmentation and heterogeneity in topography and microclimate (Opdam and Wascher 2004, Luoto et al. 2007, Ashcroft et al. 2009, Cheung et al. 2009, Loarie et al. 2009, Harrison et al. 2010, Burrows et al. 2011, Bennie et al. 2013). Habitat fragmentation – breaking up of the landscape – can constrain climate-driven range shifts by reducing the accessibility of suitable habitat to dispersing inhabitants (Honnay et al. 2002, Opdam and Wascher 2004, Holyoak and Heath 2016). Where foundation species – those that form habitats – shift ranges, one habitat essentially invades another, forming a fragmented, patchy ecotone landscape (Bruno et al. 2003, Hoegh-Guldberg and Bruno 2010, Osland et al. 2013, Vergés et al. 2014). As with fragmentation, the patchiness of transitional landscapes is likely to contribute to local structuring of community responses to climate change (Wiens 1976, Lomolino and Weiser 2001, Bennett et al. 2006). To understand the contingency on range distributions created by landscape patchiness, we need to 1) determine the scale(s) at which inhabitant species sort in patchy landscapes and 2) identify the habitat attributes that contribute to sorting resolution. The attributes that inform habitat use and the scale(s) at which inhabitants distinguish between habitat types within an ecotone should determine the apparency of patches along the range

edge. Patch apparency, in turn, will affect the precision of habitat associations in transitional landscapes and, thus, apparent community responses to habitat shifts with climate change (Fahrig 2013).

Habitats created by foundation species shape the occurrence of fauna and can result in whole community facilitation (van Montfrans et al. 2003, Lindsey et al. 2006, Pirtle and Stoner 2010, Silliman et al. 2011). The attributes of foundation species can ameliorate abiotic stress, moderate species interactions, and provide food resources, thereby affecting habitat quality and the formation of associated communities (Bertness and Hacker 1994, Bruno and Bertness 2001). Some facilitative attributes, such as structural complexity formed by foundation species growth, arise at small scales early in habitat establishment (Humphries et al. 2011). Once habitat patches surpass a critical size, other habitat attributes may functionally emerge – differentiate from the surrounding landscape – at the stand-level (Bissonette et al. 1997, Lomolino and Weiser 2001, Bennett et al. 2006). Where foundation species shift ranges with climate change, the specific attributes of foundation species that resident organisms respond to will likely influence the scale of community responses in patchy transitional landscapes.

Much of the influence of foundation species comes from the structural complexity of their growth forms (Kohn and Leviten 1976, Hurlbert 2004, Ishii et al. 2004, Gols et al. 2005, McAbendroth et al. 2005, Lindsey et al. 2006, Graham and Nash 2012, Loke and Todd 2016). Structural complexity, which includes the variety of elements that form the physical three-dimensional structure of a habitat, increases surface area for foraging and can provide refuge from predation (Vance et al. 1996,

Primavera 1997, Rönnbäck 1999, Laegdsgaard and Johnson 2001, Meager et al. 2005, Layman 2007, Demopoulos and Smith 2010, MacKenzie and Cormier 2012, Tokeshi and Arakaki 2012). Beyond the facilitative effect of structural complexity *per se*, specific structural forms can affect the variety and size-scaling of refuges (McAbendroth et al. 2005, Bartholomew and Shine 2008, Warfe et al. 2008, Tokeshi and Arakaki 2012, Loke and Todd 2016). Sensitivity to structural complexity should occur on the scale at which inhabitants interact with the immediate physical substrate, such that species that are sensitive to structural cues should sort – i.e., differ in abundance by environmental conditions – at fine scales, promoting precise habitat associations even in nascent patches along transitional landscapes. Inhabitant sorting with other attributes that emerge more broadly at the patch scale of meters to tens of meters could lead to coarser resolution habitat associations. Habitat recognition and colonization based on stand-level attributes may not occur until vegetation patches reach some threshold area, below which cues and/or habitat extent are insufficient to elicit an associative response (e.g., small island effect; Lomolino and Weiser 2001, Fahrig 2013). Alternatively, species response to both stand-level habitat attributes and fine-scale structural cues could promote early community differentiation that develops further as habitat patches grow and establish.

Here, I evaluate marine macrofauna community sorting across spatial scales in a patchy wetland ecotone along the Atlantic Coast of Florida, USA. The mangrove and marsh species that compose the ecotone occupy comparable emergent intertidal zones, leading to equivalent inundation and availability to mobile marine macrofauna. However, they differ dramatically in production, seasonality, shading, and growth

form (woody or herbaceous, branching, emergent or overhanging; Ellison and Farnsworth 2001, Pennings and Bertness 2001, Friess et al. 2012). Where mangroves emerge within the marsh landscape during expansion with climate change (Saintilan et al. 2014), microhabitat changes in structural complexity are nested within changes in other attributes that become apparent at the broader patch scale as habitats establish. Especially in this tidal system, attributes such as production and shading emerge at the stand-level. Production, for example, is tidally exported from mangroves and marshes and thus is likely swamped by matrix vegetation production until emerging patches become extensive (Wolanski 1992, Odum et al. 1995, Lee 1995, Odum 2002).

Taken together, I hypothesized 1) that each mangrove and marsh vegetation type provides distinct habitat that is differentially inhabited by macrofauna, 2) that physical structural cues are among the suite of attributes that shape habitat quality and thus faunal response to each vegetation type, and 3) that sensitivity to these cues results in fine-scale associations that should enable precise habitat matching even within a patchy, shifting habitat landscape. I used a fully crossed manipulative field experiment to isolate the influences of vegetation structural complexity from other habitat attributes. I did not manipulate the specific attributes of complexity, but rather isolated the effects of vegetation structure from other habitat attributes at the stand level. The structural units included only the sub-tidal and inter-tidal elements of each wetland vegetation, which marine species interact most closely with. Thus, influences such as shading were captured at the habitat stand level. I used alternative groupings of samples to evaluate the scale(s) of community structuring and to disentangle the

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influences of vegetation structural complexity from broader habitat attributes. The results reveal structure in community composition across spatial scales, demonstrating sensitivity to both structural and non-structural attributes. Community sorting and responsiveness to cues across nested spatial scales in a patchy frontier landscape suggests that precise habitat associations minimize local influences of habitat configuration on community response to climate-induced range shifts.

Methods

Study sites

I established a manipulative landscape-scale field experiment to assess macrofauna (i.e., decapod crustacean and fish) habitat and structural associations along the patchy and shifting mangrove-marsh ecotone (Osland et al. 2013, Saintilan et al. 2014, Cavanaugh et al. 2014). Three vegetation types with distinctive structural forms dominate the ecotone landscape: *Spartina alterniflora* (smooth cordgrass) produces emergent shoots; *Avicennia marina* (black mangrove) produces emergent pneumatophores (i.e. snorkel roots); *Rhizophora mangle* (red mangrove) produces overhanging prop roots (Figure 3.1A). Throughout the study, genenric names refer to habitat-level attributes, while growth structures refer to physical structural complexity.

Structural complexity was manipulated by fitting 0.25 m^2 retrievable panels with vegetation mimics. Panels were deployed in patches of each habitat type such that comparisons of panel samples within and across habitats were used to test each prediction (Figure 3.2). The experiment was conducted along Halifax River and

Matanzas River to characterize patch use dynamics within the mixed vegetation ecotone (Figure 3.1b). Both sites are characterized by interspersed patches of vegetation covering tens of meters. The Halifax River site (29.09°, -80.94°) is a mangrove-dominated wetland north of Cape Canaveral that has small patches of *Spartina* that persist along shallow, sandy banks. Seventy kilometers north, the Matanzas River site (29.67°, -81.24°) is a historically saltmarsh-dominated wetland south of St Augustine where mangroves have proliferated in recent decades (Zomlefer et al. 2006, Cavanaugh et al. 2014, Rodriguez et al. 2016); *Avicennia* are abundant; *Rhizophora* are still rare (Williams et al. 2014).

At each site, experimental arrays were deployed adjacent to main waterways within 4.5 km of the inlet to minimize spatial variation in larval supply and estuarine environmental attributes (e.g. temperature, currents; Etherington and Eggleston 2000, Paula et al. 2001). During the study, sites had comparable salinity (mean±SE: 29±0.5ppt, Welch's t-test: df=145.78, p=0.95) and water temperature (26±0.4°C, Welch's t-test: df=134.25, p=0.22). Across sites, habitat patches were selected to provide a continuous edge of a single vegetation type with a total patch area >15 m^2. All patches had mixed sand, mud, and oyster substrates. A total of four patches per vegetation type were selected (n=12 patches total), with six patches at each site allocated according to the natural abundance of each vegetation type (three *Spartina*, two *Avicennia*, and one *Rhizophora* patch at Matanzas; one *Spartina*, two *Avicennia*, and three *Rhizophora* patches at Halifax). This design permitted me to test mobile macrofauna species sorting by habitat and vegetation structure type across the

ecotone to understand the factors shaping the community in a climate-shifted landscape. The study was conducted from May through November 2014.

Panel specifications

To test macrofauna responses to vegetation structure, I constructed retrievable 61 x 61 cm panels from ½ inch non-pressure treated plywood and populated each with artificial vegetation structures. Vegetation structures were affixed to the central 50 x 50 cm (0.25 m^2), leaving a 5 cm outer border for anchoring and retrieval. Mimics incorporated live vegetation but not detritus or encrusting organisms. Pneumatophores were constructed from ¼ inch birch dowels (24-27 cm tall). Prop roots were constructed from a variety of ½ to ¾ inch (1.3 and 1.9 cm) birch dowels, composed of six to seven "mainstems" with two to three lateral roots each affixed at ~60 degrees. Grass shoots were composed of 1/8th inch (0.3 cm) PVC rod with silk/polyester leaves glued at regular intervals (five blades per shoot); green plastic straws were placed over the lower stem to increase the diameter to ~4.6 mm. Within the 0.25 m^2 center of each panel, one of the three vegetation types was added at natural densities (227±99SD pneumatophores, 85±35 prop roots, or 150±41 shoots per m^2; Appendix I).

Experimental design & sampling

To characterize macrofauna composition across habitat types and vegetation structures, I deployed the artificial vegetation panels along the periphery of habitat patches in a balanced design across the pair of sites (Minello et al. 2008, Sheaves et

al. 2016). Each panel was deployed flush with the benthos and weighted with a brick and anchored with bent threaded steel rod at two opposite corners. Panels were then deployed in triplicate, including one of each vegetation structure within each habitat type (n=36 panels total or 12 per structure type across habitats and 12 within each habitat type; method as in Lindsey et al. 2006, Pardo et al. 2007; Figure 3.2). Control panels had structure that match their model habitat (e.g. grass shoots within a *Spartina* patch, Figure 3.2). Structural manipulation panels were distinct from their host patch (e.g. prop roots within a *Spartina* patch). Thus, panel treatment responses indicate the effects of physical structure alone, while productivity and other attributes remain controlled by the habitat matrix at the patch level.

Panels were sampled every other week from mid-May through early November (n=13 sampling events) within three days of full and new moons. The panel sampling method mimics widely used reef monitoring approaches (NOAA autonomous reef monitoring structures [ARMS]; Brainard et al. 2009). To sample the panel contents, a PVC-framed cube (55 cm per side) lined with 1 x 2 mm mesh on all but one side – edged with foam-rubber – was quickly placed over a panel and pressed down to create a seal. The cube was strapped to the panel, and the entire unit was lifted and flipped over so that the panel could be rinsed into the cube. Panel contents were concentrated in the mesh cube and then rinsed through a 500 µm sieve. Decapod crustaceans and fish were measured by carapace width or total length, identified to (morpho)species, and released in compliance with University of Maryland IACUC protocol (R-12-64). The retrieval method was designed to capture nursery stage individuals – primarily juvenile crustaceans and fish. Although the sampling design

was not optimal for capturing large or fast-swimming individuals, finfish and

swimming crabs were captured regularly. Retained individuals ranged from 0.5 mm

to 100 mm. After sampling, panels were immediately redeployed. May samples were

used to establish species identities. Results are reported for samples collected from

June through November 2014 (n=11 sampling sessions). Samples grouped by panel

structure, habitat type, or treatment (control or manipulation) allowed me to test for

differences in macrofauna community composition across each predictor.

Analysis

Analyses were conducted by morphospecies (most identified to genus or species) and

excluded species that occurred two or fewer times. Community composition was

tested relative to habitat type (*Rhizophora, Avicennia, Spartina*) and structure type

(prop roots, pneumatophores, grass shoots) predictors, though the effect of site was

also evaluated. Panel treatment (control or manipulation) was used primarily to

constrain data for hypothesis testing. All analyses were conducted within the program

R version 3.2.3 (R Core Team 2015). Dispersion was evaluated with the betadisper

function in the vegan package in R. Dispersion was generally uneven between

predictor levels (violating the PERMANOVA assumption of homogeneity of

variances), thus I conducted all community analyses with generalized linear mixed

effects models (GLMM) with species counts modeled with the Poisson distribution

link function in the glmer function in the lme4 package in R (Bates et al. 2015).

Within GLMMs, I used the random effect model structure "(1+predictor|species)" to

write random slopes models that allow changes in community composition via

species-specific responses (Bolker et al. 2009, Johnson 2014). All models also included the predictor as a fixed effect to account for overall differences in abundance. Model performance was optimized with the "bobyqa" control function to adjust for over-conservatism in model convergence in later versions of lme4 (K. Edwards, *personal communication*). Diagnostics and model selection follow (Bolker et al. 2009); specifically, the significance and explanatory contribution of each predictor was determined from Likelihood Ratio Tests and changes in information criterion scores (AICc) between full and simplified models; terms that elicit greater score changes (ΔAICc) have more explanatory power. I also used the r.squaredGLMM function in the MuMIn package (Barton 2015) to calculate pseudo-R^2 values that represent the absolute value of goodness-of-fit for each model (Nakagawa and Schielzeth 2013, Johnson 2014); marginal R^2_{GLMM} indicates the amount of total variation explained by the fixed effects, while conditional R^2_{GLMM} indicates the combined explanatory power of fixed and random effects. The explanatory power of fixed effects was often very low, so here I do not report marginal R^2_{GLMM} in cases where it fell below 0.01; in those instances fixed effects were negligible, so conditional R^2_{GLMM} effectively measured random effects. Species contributing to significant groupings were identified by plotting modeled species-specific responses to each predictor (Appendix 3.1). For visualization, community composition data were standardized within each sample to control for abundance and then plotted relative to each predictor with a Bray-Curtis distance metric in a constrained ordination (canonical analysis of principle components: CAP) using the vegan package in R.

I first checked for community differences by site, corresponding to differences in the local species pool. Combining data across sites, I tested whether community composition differs between mangrove and marsh vegetation types, given the entire suite of cues. To determine whether structural cues and/or stand-level habitat attributes alone were sufficient to stimulate community sorting, I compared communities only on panels deployed out of context (i.e., in patches other than their model habitat). For these, community pattern by panel type indicated independent influences of structural complexity, while community pattern by habitat type indicated independent influences of non-structural habitat attributes (emerging at the stand-level). Finally, I held habitat constant while varying structure and held structure constant while varying habitat to determine contributory influences and interactions of the two predictors. Finally, I conducted a dispersion analysis using the PERMDISP function in the vegan package in R to test 1) whether community composition was more diffuse when structural cues and habitat context were mismatched (Dixon 2003) and 2) whether *Avicennia* presents a transitional habitat with higher dispersion due to community mixing (Kark 2013).

Results

Out of 396 retrieved panels, three-hundred and eighty-three (383) were occupied. I ultimately sampled and characterized 1920 individuals from Matanzas River and 1122 individuals from Halifax River. The final data included twenty-four species and morphospecies, predominantly crabs, shrimp, and fish. Several taxa were at least one order of magnitude more abundant than all other species. At the

taxonomic resolution identified, particularly abundant taxa were caridean shrimp (infraorder Caridea), penaeid shrimp (Penaeidae), *Gammarus* amphipods (Gammaridae), gobies (Gobiidae: Gobiinae and Gobionellinae), *Aratus pisonii* (Sesarmidae), and *Callinectes* spp. (Portunidae). Abundant isopods (order Isopoda) included members of Limnoriidae, but other families also may have been represented.

Contributing predictors

Community composition on retrievable panels (n=383 repeated observations) was significantly distinguishable between sites, habitats, and structure types. Site had the strongest effect on macrofauna composition (ΔAICc=858 from combined GLMM; individually tested: Likelihood Ratio Test χ^2=1122, df=5, p<0.0001, conditional R^2_{GLMM}=0.22). Caridean shrimp and gobies were more strongly associated with the marsh-dominated site (Matanzas River), while *Gammarus* amphipods, *A. pisonii*, *Callinectes* spp., isopods, and penaeid shrimp were associated with the mangrove-dominated site (Halifax River) (Figure A3). Despite differences in species composition between sites, macrofauna composition responded significantly to habitat (ΔAICc =213) and physical structure (ΔAICc =219) at smaller scales.

Community differentiation by habitat type: baseline assessment

To get a baseline understanding of how communities differ by vegetation type within the ecotone, I first examined macrofauna community composition by habitat type on control panels, where structural complexity matches the surrounding habitat patch. This comparison confirmed that mangrove and marsh vegetation types were

used differently by macrofauna, leading to significant differences in community structure across vegetation types in the ecotone (GLMM: χ^2=287.58, df=9, p<0.0001, conditional R^2_{GLMM}=0.22). Vegetation type explained at least 10% of the variation in community composition (CAP: df=2, pseudo-F=6.19, p=0.001; Figure 3.3A). Composition differences were due primarily to the associations of caridean shrimp and amphipods with *Spartina*, penaeid shrimp and *Callinectes* spp. with both mangrove species, isopods and *A. pisonii* with *Rhizophora*, and gobies with *Avicennia* (Figure A3). *Avicennia* communities fell intermediate to *Rhizophora* and *Spartina* communities in ordination space (Figure 3.3A).

Contributory influences of stand-level attributes and physical structure

Based on manipulation panel samples – those for which physical structure is independent from other habitat-level attributes – habitat alone, with any attributes controlled at the patch level, was sufficient to elicit distinct community assemblages (GLMM: χ^2=339.97, df=9, p<0.0001, conditional R^2_{GLMM}=0.18). Stand-level habitat attributes explained at least 2% of the variation in community composition (CAP: df=2, pseudo-F=2.52, p=0.001; Figure 3.3B). Caridean shrimp were associated with *Spartina*, penaeid shrimp and *Callinectes* spp. with *Rhizophora*, and isopods with mangrove habitat in general (Figure A3).

Manipulation panel samples revealed that vegetation physical structure alone also was sufficient to elicit distinct community assemblages (GLMM: χ^2=125.53, df=9, p<0.0001, conditional R^2_{GLMM}=0.17). Physical structure explained at least 2% of the variation in community composition (CAP: df=2, pseudo-F=1.97, p=0.004;

Figure 3.3C). Caridean shrimp, *Callinectes* spp., and amphipods were associated with shoots, *A. pisonii* with prop roots, and penaeid shrimp with pneumatophores. Gobies were associated with mangrove structures in general (Figure A3).

Explanatory power was higher on control panels, where physical and stand-level cues match, compared to manipulation panels (conditional $R^2_{GLMM} = 0.22$ and 0.18, respectively; Figure 3.3A,B). Accordingly, community composition was expected to be more dispersed in ordination space on manipulation structures compared to controls. Dispersion was greater on structural manipulations compared to controls in *Rhizophora* (F=3.09, Tukey's adjusted p=0.048) and *Spartina* habitats (F=19.9, Tukey's adjusted p<0.0001), but the opposite pattern emerged in *Avicennia* (F=16.9, Tukey's adjusted p=0.002; Figure 3.4).

Finally, if *Avicennia* serves as a transitional habitat, as suggested by prior results that place communities in *Avicennia* intermediate to those in *Rhizophora* and *Spartina*, then communities there may be more dispersed in ordination space. However, dispersion did not differ significantly between *Rhizophora*, *Avicennia*, and *Spartina* habitats (p>0.05).

Discussion

The scales of community structure in patchy landscapes can help reveal the cues and processes that drive species sorting and habitat associations (Hovel and Fonseca 2005, Pallas et al. 2006, Henry et al. 2013, Bennie et al. 2013). By monitoring mobile marine fauna community composition across a patchy wetland ecotone, I found that macrofauna responses to structure and habitat were strong

enough to override community differences between mangrove- and marsh-dominated ecotone sites. Inhabitant communities differed between each mangrove and marsh vegetation type overall and in response to isolated stand-level attributes and structural complexity. Community differences by structure and habitat type suggest that macrofauna are sensitive to a suite of cues and habitat attributes that allow them to distinguish between and occupy mangroves and marshes at nested scales, from microhabitat to landscape, even along the habitat range edge. Indeed, site differences suggest a kilometer-scale response to habitat dominance (Fahrig 2013). Each predictor explained unique variation in community composition and contributed to the overall community response to mangroves and saltmarsh within the mixed vegetation ecotone.

Each set of cues (structural and non-structural) was sufficient to shape the community, but neither was necessary for the formation of distinct habitat-associated communities. As I hypothesized, both smaller-scale vegetation structural cues and broader habitat attributes contributed to community responses. Each mangrove and marsh vegetation type hosted distinctive macrofauna communities, which were most distinguishable where physical structure matched habitat type (i.e., lower variance on control panels). The use of constructed structural mimics on the panels isolated the influence of physical structure, making the driver of small scale associations clear, but patch-scale associations could originate from sensitivity to a broad suite of stand-level attributes. Especially in tidally-controlled systems, productivity and associated chemical cues are exported during outwelling, such that both are effectively controlled by stands of habitat (Odum 2002). Some physical features, such as

shading, may also depend on the presence of a threshold area of habitat and thus

emerge at the patch level (Dibble et al. 1996, Ellis and Bell 2004, Verwey et al.

2006). Each of these patch-level attributes is known to affect marine communities,

and any of them could be driving the differences in community composition at the

habitat scale in this study (Glasby 1999, Morinière et al. 2003, Ellis and Bell 2004,

Verwey et al. 2006, Nagelkerken et al. 2008, Dixson et al. 2014). Further

experimentation will be needed to identify the specific attributes driving patch-level

community sorting.

General community sorting across vegetation types in the ecotone

Community structure among vegetation types was most distinctive in the

presence of matching structural and stand-level attributes. Community composition in

Spartina – the recipient habitat type – differed more from composition in *Rhizophora*

than from composition in *Avicennia*. There are several possible explanations for this

pattern. First, *Avicennia* is the pioneer species that extends farthest into the temperate

marsh landscape (maximum latitude 30.48°) and likely has been intermixed the

longest (Williams et al. 2014, Cavanaugh et al. 2015, M. Hayes, pers. comm.).

Avicennia dominate the ecotone landscape, providing a transition between *Spartina* to

the north and *Rhizophora* to the south (maximum latitude 30.41°; Williams et al.

2014, M. Hayes, pers. comm.). As such, *Avicennia* may receive the most exposure to

marine fauna that are common in both landscapes, leading to a hybrid and therefore

less differentiated assemblage in the transitional *Avicennia* habitat (Attrill and Rundle

2002, Kark 2013). However, the community in *Avicennia* was not more dispersed in

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ordination space than communities in the other habitats, casting doubt on the hybrid zone hypothesis. Alternatively, the greater similarity between *Spartina* and *Avicennia* communities could arise from similarity in their intertidal growth structures. *Spartina* shoots and *Avicennia* pneumatophores are both thin, emergent, and densely spaced (Appendix 1). *Rhizophora* prop roots are broader, woodier, and grow downward from overhanging branches. Finally, pneumatophores may simply provide poor structural refuge and weak associated cues, leading to fewer species associations and weaker community sorting in *Avicennia* habitat (Primavera 1997). Differences in assemblages in each habitat type may originate from species-specific responses to these structural or stand-level attributes.

Sorting by specific attributes

Identifying the scales of habitat associations and their relation to particular habitat attributes can help us understand how ecological communities are likely to respond to changes in habitat availability and arrangement as climate change shifts the ranges of habitat-forming species (Loarie et al. 2009, Saintilan et al. 2014, Vergés et al. 2014). Habitat selection and use can be shaped by a variety of cues, including those from predators and conspecifics and from habitat productivity and structural complexity; responses to these cues vary with spatial scale (Rittschof et al. 1998, Forward et al. 2001, Diele and Simith 2007, Dixson 2011, Dixson et al. 2014). Compared to overall associations by vegetation type as a baseline, responses to isolated structural or stand-level attributes reveal the underlying drivers of individual species' associations in the mangrove-marsh ecotone.

The general vegetation affinities of peneaid shrimp, isopods, and *Callinectes* spp. corresponded to their preference for stand-level habitat attributes independent of structural cues. Isopods were associated with both mangrove habitats (*Rhizophora* and *Avicennia*); penaeid shrimp and *Callinectes* spp. were associated with *Rhizophora* habitat. Isopods and penaeid shrimp are both broadly mangrove-associated (Primavera 1997, Warne 2013), due at least in part to their dependence on woody substrate for boring and direct consumption, respectively. *Callinectes* spp., which were predominantly juveniles in this study, have not been well studied within mangroves, so their affinity for *Rhizophora* habitat requires further study (see Chapter IV).

Notably, *Callinectes* spp. and penaeid shrimp also demonstrated affinities based on structural complexity, but not for the same vegetation type that they preferred overall. Both species were associated with *Rhizophora* habitat, but *Callinectes* spp. preferentially occupied grass shoots, while penaeid shrimp occupied pneumatophores. Both taxanomic groups may be drawn to *Rhizophora* attributes available at the stand level such as primary production or shade, while preferring to occupy other, finer structure (Minello and Zimmerman 1985, Forward et al. 1996, Minello and Webb 1997, Primavera 1997, Johnston and Lipcius 2012). In many biogenic habitats, one foundation species supports smaller foundation species that secondarily facilitate inhabitant fauna (a facilitation cascade; Angelini et al. 2011, Bishop et al. 2013). Mangroves, especially *Rhizophora*, often support epibionts such as oysters, sponges, and algae that form finer secondary structures that provide more effective refuge for inhabitant communities than the mangrove roots themselves

(Bishop et al. 2013, Schutte 2014, Hughes et al. 2014). Thus, the counterintuitive affinity for finely structured shoots and pneumatophores despite preference for *Rhizophora* habitat is likely explained by inhabitants' use of secondary habitat structures, resolving the apparent discrepancy between habitat preference and structural affinity.

Physical structure alone also was sufficient to affect community composition when experimentally controlling for the surrounding habitat type. Gammarid amphipods and *Aratus pisonii* (mangrove tree crab) habitat associations matched their responses to independent cues of structural complexity, suggesting that structure provides the key cue that informs their associations with *Spartina* shoots and *Rhizophora* prop roots, respectively. *Aratus pisonii* depends on the woody structure of mangroves for foraging and refuge (Wilson 1989, Sheridan 1992). Although *A. pisonii* also occupy *Avicennia*, they generally inhabit the trunks and branches, which were not included in this study of intertidal structures. Of the elements structuring the low intertidal, only *Rhizophora* prop roots provide sufficiently woody structure for *A. pisonii*. The origin of gammarid amphipod's structural affinity is less clear. They are epiphytic grazers and detritivores that occupy and often find refuge within seagrasses and macroaglae (Zimmerman et al. 1979, Duffy 1990, Duffy and Hay 1991). Dense and structurally complex grass shoots may supply small spaces and high surface area that provide an optimal combination of epiphyte food supply and refuge.

Finally, sensitivity to habitat attributes was not always discordant or independent between scales capturing structural and non-structural effects: caridean shrimp strongly preferred grass habitat, based on the independent influences of both

fine scale structure and stand-level non-structural attributes. Gobies were associated

with *Avicennia* vegetation overall, matching their previously documented preferences

(MacKenzie and Cormier 2012), but showed no particular association with

independent physical structure or stand-level attributes. However, they were more

prevalent at the Matanzas River site, where *Avicennia* is abundant in the landscape.

Many other species had nuanced responses to habitat and structure or demonstrated

no sensitivity to either set of attributes. Notably, the short sampling interval (two

weeks) and small grain size (50 cm^2) of the experiment make my estimates of

community sorting conservative. Nonetheless, I found that macrofauna sort quickly

and finely among alternative, co-occurring habitats. Inhabitants' responses to habitat

type and vegetation structure indicate 1) that the marine community is sensitive to

shifts in wetland composition and 2) the spatial and temporal scales at which wetland

changes elicit macrofauna community responses.

Scales of sorting: Implications for community structure in the ecotone

The documented sensitivities to specific structure types contradicts prior

evidence that structure *per se* is more influential than structure type (Primavera 1997,

1998, Rönnbäck 1999, Heck et al. 2003, Ellis and Bell 2004, Nagelkerken et al. 2010,

Grol et al. 2011, MacKenzie and Cormier 2012). Studies often use rough proxies such

as rocks versus sand to examine responses to structured and unstructured habitat

(Moksnes 2002, Lindsey et al. 2006). Others have examined effects of complexity by

deploying sampling units on bare substrate, which can inflate settlement responses

due to thigmotaxis within a barren landscape (Paula et al. 2006, Pallas et al. 2006,

Pan et al. 2010). Both of these study approaches likely bias results towards highlighting the effects of structure *per se* over the effects of specific structural attributes. The added realism of structural mimics deployed among patches of vegetated habitat may have helped reveal the sensitivity to specific structural forms documented here. Moreover, the importance of specific structural forms may have been underestimated in prior studies if, as seen here, structural affinity is not always closely tied to structural refuge from predation, which has been most commonly studied. Structure may also be influential if it is necessary for basic behavior and functions, such as foraging by arboreal crabs and epiphytic grazers.

Evaluating use of alternative habitats in a patchy landscape can help us understand how ecotone landscapes affect inhabitant community responses to foundation species expansion with climate change. By identifying the cues that drive associations and the scales at which those associations arise, we can begin to understand how much habitat or which habitat attribute is necessary to elicit a community response to foundation species emergence along range edges (Henry et al. 2013, Fahrig 2013). Within the wetland ecotone, marine fauna sorted among mangrove and marsh vegetation types. Fauna responded to both fine-scaled physical structure and broader stand-level attributes. Thus, I expect immediate and fine scale responses of fauna to the emergence of mangrove structure in the landscape, with sorting becoming stronger as mangrove patches expand and stand-level attributes emerge. This nested and finely structured response suggests that marine fauna will remain closely associated with expanding mangroves even where they occur patchily along the range edge. This study joins a growing body of literature that demonstrates

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that small-scale factors can influence species' responses to climate-driven range shifts by shaping their use of patchy landscapes (Honnay et al. 2002, Opdam and Wascher 2004, Lenoir et al. 2010, Bennie et al. 2013, Moritz and Agudo 2013, Holyoak and Heath 2016). Based on the fine and nested scales of community sorting documented here, the patchiness of the ecotone is unlikely to diminish associations near the mangrove range edge. Similar studies of the scales and attributes that influence community sorting may help explain species associations in other climate-shifted systems where range edges form patchy habitat landscapes.

FIGURES

A)

B)
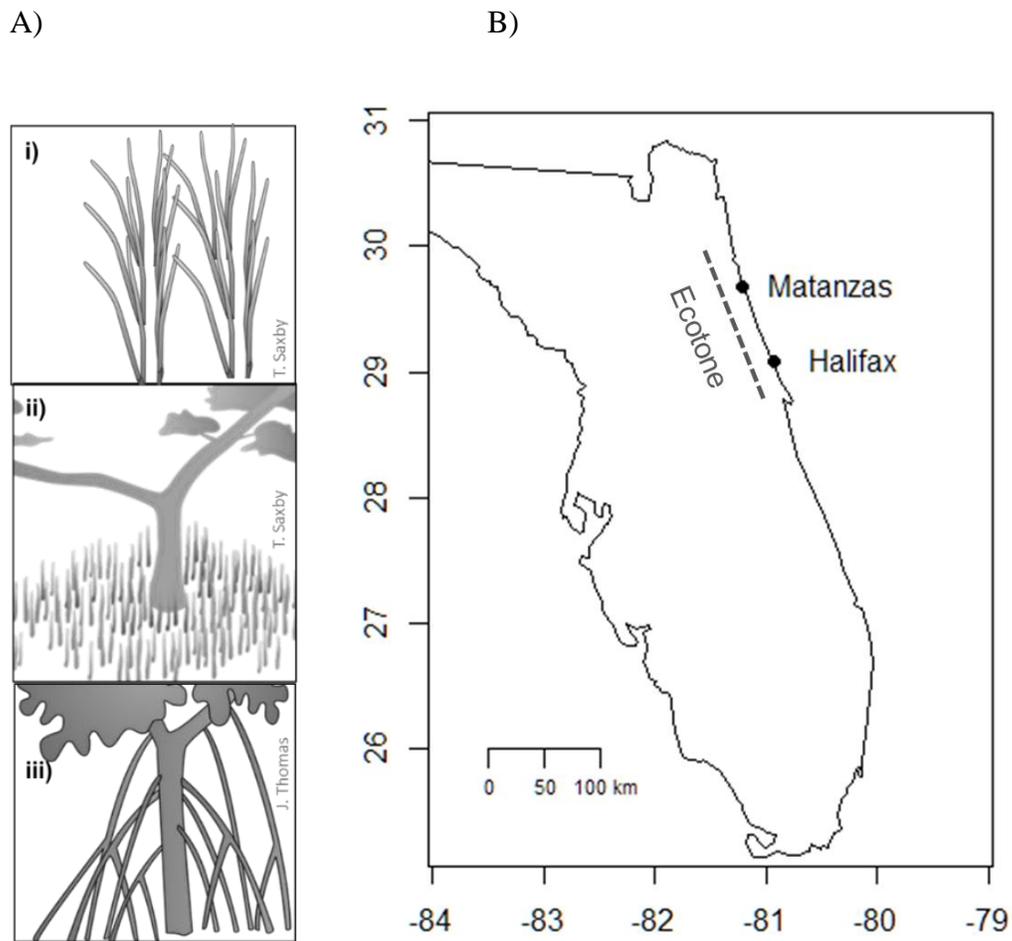
Figure 3.1: The study of habitat use by mobile marine macrofauna included (A) the three vegetation types i) *Spartina alterniflora* (smooth cordgrass) shoots, ii) *Avicennia germinans* (black mangrove) pneumatophores, and iii) *Rhizophora mangle* (red mangrove) prop roots where they co-occur at two sites (B) along the ecotone.

A)
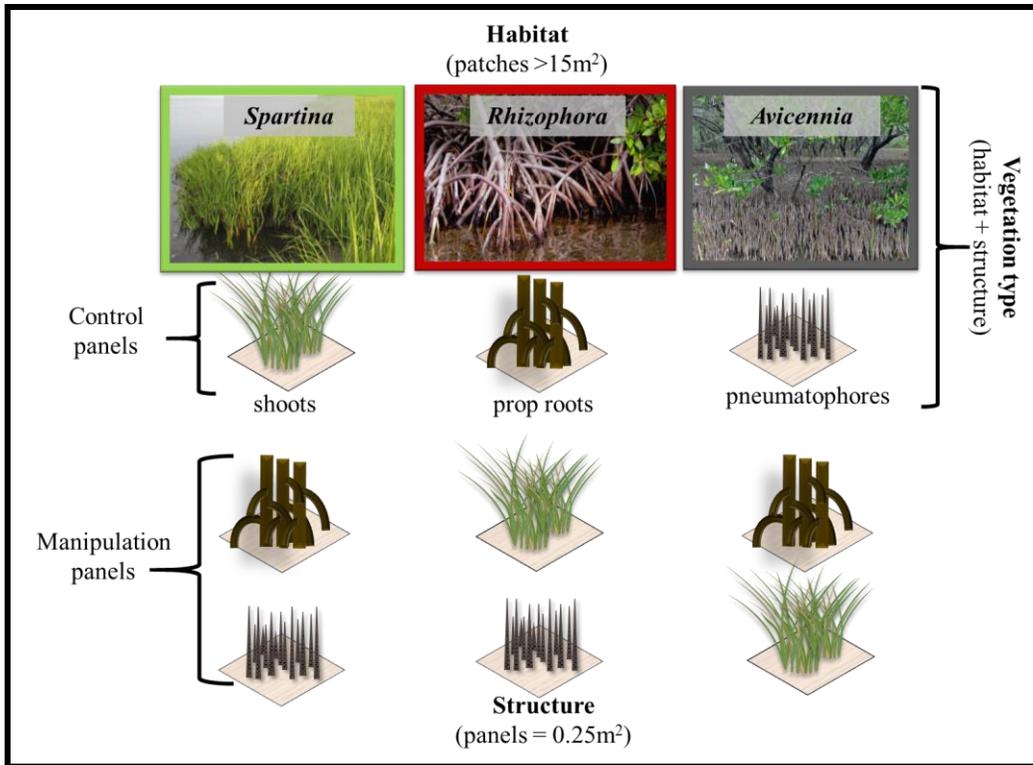
B)   C)

Figure 3.2: A) For the study, a series of retrievable panels outfitted with vegetation structural

mimics were deployed among habitat patches in the field; the fully crossed design allows the

effects of structural complexity to be isolated from stand-level habitat attributes based on

various groupings of samples by patch and panel type. B) A complete set of structures on

retrievable panels deployed along the margin of a *Rhizophora* patch. D) Control panels, where the artificial structure (grass shoots, right) matched the surrounding habitat patch (*Spartina*, left), were used to test overall differences in community composition by vegetation type, given all habitat cues.

A)
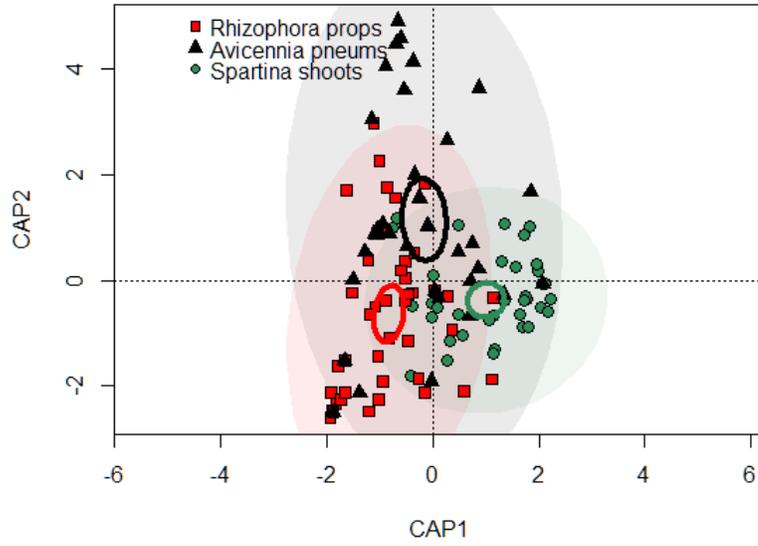
B)
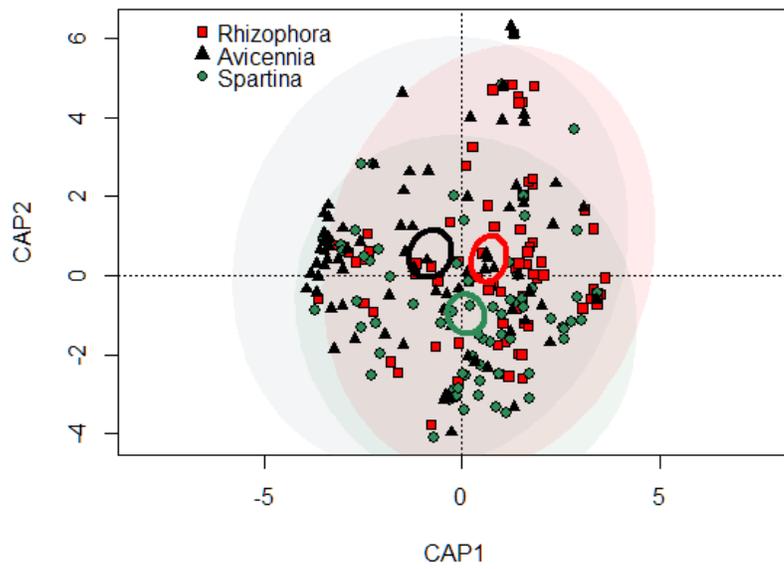
C)
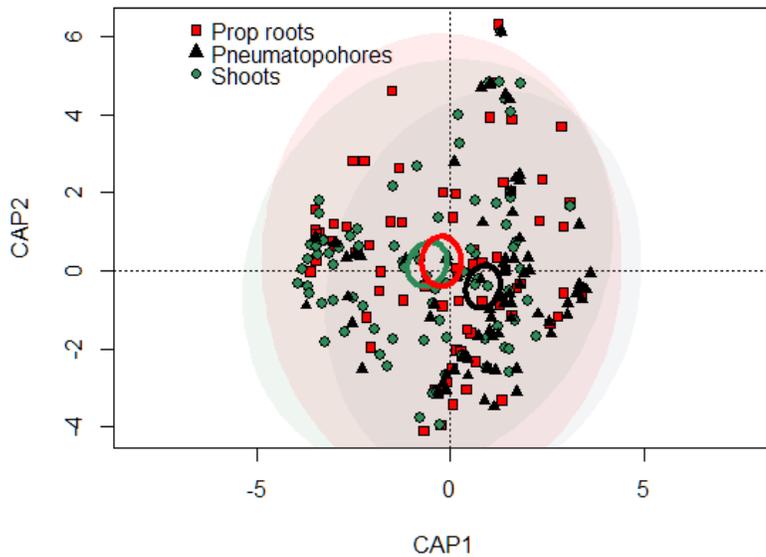
Figure 3.3: CAP constrained ordination illustrates that (A) community composition differs between vegetation types when compared on control panels, where physical structure matches broader habitat cues (e.g. prop roots within *Rhizophora*). On control panels, communities are most distinctive between *Spartina* and *Rhizophora* habitat, with communities in *Avicennia* falling more intermediate. CAP1 and CAP2 incorporate 78% and 22% of the constrained variation, respectively. Figure panels B and C depict comparisons of samples from manipulation panels (without two outliers that contained only one species each), where structure is independent of broader habitat attributes. For both, CAP1 and CAP2 incorporate 52% and 28% of the constrained variation, respectively. (B) Community composition differs by habitat type, regardless of the immediate physical structure. (C) Community composition differs by physical structure, regardless of surrounding habitat. Shaded ellipses delineate 95% confidence SD; circles indicate 95% SE of the centroid. Differences in the number of points between the two plots is due to 1/3 of panels categorized as control, while 2/3 are characterized as manipulations.

Rhizophora
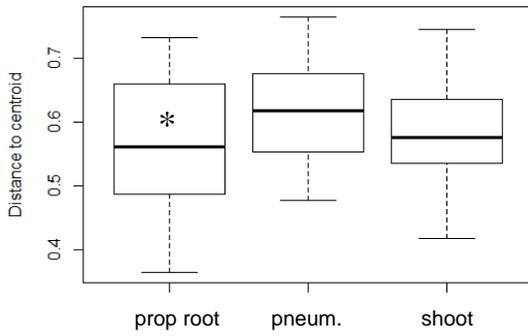
Spartina
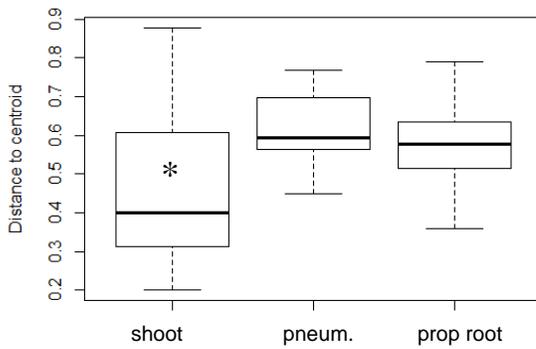
Avicennia
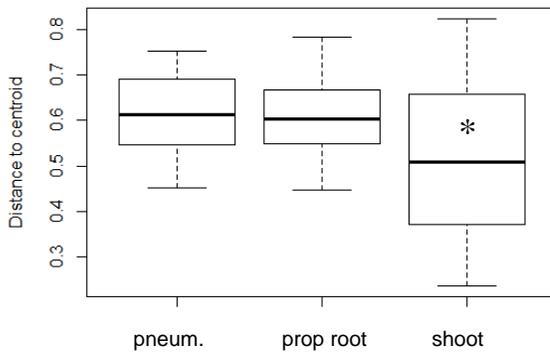
Fig 3.4: In *Spartina* and *Rhizophora* habitats, dispersion patterns indicate that communities are more distinct (less dispersed in ordination space) on control panels compared to other panels that represent a mismatch between structural and habitat cues. The pattern does not hold in *Avicennia* habitat. Control panels are always on the left.

Chapter 4: Mangrove expansion into temperate marshes alters habitat quality for recruiting estuarine fauna

Abstract

Climate change is driving geographic shifts in species distributions. Range shifts by foundation species can cause one biogenic habitat to be replaced by another, such that climate change is causing indirect changes in habitat beyond direct habitat reductions. To evaluate how climate-driven shifts in habitat-forming species affect inhabitant population dynamics, I evaluated marine fauna use of mangrove and marsh habitats where they co-occur, with particular attention to differences in structural attributes and their effects on habitat quality. I coupled recruitment surveys and lab experiments to assess the influences of foundation species structural and non-structural attributes on portunid crab recruitment, preference, and survival among mangrove and marsh habitats. Recruitment was evident only in *Spartina alterniflora* and *Rhizophora mangle* intertidal habitats, which share a complex, branched growth architecture. In lab trials, the branched growth structures also were preferred in the presence of predation risk and provided the highest probabilities of survival, indicating that settlers can distinguish among ecotone vegetation types, and that their choices correspond to habitat quality. The change in habitat quality and use with mangrove expansion into saltmarshes highlights the influence that changes in foundation species, and their structural attributes, can have on inhabitant marine fauna population dynamics. Shifts between biogenic habitats need to be more

carefully studied and, where appropriate, added to measures of climate-driven habitat loss.

Key words: biogenic habitat, climate change, ecotone, foundation species, habitat preference, post-settlement mortality, Portunidae, range shifts, structural complexity

<u>Introduction</u>

Population dynamics depend on the habitat that a species occupies. Recruitment and vital rates often vary even among co-occurring habitat types (Minello et al. 2003, Pirtle and Stoner 2010, Grol et al. 2011, Johnston and Lipcius 2012). During settlement, many species select habitat to optimize survival before making choices that optimize growth (Halpin 2000, Dahlgren and Eggleston 2000, Johnston and Lipcius 2012). Biogenic habitat created by the growth of foundational organisms plays an important role in increasing survival by providing refuge from predation (Halpin 2000, Dahlgren and Eggleston 2000, Beck and et al 2001, Bruno and Bertness 2001, Grol et al. 2011, Johnston and Lipcius 2012, Tokeshi and Arakaki 2012). Habitat structural complexity – the three-dimensional arrangement of structural elements – mediates survival by shaping the availability, diversity, and suitability of refuges (Bartholomew et al. 2000, Dahlgren and Eggleston 2000, Bartholomew and Shine 2008, Nagelkerken et al. 2010, Johnston and Lipcius 2012). Accordingly, marine macrofauna reliably prefer structurally complex habitats (Minello and Zimmerman 1985, Tupper and Boutilier 1997, Halpin 2000, Heck et al.

2001, 2003, Minello et al. 2003, van Montfrans et al. 2003, Schofield 2003, Pallas et al. 2006, Nagelkerken et al. 2010).

Climate change and anthropogenic stressors are modifying marine habitat around the globe by reducing the abundance of habitat-forming species and shifting species distributions (Harley et al. 2006, Hoegh-Guldberg and Bruno 2010). Sea level rise, warming temperatures, eutrophication, and coastal squeeze are all contributing to regime shifts and the loss of habitat-forming species (Scavia et al. 2002, Alongi 2008, Hoegh-Guldberg and Bruno 2010). Climate change is also redistributing species geographically, which can cause foundation species to replace one another without a loss of biogenic habitat *per se* (Stachowicz et al. 2002, Poloczanska et al. 2013). Where foundation species are lost, secondary declines of inhabitant fauna are attributed to reduced habitat quality with the loss of structural complexity (e.g., transitions from coral reef to algal turf and kelp forest to urchin barrens; Knowlton 2001, Steneck et al. 2002, Feary et al. 2007, Hoegh-Guldberg et al. 2007, Ling 2008, Baker et al. 2008, Dixson et al. 2014, Vergés et al. 2014). Inhabitant fauna have declined less markedly where one structurally complex habitat is replace by another (e.g., seagrass to macroalgae; Johnston and Lipcius 2012). To better understand how climate-driven shifts in foundation species affect inhabitant species, I evaluated species sorting among alternative biogenic habitats where they co-occur, paying particular attention to the effects of differences in vegetation structural attributes on habitat quality.

Throughout the world, coastal wetlands are being reshaped by the poleward shift of tropical mangroves into temperate saltmarshes (Osland et al. 2013, Saintilan

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et al. 2014, Cavanaugh et al. 2014). Many macrofauna species use mangroves or saltmarshes as nursery habitat, but the habitats likely differ in quality because their intertidal components differ in growth form (Robertson and Duke 1987, Primavera 1998, Rönnbäck 1999, Laegdsgaard and Johnson 2001, Minello et al. 2003, Sheridan and Hays 2003, Grol et al. 2011, Friess et al. 2012). The ecotone along the Atlantic coast of Florida (USA) is dominated by three plant species with distinct intertidal growth structures: *Spartina alterniflora* (smooth cordgrass) shoots and *Rhizophora mangle* (red mangrove) prop roots are tall, with a branched architecture in which secondary structures (leaves or secondary roots) branch from primary elements (stems or main roots). *Avicennia germinans* (black mangrove) produce shorter, simple pneumatophores (Figure 1.2 and 4.1B). Thus, I hypothesize that structural differences between mangrove and marsh vegetation influence inhabitant population dynamics through differences in habitat quality and use (Friess et al. 2012, Sepúlveda-Lozada et al. 2014). Examining the patterns and drivers of habitat use by representative macrofauna where mangroves and marshes co-occur along a transitional ecotone can help illuminate the implications of shifts between foundation species on nursery-seeking wetland fauna.

Along the mangrove-marsh ecotone, I 1) evaluate marine fauna use of alternative biogenic habitats, 2) determine any differences in habitat quality between the vegetation types, and 3) assess the influence of structural complexity on quality and use. To compare habitat use and the influence of structural cues, I monitored a recruiting cohort of *Callinectes* spp. (Decapoda: Portunidae) on an experimental array deployed in patches of mangrove and marsh vegetation in the ecotone (Figure 4.1A).

I expected recruits to prefer the safety of structurally complex vegetation. I modeled cohort abundance by habitat type over time to identify recruitment pulses. Optimal habitat was characterized by high recruit arrival, followed by high or comparable recruit persistence. I expected that differences in habitat use originate from active habitat selection (hereafter "preference") or from subsequent post-settlement mortality; I evaluated each in turn (Houde and Hoyt 1987, Etherington and Eggleston 2000, Heck et al. 2001). The underlying drivers of habitat use patterns were tested with settling *Callinectes* spp. in the lab. Habitat preference was tested in choice trials with all three vegetation types in an arena with or without predator cues. Increased preference in the presence of risk suggests that habitat is selected for refuge (Forward et al. 1996, 2001, Welch et al. 1997). I further evaluated that assumption by testing settler survival with a predator in each vegetation type. I expected that habitats that were preferred in trials with risk cues should confer a higher probability of survival, indicating better habitat quality (Schofield 2003). The differences in habitat use, preference, and survival identified in this study suggest that mangrove expansion is altering wetland habitat for marina fauna like *Callinectes* spp. It also reveals that differences in structural complexity, and not just the loss of structure *per se*, can affect habitat quality, such that foundation species may not replace one another functionally where they displace each other spatially.

Study system

An undifferentiated mix of *Callinectes sapidus* and *Callinectes similus* (hereafter *Callinectes*) were the focal organisms in all study components. These swimming crabs settle as megalopae in near-shore nursery habitats, especially open bays and wetlands, after a brief pelagic larval stage (Hsueh et al. 1993). They are distributed along the Western Atlantic from Maine, USA to Argentina (Williams 1984). To evaluate changes in habitat quality for *Callinectes* with mangrove expansion, I examined habitat formed by temperate *Spartina alterniflora* (saltmarsh cordgrass) and tropical *Avicennia germinans* (black mangroves) and *Rhizophora mangle* (red mangroves), hereafter referred to by generic names. Specifically, I evaluated habitat value and crab use of the vegetation components that occupy the intertidal water column – grass shoots and aerial mangrove roots. Based on the encroachment of mangroves into saltmarsh landscape, *Spartina* was specified as the intercept for all linear model analyses.

Field studies

Recruitment

I established a landscape-scale field experiment to assess habitat associations of recruiting *Callinectes* in the mangrove-marsh ecotone throughout the recruitment season (May to November 2014). The emergent and overhanging growth forms of mangroves and marsh vegetation inhibit the use of standard sampling methods (e.g. throw traps, suction samplers, seines) across all vegetation types. Instead, I used an array of retrievable panels to conduct equal sampling with a single method across

emergent shoot and pneumatophore and overhanging prop root vegetation structures. The panels were deployed in May 2014 and checked biweekly for recruitment. Once recruitment began in late summer, the recruiting *Callinectes* cohort was monitored biweekly through early November – until water temperatures fell, abundance returned to pre-recruitment levels, and crabs reached 15-20 mm carapace width (CW), when secondary dispersal is expected (Lipcius et al. 2007). I used the 10 weeks of cohort occurrence data to examine differences in recruitment dynamics, especially arrival and persistence, by habitat type (Figure 4.2B).

The experiment was designed to test recruitment response both 1) by habitat type at the scale of tens of meters and 2) by structural complexity at the scale of tens of centimeters. Retrievable panels were fitted with artificial vegetation mimics and deployed in patches of each habitat type. Comparisons by panel indicate the influences of physical structural complexity, while grouping by habitat type indicates responses to broader habitat attributes such as chemical cues, production, or shading (Figure 4.1C). Recruitment was monitored across two sites – Halifax River and Matanzas River, Florida – within the mixed vegetation ecotone (Figure 4.1A). Both sites are characterized by interspersed patches of vegetation covering tens of meters. Halifax River (29.09°, -80.94°) is a mangrove-dominated site north of Cape Canaveral that has small stands of *Spartina* that persist along shallow, sandy banks. Seventy kilometers north, Matanzas River (29.67°, -81.21°) is a historically saltmarsh-dominated site south of St Augustine where mangroves have been proliferating (Cavanaugh et al. 2014, Rodriguez et al. 2016); *Avicennia* are abundant; *Rhizophora* are still rare.

At each site, habitat patches were selected adjacent to main waterways within 4.5 km of the inlet to minimize spatial variation in larval supply and environmental conditions (Etherington and Eggleston 2000, Paula et al. 2001). Across sites, habitat patches were selected to provide a continuous edge of a single vegetation type with a total intertidal patch area >15 m^2. All patches had mixed sand, mud, and oyster substrates. A total of four patches per vegetation type were selected (n=12 patches total), with six patches at each site allocated according to the natural abundance of each vegetation type (three *Spartina*, two *Avicennia*, and one *Rhizophora* patch at Matanzas; one *Spartina*, two *Avicennia*, and three *Rhizophora* patches at Halifax). This design allowed me to determine the influences of vegetation structure and habitat type on *Callinectes* recruitment into co-occurring patches of mangroves and marsh.

To conduct the study, retrievable 61 x 61 cm panels were constructed from ½ inch non-pressure treated plywood and populated with artificial vegetation structures. Vegetation structures were affixed to the central 50 x 50 cm (0.25 m^2), leaving a 5 cm outer border for anchoring and retrieval. *Avicennia* pneumatophores were constructed from ¼ inch birch dowels (24-27 cm tall). *Rhizophora* prop roots were constructed from a variety of ½ to ¾ inch (1.3 and 1.9 cm) birch dowels, composed of 6-7 "mainstems" with 2-3 lateral roots each affixed at ~60 degrees. *Spartina* shoots were composed of 1/8th inch (0.3 cm) PVC rod with polyester leaves glued at regular intervals (5 blades per shoot); green plastic straws were placed over the lower stem to increase the diameter to ~4.6 mm. Within the 0.25 m^2 center of each panel, one of the

three vegetation types was added at natural densities (mean±SD: 227±99

pneumatophores, 85±35 prop roots, or 150±41 shoots per square meter; Appendix 1).

Panels were deployed along the periphery of habitat patches in a balanced

design across sites (Minello et al. 2008, Sheaves et al. 2016). Each panel was

deployed flush with the benthos, weighted with a brick and anchored with bent

threaded steel rod at two corners. Panels were deployed in triplicate, placing each

vegetation structure within each habitat type (n=36 panels total or 12 per structure

type across habitats and 12 within each habitat type; method as in Lindsey et al 2006,

Pardo et al 2007; Figure 4.1C). Panels were monitored biweekly from mid-May

through early November, within 3 days of full and new moons to maximize

recruitment detection. During panel sampling, a cube lined with 1 x 2 mm mesh on all

but one side – edged with foam-rubber – was placed over a panel, pressed down to

create a seal, and secured (Brainard et al. 2009). The entire unit was retrieved, and the

contents were rinsed through a 500 µm sieve and examined for recruits. Recruits were

measured and released. Panels were immediately redeployed. Recruits first occurred

on the panels in early September.

For analysis, data was constrained to samples from early September through

mid-November, when the recruiting cohort was present. A generalized additive model

(GAM) was used to fit smoothing functions to recruitment abundance in each habitat

across dates (mgcv package in R; Wood 2006, R Core Team 2015). GAMs fit data by

connecting a series of curves at points called knots. GAMs were fit per habitat type

using six knots – the number of sampling events – such that a curve was fitted to each

interval between sampling events. GAM fits that were significantly better than linear

(null) indicate a recruitment pulse. Based on Akaike Information Criteria adjusted for small samples (AICc), the best model included a fixed effect of habitat type and separate smoothers for salinity and for habitat type by sampling date but not structural complexity by sampling date.

To further characterize recruitment dynamics, I analyzed abundance by habitat type at peak recruitment in late September. I also analyzed abundance by habitat type at subsequent dates until differences were no longer significant ($p > 0.05$). Differences in abundance were analyzed with generalized linear models (with a log-link negative binomial family to adjust for overdispersion) in the mass package in R. Predictor level responses were assessed with Tukey post-hoc comparisons using the glht function in the multcomp package (Bretz et al. 2016). Together, recruit arrival and persistence were used as indicators of habitat use and quality (Figure 4.2A).

Laboratory Experiments

I conducted a series of habitat preference and survival studies with settling crabs during peak *Callinectes* recruitment in May, August, and September 2015 and May 2016. Both studies were conducted at the Smithsonian Marine Station in Fort Pierce, Florida. Seawater was provided via a flow-through system that delivers sand-filtered water directly from the adjacent Indian River Lagoon. During the study dates, lagoon waters near the study site had a mean salinity ($\pm$SD) of 33$\pm$4 ppt and mean temperature of 25$\pm$3 °C (sensor 0054, Harbor Branch Oceanographic Institute Land/Ocean Biogeochemical Observatory). Vegetation used in each study was collected fresh, scrubbed, and rinsed with fresh water to remove biofilms and epibionts (van Montfrans et al. 2003).

To populate the studies, megalopae and early juvenile (hereafter J1) *Callinectes* were collected in a 250 µm plankton net in Fort Pierce Inlet (27.48°, -80.31°) during incoming night tides within a week of full or new moon. Each study was populated with high but realistic densities of settlers (110-120 megalopae or 65-88 J1 per m^2 in preference trials and 75-94 megalopae or J1 per m^2 in survival trials; maximum documented natural recruitment is ~150 megalopae per m^2: (Moksnes 2002, van Montfrans et al. 2003). Developmental stage did not influence results in any trial, thus megalopae and J1 data are analyzed and presented together. I used sub-adult portunid crabs, which readily cannibalize conspecific recruits and first instar juveniles, as the predators in survival and risk trials (Smith 1995, Hines and Ruiz 1995, Moksnes et al. 1997, Aumann et al. 2006). Small portunids (16-36 mm carapace width) were collected with a push net in shallow sand, cobble, algae, and seagrass flats adjacent to the lab, then held in separate ~2 L tanks until each experiment (<48 hours holding time).

Preference

Settler preference for mangrove and marsh vegetation with and without risk (predator cues) was tested at night in ambient, mildly shaded outdoor conditions with a pair of multi-section arenas. In preference tests, I simultaneously offered each vegetation type to settling crabs within a subdivided circular arena (van Montfrans et al. 2003). Each 200 L arena (bottom surface = 0.28 m^2) contained a center stand pipe for infrastructure, aeration, and drainage (Figure 4.3A). Removable dividers split each arena into three individually draining 900 cm^2 sections. Sections were outfitted with freshly harvested mangrove or marsh vegetation that was fixed to plastic mesh

screens at low natural densities (55 prop roots, 110 pneumatophores, or 92 grass

shoots per m^2; Appendix 1). Vegetation was assigned to randomized arena sections,

then sand pre-sieved to <500 µm grain size was added until the mesh was covered

and the vegetation stood upright (~5 cm sand depth). The arenas were filled to 30 cm

with sand-filtered ambient seawater. To assess the influence of risk on habitat

preference, two portunid predators (described above) were added to each standpipe in

half the trials. Mesh-covered openings between the standpipe and each section

allowed predator chemical cues to enter the arena without any risk of actual

predation. Aeration within each standpipe increased water flow, circulating predator

cues from the pipe into the broader arena. Arenas, sand, and vegetation were

thoroughly rinsed with fresh water between trials.

At the start of each trial, dividers were placed between the vegetation types.

Equal numbers of settling crabs (6-8 J1 or 10-11 megalopae) were added to each

section to simulate a random distribution – the expected condition for no preference.

After five minutes of acclimation, dividers were removed to allow crabs to freely

move about the arena for 12-14 hours between 18:30-09:30, when megalopae are

most active due to natural nocturnal ingress behavior (Epifanio 1995, Tankersley et

al. 2002, van Montfrans et al. 2003, Moksnes and Heck 2006). At the end of each

trial, dividers were simultaneously returned to each arena and water was drained

down to ~10 cm depth through the central standpipe (lined with <500 µm mesh to

prevent settler loss). Section plugs were then removed simultaneously so that the

remaining water, sand, and settlers drained in unison from each section into a

corresponding bucket below. Vegetation was rinsed and visually inspected for

settlers. Finally, the drained contents of each section were filtered through a 710 µm

sieve, allowing the <500 µm sand to pass through while retaining the ~1 mm settled

crabs. Preference and avoidance were evaluated as changes in the number of crabs per

section from the initial even distribution using a repeated G-Test (Chi-Square

framework) in R version 3.2.3 (R Core Team 2015). Only trials with ≥80% recapture

efficiency were included in final analyses. Expected values for each habitat per trial

were calculated as 1/3 (three habitats per tank) of the total number of recovered

settlers per trial. For significant G-Test results, the habitats driving overall differences

were identified as those with standardized residuals >|2| from corresponding Chi-

Square tests, indicating significant deviation from the null expectation for a given

habitat (Sharpe 2015).

Survival

Settler survival was assessed during the day under ambient conditions in an

open air flow-through lab. Each sub-adult predator was fasted for 12 hours prior to

survival trials (8-10 hour stomach clearing time; McGaw and Reiber 2000). Satiation

trials were conducted to ensure that juvenile portunids are effective megalopae

predators and that consumption in survival trials was not limited by predator satiation.

To test satiation, individual fasted portunid predators (n=32) were added to tanks

containing only seawater, an airstone, and four J1 or six megalopae (4-5 maximum

used in survival trials). After 7 hours (comparable to survival trial duration), predators

were removed and surviving settlers counted. Ninety percent of prey was consumed

on average, with 100% consumed in 70% of satiation trials, indicating that predator

satiation is not a limiting factor in our survival trials.

Differences in survival by vegetation type were tested in a series of 530 cm^2 circular tanks containing only one vegetation type each. Tanks were haphazardly assigned to each vegetation type or an unvegetated sand treatment. Treatment tanks were outfitted with mangrove or marsh vegetation fixed to plastic mesh screens as in preference trials (above). Pre-sieved and rinsed sand (<500 µm grain size) was added until the mesh was covered and the vegetation stood upright (~5 cm sand depth). The unvegetated control treatment received only 5 cm of sand. Tanks were filled to 30 cm with sand-filtered ambient seawater and aerated with a single air stone. Four J1 or five megalopae were placed in each tank and given 20 minutes to acclimate before one portunid predator (described above, 22±0.4SE mm mean carapace width) was added to each tank. Trials were run for ~6 hours in ambient daylight between 09:00 and 19:00. At the end of each trial, predators were removed and tanks were drained, rinsed, and sieved as in preference trials. A series of predator-free control trials (n=10 sets of four) revealed that settler recovery was 95-100% efficient in the absence of predators, indicating no vegetation-specific recovery bias. Thus, all settlers missing from predation trials were considered depredated. Survival probability was measured as the proportion of settlers recovered. Based on my hypotheses, survival was analyzed relative to habitat type, structural complexity (branching or simple), and predator size with generalized linear models with a quasibinomial family to account for overdispersion in R version 3.2.3 (R Core Team 2015). Treatment level responses were assessed with Tukey post-hoc comparisons between predictor levels with the glht function in the multcomp package (Bretz et al. 2016).

Results

Recruitment

A recruiting cohort was first detected in early September 2014 and reached peak abundance in late September. Recruits were twice as abundant, on average, at the Halifax River site (mangrove dominated; 1.9 recruits per panel on average compared to 0.9 at Matanzas River); nonetheless, habitat associations were consistent when standardized by recruit availability for each site and sampling date, thus results are presented for modeled raw data. Significant recruitment pulses were detectable in *Spartina* (GAM temporal smoother χ^2=19.5, p=0.0006) and *Rhizophora* habitats (χ^2=21.4, p=0.0003), but not in *Avicennia* (χ^2=3.1, p=0.21; Figure 4.2B). In recruitment comparisons by date, peak abundance in late September was significantly higher in *Rhizophora* habitat (mean±SE: 32±8 settlers per m^2) compared to *Spartina* (13±4 settlers per m^2, GLM residual df=31, p=0.005) and *Avicennia* (8±3 settlers per m^2, p<0.0001; Likelihood Ratio Test χ^2=17.2, n=4 patches per habitat type, with recruits sampled on three panels in each patch; Figure 4.2C). Among vegetation structures, recruit abundance was highest on grass shoots (30±9 settlers per m^2); recruitment was significantly lower on pneumatophores (13±4 settlers per m^2, GLM residual df=32, p=0.02) and prop roots (10±3 settlers per m^2, p=0.001; χ^2=12.7, n=12 panels per structure type; Figure 4.2C). Recruit persistence was lowest in *Rhizophora* habitat, with higher persistence in *Avicennia* and *Spartina*. Thus, within two weeks (early October) recruit occupancy was no longer significantly different by habitat type or structural complexity (GLM residual df=30, p>0.05; Figure 2D).

Preference

To determine whether recruitment patterns in the field are driven by active preference, I tested settler habitat preference in the lab. In the absence of predation risk, settlers did not display a preference between habitat types (individual G-test for no risk: n=16 trials, df=2, p=0.58). Although they remained non-significant, differences in habitat preference strengthened markedly in the presence of predation risk (heterogeneity G-test by risk presence/absence: df=2, p=0.09). In risk trials, *Spartina* shoots were preferred marginally over mangrove vegetation (individual G-test for risk: n=16 trials, df=2, p=0.07). Unexpected variation in preference by season emerged, with settlers distinguishing between habitat significantly more in the fall than spring (heterogeneity G-test by season: df=2, p=0.005, Figure 4.3B). In the fall, *Spartina* shoots were preferred over mangrove vegetation (individual G-test for fall: n=11 trials, df=2, p=0.009). In the spring, settler recovery was higher in *Rhizophora* prop roots, but the distinction was not significant (individual G-test for spring: n=21 trials, df=2, p=0.24). When vegetation was grouped by structural complexity (with an expected distribution of 2/3 branching:1/3 simple; Appendix 4), there was still no difference in habitat preference without risk. But, with risk, recruits significantly preferred complex habitat (*Rhizophora* prop roots and *Spartina* shoots) over simple *Avicennia* pneumatophores across seasons (individual G-test: G=3.69, df=1, p=0.05; Figure 4.3C).

Survival

Stronger preference in the presence of predator cues suggests that preferred habitats confer higher survival, so I also evaluated settler survival in each vegetation

type. The relationship between probability of survival and predator size varied with habitat type (GLM, residual df=52, p=0.019). Probability of survival was negatively correlated with predator size in the sand treatment (slope=-0.05; ANCOVA, df=1, adjusted R^2=0.38, p=0.008). That relationship disappeared in the presence of vegetation (p>0.05 for each). Settler probability of survival was two-fold higher in vegetation (mean±SE: 0.45±0.04) than in unvegetated bare sand substrate (0.23±0.06; GLM, residual df=58, p=0.018). In particular, survival was significantly higher only in vegetation with more complex (branching) structure (0.50±0.05, residual df=57, p=0.02), while survival in simple vegetation (0.36±0.07) was not significantly different from survival in sand (0.23±0.06; residual df=57, p=0.43; Figure 4.4A). Among the complex habitats, only *Spartina* shoots provided a probability of survival that was significantly higher than the unvegetated treatment (0.54±0.07; residual df=56, p=0.028; Figure 4.4B). Survival was unrelated to any other vegetation attribute examined (Appendix 4).

Discussion

Climate change is redistributing foundation species, with the potential to affect the population dynamics of inhabitant species if alternative habitats differ in quality. I used studies of recruitment, preference, and survival to determine the suitability of mangrove and marsh vegetation as habitat for *Callinectes*. Overall, I expected more complex vegetation types such as *Rhizophora* prop roots and *Spartina* shoots to provide higher quality habitat, evident through higher recruitment and survival (Minello and Zimmerman 1985, Tupper and Boutilier 1997, Halpin 2000,

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Beck and et al 2001, Heck et al. 2001, Schofield 2003, Scharf et al. 2006, Feary et al. 2007, Graham and Nash 2012, Brooker et al. 2013). Habitat use in the field revealed that recruitment pulses occurred only in those branching habitats. As expected, independent experimentation in the lab demonstrated that the structurally complex habitats conferred higher survival and were more strongly preferred in the presence of predation risk. However, survival and preference varied even among the complex vegetation forms. Together, the differences in habitat use, preference, and survival indicate that mangrove and marsh vegetation differs in habitat quality and use, such that shifts in their distribution changes the wetland habitat landscape for marine fauna like *Callinectes*.

Recruitment

Patchy recruitment has the potential to reduce settlement-based population attrition if recruits preferentially settle in habitats that provide higher probability of survival (Halpin 2000, Dahlgren and Eggleston 2000, Johnston and Lipcius 2012). The evolution of transient, mobile settler stages (e.g. megalopae) is attributed in part to the importance of finding and recruiting to optimal habitat by recognizing and choosing among cues for structure, food, and reduced predation (Welch et al. 1997, Rittschof et al. 1998, Tapia-Lewin and Pardo 2014). As expected, significant pulses of settlers recruited into structurally complex *Spartina* and *Rhizophora* but not into simple *Avicennia*. Recruitment was four-fold higher in *Rhizophora* and two-fold higher in *Spartina* compared to neighboring *Avicennia*. Recruitment peaked simultaneously across vegetation types, indicating that initial differences in

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abundance arose immediately upon recruitment, rather than due to secondary dispersal (Heck et al. 2001, Moksnes 2002, Moksnes and Heck 2006).

Callinectes often distinguish between habitats upon initial settlement (Welch et al. 1997, Moksnes and Heck 2006, Johnston and Lipcius 2012); however, settlement patterns are not always indicative of later population distribution, which is more readily attributed to juvenile survival and secondary dispersal (Heck et al. 2001, Moksnes 2002, Moksnes and Heck 2006). Thus, recruit persistence was expected to vary by habitat according to quality. Indeed, within two weeks, lower persistence in *Rhizophora* habitat erased differences in settler abundance between *Rhizophora* and *Spartina* habitat. Continued recruit loss over time could be explained by a number of mechanisms. 1) Mortality would lead to decreasing recruit abundance over time. 2) Redistribution could also lead to decreased occurrence, but secondary dispersal is unlikely to be confounding because the sampled crabs did not surpass 20 mm CW – the expected size at secondary dispersal (Lipcius et al. 2007, Pardo et al. 2007, Johnston and Lipcius 2012). 3) It is possible that recruit attrition was due in part to less effective capture of large or fast-swimming individuals with the panel retrieval method; however, finfish and swimming crabs ranging in size from 0.5 mm to 100 mm were regularly captured. Thus, some combination of mortality and local redistribution are the most likely explanations for recruit attrition. Optimal habitat should host high initial arrival, followed by recruit persistence; these conditions were most apparent in *Spartina* habitat. Differences in habitat use may originate from some combination of active preference and post-settlement mortality (Houde and Hoyt 1987, Etherington and Eggleston 2000, Heck et al. 2001), so I evaluated each in turn.

Preference

Juvenile habitat use is driven foremost by mortality avoidance (Halpin 2000, Dahlgren and Eggleston 2000, Johnston and Lipcius 2012), so preference for a specific habitat should reflect its structural complexity and value as a refuge, especially in the presence of predation risk (Welch et al. 1997, van Montfrans et al. 2003, Schofield 2003). When vegetation was grouped by complexity (*Rhizophora* prop roots and *Spartina* shoots as branched, *Avicennia* pneumatophores as simple), crabs strongly preferred complex habitat in the presence of predator cues, regardless of season. When considering vegetation types separately, preference was more nuanced, including a seasonal effect. *Spartina* shoots were strongly preferred in the fall in the presence of risk. There was a compelling pattern that preference switched to *Rhizophora* prop roots in the spring. Low statistical power in preference trials means that failure to reject the null of no difference between vegetation types should be interpreted cautiously. The origin of seasonal variation is unknown, but it may relate to grass emergence in spring and senescence in fall. This hypothesis is supported in part by crab preference for *Spartina* wrack and detrius as structural refuge (Smith et al. 2016). Across seasons, preference was stronger in the presence of predator cues and always favored complex vegetation forms.

Although juvenile portunid crabs are voracious and effective predators on conspecific megalopae, in the preference study, juvenile cues could have been perceived as conspecific or predator cues (Smith 1995, Hines and Ruiz 1995, Moksnes et al. 1997, Aumann et al. 2006). Conspecific cues enhance settlement and metamorphosis (Forward et al. 2001, Diele and Simith 2007), while predator cues

generally reduce metamorphosis or accentuate habitat choices (Welch et al. 1997, Moksnes et al. 1997). If the juvenile cue treatment was perceived as conspecifics, I would have expected settler distributions to remain even among habitat types. If anything, conspecific cues should increase the rate of metamorphosis, resulting in more first instar juveniles (J1s) recovered from megalopae trials with the cue treatment. Instead, differences in habitat use became stronger and recovery of metamorphosed J1s was reduced by more than half in the presence of juvenile cues (1.2 compared to 3.6 average J1 recovered per habitat). Both results indicate that juveniles were perceived as predators rather than conspecific settlement cues. Thus, consistent preference for structurally complex vegetation in the presence of predation risk cues suggests that those habitats are likely of higher quality and should confer higher probability of survival.

Survival

In studies that compare vegetated (i.e. seagrass and salt marsh) habitat to mud and sand areas, the vegetated habitats always enhance survival and growth of juvenile fish and invertebrates (Minello and Zimmerman 1985, Halpin 2000, Heck et al. 2001, Minello et al. 2003, Schofield 2003, Johnston and Lipcius 2012, Brooker et al. 2013). Vegetation also enhanced survival of settlers in this study. More specifically, survival probability depended on vegetation structural complexity. Short, structurally simple *Avicennia* pnuematophores yielded low survival probabilities comparable to unvegetated sand substrate, whereas only structurally complex vegetation with a branched architecture significantly improved survival. These results align with prior

evidence that post-settlement survival of fish and invertebrates is highest in the most complex habitat available, such as sponge clusters (Scharf et al. 2006), rocky reefs (Tupper and Boutilier 1997), or branching macroalgae (Johnston and Lipcius 2012), compared to habitats of intermediate complexity such as shell and cobble substrates or seagrass. In particular, survival was highest in *Spartina* vegetation. *Spartina* shoots provide structure with a branched architecture at high densities (Appendix 1); this combination of traits may provide the most effective size-scaling between vegetation structures and small settling crabs. Similarly, *Callinectes sapidus* survive better in finely branching macroalgae than in seagrass in Chesapeake Bay (Johnston and Lipcius 2012).

Overall, the differences in survival probability associated with habitat structural attributes suggest that 1) species are dependent on the refuges provided by structurally complex habitats and that 2) not all complexity provides equally beneficial habitat. Differences in survival likely originate from differences in refuge quality, particularly size-scaling and influences of vegetation structure on relative predator and prey mobility. Here, larger predators were able to eat more prey in sand, but vegetation mediated that relationship, likely because structural complexity impedes the movement of larger predators (Bartholomew et al. 2000). Survival results from this study support prior findings that structurally complex nursery habitats (here *Spartina* shoots and *Rhizophora* prop roots) provide better refuge and higher survival of vulnerable marine settlers and early juveniles (Tupper and Boutilier 1997, Halpin 2000, Beck and et al 2001, Heck et al. 2001, 2003, van Montfrans et al. 2003, Almany 2004). Taken together, differences in survival across ecotone vegetation

types indicate that mangroves and marsh each provide distinctive habitat quality, based in part on the complexity of their structural forms.

Implications of mangrove expansion

This study demonstrates that the shift of mangroves into saltmarsh is changing wetland habitat for *Callinectes*. Recruiting *Callinectes* selectively settled among mangrove and marsh vegetation types based on both structural and non-structural habitat attributes. The preferred structurally complex habitats provided the highest probabilities of survival in lab experiments, suggesting that settlers can distinguish among ecotone vegetation types and that their choices correspond to habitat quality. Stronger preference in the presence of predation risk further supports the inference that selective settlement into structurally complex habitats is driven at least in part by mortality avoidance.

Based on these findings, *Avicennia* intrusion into saltmarsh represents effective habitat loss for *Callinectes* that will be partially alleviated with the subsequent emergence of more structurally complex *Rhizophora*. In both mangrove types, however, there is either low recruitment or low post-recruitment persistence. Poor recruit persistence in *Rhizophora* could represent an ecological trap or population sink (Battin 2004, Patten and Kelly 2010); high recruit arrival there should not be interpreted as good habitat quality. Further studies are needed to identify the cues stimulating high *Callinectes* settlement in suboptimal *Rhizophora* habitat. Prior studies have reported contradictory evidence about the importance of structural and non-structural cues in *Callinectes* selection of *Spartina* habitat (Forward et al. 1996,

Diaz et al. 1999). Responses to both structural and non-structural cues were evident in this study. Additional studies will be needed to determine 1) the non-structural attributes that shape habitat use and 2) differences in food availability and recruit growth rates among habitats. This study provides clear implications for the difference in habitat at settlement, but given the transience of settlement dynamics in portunids (Etherington and Eggleston 2000, Moksnes and Heck 2006), further studies are needed to determine late juvenile (>20 mm carapace width) and adult habitat use among mangroves and marshes.

With this study, mangroves and saltmarshes join the suite of habitats that *Callinectes* distinguish among during settlement. Even though *Spartina* wetlands often provide poorer habitat quality than co-occurring seagrass for marine fauna (Minello et al. 2003, Bloomfield and Gillanders 2005), here I found that *Spartina* is superior habitat to tropical mangrove vegetation. As such, mangrove expansion is likely to have a negative impact on *Callinectes* populations. *Callinectes* are highly connected species within estuarine food webs (McCann et al 2016); thus, the shift in habitat quality for *Callinectes* with climate-driven wetland shifts is likely representative of changing conditions and cascading impacts for the broader estuarine macrofauna community. Beyond this system, these findings shed light on the habitat attributes that shape *Callinectes* habitat use. Their reliable response to structural complexity indicates that shifts between habitats of differing structural complexity should be safely considered a change in habitat quality, especially in terms of survival. Such shifts should be evaluated so that differences in quality can be taken

into consideration when characterizing habitat availability and developing fisheries management plans.

Conclusion

      Climate change is altering marine ecosystems primarily through the loss of complex habitat, but it is also driving the redistribution of foundation species (Harley et al. 2006, Hoegh-Guldberg et al. 2007). *Callinectes* use of mangrove and marsh vegetation along the ecotone reveals that differences in structural complexity, not just the presence of habitat structure *per se*, shape habitat quality. Thus, the displacement of one foundation species by another can alter habitat quality and availability without the net loss of structured habitat. To fully evaluate the impacts of climate change on marine communities that depend on biogenic habitat, we need to account for not just the loss of structural habitat, but also for shifts in foundation species where differences in the quality of their biogenic habitats affect inhabitant population dynamics.

A)
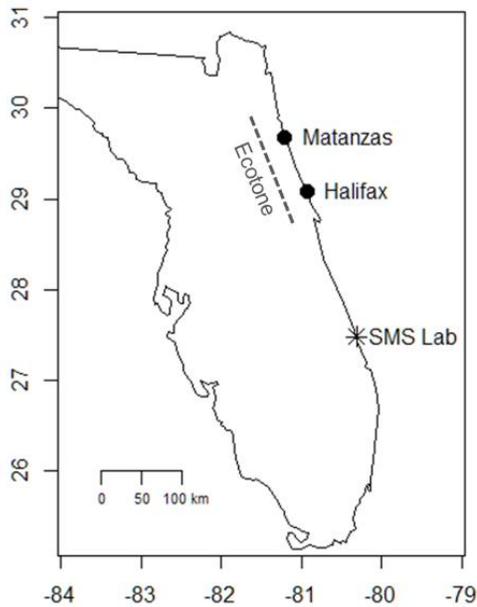
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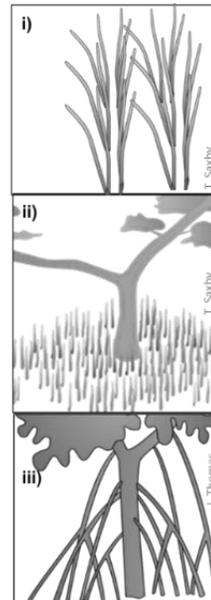
C)
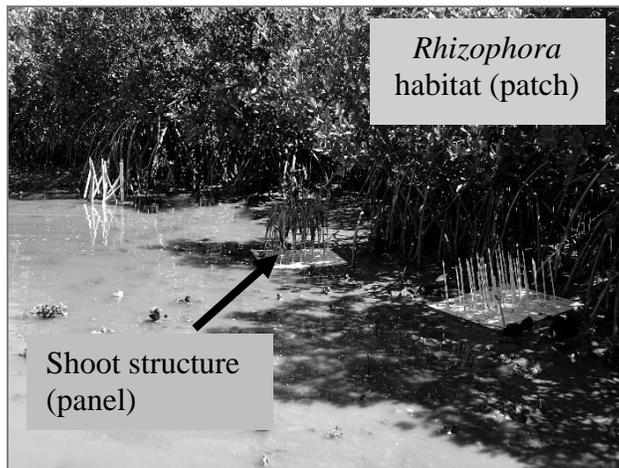
Figure 4.1: (A) Recruitment was studied at two sites (black circles) along the ecotone. Lab

trials were conducted at the Smithsonian Marine Station in Fort Pierce (asterisk). (B) The

three vegetation types studied are i) *Spartina alterniflora* (cord grass) shoots, ii) *Avicennia*

germinans (black mangrove) pneumatophores, and iii) *Rhizophora mangle* (red mangrove)

prop roots. (C) For the recruitment study, 0.25 m^2 panels outfitted with each structure type were deployed in sets in patches of each habitat type; a full set of panels deployed along the margins of a *Rhizophora* patch is shown.

A)

B)

Time

Frequency

Modeled abundance per panel (0.25m^2)

25 Aug   8 Sept   24 Sept   8 Oct   23 Oct   6 Nov

C)

Late September (week 0)

D)

Early October (week 2)
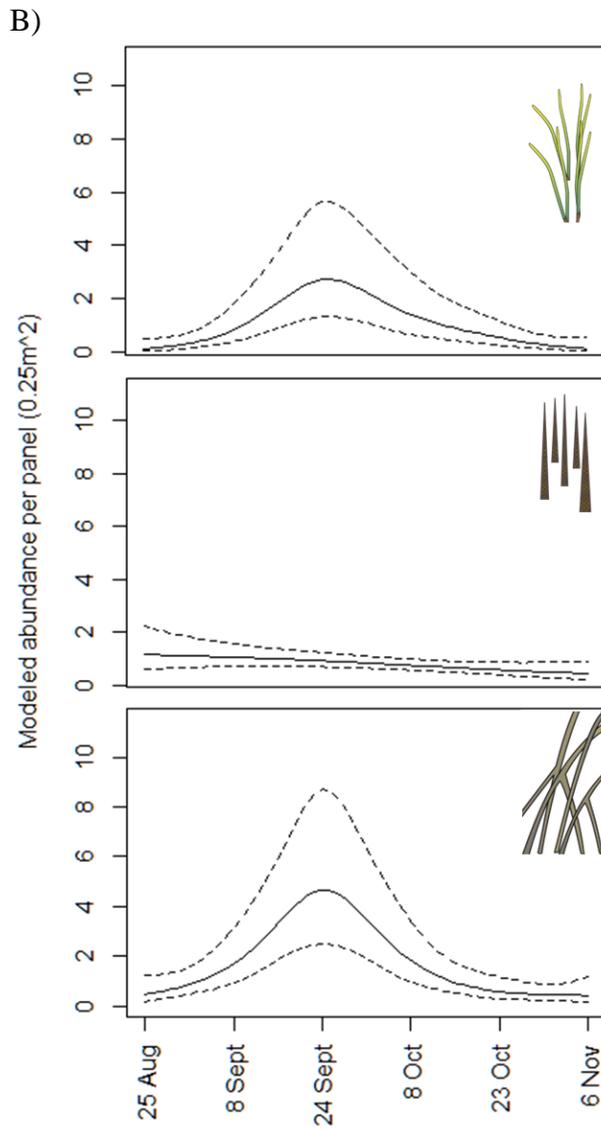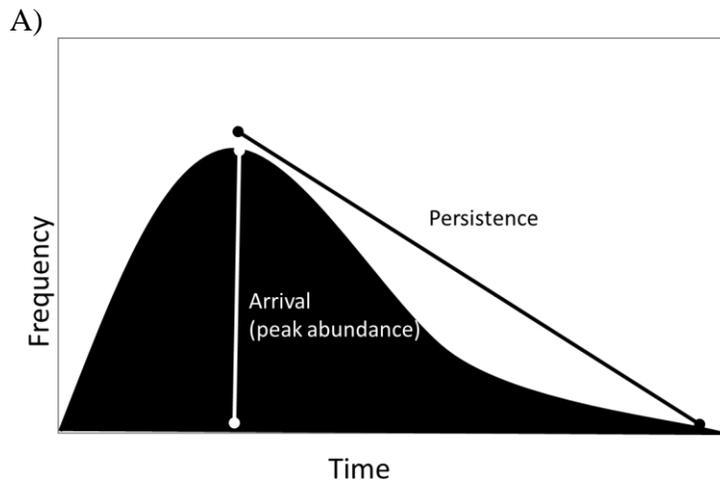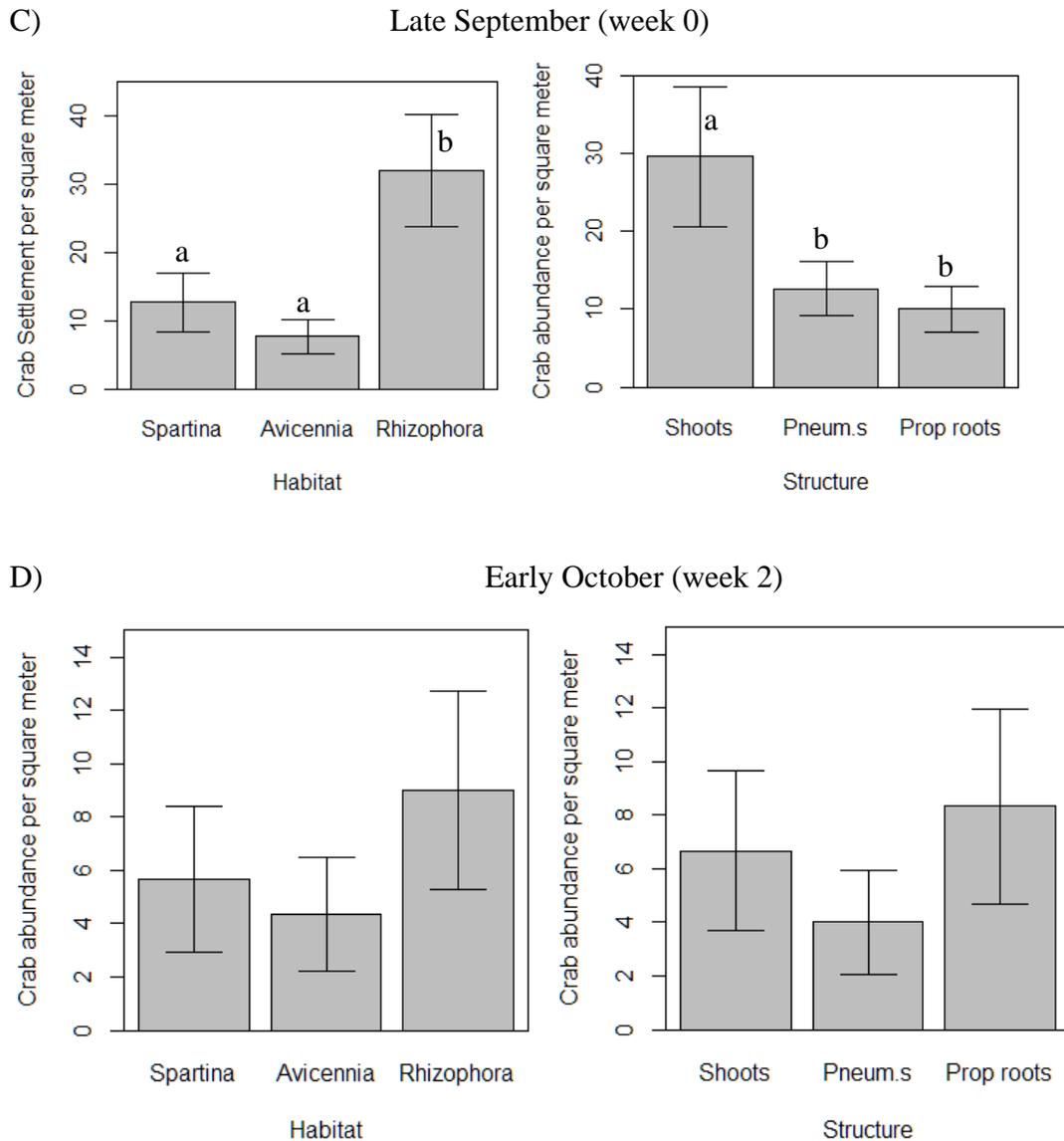
Figure 4.2: (A) Recruitment was evaluated in terms of initial arrival and subsequent recruit persistence. The optimal habitat would have high peak abundance followed by high persistence (i.e., shallow slope). (B) Recruitment was habitat specific, as characterized by abundance over time with habitat-specific smoothing functions in a generalized additive model (GAM). Recruitment peaks (significantly nonlinear) were found in *Spartina* and *Rhizophora* but not *Avicennia* habitat. (C) Arrival (i.e., peak recruit abundance) was

significantly higher in *Rhizophora* habitat (left) and grass shoots (right). (D) Due in part to low persistence in *Rhizophora* habitat (see slope in 4.2B), recruit abundances were no longer significantly different between habitats or structures within two weeks (early October) after peak recruitment. Note difference in abundance scales between September and October.

A)

B)

C)
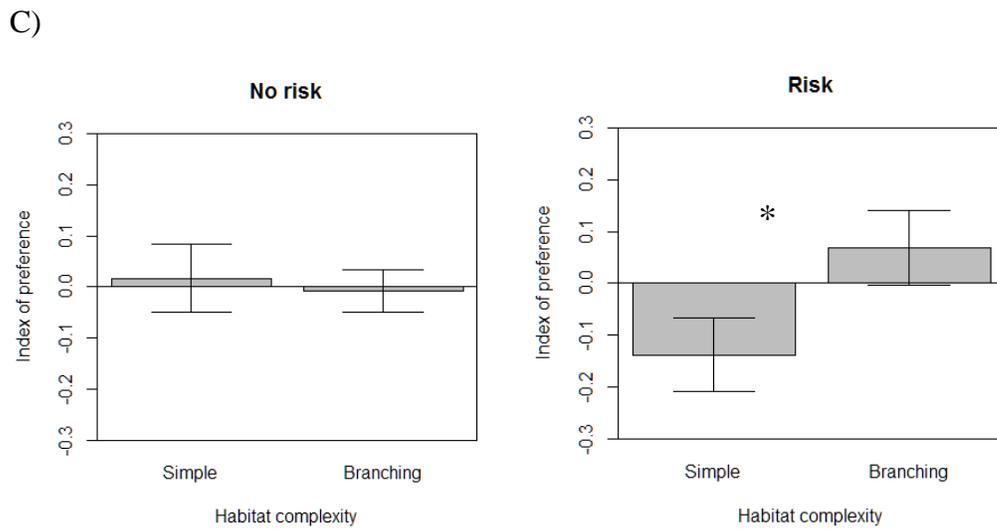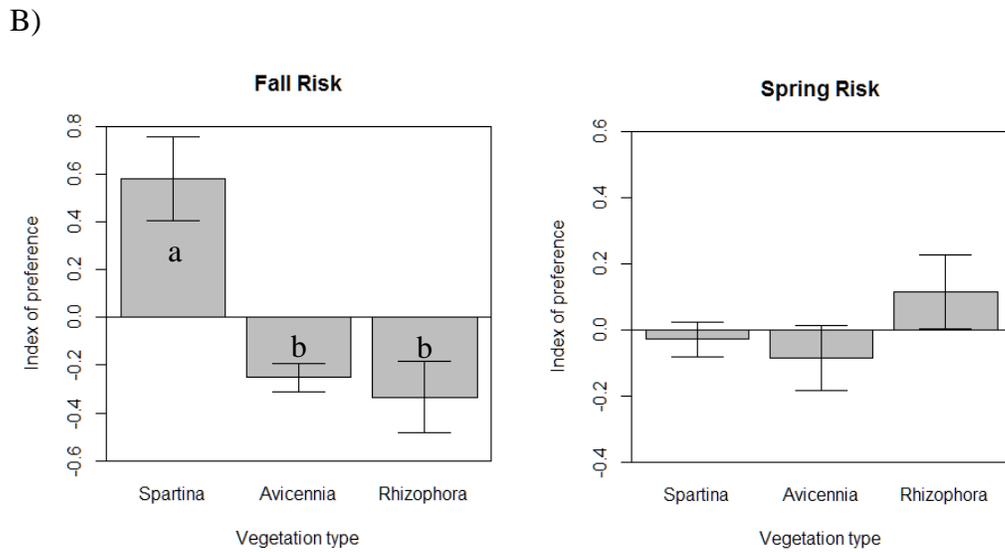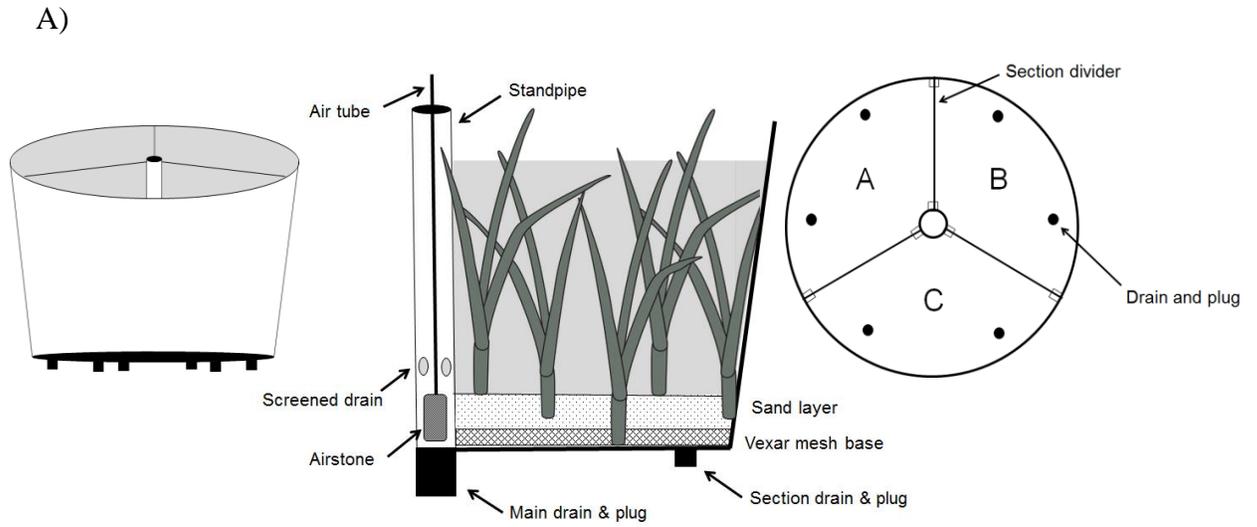
Figure 4.3: A) Preference arena design: side view (left), cross section (center, shown with *Spartina*), and aerial view (right). B) The particular complex vegetation type that was preferred varied by season, but preferences were only significant in fall trials. C) With risk, habitats with complex branched architecture (*Spartina* shoots and *Rhizophora* prop roots) were preferred across all seasons. Preferences for vegetation type were never significant in the absence of predation risk. Values >0 indicate preference; values <0 indicate avoidance. Letters and asterisks indicate significant differences. Arena illustration: O. Caretti.

A)

B)
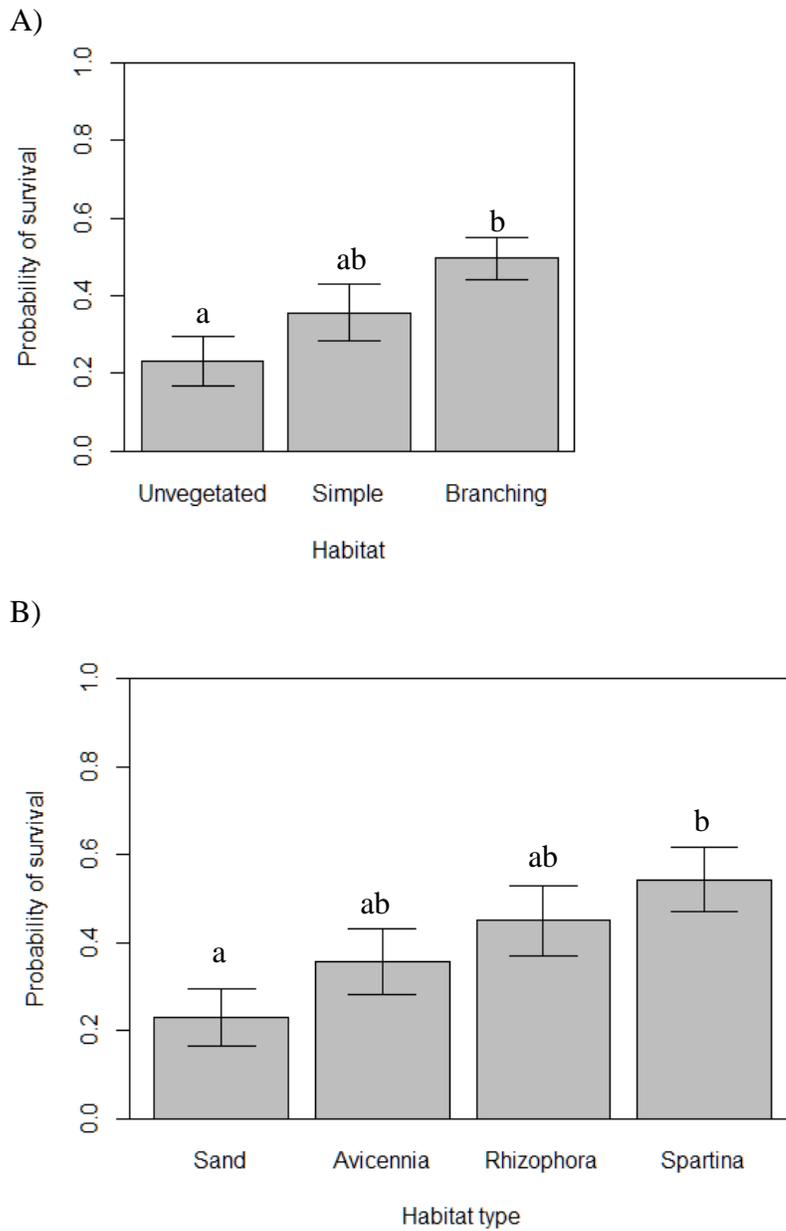
Figure 4.4: *Callinectes* spp. survival varied with habitat type; it was highest in vegetation with complex, branched architecture (A), particularly in *Spartina* shoots (B). Lettering indicates significant differences.

Appendices

Appendix 1: Measures of vegetation structural complexity

Introduction

Mangroves and marshes interface along a narrow strip of coastline (~3 degrees of latitude) around the world. They inhabit largely mutually exclusive ranges, with mangroves in tropical regions and saltmarsh grasses in temperate zones. However, within their respective ranges they inhabit comparable emergent intertidal zones, forming parallel coastal ecosystems (Friess et al. 2012). One of their important roles is as nursery habitat for marine organisms, especially the vulnerable juvenile stages of fish, crabs, and shrimp that eventually emigrate into surrounding ecosystems, including coral and oyster reefs (Mumby et al. 2004, Jones et al. 2010). With climate change, mangroves are shifting poleward, displacing saltmarshes (Saintilan et al. 2014). This shift adds an urgency to compare and contrast mangroves and marshes as marine habitat.

Differences in growth form between vegetation types will influence structural complexity, defined as the three-dimensional arrangement of structural elements (Tokeshi and Arakaki 2012). Differences in structural complexity could affect marine inhabitant communities through differences in size scaling, refuge availability and effectiveness, and resource partitioning (Dahlgren and Eggleston 2000, Johnston and Lipcius 2012). In order to attribute differences between vegetation types to structure, we need a basis by which to compare their complexity. Here, I measured basic structural traits of emergent intertidal growth structures (hereafter "elements") of

mangrove and marsh vegetation, specifically pneumatophores of *Avicennia germinans* (black mangrove), prop roots of *Rhizophora mangle* (red mangrove), and shoots of *Spartina alterniflora* (smooth cordgrass) (Figure A1.1a). I collected measurements to characterize and compare the density, dimensions, spacing, and orientation of each element type. These measures were chosen to characterize the features that are likely to influence structure:body scaling and other aspects of refuge and habitat use. Mean traits may be important for determining basic habitat suitability (e.g. structure:body size scaling), but the variety in structure is likely to be particularly important, promoting species coexistence by partitioning spaces to limit competition or by creating refuge from a broad suite of predator sizes (Cuddington and Yodzis 2002, McAbendroth et al. 2005). Differences in the mean or variety of attributes between vegetation types are discussed in reference to potential implications for differences in habitat provisioning, which will become of particular importance in assessments of habitat area as mangroves displace marshes.

Methods

To assess biologically-relevant traits of complexity, I measured size, spacing, articulation, branching, water column occupancy (height relative to high tide line), and growth form of vegetated habitats (Figure A1.1b; Bartholomew et al. 2000, Gratwicke and Speight 2005, Kovalenko et al. 2012). Measures were taken at five sites spanning the mangrove-marsh ecotone along the Atlantic Coast of Florida in 2013. Each vegetation type was surveyed in at least three sites. Structural characteristics are attributed to a particular vegetation type in any plot where it made up >80% of the vegetation cover.

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Sampling areas were identified by selecting a randomly drawn number between zero and ten that corresponded to points along a haphazardly chosen strip of shoreline. Within a 1 m^2 plot at each sampling area, I recorded vegetation cover and composition, number of elements, nearest neighbor distances from a central element, and water column occupancy. Nearest neighbor distances were used to establish a coarse measure of spacing between elements in each vegetation type; I selected the centermost stem in each plot and then measured distance to the nearest element within each of four 90° arcs, delineated by cardinal directions. This method provides an unbiased average and range of spacing distances between elements (Bartholomew et al. 2000, Bell et al. 2003). Water column occupancy was determined by dividing the vegetation height by the mean high tide line: vegetation that scores one (1) or greater completely vertically occupies the water column and emerges even at high tide; vegetation scoring less than one does not reach the surface at high tide. Water column occupancy is more accurate and biologically relevant than standard vegetation height since (1) some forms grow down into the substrate while others grow up out of it and (2) structural refuge is more complete when predator access is limited vertically as well as laterally (Nagelkerken et al. 2010). Vegetation that does not fully occupy the water column may leave inhabitants vulnerable from above or below.

The main plot was then subdivided into quarters, one of which was randomly selected as a 0.5 m^2 subplot for finer measurements. Within the subplot, I measured element diameters and the height and angle of branch points. Heights of branch points – including leaves on *Spartina* stems and lateral roots on *Rhizophora* prop roots –

were measured from the substrate. Diameter was measured ~10 cm above the sediment to keep it comparable between vegetation of different heights.

For attributes with homogeneous variances, data were analyzed with ANOVA; contrasts are reported from Tukey's Honest Significant Differences. All others were analyzed with generalized linear models with an appropriate distributional family. All analyses were conducted in R version 3.2.3 (R Core Team 2015). To emphasize attribute variation, values for each measure are reported as mean ± standard deviation (Table A1).

<u>*Results*</u>

For density of elements, variances are comparable (p=0.09), but mean densities differ significantly between each vegetation type (df=2, p<0.0001; Figure A1.2). Spacing (NND) variance and means are equivalent between vegetation types (for variance p=0.9; for means df=2, p=0.3; Figure A1.3). Vertically, *Rhizophora* and *Spartina* fully structure the water column, while *Avicennnia* pneumatophores structure only 0.66±0.3 of the water column (Figure A1.4). At 10cm above the sediment, *Rhizophora* prop root diameter had greater variance (p<0.0001) but also appears to be broader on average than the structural elements of the other vegetation types (Figure A1.5). *Avicennnia* pneumatophores generally lack branching points and thus were excluded from analyses of articulation. Variance in branch point height was equal between the branching habitats, but branch points were significantly higher on average in *Rhizophora* prop roots than in *Spartina* shoots (df=1, p=0.0385; Table A1, Figure A1.6). *Rhizophora* prop roots and *Spartina* shoots had comparable variance in angle of articulation. *Rhizophora* prop roots have a significantly greater angle of

articulation compared to *Spartina* (df=1, p<0.0001; Figure A1.6). Both vegetation types also differed significantly in the position of branch points – angle corrected for vertical position: <90 opens downward ("^"), >90 opens upward ("v") (df=1, p<0.0001; Figure A1.6).

Discussion

Mangrove roots and marsh shoots differ in a number of structural attributes. *Spartina* shoots are herbaceous, while mangrove roots are woody. The difference in tissue type likely influences rigidity and decomposition, but it does not correspond to other differences in form and specific structural attributes. Each vegetation type had a unique density of structural elements; element density was highest in pneumatophores, followed by shoots, and then prop roots. Despite differences in density, spacing between elements was comparable across vegetation types. This counterintuitive pattern arises because the vegetation with the lowest element density has the greatest element diameter, while those with high densities are smaller in diameter. These distinct combinations mean that spacing is comparable between individual elements but occurs between fewer elements within the low density, high diameter prop roots (i.e., spaces are the same size but there are fewer of them). Functionally, *Rhizophora* prop roots provide a wider variety of diameters than *Avicennnia* or *Spartina* vegetation. Prop roots are more than double the diameter of the other vegetation types on average, but the spread of variances is also at least twice as high in prop roots. Differences in diameter alone can affect habitat quality, because surface area can affect cover and foraging (Newell et al. 1995, Sheridan and Hays 2003, Layman 2007, Demopoulos and Smith 2010).

Branching architecture can affect habitat by shaping the number and width of spaces available as refuge. More articulated forms should be more fractal, such that spaces are replicated across scales, leading to partitioning and coexistence of a greater size range of inhabitants (Cuddington and Yodzis 2002, McAbendroth et al. 2005, Tokeshi and Arakaki 2012). Only *Rhizophora* prop roots and *Spartina* shoots have second order structural elements, creating articulation at branch points. The height of branch points is only slightly higher in prop roots, but this small (2cm) difference in branch height could have inordinate consequences for habitat provisioning, because branches with higher origins will have broader spaces between them by the point where they contact the sediment (or water surface). This effect is compounded by the already greater angle of articulation in prop roots. The angles between *Rhizophora* prop roots are one and a half-fold wider than between *Spartina* stems and leaves. Moreover, *Rhizophora* prop roots open downward (^) while *Spartina* opens upward (v). Thus, even among the branching habitats, the specific attributes of their branching patterns create very different habitats. For example, the upward branching of *Spartina* leaves may provide less benefit for benthic invertebrates.

In addition to the added structural complexity from branching, *Rhizophora* prop roots and *Spartina* shoots occupy the water column completely, while *Avicennnia* pneumatophores occupied little more than half the water column at high tide on average. Full structuring of the water column provides the added benefit of inhibiting predator access from above (or below in overhanging prop roots; Nagelkerken et al. 2010).

Broader inference

Marsh and mangrove vegetation types not only differ among the attributes measured, they differ in such a way that they could be used in comparative habitat use studies to test which structural attributes drive habitat preference and quality. *Spartina* differs from both mangroves in tissue type (and likely rigidity, though not tested here). *Avicennnia* pneumatophores and *Spartina* shoots are comparable in diameter, while *Rhizophora* prop roots are broader. *Spartina* and *Rhizophora* share branching structures, while *Avicennnia*s pneumatophores are simple. Thus, alternative groupings of these vegetation types can effectively test the roles of diameter, branching, and woodiness on habitat preferences, use, and quality.

Conclusion

The differences in structural attributes between mangrove and marsh vegetation types documented here highlight that mangrove shifts into temperate saltmarshes are likely to affect habitat quality and availability for wetland inhabitants. Mangroves and marshes should not be considered equivalent wetlands; habitat quality and use need to be critically evaluated for each vegetation type in order to determine how the habitat landscape is changing with climate-driven mangrove expansion.

TABLES

Table A1: Vegetation attributes, reported as mean±SD. Significantly different groups are distinguished with **bold** lettering.

| Attribute	*Spartina alterniflora*	*Avicennia germinans*	*Rhizophora mangle*	Contrast
Element	shoots	pneumatophores	prop roots	-
Tissue	**herbaceous**	woody	woody	Spart v Avic/Rhiz
Density (m^{-2})	**150±41**	**227±99**	**86±35**	unique
Spacing (NND, cm)	10±9	10±13	13±7	equal
Water column occupancy (ht/HTL)	1±0.02	**0.66±0.3**	0.99±0.03	Avic v Spart/Rhiz
Diameter (mm)	8±5	8±2	**23±9**	Rhiz v Spart/Avic
Branching height (cm)	**26±13**	N/A	28±12	Spart v Rhiz
Branching angle (degrees)	23±17	N/A	**37±16**	Spart v Rhiz

a)   b)
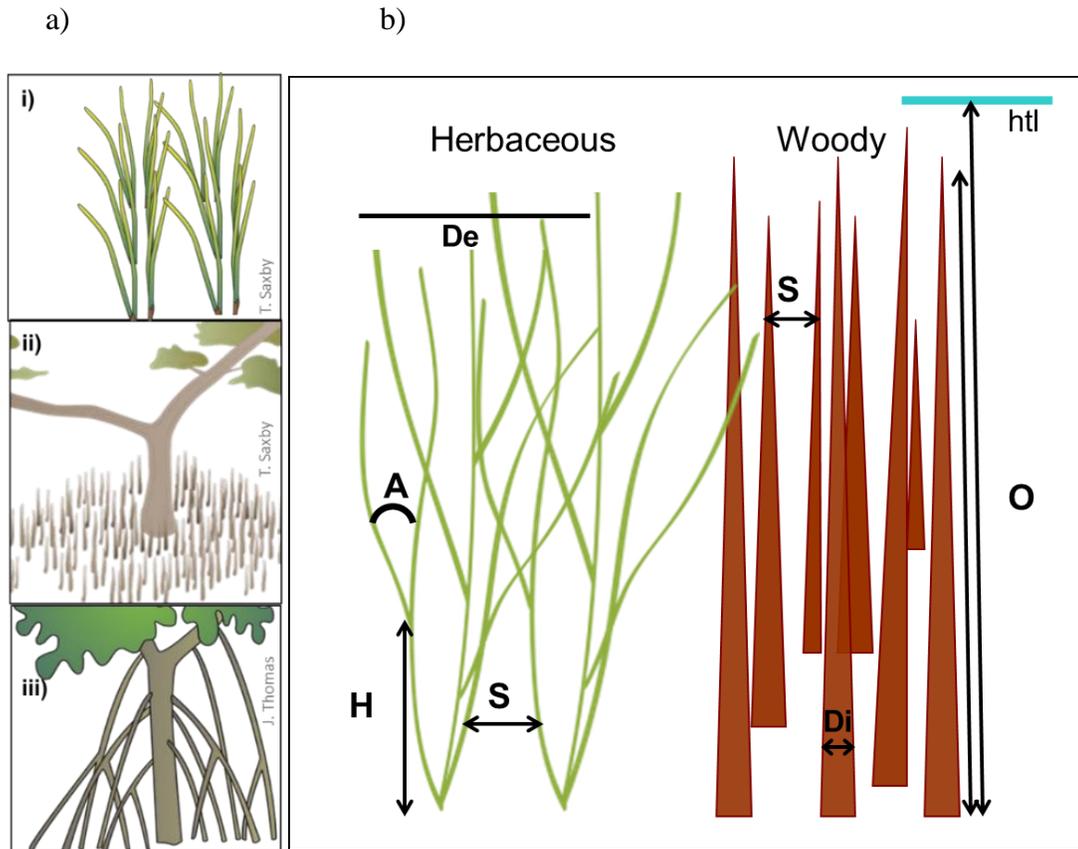
Figure A1.1: a) The three vegetation types studied are i) *Spartina alterniflora* (smooth

cordgrass) shoots, ii) *Avicennia germinans* (black mangrove) pneumatophores, and iii)

Rhizophora mangle (red mangrove) prop roots. b) Structural aspects measured and compared

between mangrove and marsh species are density (De), spacing (S), height of branch points

(H), diameter (Di), articulation (A) , and water column occupancy (O, measured as a ratio of

vegetation height to high tide line[htl]). Growth form (woody vs. herbaceous) is qualitative.
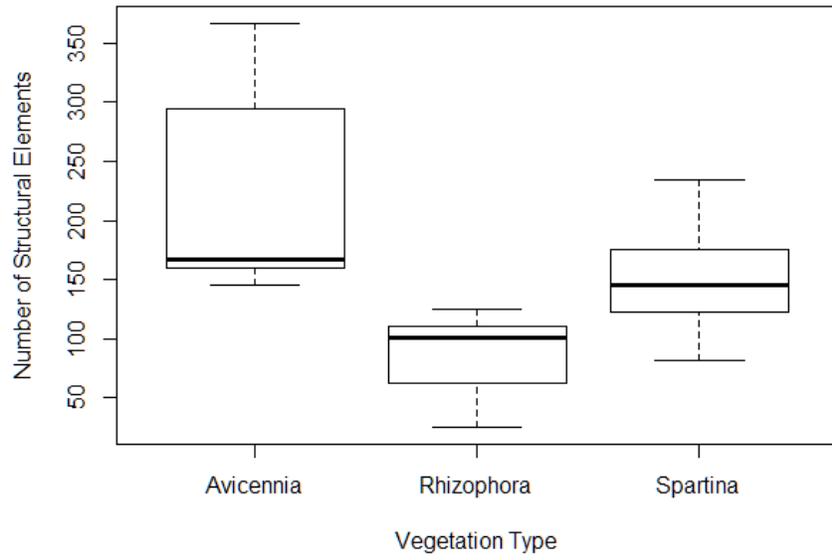
Figure A1.2: Density (number per square meter) of structural elements were significantly different for each vegetation type.
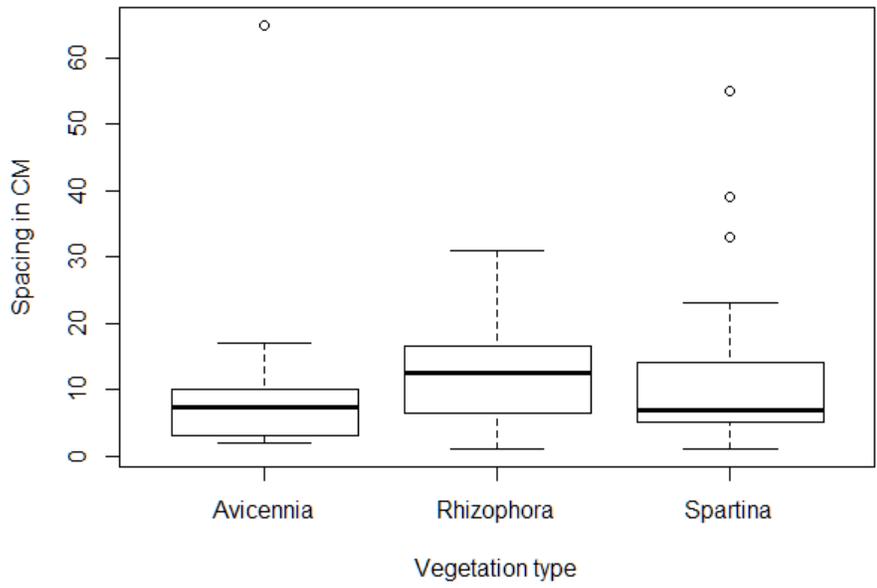
Figure A1.3: Spacing between elements was no different between vegetation type.
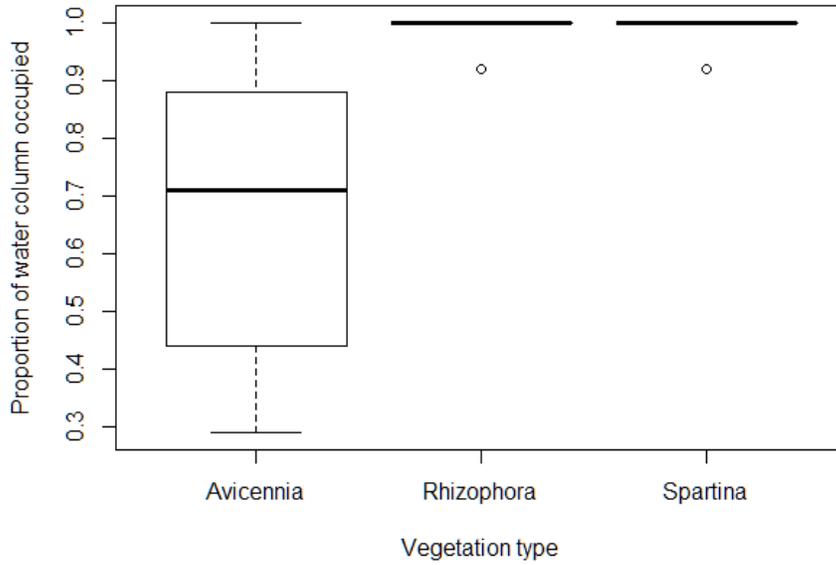
Figure A1.4: Compared to the high tide line, *Rhizophora* prop roots and *Spartina* shoots occupied the entire water column. *Avicennnia* pneumatophores are rarely tall enough to emerge at high tide.
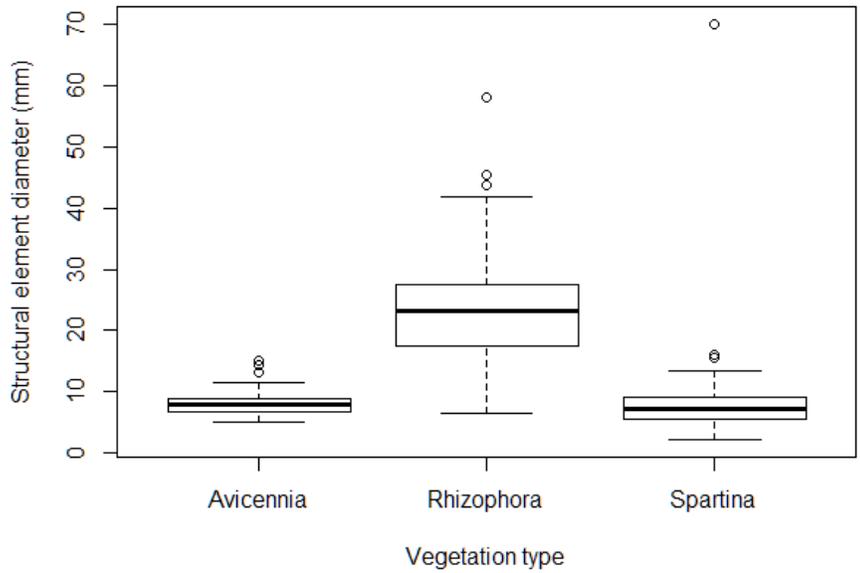
Figure A1.5: Both the mean and variance of element diameter differ between *Rhizophora* prop roots and the structural elements of the other vegetation types.
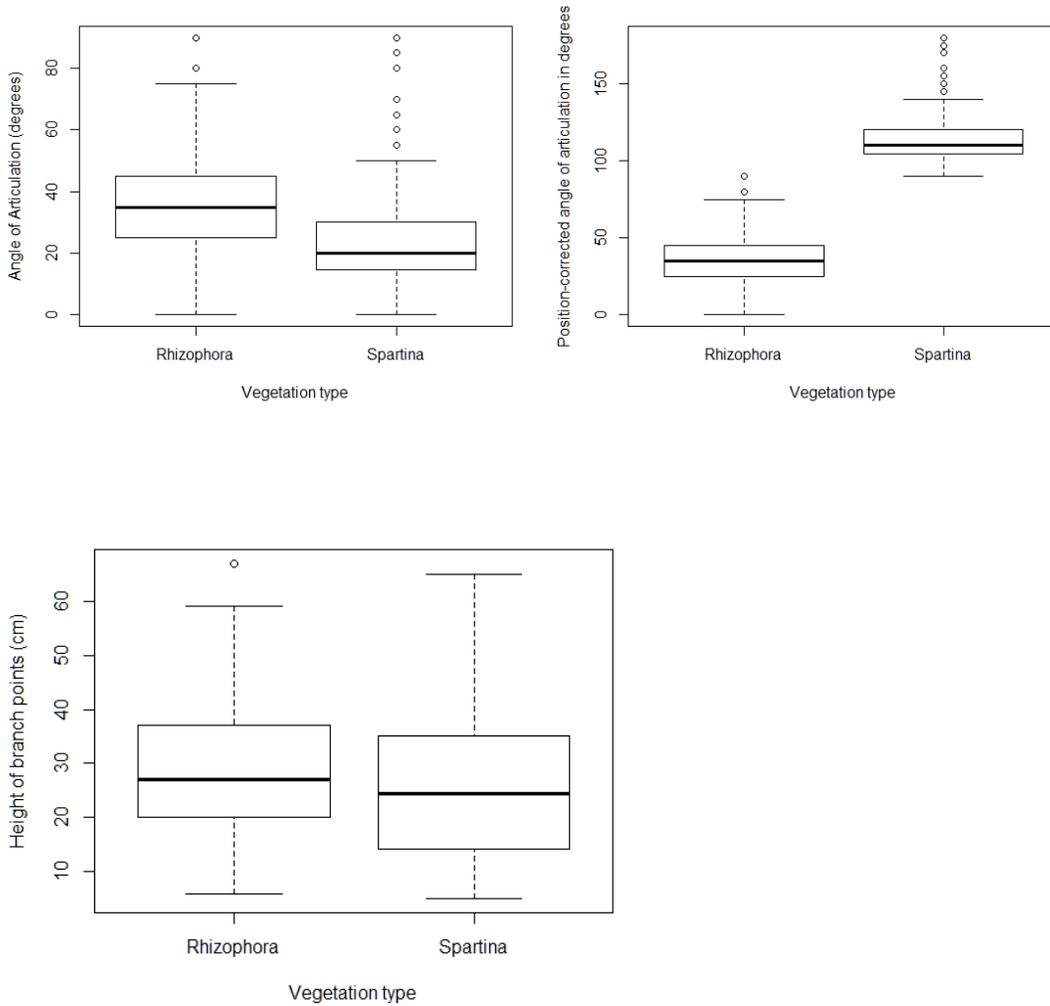
Figure A1.6: Angle of articulation (essentially size of spaces created), position of articulation (angle adjusted for vertical position – essentially direction of opening), and height of branch points (cm).

Appendix 2: Modeled species-specific responses in the settled crab community

A)

B)

C)

D)
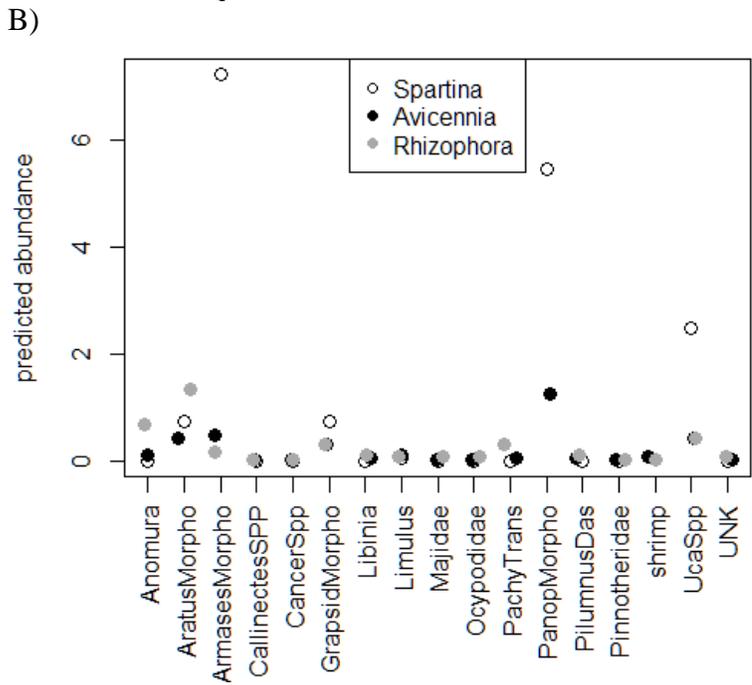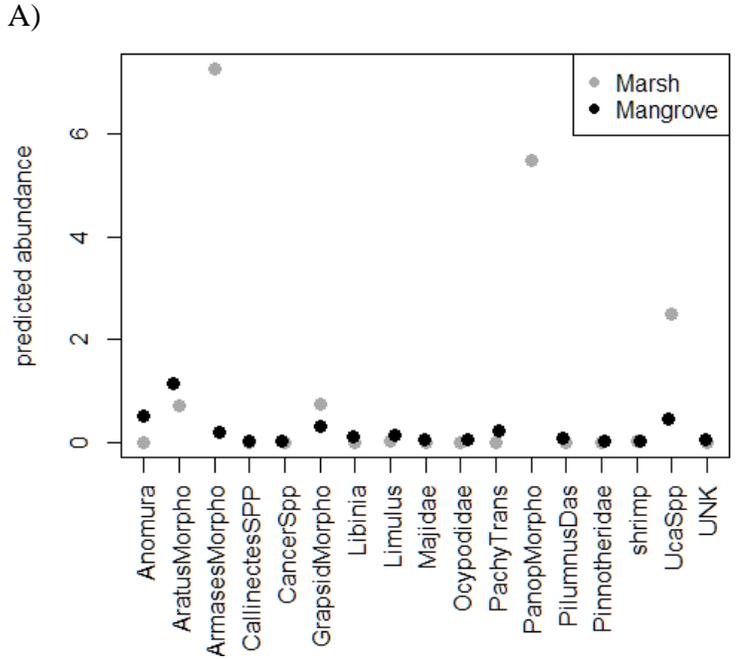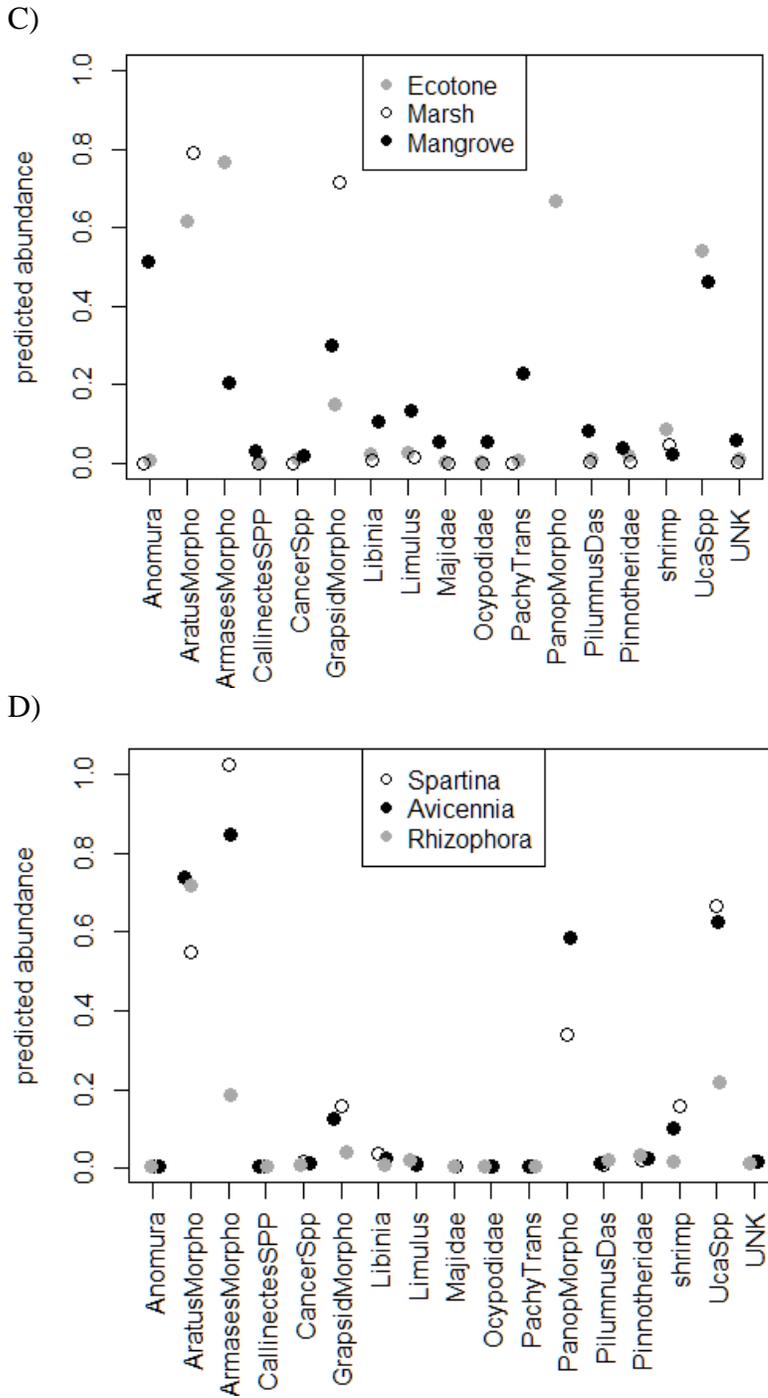
Figure A2: Modeled species-specific responses of the settled crab community to focal

predictors in each landscape. High predicted abundance indicates strong species occurrence

in a given habitat. Species that were abundant in a single habitat were considered strongly

associated with that habitat. (A) Associations by landscape type only in baseline landscapes

dominated by mangal forest or saltmarsh. (B) Associations by habitat type within the same

baseline landscapes. (C) Associations by landscape type, including the ecotone. (D)

Associations by habitat type solely within the mixed vegetation ecotone.

Appendix 3: Modeled species-specific responses across scales and cues

A)
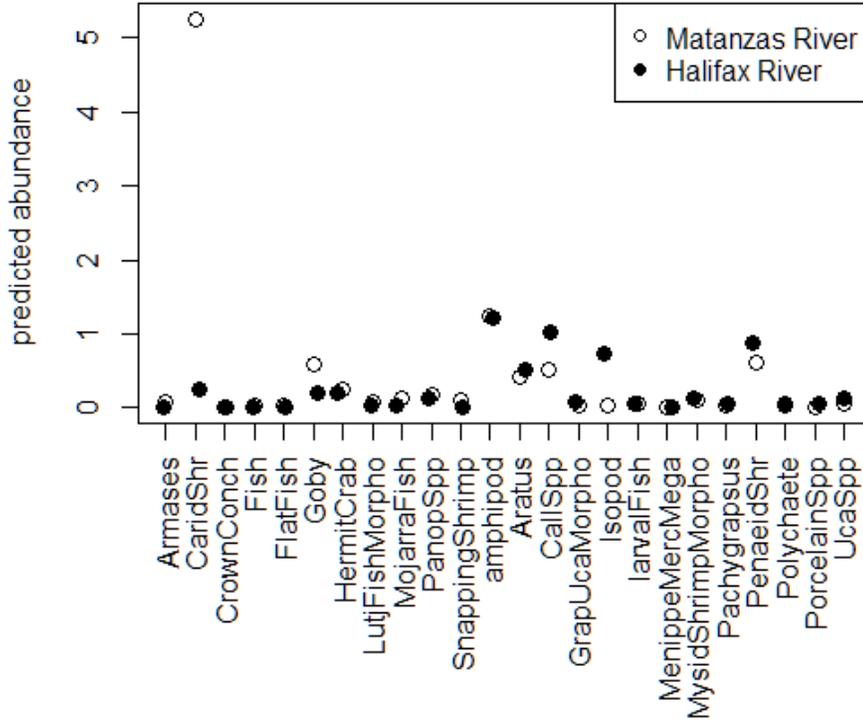
B)
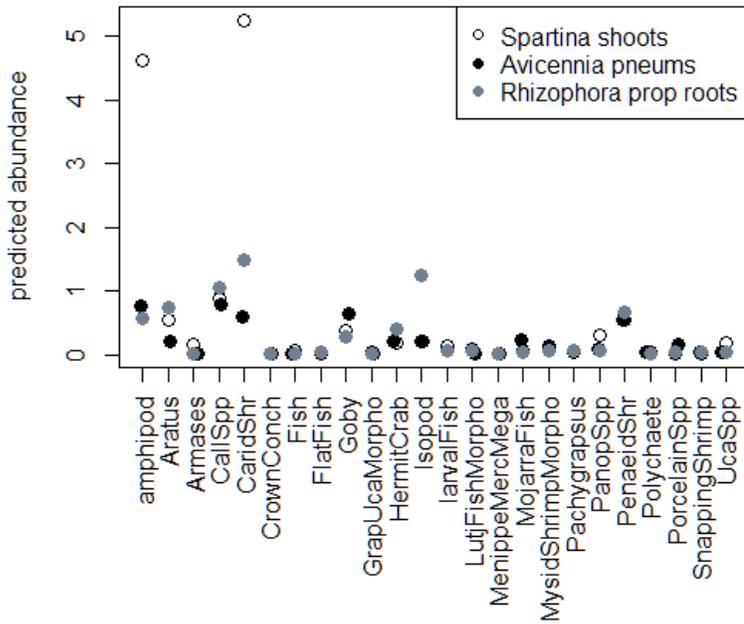
C)
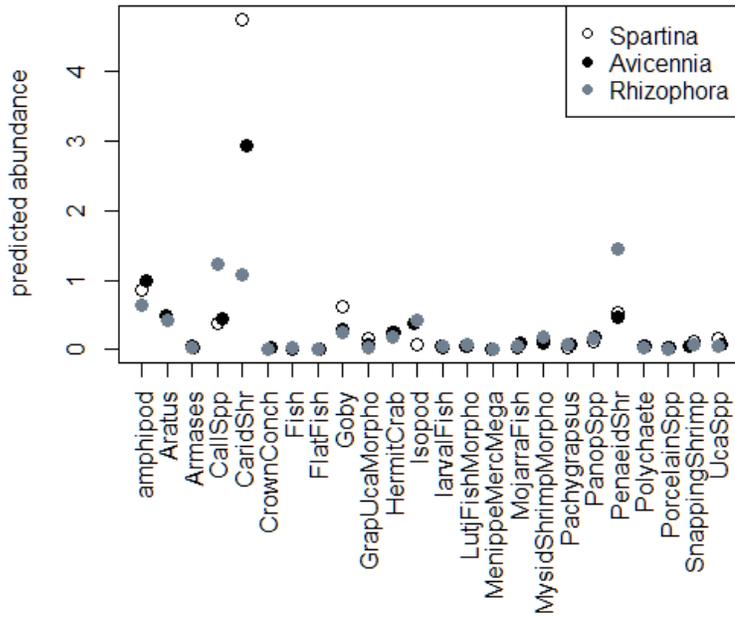
D)
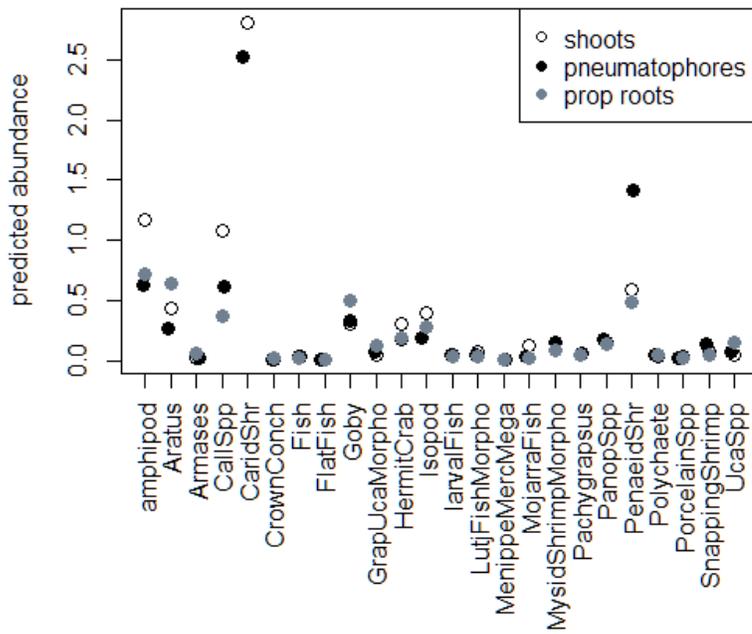
Figure A3: Modeled species responses by predictor level; species with a higher predicted abundance at a particular level were more strongly associated with that level. (A) Species associations by site. For site, species have been grouped so that those to the left show some

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affinity for Matanzas River (marsh-dominated), while species to the right were more closely

associated with Halifax River (mangrove-dominated) (Figure 3.1B). For all other plots,

species are listed alphabetically. (B) Modeled species responses by vegetation type on control

panels, which include both structural and stand-level habitat attributes. (C) Modeled species

responses by habitat type, incorporating any stand-level attributes. (D) Modeled species

responses by structural features.

Appendix 4: Habitat attributes and their influence on survival patterns

Table A4: Categorization of attributes of each microhabitat – the growth form of each vegetation type that occupies the intertidal water column. Assignments are based on analysis of data from vegetation plots in the field (Appendix 1). Result refers to differences in survival across a given attribute.

Attribute	Categorization by habitat type			Analysis	
	Spartina	*Avicennia*	*Rhizophora*	**Test grouping**	**Result**
Element	shoots	pneumatophores	prop roots	vegetation type	NS*
Density (m^{-2})	150±11SE	227±44SE	86±9SE	vegetation type	NS*
Spacing	-	equivalent (NS)	-	N/A	
Tissue	herbaceous	woody	woody	Spart v Rhiz+Avic	NS
Diameter	<10cm, low variance	<10cm, low variance	>10cm, high variance	Rhiz v Spart+Avic	NS
Arrangement	branching	simple	branching	Avic v Rhiz+Spart	P=0.008

* p>0.05 when compared between vegetation types; p<0.05 for grass when each vegetation was compared to unvegetated sand substrate

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