

**Assessing seascape-wide ecological connectivity in support of conservation
and restoration efforts in the Florida Keys, USA**

by

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Abstract

Multi-habitat use is a widespread strategy for marine organisms, including numerous coral reef fish and invertebrate species of ecological and economic importance. Through daily, seasonal, or ontogenetic migrations, these species play vital roles in maintaining functional connectivity, i.e., the exchange of organisms, energy, nutrients, and other matter between habitats in spatially and topographically heterogeneous seascapes. However, stressors operating over multiple spatiotemporal scales, including global ocean warming and acidification, land-use change, and resource overexploitation, are degrading and fragmenting marine habitats, threatening functional connectivity. Identifying, protecting, and restoring habitat patches and corridors responsible for maintaining multi-scale and multi-species functional connectivity is essential for marine conservation. In this thesis, I address key knowledge gaps in our understanding of the spatial and environmental conditions supporting the cross-shelf (> 5 km) ontogenetic migrations of two mesopredatory reef fish species occupying a heavily modified coastal seascape in the Florida Keys, USA—gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*). In addition to supporting local fisheries, both species play a critical role in shaping ecosystem function by delivering allochthonous nutrient subsidies and modifying rates of herbivory, corallivory, and predation by other community members, yet their ontogenetic habitat shifts remain difficult to track using conventional techniques due to their small body size at migration and the broad spatiotemporal scales over which they move. In Chapter 2, I first compared two techniques for modeling seascape-wide habitat suitability for the migratory sub-adults of each species—penalized logistic regressions and Maximum Entropy (MaxEnt) modeling—using fish records from SCUBA-diver surveys and high-resolution spatial data on bathymetry, seasonal water conditions, habitat configuration, and seascape surface geomorphology. I found that across species and

suitability thresholds, MaxEnt’s discriminatory ability exceeded that of the penalized regressions. Furthermore, MaxEnt’s patchy suitability predictions, which were driven primarily by benthic habitat composition, depth, and broad-scale seafloor features, more closely aligned with the known ecology of the study species. Then, in Chapter 3, I modeled potential functional connectivity for sub-adult *L. griseus* and *H. sciurus* using a spatial graph-theoretic approach in which MaxEnt-derived nodes (i.e., suitable habitat patches) and edges (i.e., least-cost paths predicted over species-specific resistance surfaces) were used to quantify and visualize the probability of connectivity at both the local and seascape scales. I then used the resulting connectivity networks to evaluate and rank the contributions of candidate sites prioritized for coral restoration as part of the spatial design of a broad-scale, multi-million dollar (USD) coral reef restoration program recently established in the Florida Keys—*Mission: Iconic Reefs*—to seascape-wide connectivity. I hypothesized that sites located adjacent to potential mangrove and seagrass nurseries would support higher levels of connectivity for both species, and thus be of greatest value for restoration. Spatial graph analyses revealed that, across scales, the Florida Keys seascape presently supports a higher level of potential connectivity for sub-adult *H. sciurus* relative to *L. griseus*. Moreover, these models suggest that the *Mission: Iconic Reefs* sites are more likely to benefit from ecological interactions with migrating *H. sciurus* compared to *L. griseus* based on their spatial configuration. Contrary to my hypothesis, however, site-specific connectivity contributions were not found to be related to nursery proximity. This thesis demonstrates how spatial graph connectivity analyses informed by habitat suitability modeling can be leveraged as a tool in support of marine habitat restoration planning through the development of data-driven spatial priorities and joins previous research showcasing the ecological benefits of integrating multi-species connectivity in marine reserve design, including productivity and diversity enhancements.

Preface

This thesis is an original work by Courtney E. Stuart. This research was supervised by Dr. Stephanie J. Green (University of Alberta) and was conducted in collaboration with Drs. Lisa M. Wedding and Simon J. Pittman (University of Oxford). S.J.G. and I (C.E.S.) conceived the research. I developed the research methods and conducted all analyses, with input from S.J.P., L.M.W., and S.J.G. I produced the tables, figures, and maps, and wrote the manuscripts. All co-authors provided editorial feedback and approved the final products.

Chapter 2 of this thesis (pages 9–50) was previously published in the *Diversity* Special Issue: “Ecological Connectivity among Tropical Coastal Ecosystems,” as: Stuart, C. E., Wedding, L. M., Pittman, S. J., & Green, S. J. (2021). Habitat suitability modeling to inform seascape connectivity conservation and management. *Diversity*, 13(10), 465.

Chapter 3 of this thesis (pages 51–85) is currently in preparation for *Restoration Ecology* as: Stuart, C. E., Wedding, L.M., Pittman, S.J., & Green, S.J. Connectivity modeling in support of coral reef restoration design.

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List of Abbreviations

AUC	Area under the receiver-operator curve
BNP	Biscayne National Park
BPI	Bathymetric position index
BTM	Benthic Terrain Modeler
EC	Equivalent Connectivity
FKNMS	Florida Keys National Marine Sanctuary
GIS	Geographic information systems
HSI	Habitat suitability index
HSM	Habitat suitability model
IF	Interaction Flux
Max SSS	Maximum sum of sensitivity and specificity
MVS	Mangrove Visual Survey
NOAA	National Oceanic and Atmospheric Administration
PC	Probability of Connectivity
RVC	Reef Visual Census
USA	United States of America
USD	United States Dollar
VIF	Variance inflation factor

Chapter 1: General introduction

1.1 Background

Relationships between spatiotemporal patterns and ecological processes have long fascinated geographers and ecologists alike. This interest was officially formalized in the 20th century by the rise of the landscape ecology discipline. *Landschaftsökologie*, or landscape ecology, was initially coined in 1939 by German biogeographer Carl Troll, who, over subsequent decades, came to define the discipline as, “The study of the main complex causal relationships between the life communities and their environments in a given section of a *Landschaft* (landscape),” going on to say that, “These relationships are expressed regionally in a definite distribution pattern (*Landschaft* mosaic, *Landschaft* pattern),” (Troll 1939, 1968, 1971). This early definition emphasized the holistic, spatially explicit nature of landscape ecology research and triggered a paradigm shift in ecology where environments were no longer assumed to be spatially homogeneous, but rather dynamic, heterogeneous units interacting with and responding to disturbances across scales in space and time (Turner 1989, 2005). Incipient landscape ecologists in Europe, who typically followed a human-centered approach, focused on nomenclature and classification, along with spatial planning in built systems. In contrast, their North American counterparts, whose numbers surged around the 1980s, followed hypothesis-driven, ecocentric approaches with an emphasis on spatial modeling, advancement of theory, and natural resource management (Pittman et al. 2017). Bolstered by improvements in geographic information systems (GIS), remote sensing technologies, computer science, and spatial statistics, modern landscape ecology provides a unified framework for studying pattern-process interactions in human-nature systems that explicitly considers scale, enabling researchers to answer a suite of basic and applied questions ranging from biodiversity modeling to cultural landscape preservation (Turner 2005; Pittman et al. 2017).

Despite a long and rich history in terrestrial systems, application of landscape ecology theory and techniques to marine landscapes (i.e., seascapes) remained relatively rare up until the turn of the 21st century. However, growing recognition of seascapes as dynamic, heterogeneous entities altered by natural and human disturbances in much the same way as terrestrial landscapes prompted the development of a new discipline, seascape ecology (Pittman 2017). This emerging, pattern-oriented science, which borrows and modifies landscape ecology concepts and methodologies developed in terrestrial environments (Wedding et al. 2011), has gained significant

traction in coastal seascapes, where multi-scale land- and ocean-based stressors interact to visibly alter seascape structure (Halpern et al. 2008, 2019). Indeed, loss, fragmentation, and degradation of coastal habitats, such as seagrasses and mangroves (Orth et al. 2006; Waycott et al. 2009; Polidoro et al. 2010), now mirror that of terrestrial grasslands and forests, with potentially cascading effects on ecological function. Understanding the causes and consequences of spatial heterogeneity and patchiness are now pressing goals in seascape conservation and management initiatives, including marine spatial planning, reserve design, and habitat restoration (Olds et al. 2016; Carr et al. 2017; Balbar & Metaxas 2019). Seascape ecology has revolutionized the way marine ecologists, resource managers, and restoration practitioners address these objectives by emphasizing seascape context, configuration, connectivity, and consideration of scale, known collectively as the 4Cs (Pittman et al. 2021).

Seascape ecology has encouraged a shift from patch- and biotope-specific thinking to exploration of entire seascape mosaics as focal units. This shift in perspective stems from the realization that focal patches do not exist and operate in isolation, but are rather influenced by the size, composition, and arrangement of surrounding edge, patches, and ecotones, as well as the identity and abundance of their inhabitants, over a range of spatiotemporal scales (Turner 1989). Determining how the structural and compositional attributes of seascapes effect the exchange of organisms, energy, nutrients, and other materials between their elements (i.e., functional connectivity) has become a central goal in seascape ecology (Grober-Dunsmore et al. 2009; Pittman 2017). However, direct measures of functional connectivity are complicated by complex interactions between biological, physical, and social regimes, including human interference (Turner 1989). Furthermore, functional connectivity is an emergent, scale-dependent (i.e., non-generalizable) property of seascapes, with individual species and processes reacting to spatial heterogeneity over unique spatial and temporal scales. Thus, functional connectivity research necessitates an organism- or process-centered view of seascapes that accounts for multiple drivers of change (Turner 1989; Costa et al. 2017; Pittman et al. 2021). Globally, burgeoning land- and ocean-based anthropogenic activities threaten to degrade and fragment critical habitat for countless marine species, with implications for the distribution, functioning, and persistence of ecological communities (Halpern et al. 2019). Identifying, preserving, and, where applicable, restoring, the spatial and environmental conditions necessary to support healthy, diverse, and well-connected communities is therefore essential to effective marine conservation and stewardship, and will be

particularly important as we enter the United Nations (UN) Decade on Ecosystem Restoration (2021-2030) (Waltham et al. 2020).

Quantifying seascape functional connectivity, whether the directed movements of nekton or current-driven fluxes of suspended materials, in support of conservation and restoration efforts is often hindered by the broad spatiotemporal scales over which these processes operate (Turner 1989). Although functional connectivity may be measured over finer scales using tagging, tracking, or conventional experimental approaches, seascape ecologists increasingly turn to spatial modeling to inform broad-scale issues. Furthermore, connectivity mapping and modeling efforts are becoming more practical and urgent as the pace, magnitude, and scale of environmental challenges continue to rise (Pittman 2017). One modeling approach that has received substantial attention and progress over recent decades stems from graph theory, a branch of mathematics interested in functional connections between discrete entities (Urban & Keitt 2001). A graph is defined as a set of nodes connected to some extent by edges and has long been used to represent and analyze data in the computer, information, and social sciences. More recently, graphs have been updated to retain geographic coordinate system information, resulting in *spatial graphs* in which the geographic location and geometric attributes of nodes and edges are preserved (Fall et al. 2007; Urban et al. 2009). In the context of seascape ecology, spatial graphs have been applied to estimate potential functional connectivity (hereafter, potential connectivity) arising from the dispersal of organisms between suitable seascape patches embedded in a matrix of lower quality habitat, where connectivity is assumed to be driven by interactions between the focal species' behavioral and life-history traits and the spatial arrangement of seascape elements (Fagan & Calabrese 2006). Spatial graphs are therefore a valuable, data- and -computationally efficient method for studying potential changes in functional connectivity over time, such as before and after implementation of marine protected areas or habitat restoration, and may be subsequently evaluated *in situ* should additional time or resources become available (Fagan & Calabrese 2006). However, defining and delineating the boundaries of suitable seascape patches to use as nodes in spatial graphs remains challenging for highly heterogeneous seascape mosaics and species with multi-habitat life histories.

In this thesis, I merge species- and life stage-specific habitat suitability models (HSMs) and spatial graphs to better understand potential connectivity for two abundant reef fish species occupying a spatially heterogeneous coastal seascape in the Florida Keys, USA. Like many other

reef fishes (Nagelkerken et al. 2000b, 2015), the species at the heart of this research—gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*)—undertake cross-shelf ontogenetic migrations as sub-adults from coastal mangrove and seagrass nurseries to adult habitat on offshore coral reefs (Faunce & Serafy 2007). However, the migrations of these and other economically and ecologically valuable mesopredators have and continue to be threatened by anthropogenic habitat alterations (Ault et al. 2005), with implications for seascape-wide functional connectivity and metapopulation persistence. To forestall further environmental degradation, habitat restoration programs have proliferated in the Florida Keys, including the National Oceanic and Atmospheric Administration’s (NOAA) *Mission: Iconic Reefs* program announced in 2019, which aims to recover the diversity and health of corals in the Florida Keys National Marine Sanctuary (FKNMS) (NOAA Fisheries 2019). This thesis provides baseline estimates of existing suitable habitat and potential connectivity for *L. griseus* and *H. sciurus* sub-adults ahead of coral restoration efforts, while simultaneously applying the 4Cs to reveal the coral reef restoration sites most likely to benefit from the ecological functions provided by migrating *L. griseus* and *H. sciurus*, including predation and deposition of allochthonous nutrients (Shantz et al. 2015; Ladd et al. 2018).

In Chapter 2 of this thesis, I compare two methods for mapping and modeling the distribution of suitable habitat for sub-adult *L. griseus* and *H. sciurus*—maximum entropy (MaxEnt) and penalized logistic regressions. To determine which method produces the most ecologically realistic HSMs for use in subsequent connectivity analyses, I first evaluate each model’s ability to discriminate between suitable and unsuitable locations using threshold-independent (i.e., area under the receiver-operator curve (AUC)) and threshold-dependent (i.e., accuracy, sensitivity, and specificity) assessments. Then, to better understand the spatial patterns and environmental variables driving habitat suitability for sub-adult stage *L. griseus* and *H. sciurus*, I explore the five most influential predictors of suitability from the top-performing model for each species. Finally, these influential predictors, as well as the seascape-scale continuous suitability surfaces, are compared to the known ecology of the two study species from previous experimental, observational, and tracking studies to evaluate each model’s overall quality. This thesis chapter provides evidence that spatial and environmental variables, including habitat composition and configuration, bathymetry and seafloor surface morphology, and seasonal water conditions, can be coupled with SCUBA-diver based species occurrence data to reliably predict

habitat suitability for two common reef fishes and, therefore, presents a helpful strategy for delineating suitable habitat nodes for connectivity modeling via spatial graphs.

In Chapter 3 of this thesis, I model potential connectivity for *L. griseus* and *H. sciurus* sub-adults and use these models to evaluate the spatial design of the newly established *Mission: Iconic Reefs* coral restoration program. To achieve this goal, I first construct species-specific minimum planar (spatial) graphs using suitable seascape patches (i.e., nodes) and least-cost paths (i.e., edges) derived from the MaxEnt HSMs produced in Chapter 2. These graphs are then analyzed using both global (i.e., Probability of Connectivity (PC), Equivalent Connectivity (EC)) and local (i.e., Interaction Flux (IF)) metrics to evaluate seascape-wide potential connectivity and node-scale connectivity contributions, respectively. The selected and alternate *Mission: Iconic Reefs* restoration sites are then ranked by their IF values to provide an indication of their roles in supporting potential connectivity across the Florida Keys seascape for *L. griseus* and *H. sciurus* sub-adults. This thesis chapter demonstrates a novel application of connectivity modeling to inform coral reef restoration design and emphasizes the value of connectivity and seascape context as guiding factors in habitat restoration planning.

Finally, in Chapter 4, I synthesize the findings presented in Chapters 2 and 3, and address outstanding challenges facing seascape connectivity research. I touch on future research priorities and review strategies for explicitly integrating seascape connectivity in habitat restoration design in the Florida Keys and beyond. Lastly, I conclude with a brief discussion of connectivity conservation research at the intersection of theoretical, empirical, and applied efforts.

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Chapter 2: Habitat suitability modeling to inform seascape connectivity conservation and management

2.1 Introduction

Understanding the spatial, temporal, and environmental drivers of marine species distributions is paramount to developing ecologically sound conservation and place-based management strategies (Marshall et al. 2014; Villero et al. 2017). These efforts are increasingly urgent as global climate change interacts with local and regional stressors (e.g., pollution, overexploitation) to degrade and fragment marine ecosystems (Smale et al. 2019; Gissi et al. 2021). Coastal habitats, including mangroves (Polidoro et al. 2010), seagrasses (Waycott et al. 2009), corals (Gardner et al. 2003), and salt marshes (Deegan et al. 2012), have experienced precipitous declines worldwide over the last several decades, thereby vastly reducing the suitable habitat space for many marine species. Biodiversity loss stemming from environmental degradation enhances the risk of functional collapse by reducing ecosystem resilience to interacting stressors (Duffy et al. 2016; Benkwitt et al. 2020). Identifying priority locations for protection and restoration of coastal habitats at both local and global scales is therefore one of the most important challenges in marine conservation and spatial planning (Kennedy et al. 2013; Waltham et al. 2020). Seascape connectivity is increasingly recognized as a dynamic and spatially explicit process regulating biodiversity patterns and ecosystem functions, and playing an important role in guiding coastal conservation efforts (Olds et al. 2016; Carr et al. 2017; Weeks 2017; Balbar & Metaxas 2019).

Seascape connectivity represents ecological linkages and flows across heterogeneous environments (Taylor et al. 1993, 2006), typically related to the flow of organisms, energy, nutrients, or genetic material. The magnitude and location of these exchanges are shaped by patterns of intra- and inter-habitat connectivity, with the latter being especially important for species whose movements span multiple habitat types. In tropical coastal seascapes, for example, multi-habitat use is widespread with almost half of all coral reef associated fish species having also been recorded in two or more non-reef habitats (Sambrook et al. 2019). Seascape connectivity can be categorized into two major types—structural connectivity and functional connectivity (Olds et al. 2016). Structural connectivity describes the spatial patterns and relationships of the seascape itself (e.g., patch areas, inter-patch distances, habitat corridors), whereas functional connectivity describes the degree to which animals move among resource patches in response to those structural patterns (Taylor et al. 2006; Grober-Dunsmore et al. 2009). Functional connectivity is therefore

inherently species- and life stage-specific, as it depends on the behavioral and life history traits of the organism, and on the spatiotemporal scales of their movements (Taylor et al. 2006; Tischendorf & Fahrig 2000). Thus, management programs that maximize functional connectivity across scales and communities, including through place-based conservation measures such as marine protected areas, are expected to achieve greater ecological outcomes (Olds et al. 2016; Carr et al. 2017; Weeks 2017). Facilitating these efforts are models of potential connectivity, in which limited data on species behavior or dispersal are related to metrics of seascape structure (Grober-Dunsmore et al. 2009). These include graph-theoretic approaches, in which the seascape is represented by a spatial graph constructed of suitable habitat patches (nodes) connected by a series of dispersal links (edges) (Urban & Keitt 2001). In this regard, potential connectivity models can be used to estimate connectivity thresholds, movement corridors, and stepping-stones unique to individual seascape residents, which can then serve as targets in conservation and restoration planning (McRae et al. 2012; Daigle et al. 2020).

To successfully inform conservation efforts, connectivity models must achieve a high level of ecological realism, which relies on knowledge of the current distribution of suitable habitats and species–environment relationships. One way to access this information is through habitat suitability modeling, also referred to as species distribution modeling, a method that uses known species locations and their associated environmental conditions to predict habitat suitability over space and time (Guisan & Zimmermann 2000). When used as a precursor to connectivity modeling, predictive habitat suitability models (HSMs) can reveal the locations and sizes of suitable habitat patches, which can then serve as nodes in spatial graphs (Dufлот et al. 2018). Furthermore, assuming that animals travel along pathways that minimize their ecological costs, HSMs can be inverted to produce cost surfaces over which connectivity is predicted (e.g., least-cost path models), potentially increasing the realism and precision of predicted edges (Stevenson-Holt et al. 2014). As the integration of three-dimensional surfaces alongside standard two-dimensional predictors becomes more common in spatial modeling (Lepczyk et al. 2021; Wedding et al. 2019), the value of HSMs and HSM-derived cost surfaces for connectivity analysis will likely increase. Although realistic HSMs can help bridge the gap between connectivity modeling and conservation planning, applications of this multi-step approach have been applied only to terrestrial landscapes (Dufлот et al. 2018; Poor et al. 2012; Penjor et al. 2021).

The limited availability and quality of species occurrence and environmental data represent major barriers to habitat suitability modeling in complex coastal seascapes. However, recent advancements in remote sensing technology have increased the accessibility of data on marine habitat mosaics, three-dimensional seascape terrain structure, and oceanographic conditions, which can serve as ecologically relevant spatial predictors in HSMs (Lepczyk et al. 2021; Wedding et al. 2019; Green et al. 1996). When possible, systematic surveys (e.g., SCUBA censuses) can be performed to collect detailed presence–absence data for focal species, which can then be used to predict the probability of species presence via generalized linear or additive modeling (e.g., logistic regression) (Guisan & Zimmermann 2000; Pearce & Ferrier 2000). The cost of systematic surveys, however, may limit their coverage and usefulness for seascape-wide modeling. In contrast, presence-only species data may be compiled from a variety of sources covering broad geographic and environmental space, including online biodiversity databases (e.g., gbif.org, obis.org), fishery-dependent and fishery-independent programs, and citizen science initiatives. When coupled with information on environmental conditions at a set of background points (i.e., presence-background data), these data can be used to estimate the relative likelihood of species occurrence (Guillera-Arroita et al. 2015). MaxEnt, an open-source machine learning software that uses the principle of maximum entropy to model species distributions, is a popular presence-background technique (Phillips et al. 2006; Phillips & Dudík 2008). MaxEnt and standard regression techniques have displayed similar predictive performance in several terrestrial studies (Elith et al. 2006; Gibson et al. 2007; Roura-Pascual et al. 2009; Marini et al. 2010), although the generality of these findings is still under debate (Qiao et al. 2019). Furthermore, it remains unclear whether MaxEnt’s predictive performance holds in complex seascapes and under the scrutiny of connectivity modeling.

We compared penalized logistic regression and MaxEnt models of habitat suitability for two common fish species across a spatially heterogeneous coastal seascape in the Florida Keys, United States of America (USA). Our primary objective was to determine which modeling method produced the more realistic HSM for use in subsequent connectivity assessments. To meet this objective, we examined each model’s ability to discriminate between suitable and unsuitable locations using both threshold-independent and threshold-dependent assessments. Our secondary objective was to identify the most influential environmental and spatial predictors of habitat

suitability for each species to better understand the species-seascape interactions that shape patterns of connectivity.

2.2 Methods

2.2.1 Study area

The Florida Keys—a string of islands located off the southern tip of Florida between the Atlantic Ocean and the Gulf of Mexico—were selected as a case study for this research (Figure 2.1). The seascape in this region has been described as a mangrove–seagrass–reef continuum featuring patches of shoreline mangroves, dense seagrass beds interspersed with patch reefs, and finally the Florida Reef Tract located 5–15 km offshore (Ogden et al. 1994). Despite protection from the Florida Keys National Marine Sanctuary (FKNMS) and Biscayne National Park (BNP), this region has experienced significant declines in biogenic habitat over the last 50 years. A range of local, state, and federal organizations are now focusing substantial resources on habitat restoration to combat loss and fragmentation, with the offshore reef tract being a major target (NOAA Fisheries 2019). These restoration efforts will benefit from a thorough understanding of the daily, seasonal, and ontogenetic migrations of reef fishes between spatially isolated habitats across the seascape, as these movements increase reef productivity and resilience through the transfer of nutrients, the maintenance of top-down control on coral predators, and the enhancement of grazing pressure on harmful epiphytes and macroalgae that could otherwise shift reefs into a macroalgal state (Mumby & Hastings 2008; Ladd et al. 2018; Ladd & Shantz 2020). In fact, the transfer of nitrogen and phosphorus from sheltering resident and migratory reef fishes to their host corals has been demonstrated to significantly increase zooxanthellae abundance and coral growth rates (Meyer & Schultz 1985; Holbrook et al. 2008). Fish-derived nutrient hotspots thus offer important supplements to oligotrophic tropical and subtropical coral reefs, including those of the Florida Keys (Shantz et al. 2015). Therefore, we focused on modeling habitat suitability for reef fishes in the coastal region (≤ 50 m depth) from Key Biscayne in the Upper Keys to Cudjoe Key in the Lower Keys.

2.2.2 Focal species

We selected gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) as focal species due to their complex, multi-habitat life histories. Though generally considered reef-

associated as adults, these species occupy spatially discrete patches of varying habitat type through ontogeny, resulting in them being categorized as seascape nursery species (Nagelkerken et al. 2000b, 2015). In Southern Florida, larval *L. griseus* and *H. sciurus* settle in seagrass beds around September and February, respectively, before expanding to mangroves several months later (Faunce & Serafy 2007). Juveniles often remain in nearshore nurseries for months to years, then, as sub-adults, undertake a cross-shelf migration to join adults on offshore coral reefs. Although it is clear that their ontogenetic migrations play an important role in maintaining seascape-wide ecological connectivity, there remains a paucity of information on habitat suitability across the seascape for *L. griseus* and *H. sciurus*. Additionally, there may be considerable inter-species variation in habitat suitability, and consequently, functional connectivity, stemming from unique preferences for nearshore strata (Faunce & Serafy 2007, 2008), tolerances to salinity fluctuation (Serafy et al. 1997), and motivations for movement (Cocheret de la Morinière et al. 2003; Nemeth 2009). Addressing these knowledge gaps is of critical importance as *L. griseus* and *H. sciurus* play key ecological and economic roles in the region as abundant members of the fish assemblage, highly mobile predators and vectors of nutrient transfer, and valued sport and commercial fishery targets (Ault et al. 2005; Harper et al. 2000).

Data describing the size, abundance, and distributions of *L. griseus* and *H. sciurus* were obtained from two multi-agency monitoring programs coordinated by the NOAA Southeast Fisheries Science Center: the South Florida Reef Visual Census (RVC) and the Mangrove Visual Survey (MVS). Using a two-stage stratified random sampling design, the RVC program surveys fish communities on coral reefs and other hard bottom habitats biennially using a stationary visual survey method (Bohnsack & Bannerot 1986). Similarly, the MVS program conducts annual belt transect surveys alongside randomly selected mangrove shoreline sites in Biscayne Bay, Card Sound, Barnes Sound, and northeastern Florida Bay (Serafy et al. 2003; Serafy & Teare 2017). At each site, a trained diver records the identity, abundance, and size structure of all fishes encountered; RVC surveys occur within a 7.5 m-radius imaginary cylinder extending vertically from the seafloor to the surface, while MVS surveys take place over 30 × 2 m transects established parallel to the shore. These programs were designed to collect data that enables the detection of spatiotemporal changes in reef fish species composition, size, and abundance using statistical analyses. Thus, we compiled RVC and MVS data collected at unique sampling sites in 2014, 2016, and 2018 to maximize the spatial coverage of georeferenced *L. griseus* and *H. sciurus* records.

This process also ensured a temporal match between the two reef fish monitoring programs and the spatial predictors described below, which are based largely on data collected between 2014 and 2018. Considering the dynamic nature of the Florida Keys, where seafloor features change over time, we used temporal data alignment to prevent model inaccuracies.

2.2.3 *Spatial predictors*

To explore the relationship between spatial predictors and *L. griseus* and *H. sciurus* distributions, we constructed raster data layers to map the following environmental categories: benthic habitat, bathymetry and seafloor morphology, and water conditions (Table 2.1; Figure 2.2). All rasters had a grid cell resolution of 5×5 m and were referenced to the Florida East projected coordinate system (EPSG:26958) and the NAVD vertical coordinate system (EPSG:5703) where applicable.

2.2.3.1 Benthic habitat

Benthic habitat data were obtained from Florida's Unified Reef Map v2.0 (FWRI 2016), a seamless map of benthic habitats from Martin County to the Dry Tortugas derived from remote sensing imagery, high-resolution bathymetric data, and *in situ* observations using a five-tier hierarchical classification system. We supplemented the Reef Map with a separate GIS dataset of shoreline mangroves to fully capture the extent of this potentially important nursery habitat (FWRI 2017). For this research, we used Level 1 map classifications, which delineate the major benthic habitat types while maintaining agreement between the Reef Map's contributing agencies. Habitat data were rasterized, producing cells that reflected the IDs of 12 possible benthic habitats: individual or aggregated patch reef, scattered coral and rock in unconsolidated sediment, continuous seagrass, discontinuous seagrass, unconsolidated sediment, aggregate reef, pavement, reef rubble, mangrove, artificial, dredged and excavated, and ridge. We also assessed the importance of mangrove nursery proximity by constructing a raster of Euclidean distances to the nearest mangrove habitat using the *raster* R package (v3.3–13) (Hijmans 2020) in R version 4.0.2 (R Core Team 2020).

2.2.3.2 Bathymetry and seafloor morphology

NOAA's 1/9th ArcSecond Resolution Continuously Updated Digital Elevation Model served as an initial bathymetric surface for this research (CIRES & NOAA-NCEI 2014). Seafloor

morphology was quantified from the bathymetric surface by applying metrics of slope, curvature, rugosity, bathymetric position index (BPI), and standard deviation of depth using the Benthic Terrain Modeler ArcGIS extension (BTM v3.0) (Wright et al. 2012) in ArcGIS v10.7.1. These rasters captured detailed information on the structure and complexity of the seafloor, including the locations of crests, flats, and valleys, the direction of benthic flow, and the roughness of the local surface (Walbridge et al. 2018). The influence of seascape surface morphology on the distribution of tropical reef fishes has been demonstrated in coral reef ecosystems in the U.S. Caribbean (Pittman & Brown 2011; Costa et al. 2014), Hawaii (Wedding et al. 2019; Wedding & Friedlander 2008; Stamoulis et al. 2018), and elsewhere (Borland et al. 2021); however, this approach has not been applied at a seascape scale to fishes of the Florida Keys.

2.2.3.3 Water conditions

Seasonal water conditions, in addition to habitat availability and seafloor morphology, may play a role in shaping the distributions of *L. griseus* and *H. sciurus*. We investigated this possibility using raster data layers of mean bottom temperature, salinity, and dissolved oxygen. Using ordinary kriging via the *krige* function of the *gstat* R package (v2.0–6) (Pebesma 2004), we interpolated water quality data from sites that were sampled regularly over the 2014–2018 period by the Southeast Environmental Research Center’s Water Quality Monitoring Network and the Miami-Dade County Surface and Groundwater Quality Viewer. Our research focused on two critical seasons—winter (January–March) and summer (July–September)—to capture not only annual extremes, but also important periods in the life histories of *L. griseus* and *H. sciurus*, including habitat expansion and spawning activity (Faunce & Serafy 2007; Munro et al. 1973; Domeier et al. 1996).

2.2.4 Model development

2.2.4.1 Filtering and partitioning of occurrence records

As functional connectivity for *L. griseus* and *H. sciurus* across the Florida Keys seascape is maintained primarily by the cross-shelf (5–15 km) ontogenetic migrations of their sub-adult life stage, we focused our habitat suitability modeling efforts specifically on this subpopulation. Therefore, we restricted *L. griseus* and *H. sciurus* records using the size cut-offs defined in a previous Florida study (Faunce & Serafy 2007), where sub-adults are those between the size at year 1 and the size at maturation (Table 2.2). Prior to habitat suitability modeling, species

occurrence records were partitioned into calibration (70%) and evaluation (30%) subsets following a random split approach (Table 2.2).

2.2.4.2 Selection of spatial predictors

Pearson correlation coefficients (r) and variance inflation factors (VIF) were used to assess collinearity among the environmental raster data layers using thresholds of $|0.7|$ and 5 for r and VIF scores, respectively (Montgomery et al. 2012). Four spatial predictors were removed due to multicollinearity issues—standard deviation of depth, plan curvature, and dissolved oxygen across both seasons. Of the 12 predictors retained for modeling, the highest correlation was between summer and winter salinities ($r = 0.61$) and the largest VIF score, belonging to depth, was 2.63 (Table A2.1; Figure A2.2).

2.2.4.3 Penalized logistic regressions

Penalized logistic regressions predicting habitat suitability for sub-adult *L. griseus* and *H. sciurus* were constructed in R using the *glmnet* (v4.1.1) (Friedman et al. 2010) and *caret* (v6.0.86) (Kuhn 2021) packages, in R version 4.0.2. (R Core Team 2020). For each species, two logistic regressions were fit via penalized maximum likelihood. The first set of models applied the lasso penalty (i.e., L1-regularization, $\alpha = 1$), a method that minimizes the absolute magnitude of the regression coefficients (Tibshirani 1996). The lasso penalty reduces variance by shrinking or assigning a value of zero to some coefficients, thereby finding the optimal balance between model fit and complexity. The second set of models applied the ridge penalty (i.e., L2-regularization, $\alpha = 0$), a method that minimizes the sum of the squared coefficients (Hoerl & Kennard 1970). Unlike lasso, the coefficients in ridge regression can only asymptotically approach a value of zero. We applied these penalty terms independently to determine whether predictive performance varies based on regularization strategy.

The appropriate shrinkage parameters (λ) for lasso and ridge were determined based on 10-fold cross validation using the *cv.glmnet* function of the *glmnet* package (Friedman et al. 2010). Penalized logistic regressions were then fit for each species separately using *caret*, again using 10-fold cross validation for model calibration. Thus, each model was fit using the 70% of presence–absence records set aside for model calibration and the 12 spatially explicit

environmental predictors. Finally, the fitted training models were used to extrapolate predictions across the study area via the predict function of the R package *raster* (Hijmans 2020).

2.2.4.4 MaxEnt models

Maximum entropy models predicting relative habitat suitability for sub-adult *L. griseus* and *H. sciurus* were constructed using MaxEnt version 3.4.1. (Phillips et al. n.d.). MaxEnt automatically applies L1-regularization to find the most parsimonious model (Phillips et al. 2006; Elith et al. 2011). The default regularization multiplier is 1.0, however, we used species-specific tuning to identify the regularization value and feature classes (i.e., functions of continuous environmental covariates) that enhanced predictive ability while minimizing overfitting (Anderson & Gonzalez 2011; Radosavljevic & Anderson 2014). After comparing five potential regularization multipliers (0.25, 0.5, 1.0, 2.0, and 5.0) using the *ENMEval* R package (v0.3.1) (Muscarella et al. 2014), it was determined that a value of 5.0, in combination with linear, quadratic, and hinge features, was optimal for constructing presence-background HSMs for sub-adult *L. griseus* and *H. sciurus*. Additionally, to prevent environmental bias stemming from spatially biased occurrence data (Phillips et al. 2009; Fourcade et al. 2014), we created a Gaussian kernel density surface to capture the distribution of RVC and MVS sampling effort. This bias grid was fed into MaxEnt via the “bias file” option, enabling the sampling distribution to be factored out during construction of the training algorithm.

MaxEnt models were constructed using the 12 spatially explicit environmental predictors and the 70% of presence-only records designated for model calibration. Initial tuning and subsequent modeling were conducted using 10-fold cross validation and a set of 10,000 background points selected according to the bias file described above. The complementary log–log (cloglog) transformation was used, producing surfaces that reflected the predicted relative habitat suitability (or relative likelihood of occurrence) on a scale of 0 to 1.

2.2.5 Model assessment

2.2.5.1 Discriminatory ability

Predictive performance was compared between penalized logistic regression and MaxEnt models using the area under the receiver-operator curve (AUC). AUC is a threshold-independent, rank-based statistic that indicates a model’s ability to discriminate between a random absence (or

background) point and a random presence point (Phillips et al. 2006). By assessing model performance over a variety of thresholds, the AUC test statistic provides an indication of discriminatory ability on a continuous scale and enables comparisons between modeling algorithms. AUC values range from 0 to 1, with the latter representing perfect discrimination. AUCs ≤ 0.5 suggest random or worse than random performance (Hosmer et al. 2013).

2.2.5.2 Binary predictive performance

We assessed the binary classification accuracy of each model using the 30% of presence–absence records set aside during the initial train–test split. The predicted suitability surfaces for each species were first discretized to a binary scale using a standard threshold of 0.5 for the predicted probability (penalized regression) or relative likelihood (MaxEnt) of presence. A confusion matrix was then calculated for each species–model combination, and the accuracy (i.e., percentage of correct classifications), sensitivity (i.e., percentage of correctly predicted presences), and specificity (i.e., percentage of correctly predicted absences) were examined. Though this standard threshold enables a general comparison of predictive accuracy between modeling algorithms, it likely will not represent the suitability cut-off at which the models optimally distinguish between suitable and unsuitable locations, which is an essential goal when defining nodes for subsequent connectivity modeling. Thus, we also identified the suitability thresholds at which each model achieved a maximum sum of sensitivity and specificity (max SSS). Max SSS provides an indication of how conservative of a suitability cut-off must be used to maximize discrimination between the presence and absence (or suitable and unsuitable) locations (Liu et al. 2013).

2.2.5.3 Variable importance

Variable importance scores were also calculated for each species across the three modeling techniques. For penalized logistic regressions built using *glmnet* and *caret*, variable importance was assessed using `varImp`, a function of the *caret* package that scales variables from 0 to 100 according to the absolute value of their standardized coefficients. For MaxEnt models, jackknife resampling was used to assess the influence of each predictor, this procedure sums the change in regularized gain (i.e., a goodness of fit measure based on a variable’s ability to distinguish species

presence sites) across the ten cross validation folds. Regardless of model type, larger values indicate a higher level of importance.

2.3 Results

2.3.1 *Discriminatory ability*

We used the AUC test statistic to determine whether penalized logistic regression and MaxEnt modeling techniques differ in their ability to discriminate between suitable and unsuitable locations across a variety of thresholds. According to the AUC statistic, regularization strategy had little effect on the discriminatory ability of regression HSMs, as lasso- and ridge-penalized models displayed similar performance within species. For sub-adult *L. griseus*, both penalized regressions achieved an AUC value of 0.74, indicating a good model fit. Discriminatory ability improved slightly for penalized regressions of sub-adult *H. sciurus* suitability, with lasso and ridge regressions producing AUCs of 0.76 and 0.75, respectively. However, regardless of the regularization strategy, the penalized logistic models were outperformed by MaxEnt, which yielded AUC values of 0.88 for *L. griseus* and 0.86 for *H. sciurus* (Table 2.3).

2.3.2 *Binary predictive performance*

To produce the discrete patches of suitable habitat (i.e., nodes) required for modeling potential connectivity, the continuous habitat suitability surfaces must be discretized to a binary scale. Therefore, we used confusion matrices to assess each model's binary predictive performance following discretization at two thresholds. When first discretized using a standard suitability cut-off of 0.5 and compared to the withheld validation data, lasso and ridge HSMs for sub-adult *L. griseus* achieved classification accuracies of 77.9% and 77.7%, respectively. Predictive accuracy was slightly lower for sub-adult *H. sciurus*, with values of 73.2% and 74.2% for lasso and ridge regressions, respectively. Relative to the penalized regressions, overall predictive accuracy for MaxEnt was low when assessed at this suitability cut-off, ranging from roughly 40–50% (Table 2.3). The models also varied in terms of sensitivity and specificity, with penalized regressions successfully identifying known absence (i.e., unsuitable) locations more frequently than known presence (i.e., suitable) locations and MaxEnt following the opposite trend.

The max SSS threshold selection strategy, which optimizes discrimination between known presence and absence localities, identified substantially different suitability cut-offs for each of the modeling algorithms (Table 2.3). In general, the penalized logistic models would have to lower

their suitability thresholds to roughly 0.30 to maximize discrimination, whereas the MaxEnt models optimized discrimination between known presence and absence sites at a threshold of 0.65, a far less conservative cut-off. Although the overall accuracy of the penalized logistic regressions exceeded those of the MaxEnt models, MaxEnt successfully predicted true positives (i.e., model sensitivity) in a framework of minimizing false positives (i.e., 1-specificity). It must be noted, however, that other results would likely be obtained if the suitability threshold was selected to maximize model sensitivity alone (as opposed to maximizing the sum of sensitivity and specificity).

2.3.3 *Variable importance*

To better understand the species–seascape interactions driving patterns of habitat suitability and, consequently, potential connectivity, we examined the continuous habitat suitability surfaces and variable importance plots produced by each model. Within species, there was a high level of agreement between the habitat suitability predictions of the three modeling techniques; however, lasso- and ridge-penalized regressions predicted smooth, gradual patterns of decreasing suitability as distance from shore increased, whereas MaxEnt captured patchy distributions of suitable habitat with noticeable fine-scale differences (Figure A2.3). Furthermore, the models revealed species-specific responses to the various spatial predictors, resulting in considerable inter-species variation in predicted suitability across the seascape (Figure 2.3). For brevity, we focus here only on the variable contributions of the top-performing continuous HSM for each species according to AUC (i.e., the MaxEnt models). Variable importance information for the penalized regressions is provided in Figure A2.4, response curves for the top five MaxEnt predictors are provided in Figure A2.5, and frequency distribution plots displaying the breakdown of predicted habitat suitability values in relation to the standard and max SSS suitability thresholds for each species-model combination are provided in Figure A2.6.

For sub-adult *L. griseus*, MaxEnt’s jackknife procedure identified benthic habitat type as the single most influential predictor of habitat suitability, followed by Euclidean distance to the nearest mangrove, slope, depth, and broad-scale BPI (Figure 2.4; Figure A2.5). Predicted habitat suitability for *L. griseus* was high in shallow waters (< 5 m depth) within roughly 200 m from mangroves, with the highest values predicted at the interface of shoreline mangroves and seagrass meadows (i.e., the seagrass fringe). Patches of high suitability were also identified along the shoreward side of the barrier reef tract, primarily in areas of increasing slope (> 5 degrees) and

over aggregate reefs and isolated patch reefs with shallow peaks surrounded by dense seagrass (Figure 2.3). In contrast, unconsolidated sediment and discontinuous seagrass were predicted to have the lowest relative likelihood of sub-adult *L. griseus* presence. Broad-scale BPI positively influenced predicted suitability levels, with broad peaks and ridges favored over flats and valleys. Though their roles were negligible relative to the top five predictors, mean winter salinity and mean summer temperature both showed negative relationships with predicted suitability when used in isolation. The remaining predictors—curvature, rugosity, fine-scale BPI, mean summer salinity, and mean winter temperature—were assigned a variable importance score of zero.

The five most influential predictors regulating the distribution of suitable habitat for sub-adult *H. sciurus* were benthic habitat type, slope, Euclidean distance to the nearest mangrove, depth, and broad-scale BPI (Figure 2.4; Figure A2.5). Similar to the *L. griseus* model, predicted habitat suitability for sub-adult *H. sciurus* was high along the seagrass fringe and over individual patch reefs and aggregate coral reefs, especially those with broad peaks (Figure 2.3). However, relative to the *L. griseus* model, MaxEnt predicted higher suitability levels for *H. sciurus* over ridges and in patches of pavement, scattered rock, and reef rubble, and lower suitability levels in seagrass with the exception of those in shallow areas immediately adjacent to mangroves. Although depths shallower than 5 m were predicted to be the most suitable, the relative likelihood of *H. sciurus* presence remained above 50% at depths down to roughly 25 m. Predicted habitat suitability for *H. sciurus* also declined rapidly as Euclidean distance from the nearest mangrove approached 200 m, however, suitability levels for this species began gradually increasing again at a distance of around 1 km rather than continuing to decline. Furthermore, the mangrove shorelines on the windward and leeward sides of the Florida Keys had consistently higher estimates of habitat suitability than those along the mainland in Biscayne Bay (Figure 2.3). Although this trend was also visible in the *L. griseus* model, it was much more pronounced for *H. sciurus*. Water conditions contributed only weakly to overall model fit, however, there were positive relationships between the relative likelihood of sub-adult *H. sciurus* presence and mean winter salinity and temperature. In contrast, curvature, rugosity, fine-scale BPI, and mean summer salinity and temperature had contribution scores of zero.

2.4 Discussion

2.4.1 Model performance

We compared penalized logistic regression and MaxEnt models of habitat suitability for two economically and ecologically critical reef fish species in the Florida Keys, USA, with the goal of identifying which modeling algorithm produces the most realistic and detailed products for use in subsequent connectivity modeling. MaxEnt's AUC values were consistently higher than those of either the lasso- or ridge-penalized logistic regressions, suggesting that MaxEnt was better able to distinguish between suitable and unsuitable locations for sub-adult *L. griseus* and *H. sciurus* when evaluated across a range of suitability thresholds. Although the overall predictive accuracy of the MaxEnt models fell below those of the penalized regressions when discretized to a binary scale using standard and max SSS suitability thresholds, MaxEnt produced similar or improved sensitivity estimates relative to the penalized regressions. MaxEnt's consistently high sensitivity values suggest that these models were able to reliably identify known presence locations, which is essential for delineating the suitable habitat nodes required to produce spatial graphs for connectivity assessment. The high-resolution suitability maps produced by MaxEnt also appear to be better suited for conversion to resistance surfaces, as these models predicted patchy distributions of suitable habitat across the seascape that more closely aligned with the known ecology of the study species, as described below in Section 2.4.2.

Consistent with our findings, MaxEnt's performance has paralleled or exceeded that of other machine learning and regression techniques in several comparative studies. For instance, MaxEnt and penalized logistic regression techniques yielded similar AUC values when used to model the distributions of several tree species in Spain, with both models outperforming standard logistic regressions (Gastón & García-Viñas 2011). Similarly, MaxEnt achieved the highest predictive performance out of five modeling methods when used to model habitat suitability for the invasive Argentine ant across the Iberian Peninsula, producing predictive distributional maps that highlighted areas susceptible to invasion (Roura-Pascual et al. 2009). MaxEnt has even performed well in spatially and topographically complex seascapes, as demonstrated by a comparative study of ten presence-only modeling algorithms applied to demersal fish species of Australia (Monk et al. 2010). Our research, therefore, joins these and other examples from the literature that illustrate MaxEnt's usefulness as a tool for mapping species distributions across a range of taxa and environmental settings, especially in scenarios where distributional patterns are thought to be driven by complex species–environment relationships. These results can likely be attributed to MaxEnt's ability to harness categorical data and linear, quadratic, hinge, and threshold

functions of continuous environmental variables, while simultaneously maintaining a balance between model fit and complexity using regularization (Elith et al. 2011). Despite its growing promise and popularity among ecologists, attempts to leverage MaxEnt products for connectivity modeling remain scarce.

2.4.2 Variable importance

Of the 12 environmental predictors assessed in our study, habitat type was identified as the main driver of suitability for sub-adult *L. griseus* and *H. sciurus*, with dense seagrass beds, shoreline mangroves, patch reefs, and shoreward aggregate reefs being especially important. According to our models, these habitats play a variable role in supporting sub-adult *L. griseus* and *H. sciurus*, depending on their geographic location. This trend was especially apparent for shoreline mangroves, with suitability predicted to be highest in mangroves along the leeward and windward sides of the Keys and surrounding Biscayne Bay's southern islands. Previous research in the region revealed a similar pattern of habitat use whereby sub-adult *L. griseus* and *H. sciurus* selected for easterly mangroves along the Keys, whereas larger-bodied adults were more common in Biscayne Bay's expansive mainland forests (Faunce & Serafy 2007, 2008). The high suitability levels predicted along the seagrass fringe and in areas within several hundred meters of a nearby mangrove shoreline likely reflect the regular diel migrations of grunts and snappers between daytime resting sites in mangroves and nocturnal foraging grounds in seagrass meadows, which cover distances of up to 1 km (Faunce & Serafy 2007; Nagelkerken et al. 2000a; Luo et al. 2009). Furthermore, patch reefs and sections of the reef tract adjacent to lush seagrass beds and mangrove shorelines, particularly those along the Keys, were predicted to have a higher relative likelihood of presence for both species compared to those located alongside unvegetated substrates. Together, these results suggest that patch reefs serve as critical stepping-stones connecting mangrove and seagrass nurseries to adult habitat on offshore reefs. However, sub-adult dispersal between back reef habitats may be limited to only immediately accessible patches of topographically complex habitat, with implications for the replenishment of adult populations across the barrier reef tract (Huijbers et al. 2013; Nagelkerken et al. 2017). These findings also suggest that nutrient supplementation and top-down control of coral predators by migratory reef fishes may be greatest in patch reef, back reef, and reef crest communities neighboring seagrasses and mangroves, with

consequences for coral growth and the placement of coral restoration efforts (Ladd et al. 2018; Shantz et al. 2015).

Beyond the type and spatial arrangement of benthic habitats, suitability varied as a function of depth and seafloor surface morphology, as quantified by slope and bathymetric position index (BPI). Generally, the likelihood of *L. griseus* and *H. sciurus* presence decreased with increasing depth, with this pattern being especially abrupt for *L. griseus*. The predicted suitability maps also displayed within-patch variation, with both species responding positively to even small increases in slope (< 5 degrees). Additionally, our models revealed that the influence of BPI on habitat suitability is both scale- and species-dependent, with broad-scale BPI having a stronger influence over predicted suitability levels for *L. griseus* than *H. sciurus*. Nonetheless, fine-scale BPI and two other fine-scale metrics of seafloor surface complexity—curvature and rugosity—were dropped entirely from both MaxEnt models. These results indicate that the distributions of sub-adult *L. griseus* and *H. sciurus* across the seascape are primarily driven by broad-scale habitat features and geographic location, a finding that is consistent with previous research on predatory reef fishes and which may be related to the high vagility and large home range sizes of these species (1–5 km) (Pittman et al. 2004; Grober-Dunsmore et al. 2008; Green et al. 2015; Shideler et al. 2017). However, previous work in the Caribbean revealed that seafloor morphology and geographic location interact to drive the distributional patterns of herbivores, in addition to invertivores and piscivores, suggesting that this trend is likely common across coastal reef fish communities rather than being restricted to mobile predators (Pittman & Brown 2011).

Although neither salinity nor temperature acted as a major determinant of suitability, these variables acted as filters to mediate the relative suitability of otherwise similar habitats. Previous research has demonstrated significant inter-species variation in salinity tolerances, with *L. griseus* being abundant in low-to-intermediate salinities and *H. sciurus* being abundant in stable, high salinities (Serafy et al. 1997; Serrano et al. 2010). These relationships were reflected in MaxEnt's predictions and were especially noticeable in Biscayne Bay, where salinity fluctuates significantly as a result of both freshwater discharge and tidal exchange. As such, the western and southwestern mainland coasts, which are characterized by extreme salinity fluctuations and lower overall means (Serafy et al. 2003), were predicted to have higher suitability levels for *L. griseus* than *H. sciurus*. In contrast, habitats along the leeward and windward sides of the Upper Keys that have narrow salinity ranges dominated by seawater were predicted to have higher suitability levels for *H.*

sciurus. Additionally, the present finding that relative suitability for sub-adult *L. griseus* decreases rapidly as summer temperatures approach 31 °C is in agreement with previous laboratory experiments that estimated 33 °C as being close to the maximum for juvenile gray snapper feeding (Wuenschel et al. 2004). Considering that settlement and grow-out occur from summer through early fall (Faunce & Serafy 2007), this temperature constraint may be an artifact of juvenile habitat selection. On the other hand, the positive relationship between mean winter temperature and predicted suitability for sub-adult *H. sciurus* may reflect the winter spawning and settlement behavior of this species, as warmer winter temperatures decrease the overwinter mortality of juveniles and increase the chances of successful sub-adult dispersal to the offshore reefs (Hare & Able 2007; Tolan & Fisher 2009).

2.4.3 Implications for seascape connectivity modeling and conservation

Based on our case study, habitat composition and arrangement, depth, and broad-scale bathymetric features are among the most important factors to consider when planning conservation efforts for reef fish species with complex, multi-habitat life histories. In particular, our models highlight the value of targeting mosaics of interconnected habitats, rather than single biotopes, when planning marine protected areas, reserve networks, and resource management (Olds et al. 2016; Carr et al. 2017; Almany et al. 2009). The importance of considering surrounding seascape context and connectivity is not limited to the protection and conservation of existing ecosystems, but also to the restoration of degraded and fragmented habitats. By strategically placing restoration activities within the seascape, restoration practitioners can enhance intra- and inter-habitat connectivity, thereby increasing dispersal and harnessing key ecological processes including herbivory and primary production, predation and secondary production, and nutrient turnover (Ladd et al. 2018). Although the application of seascape connectivity as a spatially explicit metric in restoration planning has been limited thus far, projects that have incorporated surrounding seascape context in their site selection process have seen positive outcomes (Gilby et al. 2018). Integrative approaches that combine the strengths of habitat suitability modeling and connectivity modeling are becoming increasingly common and accessible thanks to improvements in data availability and the development of decision support tools like Marxan Connect and Zonation (Weeks 2017; Daigle et al. 2020).

In conclusion, our research demonstrates that MaxEnt, a presence-background machine learning approach, outperforms traditional presence–absence techniques in terms of discriminatory ability and capacity to produce habitat suitability maps that reflect the known ecology of sub-adult *L. griseus* and *H. sciurus* in the Florida Keys. These results are consistent with previous terrestrial studies that have found similar or improved predictive performance of MaxEnt relative to standard or penalized logistic regressions (Elith et al. 2006; Gastón & García-Viñas 2011; Guillera-Arroita et al. 2014). Furthermore, our research, coupled with previous work on warm-water kelps (Franco et al. 2018), demersal fishes (Monk et al. 2010), and shallow and deep-sea corals (Couce et al. 2013; Etnoyer et al. 2018), demonstrate that MaxEnt’s promise as a fast, open-source tool for mapping species distributions extends beyond the land–sea interface. Although analogs exist from the terrestrial literature (e.g., Duflot et al. 2018; Poor et al. 2012), the application of habitat suitability modeling as a precursor to marine connectivity assessments and conservation planning remains scarce. We anticipate that MaxEnt-derived nodes and linkages can be combined with data on species biological traits to produce detailed and ecologically realistic spatial graphs for connectivity assessment. As a next step, we plan to construct and operationalize these graphs for habitat restoration planning through scenario testing, including the iterative addition or removal of nodes and linkages (i.e., restoration and fragmentation scenarios, respectively). As habitat restoration efforts ramp up across the spatially and topographically complex seascape of the Florida Keys, we encourage restoration practitioners and coastal managers to adopt a multi-step site selection strategy that harnesses the strengths of both habitat suitability and connectivity modeling.

2.5 Acknowledgements

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2.6 Data availability statement

Data, R scripts, MaxEnt command line code, and ArcGIS geoprocessing workflows associated with this research are available online at https://github.com/CourtneyStuart/FL_Habitat_Suitability (accessed on 30 September 2020). Reef fish occurrence records were obtained from two public data sources: the South Florida Reef Visual Census (<https://github.com/jeremiaheb/rvc>) and the Mangrove Visual Survey (<https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0159580>) (accessed on 30 September 2020). The Florida Keys National Marine Sanctuary and Biscayne National Park GIS shapefiles used for mapping are accessible at https://sanctuaries.noaa.gov/library/imast_gis.html (accessed on 30 September 2020) and <https://public-nps.opendata.arcgis.com/datasets/nps-boundary-1/data> (accessed on 30 September 2020), respectively. The water quality data used in this research were provided by the Miami-Dade County Surface and Groundwater Quality Viewer (<https://mdc.maps.arcgis.com/apps/webappviewer/index.html?id=3fd24515ee614f5db63924d7323a4ea7> (accessed on 30 September 2020)) and the SERC- FIU Water Quality Monitoring Network, which is supported by EPA Agreement #X7 00D024121 and NOAA Agreement #NA09NOS4260253 (<http://serc.fiu.edu/wqmnetwork/FKNMS-CD/index.htm> (accessed on 30 September 2020)).

2.7 Tables and figures

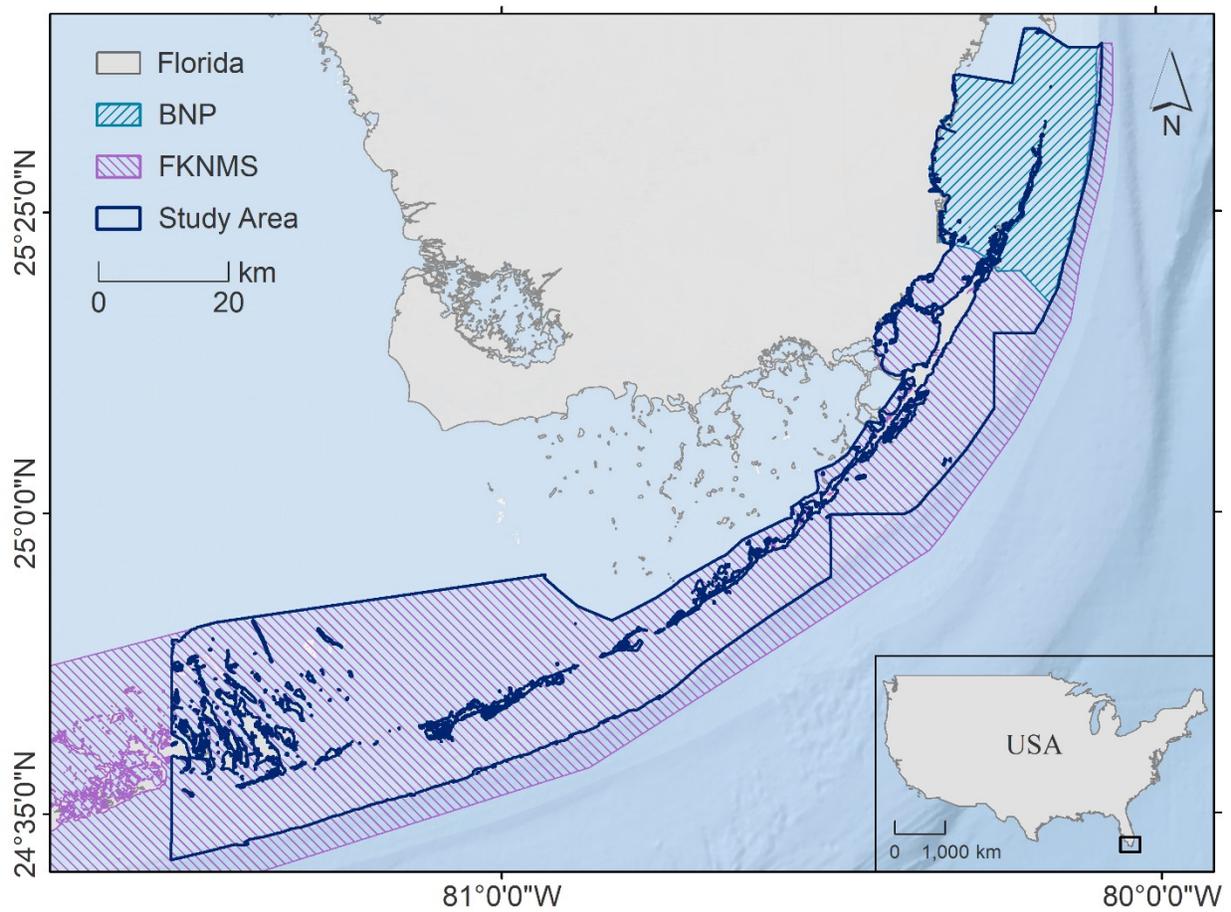


Figure 2.1. Location of the study area in the Florida Keys, United States of America (USA), which included Biscayne National Park (BNP) and portions of the Florida Keys National Marine Sanctuary (FKNMS).

Table 2.1. Spatial predictors available for habitat suitability modeling. Grayed-out predictors were removed due to collinearity issues. BTM: Benthic Terrain Modeler ArcGIS extension (v3.0). Calculations performed using a 3×3 moving window of cells, unless otherwise noted.

	Predictor	Units	Description	Tool Used
Habitat	Benthic Habitat	Categorical (12)	Bottom habitat type	Not Applicable
	Distance to Mangrove	Meters	Euclidean distance to the nearest mangrove habitat	gridDistance function in the <i>raster</i> R package
Bathymetry & Seafloor Morphology	Depth	Meters	Water depth in each cell	Not Applicable
	Depth (Standard Deviation)	Meters	Local dispersion	Calculate Metrics tool in BTM
	Slope	Degrees	Rate of maximum change in depth	Slope tool in BTM
	Curvature	$\frac{1}{100}$ th of a meter, convex (+) or concave (-)	Second derivative of the bathymetric surface	Curvature tool in ArcGIS Spatial Analyst
	Plan Curvature	$\frac{1}{100}$ th of a meter, convex (+) or concave (-)	Curvature perpendicular to the direction of maximum slope	Curvature tool in ArcGIS Spatial Analyst
	Rugosity	Ratio	Local surface roughness calculated as the ratio of surface area to planar area	Surface Area to Planar Area (slope-corrected) tool in BTM
	Broad-Scale Bathymetric Position Index (BPI)	Ridge (+), Flat (0), or Valley (-)	Depth of a cell relative to its surroundings, evaluated using concentric rings of 125 m and 1250 m	Broad-Scale BPI tool in BTM (standardized)
	Fine-Scale BPI	Ridge (+), Flat (0), or Valley (-)	Depth of a cell relative to its surroundings, evaluated using concentric rings of 5 m and 125 m	Fine-Scale BPI tool in BTM (standardized)
Water Conditions	Winter Temperature	Degrees Celsius	Mean winter (January–March) temperature	Krige function in the <i>gstat</i> R package
	Winter Salinity	Practical Salinity Units	Mean winter (January–March) salinity	Krige function in the <i>gstat</i> R package
	Winter Dissolved Oxygen	Milligrams per Liter	Mean winter (January–March) dissolved oxygen	Krige function in the <i>gstat</i> R package
	Summer Temperature	Degrees Celsius	Mean summer (July–September) temperature	Krige function in the <i>gstat</i> R package
	Summer Salinity	Practical Salinity Units	Mean summer (July–September) salinity	Krige function in the <i>gstat</i> R package
	Summer Dissolved Oxygen	Milligrams per Liter	Mean summer (July–September) dissolved oxygen	Krige function in the <i>gstat</i> R package

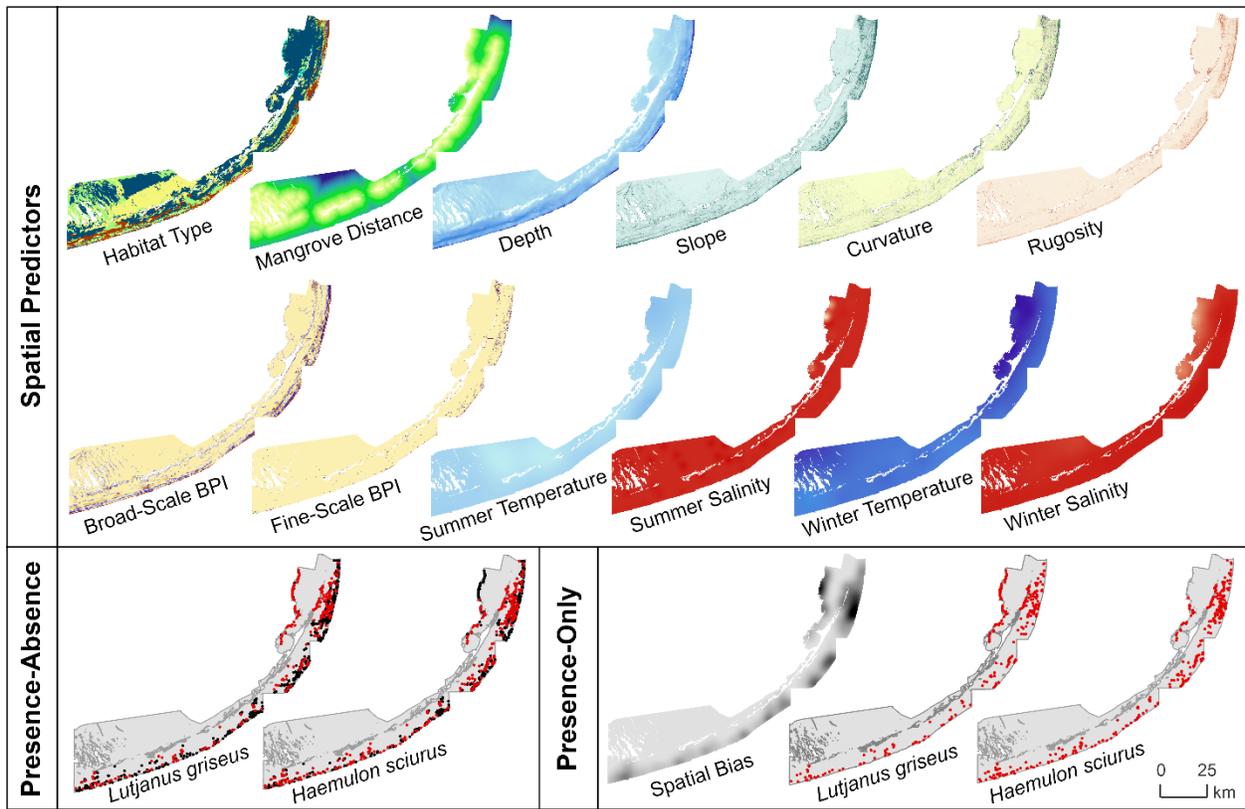


Figure 2.2. Maps of spatial predictors and sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) occurrence records used to train MaxEnt models and penalized logistic regressions of habitat suitability in the Florida Keys, USA.

Table 2.2. Sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) occurrence records in the southern Florida study area. Prior to habitat suitability modeling, data were randomly partitioned into calibration (70%) and evaluation (30%) subsets.

	Size (cm TL)	Presence Sites	Absence Sites	Total
Calibration Data				
<i>Lutjanus griseus</i>	9.51–24.71	378	1129	1507
<i>Haemulon sciurus</i>	11.90–25.33	447	1060	1507
Evaluation Data				
<i>Lutjanus griseus</i>	9.51–24.71	167	479	646
<i>Haemulon sciurus</i>	11.90–25.33	216	430	646

Table 2.3. Performance assessment for the various species–model combinations. Discriminatory ability on a continuous scale was assessed using the area under the receiver–operator curve (AUC). Binary predictive performance was assessed using confusion matrices following discretization at two suitability thresholds—a standard threshold of 0.5 and the threshold at which each model achieved a maximum sum of sensitivity and specificity (max SSS). Accuracy, sensitivity, and specificity values are displayed as percentages and thresholds represent predicted suitability levels on a scale of 0 to 1.

	Discrimination	Binary Performance (Standard)			Binary Performance (Max SSS)				
	AUC	Cut-Off	Accuracy	Sensitivity	Specificity	Cut-Off	Accuracy	Sensitivity	Specificity
<i>Lutjanus griseus</i>									
Lasso Regression	0.74	0.5	77.9	32.7	93.3	0.28	69.4	73.9	67.8
Ridge Regression	0.74	0.5	77.7	32.7	93.1	0.24	65.5	80.0	60.5
MaxEnt	0.88	0.5	50.5	84.9	38.7	0.65	59.0	80.0	51.8
<i>Haemulon sciurus</i>									
Lasso Regression	0.76	0.5	73.2	37.5	91.2	0.32	72.8	71.3	73.5
Ridge Regression	0.75	0.5	74.2	35.7	93.5	0.32	72.8	70.8	73.7
MaxEnt	0.86	0.5	41.3	79.1	24.3	0.65	51.7	72.6	42.3

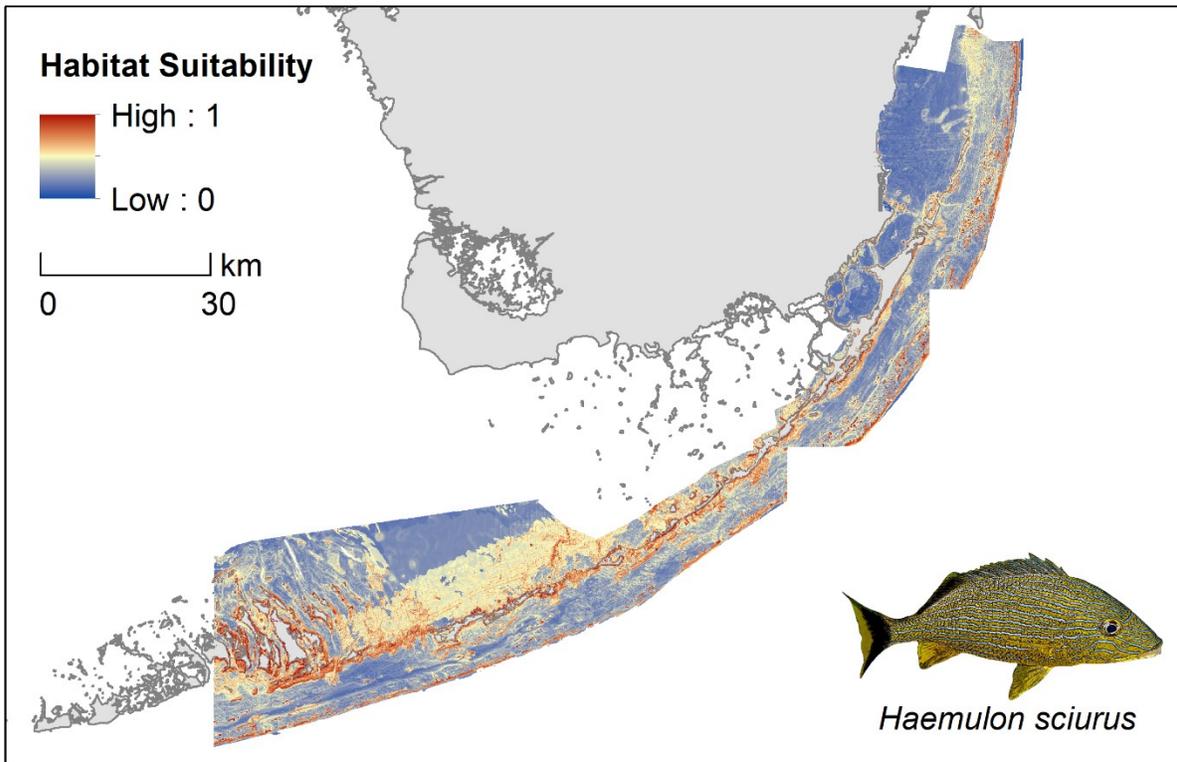
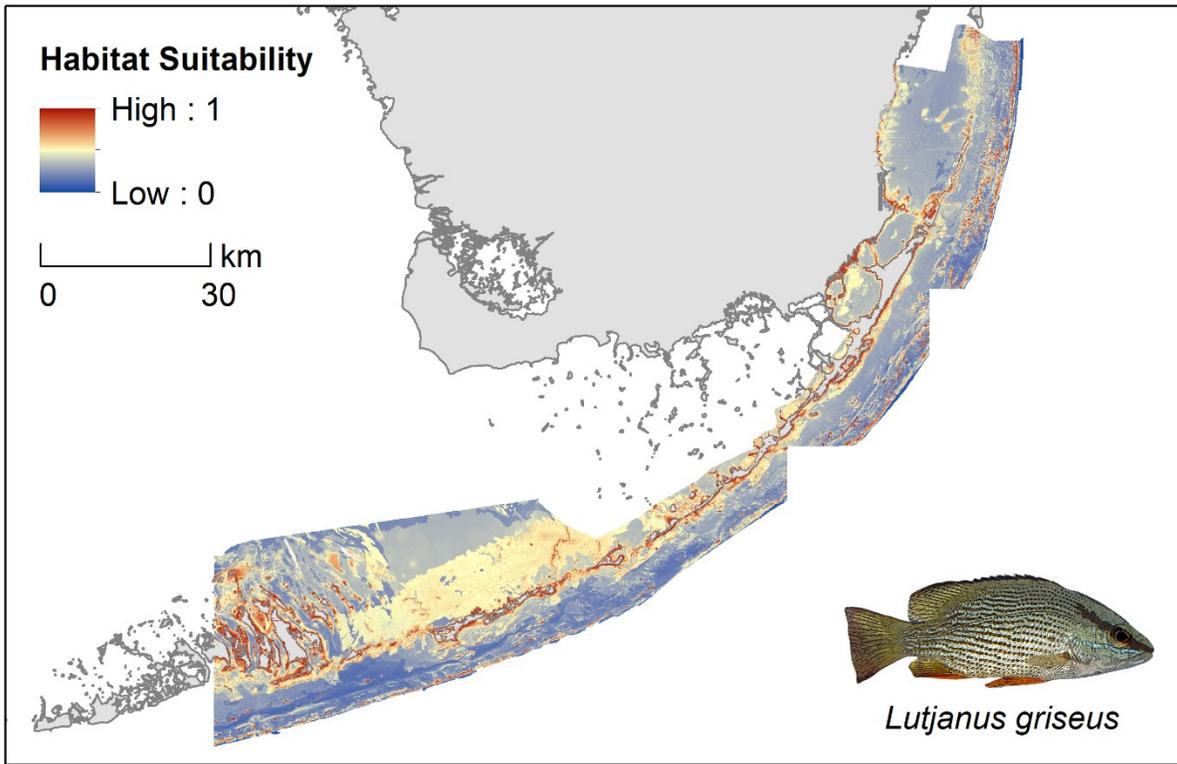


Figure 2.3. MaxEnt predictions of relative habitat suitability for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) across the Florida Keys, USA.

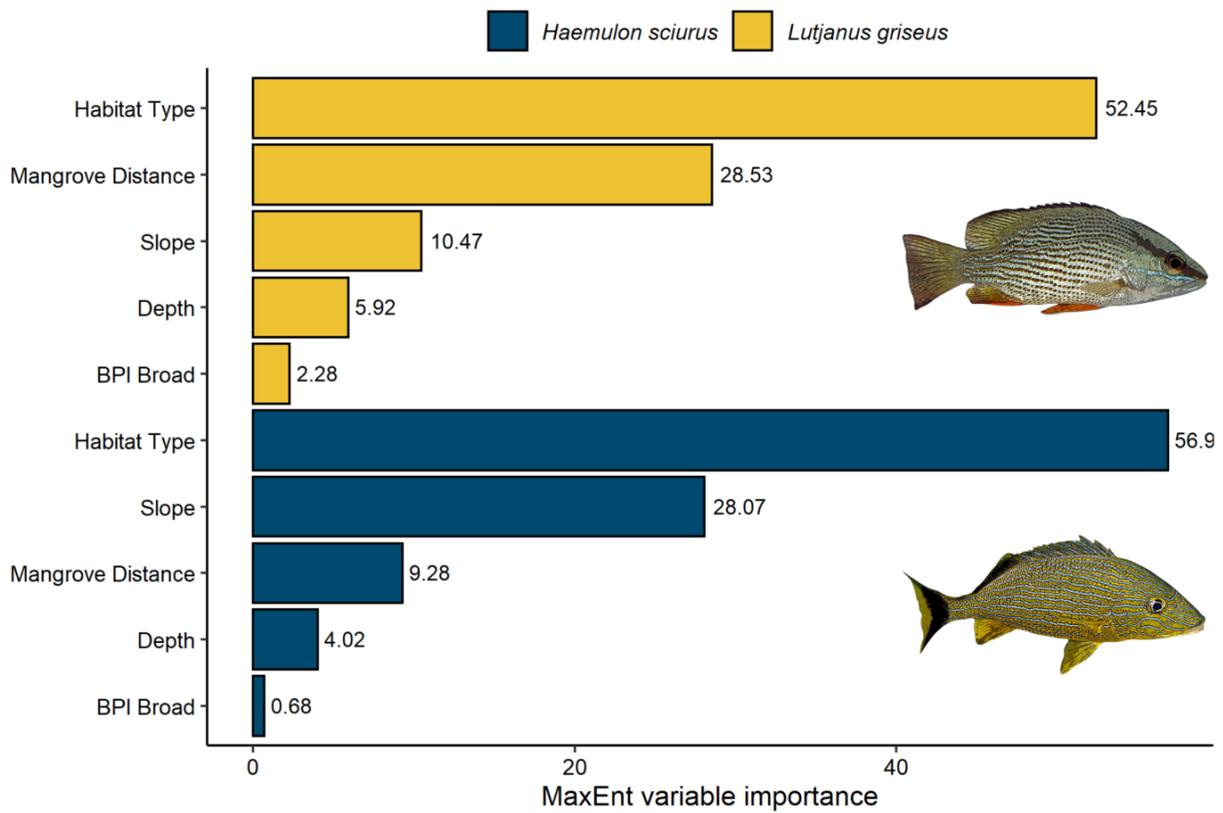


Figure 2.4. Plot of the top five most influential predictors of habitat suitability for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*), according to MaxEnt. Variable importance reflects the contribution of each variable to model fit based on the increase in regularized gain (%).

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Appendix 1: Supplementary materials for Chapter 2: Habitat suitability modeling to inform seascape connectivity conservation and management

Table A2.1. Variance Inflation Factors. Collinearity among spatial predictors was assessed using variance inflation factor (VIF) scores and Pearson pairwise correlation coefficients (r). Predictors were retained for modeling if they fell below thresholds of 5 and $|0.7|$ for VIF and r , respectively. See Table 2.1 in the main text for variable descriptions and Supplementary Figures A2.1 and A2.2 for correlation matrices.

Spatial Predictor	VIF (Full Predictor Set)	VIF (Retained Predictor Set)
Benthic Habitat	1.19	1.16
Distance to Mangrove	1.35	1.29
Depth	2.74	2.63
Depth (Standard Deviation)	688.05	-
Slope	645.26	1.69
Curvature	2.12	1.07
Plan Curvature	2.16	-
Rugosity	4.03	1.43
Broad Scale Bathymetric Position Index	1.75	1.78
Fine Scale Bathymetric Position Index	1.15	1.16
Winter Temperature	2.92	2.20
Winter Salinity	8.15	2.46
Winter Dissolved Oxygen	3.15	-
Summer Temperature	1.86	1.79
Summer Salinity	2.08	1.70
Summer Dissolved Oxygen	6.32	-

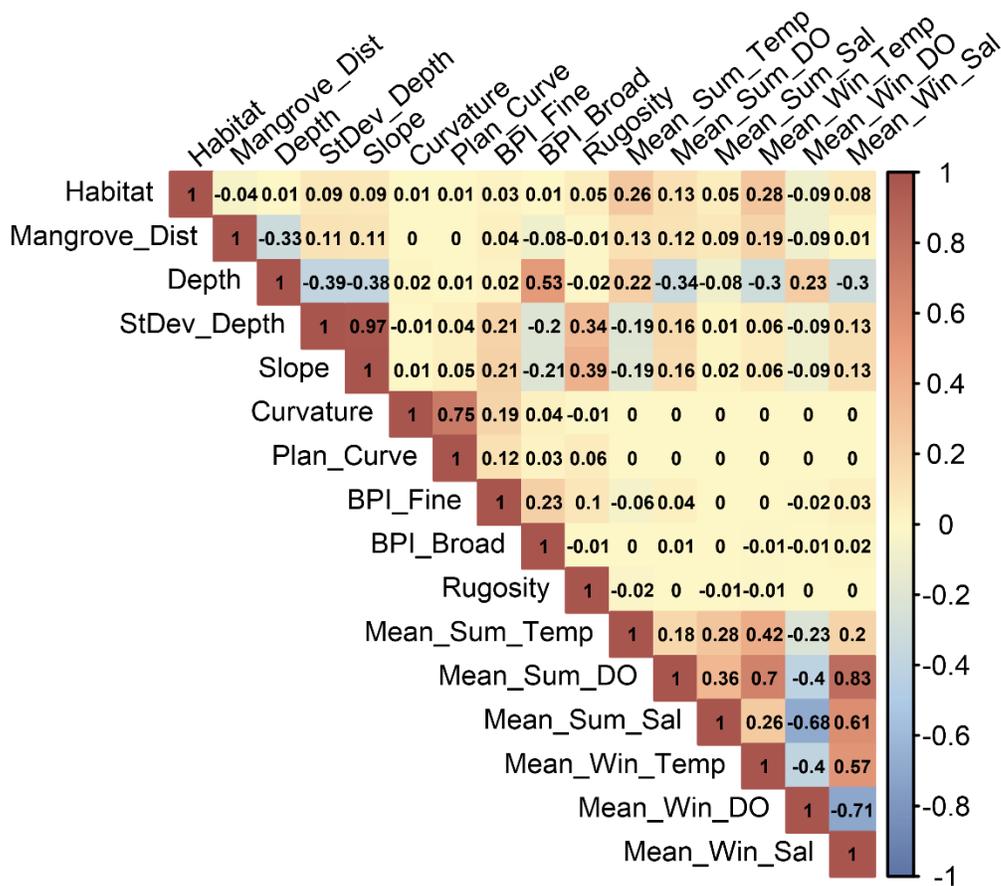


Figure A2.1. Pearson pairwise correlation matrix of all available spatial predictors. A correlation threshold of $|0.7|$ was used in concert with a VIF threshold of 5 to remove collinear variables (see Table A2.1). Abbreviations as follows: Dist = Distance, St_Dev = Standard Deviation, Curve = Curvature, BPI = Bathymetric Position Index, Sum = Summer, Win = Winter, Temp = Temperature, Sal = Salinity, DO = Dissolved Oxygen.

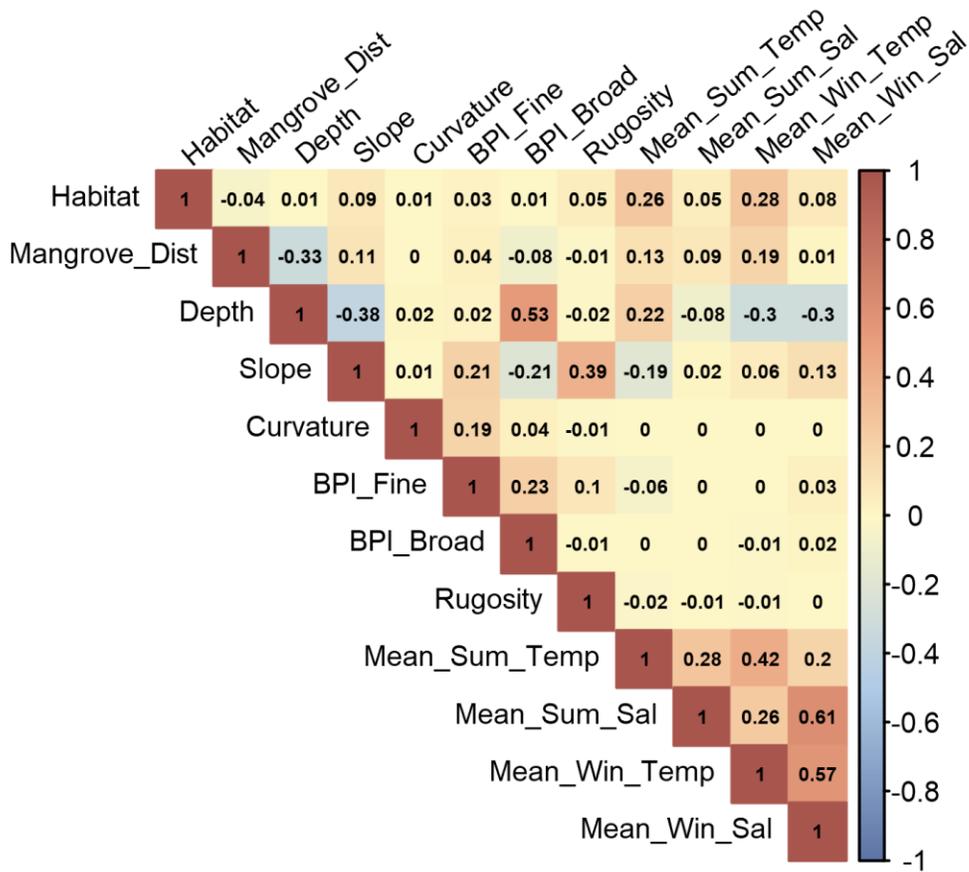


Figure A2.2. Pearson pairwise correlation matrix of spatial predictors retained for habitat suitability modeling. A correlation threshold of $|0.7|$ was used in concert with a VIF threshold of 5 to remove collinear variables (see Table A2.1). Abbreviations as follows: Dist = Distance, BPI = Bathymetric Position Index, Sum = Summer, Win = Winter, Temp = Temperature, Sal = Salinity.

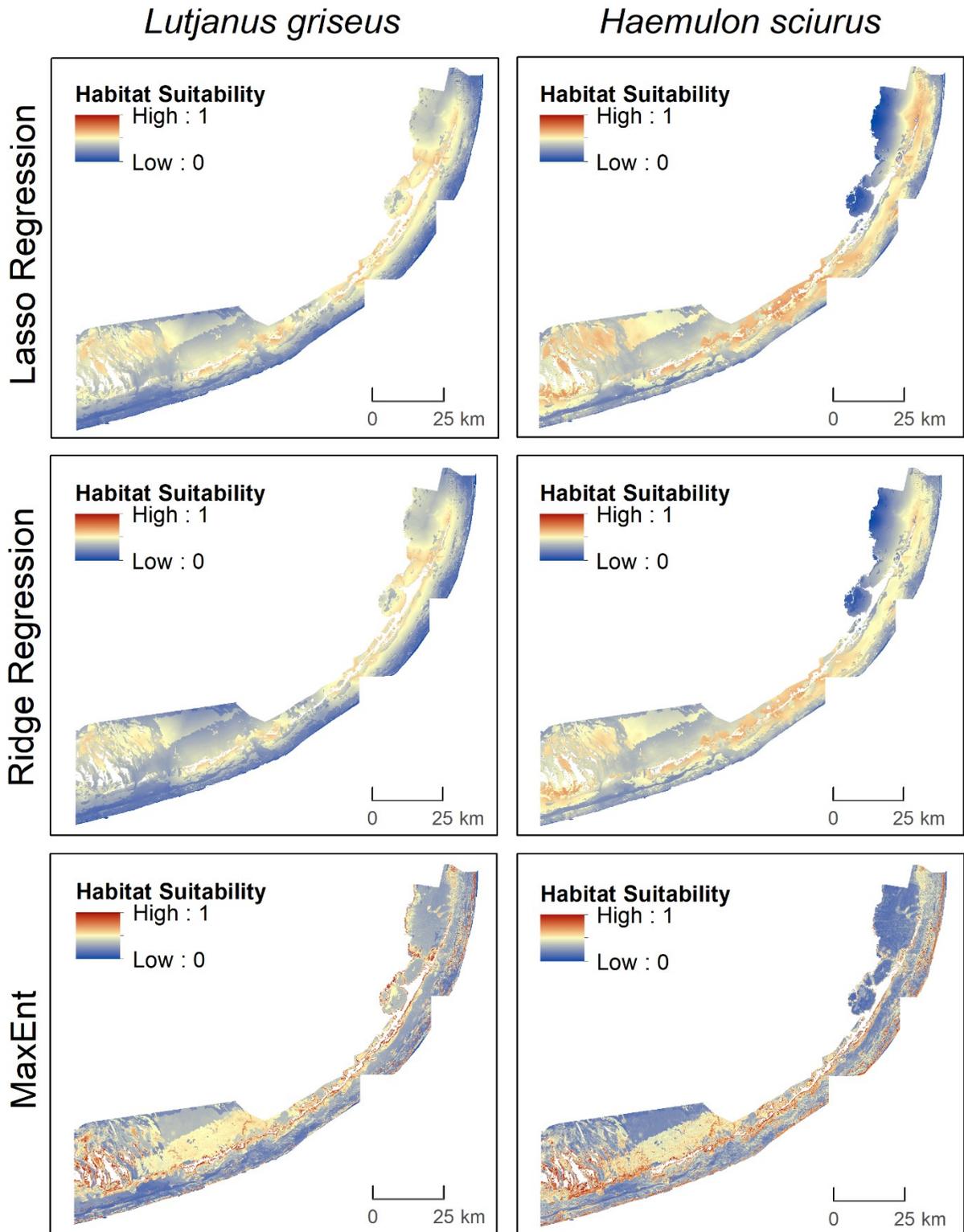


Figure A2.3. Lasso-penalized logistic regression, ridge-penalized logistic regression, and MaxEnt predictions of habitat suitability for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) in the Florida Keys, United States of America (USA).

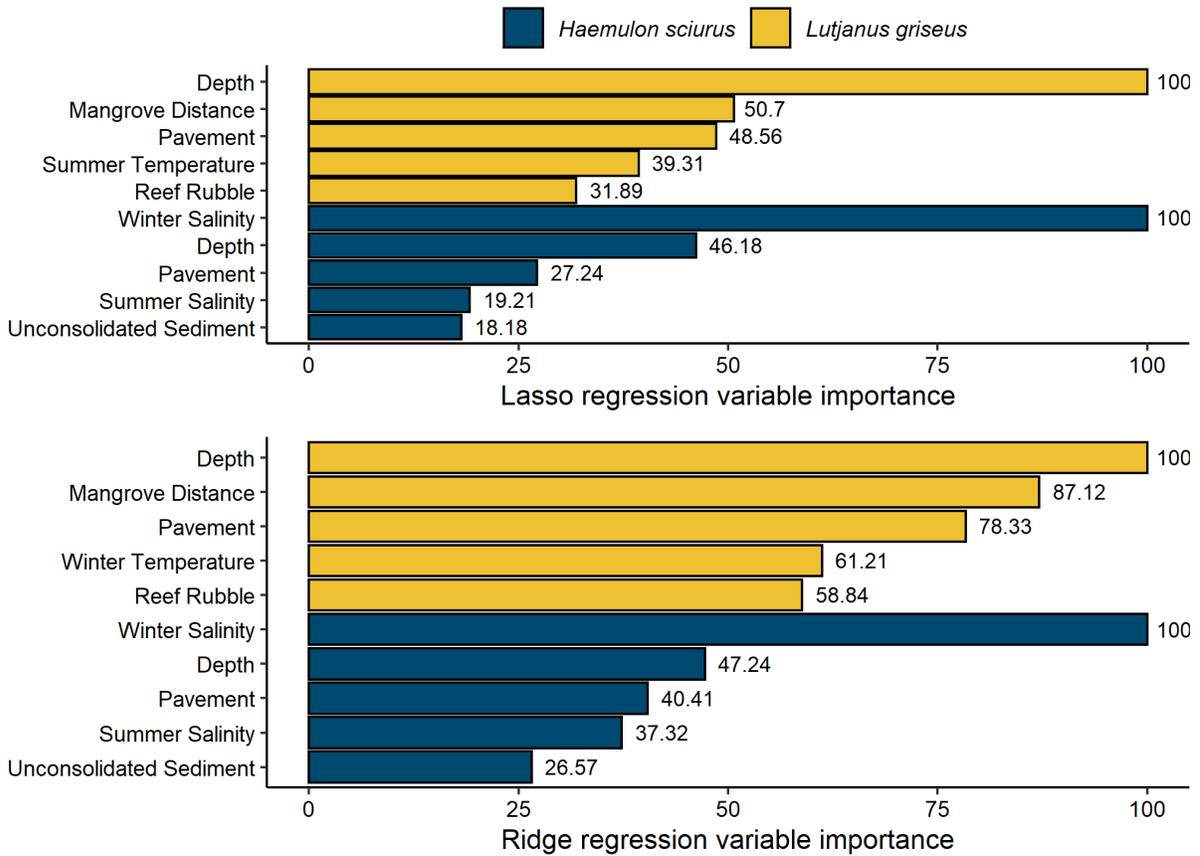


Figure A2.4. Plots of the top five most influential predictors of sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) suitability according to lasso- and ridge-penalized logistic regressions. Variable importance (scaled 0 to 100) was quantified by ranking each spatial predictor by the magnitude of their standardized coefficients.

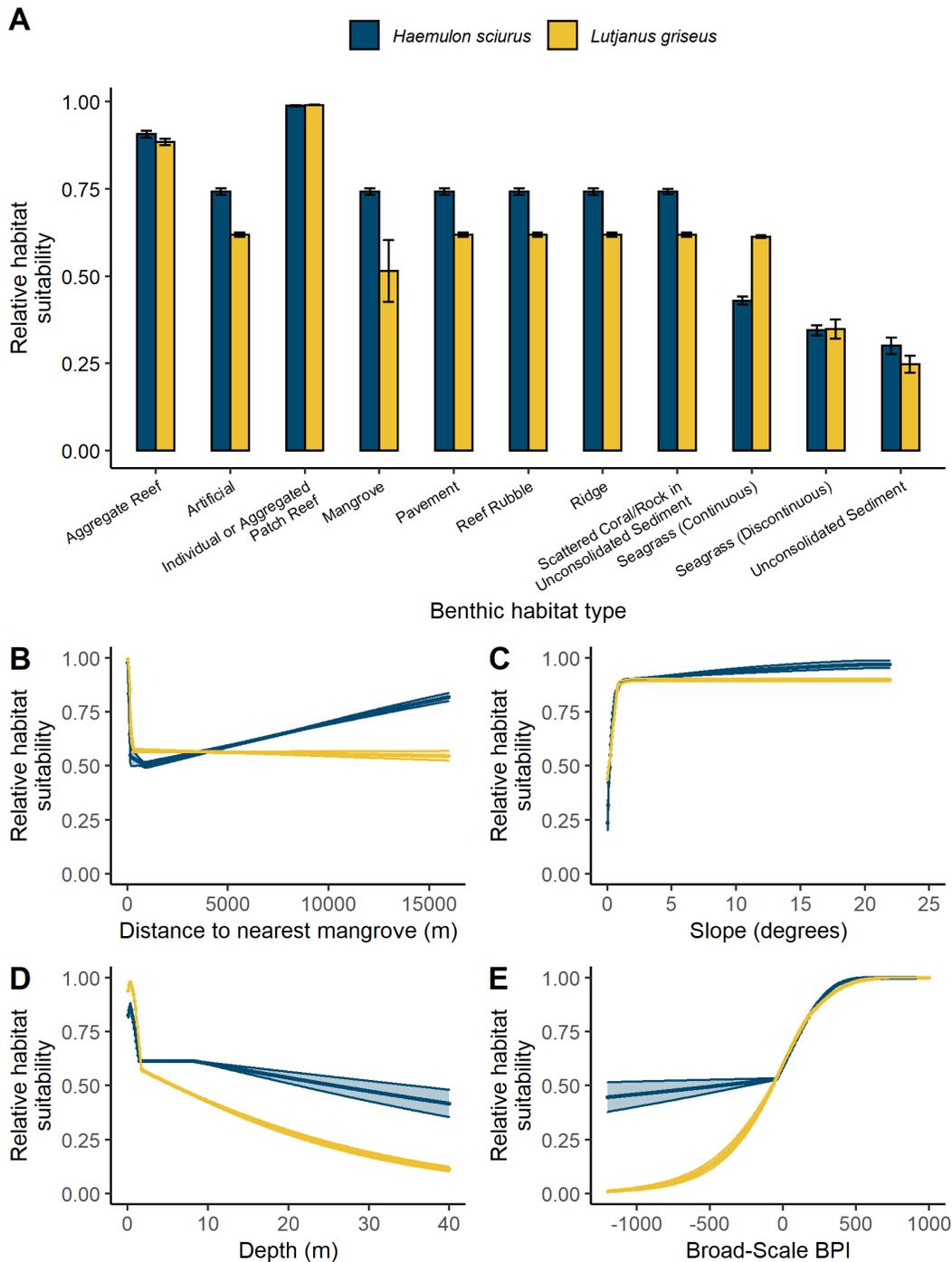


Figure A2.5. MaxEnt response curves displaying the relationship between predicted relative habitat suitability for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) and the values of the five most influential predictors: (A) benthic habitat type, (B) Euclidean distance to the nearest mangrove, (C) slope, (D) depth, and (E) broad-scale bathymetric position index (BPI). Each curve represents a different MaxEnt model created using only the

corresponding variable, displayed as the mean \pm one standard deviation calculated over 10 cross-validation folds.

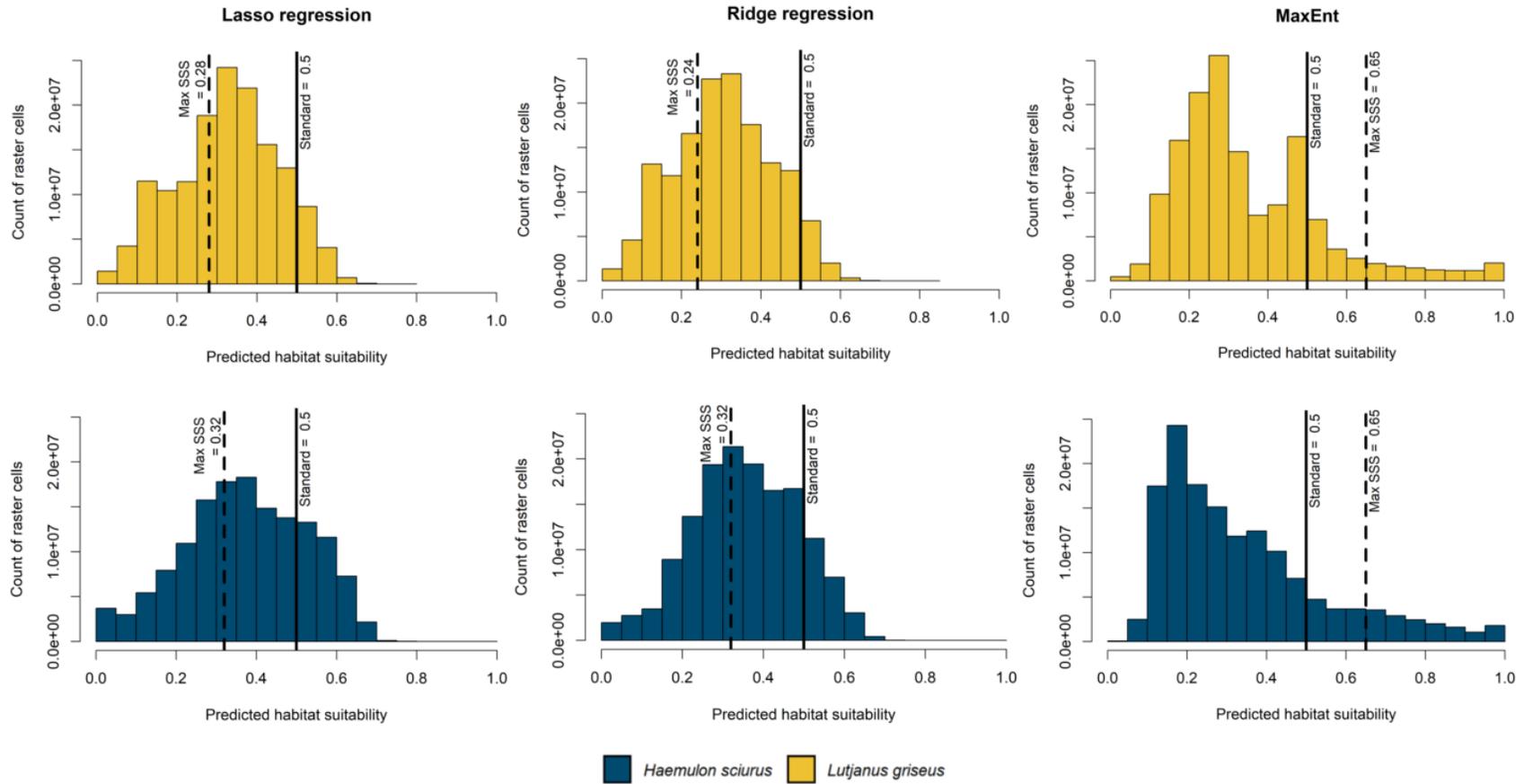


Figure A2.6. Frequency distribution plots displaying the total number of raster cells classified within each predicted habitat suitability bin. Standard (0.5) and maximum sum of sensitivity and specificity (max SSS) binary suitability thresholds are represented using solid and dashed black lines, respectively.

Chapter 3: Connectivity modeling in support of coral reef restoration design

3.1 Introduction

Seascapes, the marine counterpart of landscapes, are spatially and topographically heterogeneous areas composed of patches of varying habitat type and quality (Boström et al. 2011; Pittman et al. 2021). The structure and function of seascapes are shaped by processes operating and interacting across scales in space and time such as storm surges, current and tidal flow, and biological interactions, including human activity (e.g., Gilby et al. 2021). The magnitude and pace of seascape structural and functional changes are particularly high in coastal areas, where local human stressors, including land development, resource overexploitation, and nutrient, pollutant, and sediment run-off, are now being exacerbated by global climate change (Lotze et al. 2006; Zaneveld et al. 2016; Halpern et al. 2019). Consequently, coastal ecosystems have experienced significant degradation and fragmentation over recent decades, with coral reefs, seagrasses, and mangroves being among those most affected (Gardner et al. 2003; Waycott et al. 2009; Polidoro et al. 2010; Halpern et al. 2019). These disturbances alter seascape spatial patterns and reduce contiguity within and between patches (i.e., structural connectivity), with potentially cascading effects on ecological processes across a range of spatiotemporal scales, including the exchange of organisms, nutrients, and energy between habitats, ecosystems, and geographic regions (i.e., functional connectivity) (Crooks & Sanjayan 2006). Thus, determining how local and climate-related disturbances alter the relationship between structural and functional connectivity, and what this means for patterns of biodiversity, ecosystem functioning, and resilience, are now pressing goals in conservation and restoration planning (Olds et al. 2016; Carr et al. 2017).

As the coverage, topographic complexity, and spatial proximity of habitat patch types decline in response to anthropogenic stress (Hughes et al. 2003; Bellwood et al. 2004; Orth et al. 2006; Alvarez-Filip et al. 2009), organismal movement becomes increasingly important for maintaining connectivity in coastal seascapes. However, whether and to what extent a seascape is functionally connected by the movement of organisms varies substantially between species and ontogenetic stages depending on how their behavioral and life history traits interact with the physical seascape structure (Grober-Dunsmore et al. 2009). Coral reef fishes in shallow subtropical and tropical seascapes provide key evidence of species- and process-specific connectivity scaling (Berkström et al. 2012). For instance, the defensive and farming behaviors of herbivorous,

territorial damselfishes influence the composition and productivity of benthic communities at the scale of a few meters, thereby connecting reef microhabitats; however, the placement, size, and shape of damselfish territories are themselves influenced by physical seafloor characteristics such as rugosity and local substrata availability over scales as fine as 1–2 m (Ceccarelli 2007; Eurich et al. 2018). In contrast, the diel foraging movements and cross-shelf ontogenetic migrations of grunts and snappers influence benthic patterns over scales of tens to thousands of meters by delivering allochthonous nutrient subsidies and modifying rates of herbivory by other community members (Peterson et al. 2013; Shantz et al. 2015), yet the pathways and distances over which these processes occur appear to be heavily influenced by broad-scale bathymetric features and surrounding seascape context (Appeldoorn et al. 2009; Hitt, Pittman & Nemeth 2011; Stuart et al. 2021). Thus, structural connectivity patterns elicit unique responses from coral reef fishes depending on their scale, resulting in intra- and inter-specific variation in functional connectivity.

Given that structural connectivity drives the spatial distributions of coral reef fishes and the ecological processes to which they contribute (e.g., herbivory, predation, nutrient turnover), enhancing and maintaining connectivity serves as a valuable guiding principle for a variety of conservation activities. To date, connectivity has been demonstrated to improve multiple measures of reserve performance, including production and diversity (Olds et al. 2016). Connectivity is expected to benefit marine habitat restoration efforts as well, as has been revealed in previous terrestrial studies. For instance, in human-dominated agricultural landscapes in Costa Rica, Harvey (2000) found that structural connectivity with remnant forest patches enhanced the diversity and abundance of understory vegetation in planted windbreaks. By supporting the dispersal, breeding, and foraging activities of seed-dispersing organisms, well-connected windbreaks facilitated understory tree recruitment and passive forest regeneration. Establishing windbreaks around mature, native forest trees also benefited seedlings through the amelioration of microclimatic and edaphic conditions (Harvey 2000).

By strategically placing restoration activities in areas of high structural connectivity, or by using habitat restoration to repair structural connectivity, practitioners can similarly regulate fluxes of organisms, sediments, nutrients, and wave energy between interconnected seascape habitats (Halpern et al. 2007). For example, coral reefs and seagrasses benefit nearby mangrove habitats by dampening wave energy, and, conversely, mangroves and seagrasses benefit coral reefs by filtering land-based nutrients and suspended sediments (Gillis et al. 2014, 2017). By protecting

and improving structural connectivity, restoration practitioners can leverage these reciprocal interactions to bolster restoration success (Halpern et al. 2007). Furthermore, the recovery of structural connectivity through habitat creation or restoration, coupled with place-based management strategies such as marine protected areas, may improve functional connectivity for a variety of species, including fishes and invertebrates with complex, multi-habitat life histories (Halpern et al. 2007; Grober-Dunsmore et al. 2009). Functional connectivity is, in turn, likely to benefit restored habitats by ensuring the continuous exchange of organisms and essential ecological functions (Ladd et al. 2018).

Yet despite these potential advantages, attempts to quantify seascape connectivity and integrate it as a spatially explicit criterion in marine habitat restoration planning remain scarce (Gilby et al. 2018), potentially owing to difficulties in measuring connectivity at ecologically relevant scales. In particular, relative to structural connectivity, the quantification of functional connectivity remains challenging and represents a major barrier to its application in restoration planning and practice. A variety of methods exist to directly measure animal movement at seascape scales (i.e., actual connectivity), including advanced tagging and tracking techniques; however, the data- and resource-intensive nature of these approaches may limit their spatial and temporal scope (Fagan & Calabrese 2006). Additionally, some species and developmental stages are not amenable to tagging, due, for instance, to body size or life history constraints (Hazen et al. 2012). In contrast, potential functional connectivity (hereafter, potential connectivity) can be estimated by relating seascape structural patterns to knowledge of a species' dispersal ability (Fagan & Calabrese 2006). Potential connectivity estimates, therefore, enable conservation, restoration, and management end-users to answer more complex ecological questions than possible using structural connectivity metrics alone, while simultaneously requiring less time and fewer resources than actual connectivity measures (Grober-Dunsmore et al. 2009). Furthermore, potential connectivity can be subsequently evaluated through tracking studies should additional resources become available. For these reasons, potential connectivity models may be particularly useful tools for informing the conservation and restoration of coastal seascapes in the face of increasing anthropogenic stress. Moreover, these models are particularly relevant in the context of scaling-up predictions of functional connectivity under different restoration scenarios for species with stage-structured populations that move between spatially isolated seascape elements during their ontogeny, as is common for reef-associated fish and invertebrate species (Adams et al. 2006).

Here, we use quantitative potential connectivity estimates generated via spatial graph analyses to evaluate the spatial design of a newly established, broad-scale coral restoration program in the Florida Keys, USA—*Mission: Iconic Reefs*. This multi-million dollar (USD) coral reef restoration initiative aims to recover the diversity, health, and cover of corals at several restoration sites along and adjacent to the Florida Reef Tract, a roughly 350-mile long barrier reef whose structure and function have been heavily modified by multi-scale interacting stressors (Lirman et al. 2019; NOAA Fisheries 2019). Our potential connectivity models focused specifically on two economically and ecologically valuable reef fish species whose cross-shelf ontogenetic migrations connect a mosaic of diverse habitats. These mobile mesopredators are thought to play an especially important role in modulating coral reef restoration success by altering rates of coral growth, herbivory, and corallivory through direct trophic interactions and the delivery of cross-ecosystem nutrient subsidies (Shantz et al. 2015; Ladd et al. 2018). Thus, our overarching goal was to assess the extent to which the potential coral restoration sites identified through the *Mission: Iconic Reefs* planning process are likely to support and benefit from ecological interactions with these key migratory fishes based on their distributions across the seascape and thus should be prioritized for protection and enhancement, measured as their ranked relative contributions to seascape-wide connectivity. We hypothesized that coral reef restoration sites adjacent to nearshore mangrove and seagrass nursery habitats would coincide with corridors of the highest levels of potential connectivity for these coastal coral reef fishes. To our knowledge, this study represents one of the first applications of a spatial graph-theoretic approach to projecting the effects of ongoing habitat restoration on functional connectivity for multi-habitat reef fishes. Given burgeoning investments in coastal habitat restoration globally, our aim is to demonstrate how quantitative and spatially explicit predictions of functional connectivity can be generated and applied within site selection processes.

3.2 Methods

3.2.1 Study area

Our models of potential functional connectivity focused on subtropical coastal habitats off the Florida Keys, a group of islands located off the southern tip of Florida in the United States of America (USA) (Figure 3.1). The Florida Keys seascape, which comprises a mosaic of mangrove shorelines and islands, seagrass meadows, patch reefs, and the third-largest barrier reef in the world, has experienced significant degradation and fragmentation in recent decades in response to

stressors operating at both local and global scales (Ogden et al. 1994; Lirman et al. 2019). Indeed, topographic flattening and coral loss have been severe across the Florida Reef Tract, reducing coral cover to roughly 2% in many areas (Palandro et al. 2008; Alvarez-Filip et al. 2009; NOAA Fisheries 2019). In 2019, the U.S. National Oceanic and Atmospheric Administration (NOAA) and interdisciplinary partners announced *Mission: Iconic Reefs*, a multi-million dollar restoration project aimed at recovering the diversity and cover of corals along and leeward to the Florida Reef Tract in the Florida Keys National Marine Sanctuary over the next 30 years. To address this challenge, a group of coral restoration practitioners and coastal managers ranked 37 priority areas based on criteria such as ecosystem services, likelihood of success, size and geographic location, and community interest, leading to the selection of seven final *Iconic Reefs* (NOAA Fisheries 2019). Although connectivity, lumped together with sustainability, was included, and ranked highly by reviewers, it was assessed only qualitatively. Thus, the *Mission: Iconic Reefs* program offers a unique opportunity to compare restoration site selection between quantitative potential connectivity models and expert-based opinion, as done here for fifteen coral reef restoration sites considered under the *Mission: Iconic Reefs* initiative (5 *Iconic Reefs* and 10 alternates; Figure 3.1).

3.2.2 *Focal species*

We modeled potential connectivity across the Florida Keys seascape for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*), where sub-adults were defined as individuals between the size at age-1 and the size at maturation (9.51–24.71 cm and 11.90–25.33 cm total length (TL), respectively; Faunce & Serafy 2007). Sub-adult *L. griseus* and *H. sciurus* undertake seascape-wide ontogenetic migrations from nearshore mangrove and seagrass nurseries to adult habitat on the barrier reef tract, thereby acting as conduits of functional connectivity. The geographical pathways traveled, however, remain unclear as tagging efforts typically prioritize mature fishes (e.g., Luo et al. 2009) and often finer-scale movement patterns. Potential connectivity models are, therefore, a first step in identifying the connectivity corridors that may maintain metapopulation persistence for these commercially and recreationally valuable species in southern Florida and the Gulf of Mexico (Harper et al. 2000; Ault et al. 2005). Furthermore, knowledge of potential connectivity for sub-adult *L. griseus* and *H. sciurus* will help to inform the design of effective habitat restoration programs, including *Mission: Iconic Reefs*, as these abundant fishes play essential ecological roles as mobile mesopredators and vectors of nutrient transport. For instance, grunts and snappers have been demonstrated to create nutrient

hotspots on coral reefs in the Florida Keys, thereby increasing the cover of crustose coralline algae and enhancing rates of coral growth and grazing on nuisance macroalgae by herbivorous fishes (Shantz et al. 2015), all of which may benefit coral restoration (Ladd et al. 2018). Thus, potential connectivity models can provide insights into where these fish-derived nutrient hotspots are most likely to form and where habitat restoration might be necessary to overcome connectivity barriers (McRae et al. 2012).

3.2.3 *Model construction*

Applying a spatial graph-theoretic approach, we modeled the Florida Keys seascape as a spatial graph constructed of nodes (i.e., suitable habitat patches) connected by a series of edges (i.e., dispersal links) (Urban & Keitt 2001; Fall et al. 2007). Rather than extracting nodes from simple thematic habitat maps, we leveraged previously constructed species-specific habitat suitability models (HSMs) that related fish presence localities in SCUBA diver surveys to continuous spatial data on seasonal water conditions, habitat composition and configuration, bathymetry, and seascape surface geomorphology (Stuart et al. 2021; Chapter 2). In our initial comparative study, we evaluated the discriminatory ability of penalized logistic regression and Maximum Entropy (MaxEnt) habitat suitability modeling techniques using the area under the receiver-operator curve (AUC). We also compared predictive performance following discretization of the continuous suitability surfaces to a binary scale using the suitability threshold whereby each model achieved a maximum sum of training sensitivity and specificity (max SSS), a method that maximizes discrimination between presence and absence localities (Liu et al. 2013; Stuart et al. 2021; Chapter 2). We opted to use the MaxEnt products in this research for several key reasons. First, regardless of species, MaxEnt's discriminatory ability consistently exceeded that of the penalized logistic regressions. Second, MaxEnt's species-environment relationships and patchy suitability predictions aligned more closely with the findings of previous field- and laboratory-based studies of *L. griseus* and *H. sciurus*, revealing small patches of suitable habitat that may serve as important stepping stones supporting seascape-wide connectivity. Finally, as a free, open-source software for modeling species distributions and niches from presence-background data, MaxEnt can analyze presence records from citizen science programs, online biodiversity databases, fishery- dependent and fishery-independent surveys, and other sources, which, relative to true presence-absence data, are often more readily available to coastal managers,

restoration practitioners, and other stakeholders working in complex marine systems such as the Florida Keys (Stuart et al. 2021; Chapter 2).

Although acoustic tagging data suggest that adult fishes in the Florida Keys can make mangrove-to-reef movements in a matter of days (Luo et al. 2009), transit durations are likely longer for smaller, less mobile sub-adults. Therefore, we filtered the MaxEnt-derived binary suitability maps using a minimum node size of 100 m² to retain only those suitable seascape patches that were large enough to support the daily activity spaces of sub-adults. The 100 m² node size was selected based on previous *L. griseus* and *H. sciurus* observational and tracking studies from the greater Caribbean region that have demonstrated high short-term site fidelity to diurnal resting sites (Starck II & Schroeder 1971; Beets et al. 2003; Verweij & Nagelkerken 2007; Hitt, Pittman & Nemeth 2011; Hitt, Pittman & Brown 2011) and also ensured that the resulting spatial graphs included both small stepping stones and larger patches of long term use.

We calculated edges between pairs of nodes using least-cost distances, which integrate information about the spatial configuration of habitats and the resistance of the surrounding matrix to movement (Adriaensen et al. 2003; Rayfield et al. 2010). To produce the species-specific cost surfaces from which least-cost paths were derived, we applied a negative exponential function to transform the habitat suitability indices (HSI) of Stuart et al. (2021) to resistance values. The negative exponential transformation function is as follows (Keeley et al. 2016; Dufлот et al. 2018):

$$\begin{aligned} \text{If HSI} \geq \text{threshold} &\rightarrow \text{species habitat} \rightarrow \text{resistance} = 1 \\ \text{If HSI} < \text{threshold} &\rightarrow \text{matrix} \rightarrow \text{resistance} = e^{\frac{\ln(0.001)}{\text{threshold}} \times \text{HSI}} \times 10^3 \end{aligned}$$

This function assigns a resistance value of 1 when HSI is greater than or equal to the species-specific max SSS threshold (i.e., resistance increases linearly with distance), whereas a resistance value of 1000 is assigned when HSI = 0. The exponential shape of this function loosens the assumption that resistance increases at a constant rate with decreasing suitability, as is the case in a negative linear transformation, instead allowing resistance to increase slowly as suitability first departs from its maximum, then dramatically at lower suitability values (Keeley et al. 2016). This negative exponential relationship is expected to more accurately predict the movements of sub-adult *L. griseus* and *H. sciurus*, who may willingly explore, or be forced to traverse, areas of intermediate suitability during their cross-shelf migrations, while still reinforcing the barrier effect of low-suitability areas (Keeley et al. 2016; Dufлот et al. 2018).

We developed and evaluated species-specific spatial graphs using Graphab 2.6, a free software built for modeling, analyzing, and visualizing connectivity networks that is readily available to restoration practitioners and coastal managers (Foltête et al. 2012, 2021). Graphs were constructed using planar topology with a cell resolution of 10 x 10 m, producing minimum planar graphs in which node pairs were connected from edge-to-edge by direct, least-cost dispersal links (Fall et al. 2007). Minimum planar graphs have emerged as a helpful tool for informing landscape-scale conservation efforts, as these graphs capture the connectivity network while being more efficient to construct, analyze, and communicate than the complete graphs that they approximate (Fall et al. 2007). Once least-cost paths were predicted, we pruned the resulting graphs to retain only those paths whose metric distance was less than the estimated maximum dispersal distance of sub-adult *L. griseus* and *H. sciurus*. In a previous acoustic tracking study from the U.S. Virgin Islands, a 30 cm TL *H. sciurus* and a 30.4 cm TL *L. synagris*, a congener of *L. griseus* of similar body shape and size, moved 11.7 km and 10.6 km in a single day, respectively (Pittman et al. 2014). Luo et al. (2009) also documented reef-directed movements of roughly 10 km, with a maximum distance of 15 km, for acoustically tagged *L. griseus* adults in the Florida Keys. Thus, 10 km was used as the estimated maximum dispersal distance for sub-adult *L. griseus* and *H. sciurus*, which was converted to cost units for graph pruning via Graphab’s internal distance conversion function.

3.2.4 Model evaluation

3.2.4.1 Global connectivity metrics

To first evaluate current seascape-wide potential connectivity levels for *L. griseus* and *H. sciurus* sub-adults, we applied two global connectivity metrics: Probability of Connectivity (PC) and Equivalent Connectivity (EC). The PC index, developed by Saura & Pascual-Hortal (2007), is the probability that two animals randomly placed in a landscape (seascape) fall into habitat patches that are connected. Given a set of n nodes, Graphab calculates the PC index as follows:

$$PC = \frac{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}{A_L^2}$$

where a_i and a_j are the capacities of nodes i and j (an indicator of their demographic potential), equal by default to their areas in m^2 . A_L is the area of the study region (including both species

habitat and matrix). p_{ij}^* is the maximum product probability of all possible paths between nodes i and j , where the dispersal probability (p_{ij}) between each pair of nodes is calculated as:

$$p_{ij} = e^{-\alpha d_{ij}}$$

where d_{ij} is the edge-to-edge least-cost distance between nodes i and j , and α is a cost-distance decay coefficient set such that $p_{ij} = 0.05$ for the maximum estimated dispersal distance of the focal species. If nodes i and j are in close proximity, the maximum probability path will be the direct dispersal link between them ($p_{ij}^* = p_{ij}$). If nodes i and j are spatially separated, then the maximum probability path will include the series of intermediate steps that minimizes cost, yielding $p_{ij}^* > p_{ij}$. Finally, $p_{ij}^* = 1$ when $i = j$ (i.e., a node can always be reached from itself), and $p_{ij}^* = 0$ when nodes i and j are entirely disconnected. The PC index takes on values 0 to 1, with larger values suggesting higher seascape-scale connectivity (Saura & Pascual-Hortal 2007).

Graphab's global PC metric considers only node areas and inter-node distances as drivers of seascape-scale potential connectivity, however, connectivity for sub-adult *L. griseus* and *H. sciurus* is likely influenced by node area and suitability in an interactive manner. To account for variation in node suitability, we calculated quality-weighted areas by multiplying each node's surface area by its average suitability from the original continuous suitability surfaces of Stuart et al. (2021; Chapter 2). Using these quality-weighted areas as node capacities, we then calculated the EC index. Derived from the PC index, EC is calculated as:

$$EC = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}$$

where p_{ij}^* is as defined above and a_i and a_j now represent the quality-weighted areas of nodes i and j , respectively. EC quantifies the amount of reachable habitat across the seascape, taking into account node availability and quality, the estimated dispersal flux between nodes, and the overall topology of the network (Saura et al. 2011). Furthermore, the EC calculation does not rely on the overall area of the study region (A_L), which may be arbitrarily placed or exceedingly large relative to nodes, leading to small PC values. The EC index increases with improved connectivity.

3.2.4.2 Local connectivity metrics

To evaluate the contributions of individual nodes, including those considered for restoration under *Mission: Iconic Reefs*, to seascape-wide connectivity, we calculated the local Interaction Flux (IF). IF quantifies potential connectivity at the node-scale as the sum of the products of the focal node capacity with all other nodes, weighted by their interaction probability (Foltête et al. 2014; Sahraoui et al. 2017). IF values were calculated from each species' graph as:

$$IF_i = \sum_{j=1}^n a_i^\beta a_j^\beta p_{ij}^*$$

where p_{ij}^* is as defined above, a_i^β and a_j^β are the capacities of nodes i and j , respectively, defined here as their quality-weighted areas, and β is an optional weighting exponent, set equal to 1 in this case.

IF values can be interpreted as the contribution of individual nodes to the global EC metric and, therefore, provide a means of assessing potential connectivity at unique locations across the seascape. Thus, the geographic coordinates of the *Mission: Iconic Reefs* sites ($n = 15$; Figure 3.1) were used to extract IF values from each species' spatial graph, so long as they fell on or within 10 m (i.e., a one cell distance) from an existing node. Because nodes represent a mosaic of suitable habitats extracted from continuous HSMs, rather than coral reef habitat in isolation, we also evaluated the composition of benthic habitats in each node. Similarly, we examined whether mean Euclidean distances to the nearest nursery habitats (i.e., mangroves and continuous seagrass beds) were correlated with node- and species-specific IF values by calculating Pearson pairwise correlation coefficients (r) using the `cor()` function in base R (version 4.0.2; R Core Team 2020). Finally, to compare the connectivity contributions of the fifteen prospective coral restoration sites to the remaining nodes in each species' spatial graph, we ranked all nodes by their IF values and examined whether any of the selected or alternate restoration sites ranked in the top 100 according to their contributions to seascape-scale potential connectivity. Together, these assessments allowed us to determine how seascape context influences node-scale potential connectivity for sub-adult *L. griseus* and *H. sciurus*.

3.3 Results

3.3.1 *Spatial graph structure*

Minimum planar graphs revealed a unique network of connections across the Florida Keys seascape for each of the focal species. The sub-adult *L. griseus* graph consisted of 36,339 least-cost edges connecting 21,166 nodes, which together covered roughly 7% of the study seascape (Figure 3.2). The sub-adult *H. sciurus* graph contained a larger number of least-cost edges and nodes, with 47,427 and 27,271, respectively, the latter of which covered just over 10% of the seascape (Figure 3.3). Overall, the suitability levels of seascape nodes were similar between species, averaging 0.75 ± 0.10 for *L. griseus* and 0.74 ± 0.09 for *H. sciurus* (mean \pm SD). In contrast, node size varied substantially within spatial graphs, ranging from small, isolated patch reefs to continuous mosaics of seagrass and hard bottom habitats, with average surface areas of $12,544.61 \pm 241,400.79 \text{ m}^2$ and $13,908.58 \pm 485,274.30 \text{ m}^2$ for *L. griseus* and *H. sciurus*, respectively. Metric and cumulative cost edge distances also varied within and between species, being generally shorter and more tightly clustered around the mean for *H. sciurus* at $150.99 \pm 299.71 \text{ m}$ ($230.21 \pm 1,117.78$ cumulative cost units) relative to *L. griseus* at $190.40 \pm 424.13 \text{ m}$ ($548.17 \pm 2,712.29$ cumulative cost units). Despite this variation, the fifty most costly paths for both species fell primarily in the southwestern portion of the study area and typically consisted of either long detours over continuous seagrass beds surrounded by less favorable habitats or paths of intermediate metric length that traversed more costly patches of unconsolidated sediment and sparse seagrass.

3.3.2 Global connectivity metrics

To assess seascape-wide potential connectivity for sub-adult *L. griseus* and *H. sciurus*, we first calculated the global PC metric, which quantifies the probability of two individuals randomly placed in the seascape making contact. A PC value of 1.15×10^{-4} was calculated from the *L. griseus* spatial graph, which was exceeded by the 2.28×10^{-4} value calculated from the *H. sciurus* graph. To account for the possible influence of node suitability, in addition to size, on potential connectivity at the seascape-scale, we also calculated the global EC metric using quality-weighted areas as node capacities. The EC metric quantifies the amount of reachable, suitable habitat across the seascape. Aligning with the results of the PC analysis, the *H. sciurus* graph produced a higher EC estimate than the *L. griseus* graph, with values of 2.20×10^8 and 1.62×10^8 , respectively. Together, the global PC and EC metrics suggest that, under current conditions, the Florida Keys

study seascape supports a higher level of potential connectivity for sub-adult *H. sciurus* relative to *L. griseus*.

3.3.3 Local connectivity metrics

To evaluate the contributions of fifteen sites considered under the *Mission: Iconic Reefs* initiative to seascape-wide potential connectivity for sub-adult *L. griseus* and *H. sciurus* ahead of coral restoration, we calculated the local IF metric for each species at each site. Within species, there was substantial variation in IF values across the fifteen potential coral reef restoration sites evaluated in our study area (Table 3.1; Figure 3.4). Spatial graph analysis revealed Newfound Harbor, Sombrero Reef, French Reef, Turtle Reef, and Molasses Reef as being, in decreasing order, the five coral restoration sites with the highest levels of potential connectivity for sub-adult *L. griseus* under current conditions. These top-five ranked sites represent a variety of reef types, seascape zones, and proximities to potential seagrass and mangrove nurseries, ranging from an inshore patch reef located roughly 1 km or less from both nursery habitats (Newfound Harbor) to reef margin/fore reef sites isolated from mangroves by distances of nearly 10 km (French and Molasses Reefs) (Table 3.1). Contrary to our hypothesis, we found no correlation between IF estimates for *L. griseus* and mean distances from nodes to potential mangrove and seagrass nurseries ($r_{mangrove} = -2.24 \times 10^{-2}$, $r_{seagrass} = -3.60 \times 10^{-3}$). The *L. griseus* seascape nodes in which the top-five prospective coral restoration sites fell did, however, vary in their habitat composition, including those dominated by aggregate reef and coral rubble (French, Molasses, and Sombrero Reefs), pavement and patch reef (Newfound Harbor), or a combination of these habitats (Turtle Reef) (Figure 3.5). Of the top five, only Newfound Harbor and Sombrero Reef were sites selected for active restoration by the *Mission: Iconic Reefs* panel of coral restoration practitioners and managers (Table 3.1; Figure 3.4). The remaining three selected *Iconic Reefs* in our study area—Looe Key Reef, Horseshoe Reef, and Cheeca Rocks—were ranked sixth, ninth, and fifteenth (last), respectively, in terms of supporting seascape-scale potential connectivity for sub-adult *L. griseus*, according to their IF values (Table 3.1; Figure 3.4). Of these, Looe Key Reef and Horseshoe Reef fell in nodes of similar habitat composition to the highly ranked sites, whereas Cheeca Rocks was made up of a unique mixture of patch reef and seagrass habitats surrounded by scattered coral and rock. Finally, of the 21,166 nodes making up the *L. griseus* minimum planar graph, those containing the Newfound Harbor (*Iconic Reef*), Sombrero Reef (*Iconic Reef*), French Reef (alternate), and Turtle Reef (alternate) coral restoration sites ranked in the top-100 in terms of their

IF values, suggesting that they represent potential connectivity hotspots for the sub-adults of this species.

Node-level analysis of the sub-adult *H. sciurus* connectivity network revealed Newfound Harbor, French Reef, Molasses Reef, Sombrero Reef, and Cheeca Rocks as being the five prospective coral restoration sites with the highest levels of potential connectivity for this species, in decreasing order, according to the IF metric (Table 3.1; Figure 3.4). Similar to the findings of the *L. griseus* graph, the top-five sites for *H. sciurus* varied substantially with respect to their surrounding habitat composition, including mosaics of aggregate reef, pavement, and reef rubble (French, Molasses, and Sombrero Reefs), pavement and seagrass (Newfound Harbor), and patch reef and scattered coral/rock (Cheeca Rocks) (Figure 3.5). Of these, Newfound Harbor, Sombrero Reef, and Cheeca Rocks were sites selected as *Iconic Reefs* by the original NOAA-led evaluation, and the French and Molasses Reef restoration sites fell within the same suitable seascape node for sub-adult *H. sciurus*. Furthermore, Newfound Harbor, Sombrero Reef, and French Reef were among the top-five ranked potential restoration sites for sub-adult *L. griseus*, with the first-mentioned site taking the top spot for both species. Indeed, the Newfound Harbor IF value calculated from the *H. sciurus* spatial graph exceeded that of the other fourteen sites under consideration by roughly one-to-three orders of magnitude (Table 3.1). The remaining two selected *Iconic Reefs* in our study area, Horseshoe Reef and Looe Key Reef, were ranked sixth and eighth, respectively, in terms of their ability to support seascape-wide potential connectivity for *H. sciurus* according to the IF metric. As with *L. griseus*, we once again found no correlation between node-specific IF values for sub-adult *H. sciurus* and mean distances to potential nursery habitats ($r_{mangrove} = -7.70 \times 10^{-3}$, $r_{seagrass} = -1.70 \times 10^{-3}$). Notably, of the 27,271 total nodes in the *H. sciurus* minimum planar graph, ten containing potential *Mission: Iconic Reefs* coral restoration sites ranked in the top-100 based on their IF values—the five *Iconic Reefs* selected by the initial NOAA panel (Newfound Harbor, Looe Key Reef, Sombrero Reef, Cheeca Rocks, and Horseshoe Reef) and five alternates (Davis, Molasses, French, Elbow, and Turtle Reefs) (Table 3.2).

3.4 Discussion

3.4.1 Spatial graph performance and global connectivity

Minimum planar graphs proved to be an effective tool for visualizing and quantifying potential functional connectivity for sub-adult *L. griseus* and *H. sciurus* occupying a spatially

heterogeneous seascape in the Florida Keys, USA. In particular, spatial graphs pinpointed the suitable seascape nodes that likely play fundamental roles in supporting the ontogenetic migrations of these economically and ecologically valuable focal reef fish species. Furthermore, our findings demonstrate a desirable property of spatial graphs: their ability to represent potential connectivity as an emergent property of seascapes arising from unique interactions between species and the spatial patterns that they encounter (Pittman 2017). In fact, the spatial graph analyses conducted herein revealed species-specific connectivity appraisals, suggesting that, overall, our study seascape supports a higher level of potential connectivity for *H. sciurus* relative to *L. griseus* under current conditions. Differences in global PC and EC estimates calculated from *L. griseus* and *H. sciurus* spatial graphs were likely driven in part by variation in species-specific patterns of habitat suitability across the seascape. For instance, Stuart et al. (2021; Chapter 2) found that patches of pavement, reef rubble, and unconsolidated sediments (with or without scattered coral/rock) in the same Florida Keys seascape offered higher levels of habitat suitability for sub-adult *H. sciurus* compared to *L. griseus*. Additionally, the sensitivity of habitat suitability predictions to changes in depth varied between species, with deeper waters being associated with a higher likelihood of presence for sub-adult *H. sciurus* relative to *L. griseus* (Stuart et al. 2021; Chapter 2; Figure A2.5). Together, these differences translated to a larger quantity and surface area of accessible nodes, and thus higher PC and EC estimates of seascape-scale potential connectivity, for sub-adult *H. sciurus*.

3.4.2 *Mission: Iconic Reefs and local connectivity*

Beyond providing a means to efficiently identify, quantify, and visualize seascape-scale connectivity networks, minimum planar graphs aided in the detection of intra- and inter-specific variation in potential connectivity among nodes (i.e., suitable seascape patches). By calculating the local IF metric, representing here the contributions of individual nodes to seascape-wide connectivity according to their quality-weighted areas, we were able to compare species-specific potential connectivity levels at fifteen sites considered under the *Mission: Iconic Reefs* program—a newly established habitat restoration initiative aimed at recovering the diversity and health of reef-building coral communities in the Florida Keys National Marine Sanctuary (NOAA Fisheries 2019). The five *Iconic Reefs* selected for coral restoration in our study area by the initial panel of coral scientists and restoration practitioners—Looe Key Reef, Newfound Harbor, Sombrero Reef, Cheeca Rocks, and Horseshoe Reef—differed from the five sites that would be selected for each

species according to IF estimates of potential connectivity alone. We discuss the possible drivers and ecological implications of these differences below.

According to the local IF metric, the top-five highest-ranking coral restoration sites supporting seascape-wide connectivity for sub-adult *L. griseus* included two selected *Iconic Reefs* (Newfound Harbor and Sombrero Reef) and three alternates (Molasses, French, and Turtle Reefs) (Table 3.1; Figure 3.4). Similarly, the top-five highest-ranking coral restoration sites supporting seascape-wide connectivity for sub-adult *H. sciurus* included three selected *Iconic Reefs* (Newfound Harbor, Sombrero Reef, and Cheeca Rocks) and two alternates (Molasses and French Reefs). These results suggest that the selected *Mission: Iconic Reefs* coral restoration sites in our study area are more likely to support and benefit from existing ecological interactions with migrating sub-adult *H. sciurus* relative to *L. griseus*.

Our finding that Newfound Harbor and Sombrero Reef sites were potential connectivity hotspots for both fish species is especially promising for the success of restored corals there. Grunts aggregating at connectivity hotspots have been demonstrated to alter within- and cross-ecosystem productivity and nutrient regimes in the Florida Keys by enhancing rates of nitrogen and phosphorus delivery to coral heads by roughly 5–10 times, grazing by herbivores by 3 times, and coral growth by approximately 1.5 times, relative to sites where these fish rarely shelter (Shantz et al. 2015). As such, the combined schooling and aggregating behaviors of sub-adult *L. griseus* and *H. sciurus* on and around the Newfound Harbor and Sombrero Reef restoration sites may greatly benefit the survival and growth of out-planted coral colonies and propagules through the delivery of valuable nutrient supplements and the magnification of grazing on macroalgal competitors by herbivorous fishes and invertebrates (Shantz et al. 2015; Ladd et al. 2018). Moreover, by supporting high levels of potential connectivity for both study species, and by being in relatively close proximity to the selected restoration sites, French and Molasses Reefs will likely also facilitate beneficial, fish-driven interactions with neighboring *Iconic Reefs*, despite not being selected for restoration themselves.

To compare the connectivity contributions of the fifteen potential *Mission: Iconic Reefs* restoration sites to the remaining nodes in the sub-adult *L. griseus* and *H. sciurus* spatial graphs, we ranked all nodes by their IF values and examined the identities and attributes of those nodes that ranked in the top 100. For *L. griseus* and *H. sciurus*, the 100 highest-ranking nodes included four and ten potential coral restoration sites, respectively (Table 3.2). These highly ranked sites

contained an even mix of selected and alternate *Iconic Reefs* for both species. However, the habitat composition of these nodes varied between species, being characterized by a higher proportion of pavement, reef rubble, and scattered coral/rock for *H. sciurus* relative to *L. griseus* (Figure 3.5). Once again, we suggest that these differences stem from variation in the species-specific suitability levels of benthic habitat types (Stuart et al. 2021; Chapter 2; Figure A2.5). This would also help to explain why the Cheeca Rocks *Iconic Reef* site was ranked highly for *H. sciurus* but last for *L. griseus*, as the scattered coral and rock habitat surrounding this patch reef translated to a larger node for *H. sciurus* relative to *L. griseus* (Table 3.1). It is important to note, however, that the IF values presented herein serve as only a baseline estimate of node-level potential connectivity under present conditions and that future coral restoration efforts will increase the proportion and topographic complexity of coral habitats around selected restoration sites, likely resulting in enhanced sheltering and foraging opportunities, as well as higher habitat suitability and functional connectivity levels, for both focal species (Alvarez-Filip et al. 2009; Shantz et al. 2015; Stuart et al. 2021).

3.4.3 *Nursery habitat proximity*

In our spatial graph connectivity analyses, we examined whether mean Euclidean distances to mangrove and seagrass nursery habitats (attributes that will remain unchanged by coral restoration) influenced node-scale potential connectivity estimates for sub-adult *L. griseus* and *H. sciurus*. Regardless of species, mangrove and seagrass nursery proximities were neither positively nor negatively correlated with IF estimates of node-level connectivity. These results were contrary to our hypothesis based on the findings of previous studies. For example, Stuart et al. (2021) found mangrove proximity to be an important predictor of habitat suitability for sub-adult *L. griseus* and *H. sciurus* in the Florida Keys (Chapter 2; Figure 2.4; Figure A2.5). Nagelkerken et al. (2017) also found the enhancement of adult biomass and abundances on coral reefs by mangrove and seagrass nurseries to be highly localized for reef-associated fishes in the Caribbean Sea, including *H. sciurus*. However, as revealed by Faunce and Serafy, several coral reef fish species in the Florida Keys, including *L. griseus* and *H. sciurus*, display selective patterns of mangrove strata use driven by season, environmental conditions, and other selective processes, rather than by geographic proximity alone (2008). Moreover, the sizes and suitability levels of nurseries, along with the abundances and densities of their juvenile reef fish occupants, may play larger roles in determining functional connectivity with offshore coral reefs relative to simple Euclidean measures of distance

between habitats (Huijbers et al. 2013; Nagelkerken et al. 2017). Together, these factors may help to explain the lack of a detectable nursery proximity effect on potential connectivity for sub-adult *L. griseus* and *H. sciurus* in our study area.

3.4.4 *Model limitations and assumptions*

It is important to mention the limitations and assumptions of our modeling approach. First, the application of least-cost paths derived from MaxEnt HSMs in this research relies on two assumptions that may or may not be met *in situ*: 1) that species' migrations are driven by similar spatial and environmental factors as habitat selection, and 2) that ontogenetic migrations fatefully follow least-cost paths (Zeller et al. 2012). To minimize uncertainty around these assumptions, connectivity models could instead be derived from GPS telemetry or genetic data; however, in the absence of such data, due for instance to body size constraints, resource limitations, or migrations exceeding the spatiotemporal ranges of conventional approaches, the use of limited or indirect knowledge of a species' dispersal ability may prove sufficient (Zeller et al. 2018). Second, our application of minimum planar graphs also enforces the restrictions of planarity, including the use of only non-crossing, direct edges (i.e., those that do not cross another edge or intermediate node) (Fall et al. 2007). We feel that these restrictions are justified in the context of predicting potential connectivity for sub-adult *L. griseus* and *H. sciurus*, as we find it unlikely that fishes migrating at this vulnerable life stage would cross over suitable seascape nodes without stopping for rest, foraging opportunities, protection from predators, or other potential benefits (Krumme 2009). Despite these limitations and assumptions, we feel that HSM-derived connectivity models offer much-needed baseline estimates of potential connectivity at the local and seascape scales and are particularly relevant as foresight tools for guiding and evaluating the spatial design of conservation and restoration efforts in fragmented and degraded seascapes, as has been previously demonstrated in freshwater (e.g., Stewart-Koster et al. 2015) and terrestrial environments (e.g., Saura & Pascual-Hortal 2007; Poor et al. 2012; Stevenson-Holt et al. 2014; Dufлот et al. 2018; Préau et al. 2020).

3.4.5 *Conclusions and recommendations for coral reef restoration*

Based on the findings of our novel spatial graph connectivity analyses, we argue that restoration efforts are likely to benefit greatly from the explicit consideration of seascape context and multi-species functional connectivity during their initial planning phase. Restoration programs like *Mission: Iconic Reefs* that seek to conserve structural and functional connectivity through the

creation, restoration, and protection of essential habitats are expected to result in more diverse, healthy, and productive marine communities (Olds et al. 2016; Carr et al. 2017). In the Florida Keys specifically, these ecological benefits will also provide opportunities for economic growth, as the Florida Keys seascape supports thousands of jobs and a multi-billion dollar fisheries- and tourism-based economy, annually (Harper et al. 2000; Ault et al. 2005). Previously, challenges in quantifying and representing multi-species and multi-scale connectivity precluded their integration in marine habitat restoration planning (Gilby et al. 2018). As demonstrated in our study, spatial graphs of potential connectivity informed by habitat suitability modeling help to overcome these hurdles by providing a data- and resource-efficient technique to quantify, visualize, and communicate complex connectivity information. The analyses conducted herein for sub-adult *L. griseus* and *H. sciurus* can be repeated for other species, life stages, or functional group representatives. By stacking the results of such analyses, coral restoration practitioners and coastal managers can identify the habitat patches that play critical roles in supporting multi-species connectivity.

Due to the persistence of interacting stressors and the rapid rates of decline in reef health and topographic complexity in the Florida Keys and beyond (Hughes et al. 2003; Bellwood et al. 2004; Alvarez-Filip et al. 2009; NOAA Fisheries 2019), prioritizing coral restoration efforts at sites with intermediate-to-high levels of baseline potential connectivity across species and community levels may be a more economically efficient and ecologically effective strategy than attempting to restore corals in low-connectivity areas where they are less likely to support and benefit from animal-driven positive feedback loops (Ladd et al. 2018; Gilby et al. 2018). To further enhance the probability of coral reef restoration success, practitioners could overlay spatial maps of habitat suitability for targeted coral species with graph models of potential connectivity for functionally important community members to identify the seascape locations that are most likely to facilitate the survival, growth, and resiliency of restored corals, as well as the development of multi-species connectivity hotspots, based on their spatial and environmental conditions. Finally, information on available resources for conducting restoration (e.g., funding, time, personnel, etc.), as well as the locations of other valued natural resources, can be incorporated into this spatial prioritization framework using decision support tools (e.g., Marxan Connect, Zonation), thereby enabling stakeholders to identify the restoration sites that offer the greatest socioecological value.

3.5 Data availability statement

Data, R scripts, Graphab run settings, ArcGIS geoprocessing workflows, and other materials associated with this chapter are available online in the following repository https://github.com/CourtneyStuart/FL_Seascape_Connectivity (accessed on 12 August 2022). GIS datasets storing the geographic coordinates of prospective coral reef restoration sites were obtained from two public sources: the Florida Keys National Marine Sanctuary Map Library (https://floridakeys.noaa.gov/fknms_map/maplibrary.html?s=about) and the Coral Reef Conservation Program (CRCP) Florida Prioritization Mapping Inventory (<https://noaa.maps.arcgis.com/home/item.html?id=3787e662be3f416680c30e3253fe459f>) (accessed on 12 August 2022).

3.6 Tables and figures

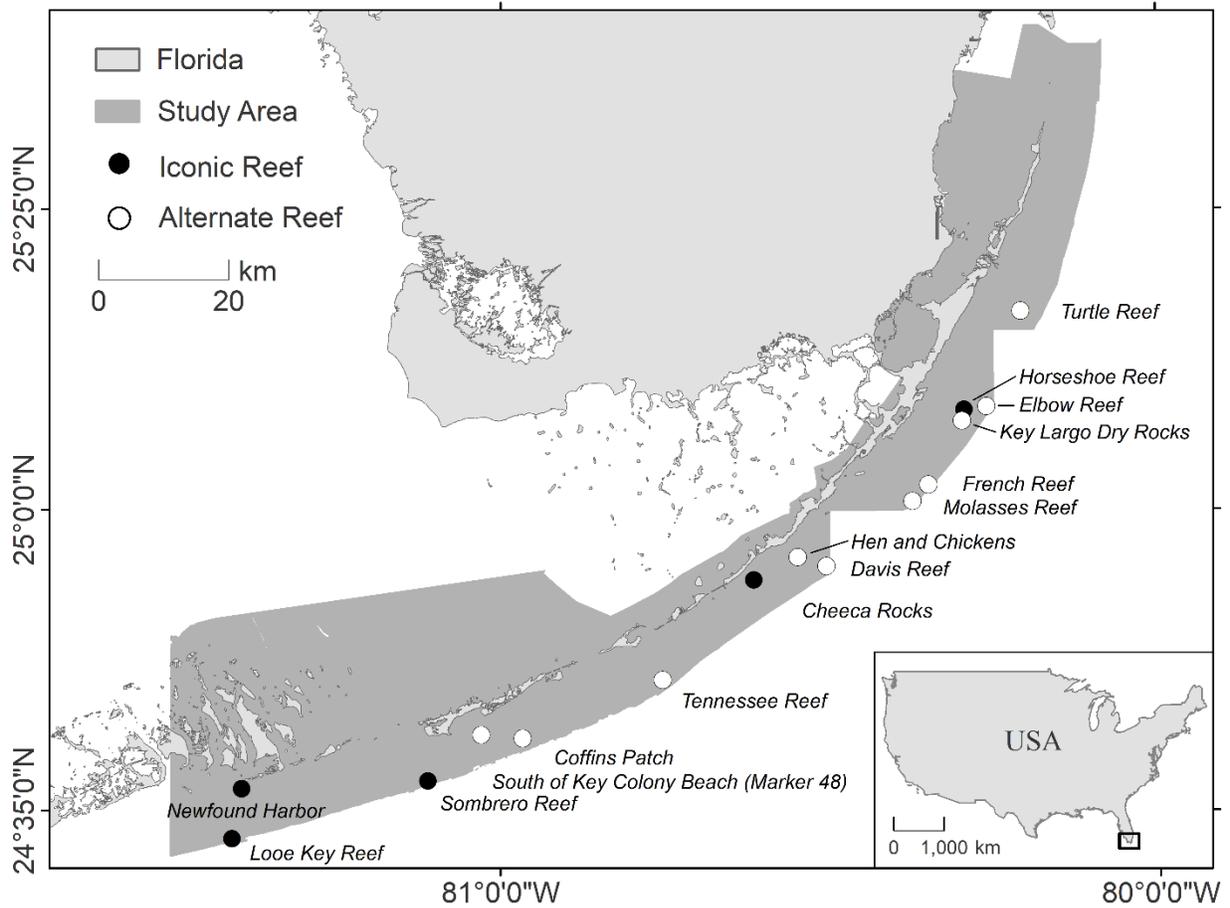


Figure 3.1. Location of the study area in the Florida Keys, USA. Potential connectivity for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) was assessed at the seascape-scale, as well as at the node-scale for fifteen sites considered under the *Mission: Iconic Reefs* coral reef restoration program (filled circle = selected *Iconic Reef*; empty circle = alternate reef).

Table 3.1. Results of spatial graph connectivity analyses focused on fifteen coral restoration sites considered under the *Mission: Iconic Reefs* program, displayed from north to south in the Florida Keys, USA (see Figure 3.1). The contributions of each site to seascape-wide potential connectivity for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) were evaluated using the Interaction Flux (IF) local connectivity metric. Site- and species-specific IF values were then related to the attributes of the nodes in which they fell, including their overall surface area and distances (mean Euclidean) to the nearest possible mangrove and seagrass nurseries.

Site	Iconic Reef	Site Description	Node Area (m ²)		Distance from Node to Mangrove (m)		Distance from Node to Seagrass (m)		Interaction Flux (IF)	
			<i>L. griseus</i>	<i>H. sciurus</i>	<i>L. griseus</i>	<i>H. sciurus</i>	<i>L. griseus</i>	<i>H. sciurus</i>	<i>L. griseus</i>	<i>H. sciurus</i>
Turtle Reef	No	Mid-channel patch reef	606400	1042000	7675.78	7744.21	893.51	860.09	2.93x10 ¹³	6.44x10 ¹³
Horseshoe Reef	Yes	Mid-channel patch reef	316500	2485400	6583.00	6817.69	1075.83	574.01	1.41x10 ¹³	1.22x10 ¹⁴
Elbow Reef	No	Reef margin/fore reef	492900	1589600	10207.00	10298.05	2647.72	2998.98	1.67x10 ¹³	8.92x10 ¹³
Key Largo Dry Rocks	No	Reef margin/fore reef	47800	56400	7309.46	7314.44	2126.55	2129.03	2.44x10 ¹²	3.13x10 ¹²
French Reef	No	Reef margin/fore reef	857200	4450600	9539.40	9098.33	729.07	1119.42	3.70x10 ¹³	2.84x10 ¹⁴
Molasses Reef	No	Reef margin/fore reef	622800	4450600	8943.65	9098.33	1288.60	1119.42	2.66x10 ¹³	2.84x10 ¹⁴
Hen and Chickens	No	Mid-channel patch reef	37800	38100	3322.17	3322.13	52.67	52.41	4.51x10 ¹²	5.73x10 ¹²
Davis Reef	No	Reef margin/fore reef	112400	451400	7693.12	7722.50	492.30	647.21	5.57x10 ¹²	4.20x10 ¹³
Cheeca Rocks	Yes	Inshore patch reef	14100	915300	6434.26	6480.71	14.09	88.84	1.86x10 ¹²	1.31x10 ¹⁴
Tennessee Reef	No	Reef margin/fore reef	175300	362400	6954.30	7061.38	1665.11	1635.42	7.44x10 ¹²	2.97x10 ¹³
Coffins Patch	No	Offshore patch reef	131700	131300	6467.76	6469.37	170.81	169.18	6.78x10 ¹²	1.06x10 ¹³
South of Key Colony Beach	No	Mid-channel patch reef	18600	18400	4283.31	4283.66	20.75	20.96	2.18x10 ¹²	2.86x10 ¹²
Sombrero Reef	Yes	Reef margin/fore reef	914900	1603300	7475.39	7508.08	1043.59	1087.57	4.28x10 ¹³	1.64x10 ¹⁴
Newfound Harbor	Yes	Inshore patch reef	486300	70519600	1072.40	1209.96	153.45	308.88	4.99x10 ¹³	1.19x10 ¹⁶
Looe Key Reef	Yes	Reef margin/fore reef	489900	950100	8957.09	9005.25	339.94	490.23	6.37x10 ¹²	7.37x10 ¹³

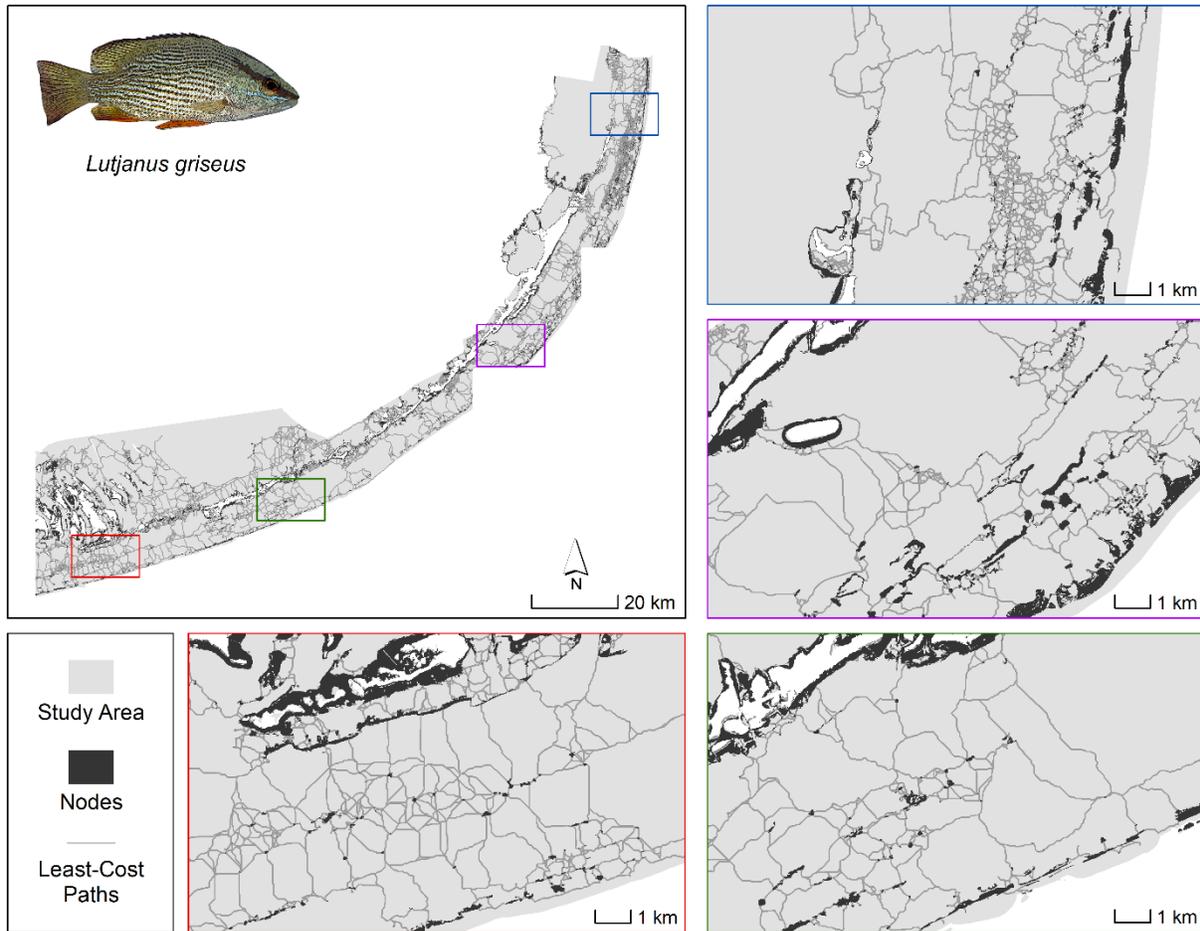


Figure 3.2. Minimum planar graph representing the connectivity network for sub-adult gray snapper (*Lutjanus griseus*) across the Florida Keys (USA) study seascape. Four zoomed-in regions are provided as examples to demonstrate the detail of MaxEnt-derived nodes and least-cost edges.

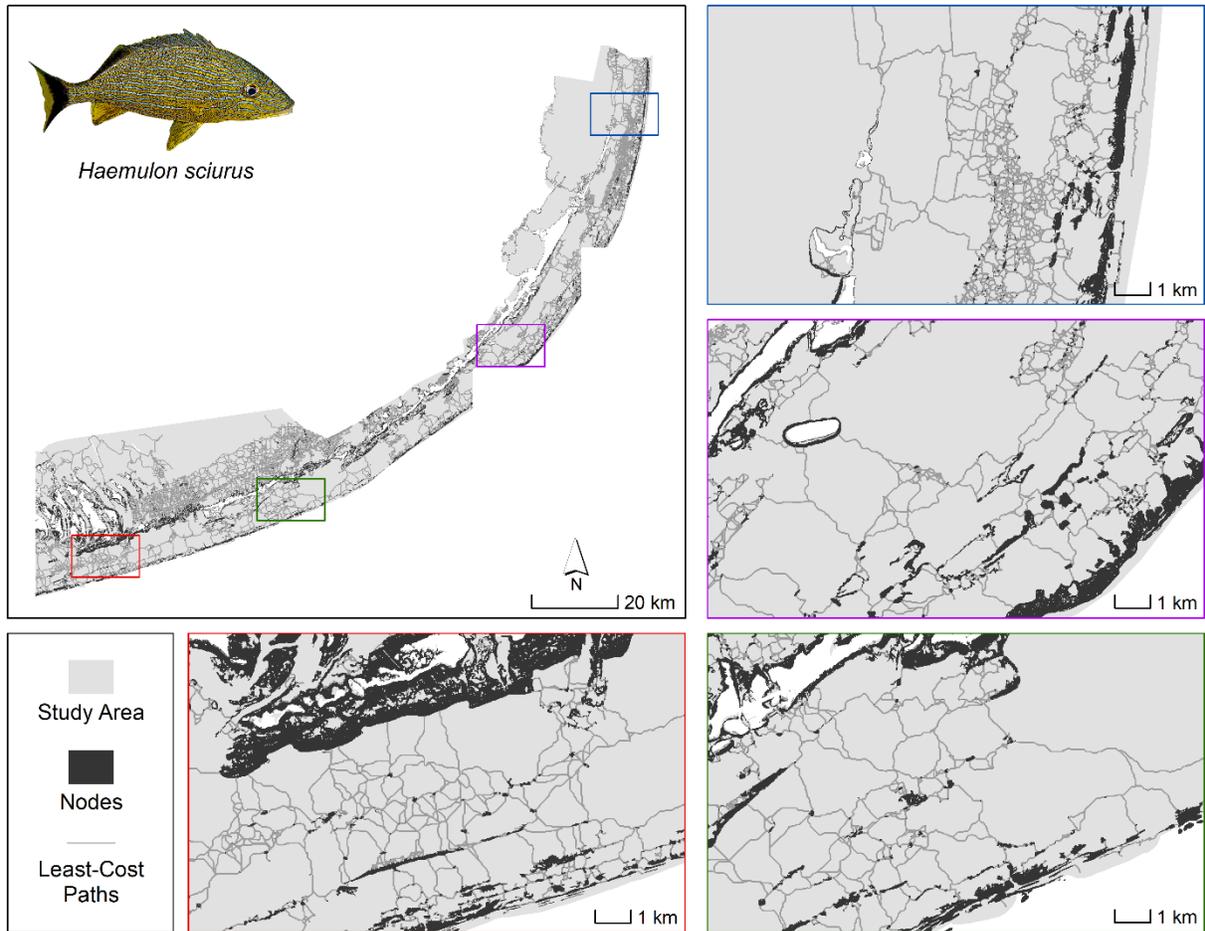


Figure 3.3. Minimum planar graph representing the connectivity network for sub-adult bluestriped grunt (*Haemulon sciurus*) across the Florida Keys (USA) study seascape. Four zoomed-in regions are provided as examples to demonstrate the detail of MaxEnt-derived nodes and least-cost edges.

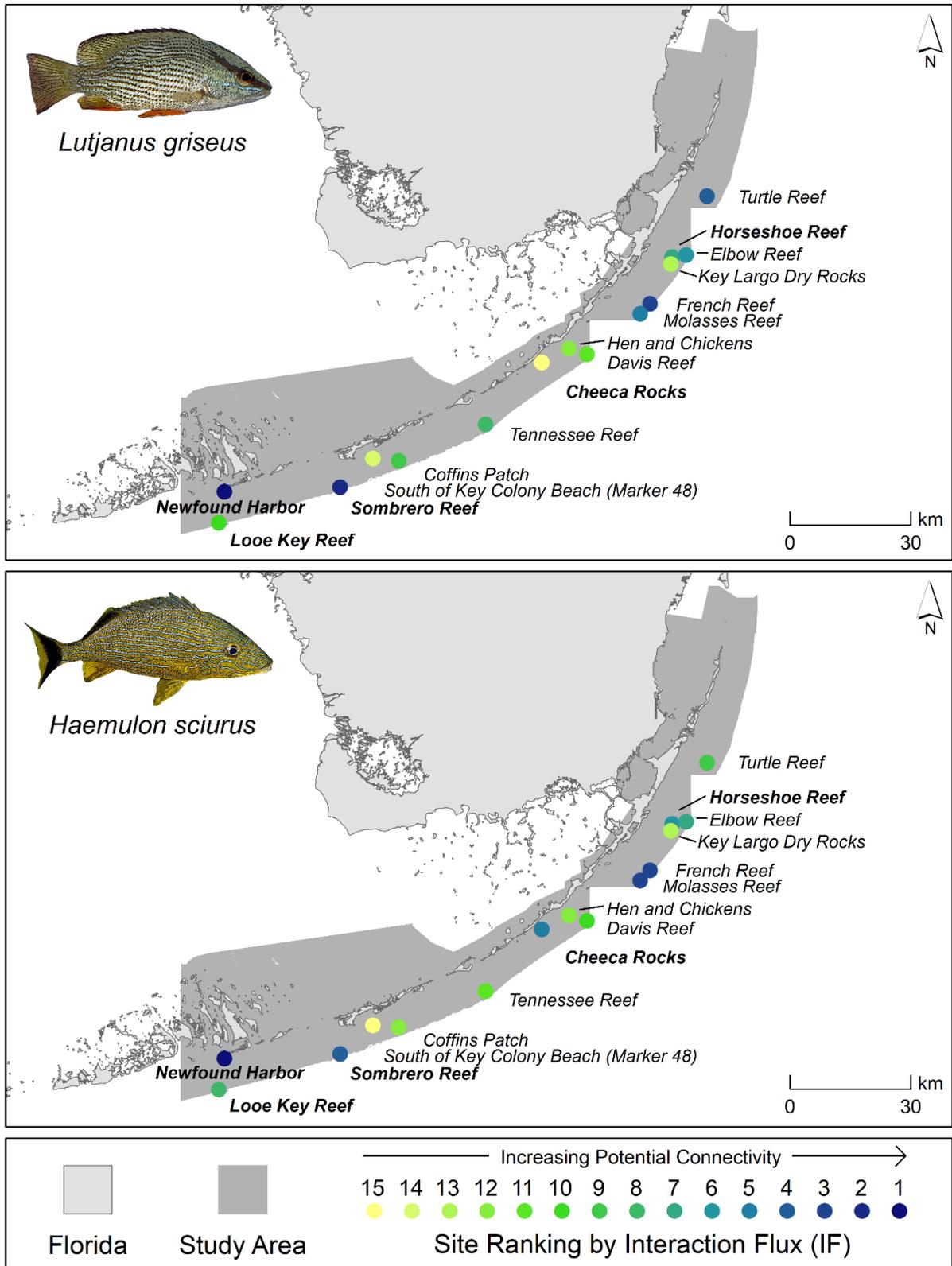


Figure 3.4. Maps of the fifteen sites considered for coral reef restoration under the *Mission: Iconic Reefs* program, where sites are colored according to their contributions to seascape-wide potential

connectivity for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) as determined by the local Interaction Flux (IF) metric. Sites highlighted in bold text were selected for restoration by the *Mission: Iconic Reefs* expert panel.

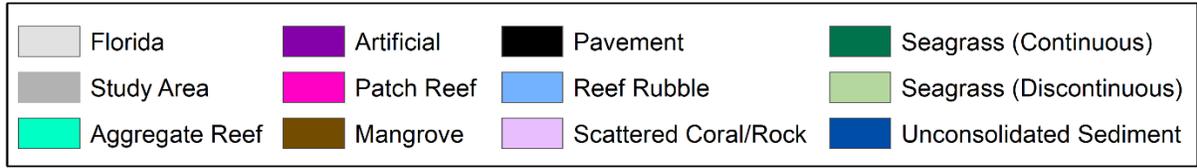
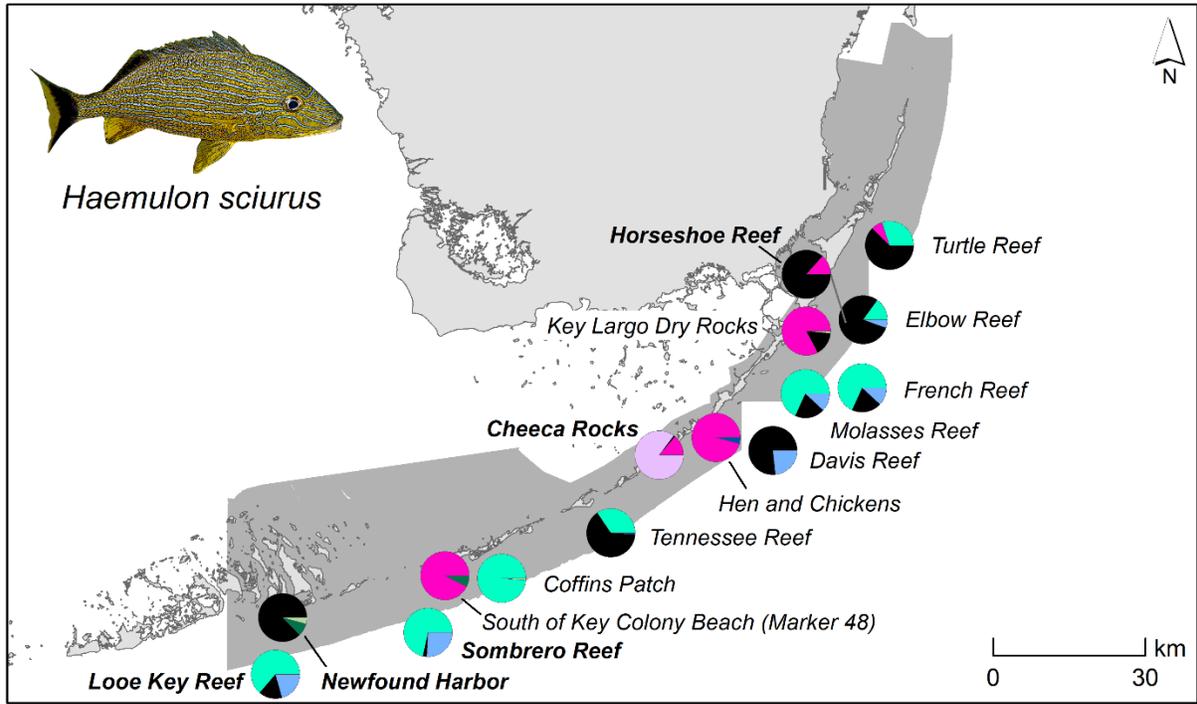
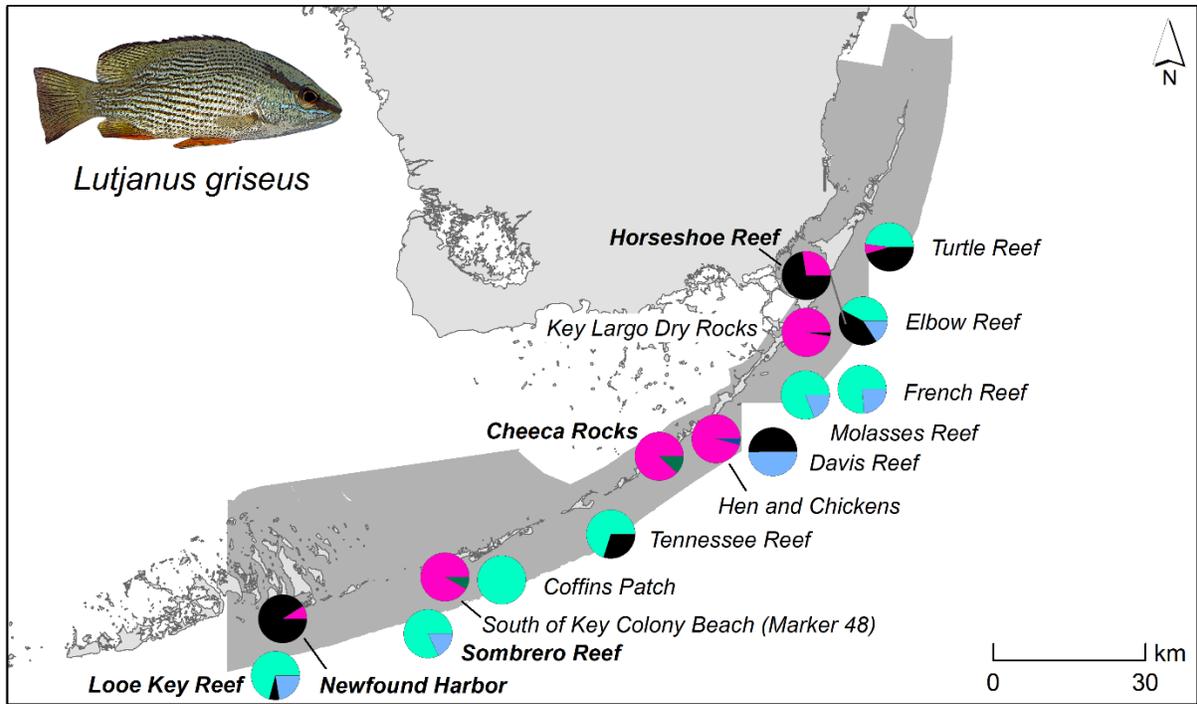


Figure 3.5. Maps demonstrating the habitat composition of nodes around each of the fifteen sites considered for coral reef restoration under the *Mission: Iconic Reefs* program. Pie charts represent

the contributions (%) of individual habitat types to the total node surface area, derived from sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) minimum planar graphs. Sites highlighted in bold text were selected for restoration by the *Mission: Iconic Reefs* expert panel.

Table 3.2. Results of spatial graph connectivity analyses focused on fifteen coral restoration sites considered under the *Mission: Iconic Reefs* program, displayed from north to south in the Florida Keys, USA (see Figure 3.1). The contributions of each site to seascape-wide potential connectivity for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) were first evaluated using the Interaction Flux (IF) local connectivity metric (see Table 3.1). IF estimates at the fifteen coral restoration sites were then compared to those at the remaining nodes in each species’ spatial graph to determine whether they ranked in the top 100.

Site	Iconic Reef	Site Description	Part of a node ranked in the top-100 according to the Interaction Flux (IF) local connectivity metric?	
			<i>L. griseus</i>	<i>H. sciurus</i>
Turtle Reef	No	Mid-channel patch reef	Yes	Yes
Horseshoe Reef	Yes	Mid-channel patch reef	No	Yes
Elbow Reef	No	Reef margin/fore reef	No	Yes
Key Largo Dry Rocks	No	Reef margin/fore reef	No	No
French Reef	No	Reef margin/fore reef	Yes	Yes
Molasses Reef	No	Reef margin/fore reef	No	Yes
Hen and Chickens	No	Mid-channel patch reef	No	No
Davis Reef	No	Reef margin/fore reef	No	Yes
Cheeca Rocks	Yes	Inshore patch reef	No	Yes
Tennessee Reef	No	Reef margin/fore reef	No	No
Coffins Patch	No	Offshore patch reef	No	No
South of Key Colony Beach	No	Mid-channel patch reef	No	No
Sombrero Reef	Yes	Reef margin/fore reef	Yes	Yes
Newfound Harbor	Yes	Inshore patch reef	Yes	Yes
Looe Key Reef	Yes	Reef margin/fore reef	No	Yes

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Chapter 4: Conclusions

4.1 Thesis objectives

My thesis applied a hierarchical landscape ecology approach to study habitat suitability and functional connectivity for two multi-habitat reef fish species occupying a spatially heterogeneous and highly-threatened subtropical seascape in the Florida Keys, USA. In Chapter 2, I compared two methods for constructing species- and life stage-specific spatial models of habitat suitability—penalized logistic regressions and maximum entropy (MaxEnt) modeling. The two main goals of this chapter were to identify the modeling algorithm that produced the most ecologically realistic products for use in subsequent connectivity assessments and to determine the environmental and spatial conditions that shaped species-specific patterns of habitat suitability across the seascape. In Chapter 3, I employed the MaxEnt habitat suitability models (HSMs) generated in Chapter 2 to model potential functional connectivity at the local and seascape scales using a spatial graph-theoretic approach. I then used spatial graph connectivity analyses to evaluate and rank the contributions of prospective coral reef restoration sites considered under Florida’s *Mission: Iconic Reefs* initiative to seascape-wide potential connectivity for both focal species. As synthesized below, the results and data products established through my thesis provide novel insights in support of conservation and restoration efforts in complex coastal seascapes, particularly those targeted at restoring, managing, and protecting functionally connected coral reef ecosystems in the face of present and future stressors.

4.2 Main findings

As anticipated, HSMs and spatial graphs both revealed species-specific patterns of habitat suitability and potential connectivity across the Florida Keys seascape (Figures 2.3; 3.2; 3.3). Intra- and inter-specific variations in the spatial distribution of suitable habitat were made particularly clear by MaxEnt HSMs, which continuously outperformed penalized logistic regressions according to the area under the receiver-operator curve and specificity metrics (Table 2.3). I suspect that these differences in model performance were driven by MaxEnt’s ability to model dynamic, multi-scale species-seascape interactions using features (i.e., sets of transformed covariates), which likely enabled this advanced machine learning approach to more accurately characterize and predict the heterogeneous nature of the focal seascape. MaxEnt HSMs suggested that benthic habitat composition, proximity to potential mangrove nurseries, slope, depth, and

broad-scale bathymetric position index (125–1250 m) were the five most influential drivers of habitat suitability for sub-adult gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*) in my study area (Figure 2.4). Aligning with previous field-based studies, MaxEnt predicted high levels of habitat suitability for both species along the mangrove-seagrass fringe and over shallow patch reefs and fore reefs, with pavement, reef rubble, and scattered coral and rock offering additional patches of intermediate-to-high suitability for *H. sciurus* (Figure A2.5). The findings highlighted in this chapter emphasize the crucial roles that seascape context, composition, configuration, and scale play in shaping species distributions, while also lending support for recent calls to “manage the mosaic” rather than patches of a single habitat type.

Quantitative, spatially explicit, and scalable modeling approaches are urgently required to better understand and anticipate the potential ecological effects of habitat fragmentation and degradation in complex seascapes. As demonstrated in my thesis, spatial graph models of potential connectivity offer great utility in this regard, especially when used in tandem with habitat suitability modeling. For instance, the habitat suitability surfaces predicted by MaxEnt in Chapter 2 offered an ecologically realistic method for delineating the nodes (i.e., suitable habitat patches) and edges (i.e., least-cost paths predicted over HSM-derived resistance surfaces) required to build connectivity networks following a spatial graph-theoretic approach. Using the Probability of Connectivity and Equivalent Connectivity global metrics, I determined that, under current conditions, the Florida Keys study seascape facilitates a higher level of potential connectivity for sub-adult *H. sciurus* relative to *L. griseus*. Furthermore, my minimum planar graphs highlighted disparities in the contributions of selected *Mission: Iconic Reefs* coral restoration sites to seascape-wide potential connectivity for the two focal species. Specifically, values of the Interaction Flux local connectivity metric suggest that the five *Iconic Reefs* selected for restoration in my study area are more likely to support and benefit from ecological interactions with sub-adult *H. sciurus* compared to *L. griseus*. My spatial graph connectivity analyses also pinpointed coral reef sites that may warrant additional restoration consideration in the future due to their roles as potential connectivity hotspots for the migratory sub-adults of both *L. griseus* and *H. sciurus*. Contrary to my hypothesis, however, these analyses did not reveal linear relationships between node-scale connectivity contributions and Euclidean distances to the nearest potential mangrove and seagrass nurseries. Nonetheless, variation in connectivity estimates did reflect the species-specific suitability levels of benthic habitat types revealed in Chapter 2, with higher suitability predictions

for *H. sciurus* across nearly all habitat types translating to a larger quantity and surface area of connected nodes for this species.

4.3 Implications for the restoration of coral reefs and other threatened ecosystems

Previous observational, experimental, and tracking studies have revealed that many marine species, including multi-habitat fishes, congregate around topographically complex seascape structures, such as coral reefs. The concentration of fish biomass around these sites leads to heterogeneous nutrient cycling, with important ecological implications in threatened coral reef communities. This is particularly evident in the oligotrophic coral reef ecosystems of the Florida Keys, where pulses of fish-derived nutrients alter the abundances and growth rates of algae and coral, along with the grazing, scraping, and bioeroding activities of herbivorous fishes on a reef-wide scale. Although coral out-planting will aid in the recovery of reef three-dimensional structural complexity, these alterations may not be enough to surpass the complexity thresholds required to attract and retain functionally important fish species and there may be significant time lags between completion of coral out-planting and the development of stable fish-derived nutrient hotspots.

Over recent decades, topographic flattening, reef fragmentation, and living coral tissue loss have reduced coral cover to < 5% in many areas along the Florida Reef Tract, and these reef-building communities continue to face unprecedented local and global threats. Considering these degraded conditions, it may be more ecologically and economically feasible to focus restoration efforts on the maintenance and protection of reef sites known to act as functional connectivity hotspots for multiple species. In doing so, restoration practitioners will not only preserve what little suitable habitat remains for reef-associated species but will also facilitate coral restoration success by safeguarding positive feedback processes.

Although explored here in the context of linking coral reef restoration design to functional connectivity for multi-habitat reef fishes in the Florida Keys, the findings presented in my thesis have relevance to marine habitat restoration planning broadly. Indeed, spatial graph-theoretic analyses informed by spatially explicit and species-specific habitat suitability models can provide critical baseline estimates of potential connectivity for a diversity of species and seascape types, thereby offering an efficient means to identify possible multi-species connectivity hotspots. These locations can aid restoration practitioners and resource managers in the selection of a set of

prospective habitat restoration sites, which can be further refined using more detailed, yet resource-intensive, in-water techniques.

4.4 Concluding remarks and the future of connectivity conservation

Coastal seascapes are open to exchanges of organisms, energy, sediments, and other materials across ecotone boundaries, including the land-sea interface. These biogeochemical fluxes underpin patterns of biodiversity and productivity in coastal mosaics and dictate the provisioning of ecosystem goods and services to the human communities that rely on them. It is therefore essential that we develop a more comprehensive understanding of the connectivity pathways required to support healthy and resilient seascapes in the face of increasing land- and ocean-based threats. We must also generate and implement adaptive restoration, management, and conservation strategies that allow us to efficiently track land-sea connectivity over space and time. Clearly, the future of connectivity conservation lies at the intersection of theoretical, empirical, and applied domains. Thus, the co-development of guiding questions and best practices by practitioners, academic scientists, and other stakeholders will help to prevent mismatched priorities, leading to more impactful seascape ecology research that meets the needs of both humans and marine communities.

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