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Contribution to the Theme Section 'Marine functional connectivity'

Seascape connectivity modeling predicts hotspots of fish-derived nutrient provisioning to restored coral reefs

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ABSTRACT: Coastal habitat quality and quantity have been significantly eroded by stressors operating and interacting across the land–sea interface, prompting a recent proliferation in coastal restoration programs worldwide. These initiatives often recognize connectivity as a critical driver of ecosystem functioning, yet most do not include connectivity as a spatially explicit, quantitative criterion during the planning process. Here, we demonstrate the use of spatial graph models to quantify potential functional connectivity for 2 multi-habitat-utilizing reef fish species known to transport nutrients from nearshore mangrove and seagrass nurseries to oligotrophic offshore reefs. Applying the method across sites considered by a multi-million dollar coral restoration program in the Florida Keys, USA, revealed locations where out-planted corals are likely to benefit most from enhanced functional connectivity in the form of nutrient provisioning and other consumer-driven processes. Opportunities for positive fish–coral interactions varied between fish species, owing to selective patterns of habitat use, highlighting the need for species-specific connectivity assessments, even within a trophic guild. Connectivity estimates for candidate restoration sites were influenced more strongly by habitat composition (which influences fish foraging and shelter resources) than by proximity to potential mangrove and seagrass nurseries, emphasizing the importance of considering both seascape composition and configuration in restoration design. Ecologically and economically effective restoration strategies are urgently required to curb rapid declines in coral reef architectural complexity, ecological function, and resilience. Our study illustrates the utility of spatial graphs as a data- and resource-efficient technique for quantifying and communicating complex ecological connectivity information in service of such efforts.

KEY WORDS: Connectivity · Coral restoration · Fish movement · Spatial graph · Nutrient hotspots · Restoration planning · Seascape ecology

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1. INTRODUCTION

Seascapes, the marine counterpart of landscapes, are dynamic, spatially heterogeneous ocean spaces shaped by multi-scale processes that influence habitat quality for marine species and life stages (Boström et al. 2011, Lepczyk et al. 2021, Pittman et al. 2021). Anthropogenic disturbances are among the most salient drivers of contemporary seascape change, and significantly alter the extent, placement, and conti-

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guity of habitat patches, referred to as structural connectivity (Crooks & Sanjayan 2006, Halpern et al. 2019). These structural modifications often have cascading effects on functional connectivity, that is, the exchange of organisms, nutrients, and energy between habitats, ecosystems, and geographic regions (Crooks & Sanjayan 2006, Carr et al. 2017). A pressing biodiversity conservation goal, therefore, is the identification of reliable strategies for restoring structurally and functionally connected seascapes that harbor diverse and resilient communities (Olds et al. 2016, Carr et al. 2017, Mcleod et al. 2019).

Coastal restoration efforts are particularly urgent in nearshore tropical and sub-tropical seascapes, where human activities have substantially reduced structural connectivity through the degradation and destruction of biogenic habitats such as mangroves, seagrasses, oyster reefs, saltmarshes, and corals (Gardner et al. 2003, Waycott et al. 2009, Polidoro et al. 2010, Gilby et al. 2021). The magnitude and pace of anthropogenic habitat modifications in the coastal zone are significant (Halpern et al. 2019), sometimes leading to unexpected changes in structural and functional connectivity that threaten essential ecosystem processes (Olds et al. 2016). Structural connectivity of benthic habitats plays a key role in determining the spatial distributions of many coastal marine species and their associated ecological processes. For example, several grunt (Haemulidae) and snapper (Lutjanidae) species undertake diel and seasonal migrations as well as ontogenetic habitat shifts through their life cycles (Hitt et al. 2011a, Appeldoorn & Bouwmeester 2022), enabled by structural connectivity. Consequently, the spatial and temporal patterns of grunt and snapper dispersal across the seascape have important ecological ramifications for patterns of fish-driven nutrient subsidies that promote reef resilience through the enhancement of crustose coralline algal cover and coral growth rates (Shantz et al. 2015, Francis & Côté 2018, Ladd et al. 2018).

Given that structural connectivity plays a critical role in determining the spatial distributions of many marine species and the ecological processes to which they contribute, enhancing and protecting structural connectivity serves as a valuable guiding principle for a variety of conservation activities (Weeks 2017, Balbar & Metaxas 2019, Hilty et al. 2020). To date, structural connectivity has been shown to improve multiple measures of marine reserve performance, including production, diversity, and resilience (Olds et al. 2016). For instance, in Moreton Bay, Australia, Olds et al. (2012) demonstrated that the richness and biomass of herbivorous reef fishes was enhanced by structural connectivity between mangrove and reef habitats. Moreover, their research revealed a synergistic effect of structural connectivity and reserve protection whereby roving herbivore biomass on protected reefs <250 m from mangroves was nearly double that on unprotected reefs within the same distance and roughly 4 times greater than that on reefs separated from mangroves by >500 m regardless of their protection status (Olds et al. 2012). These coupled reserve-connectivity effects increased herbivore grazing on protected reefs adjacent to mangroves, thereby promoting coral recruitment and growth through the removal of algal competitors, facilitating more diverse, resilient benthic assemblages (Olds et al. 2012).

Enhanced structural connectivity is posited to benefit marine restoration efforts, too, as it has for terrestrial ecosystems, yet a recent global literature review found that only 13% of marine restoration projects considered seascape attributes such as structural connectivity in their design (Gilby et al. 2018). Growing evidence highlights the need to integrate seascape context, configuration, and connectivity in multi-habitat seascape restoration planning to ensure diverse ecosystem functions (Barbier 2017, McAfee et al. 2022). For example, in coastal North Carolina, oyster reefs adjacent to saltmarsh and seagrass habitats supported greater amphipod, fish, and grass shrimp densities than those on soft-bottom control sites located within the same seascape types (Grabowski et al. 2022). Thus, by strategically placing habitat restoration activities in areas of high structural connectivity or by using restoration to repair structural connectivity, practitioners can influence fluxes of target species and ecological processes among interconnected seascape habitats (Halpern et al. 2007, Gilby et al. 2018).

Information on species-specific habitat utilization patterns and functional connectivity thresholds is particularly useful for seascape restoration planning. Although conventional tagging and tracking techniques provide such information, their spatiotemporal scope may be restricted by data, resource, or body-size limitations (Fagan & Calabrese 2006). Where direct measurements of functional connectivity are sparse or absent, potential functional connectivity (hereafter, potential connectivity) can be estimated by relating seascape structural patterns to knowledge of a species' dispersal ability (Fagan & Calabrese 2006). These efforts often follow a modified graph-theoretic approach, referred to as spatial graph analysis, in which mathematical graphs are used to represent georeferenced seascape elements connected to some extent by pathways of ecological flux (Urban & Keitt 2001, Fall et al. 2007). Spatial graph models of potential connectivity, therefore, provide qualitative and quantitative outputs that aid in the investigation of complex ecological questions, such as the identification of seascape features that may disproportionately contribute to multi-species functional connectivity.

The desired ecological and economic outcomes of restoration may be bolstered if programs are designed to deliberately enhance multi-species functional connectivity and harness facilitative relationships between restored biogenic habitats and their occupants (Halpern et al. 2007, Ladd et al. 2018). To explore this concept further, we constructed species-specific spatial graphs to estimate potential connectivity for 2 abundant and ecologically important mesopredatory reef fish species occupying a Florida Keys, USA, seascape slated for coral reef restoration. We modeled potential connectivity for sub-adult stage gray snapper *Lutjanus griseus* and bluestriped grunt *Haemulon sciurus*, 2 common Atlantic species whose ontogenetic habitat shifts from nearshore mangrove and seagrass nurseries to oligotrophic offshore reefs may augment coral 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, Huntington et al. 2017, Ladd et al. 2018). Our goal was to assess whether the predicted movement pathways of these vital fishes coincide spatially with coral reef sites identified as restoration targets under Florida's 'Mission: Iconic Reefs' program. Established in 2019, 'Mission: Iconic Reefs' is a regional, multimillion dollar (USD) initiative aiming to recover the diversity, health, and geographic extent of live coral at several sites along and adjacent to the Florida Reef Tract, a roughly 350 mile (563 km)-long coral reef system with a recent history of decline (Lirman et al. 2019, NOAA Fisheries 2019). By providing foraging opportunities and predator refugia in the form of enhanced structural connectivity and topographically complex coral habitat, the 'Iconic Reefs' sites may improve functional connectivity for migrating sub-adult *L. griseus* and *H. sciurus*. Based on the well-documented mangrove and seagrass nursery utilization patterns of the 2 focal species in the Florida Keys (Faunce & Serafy 2007, Jones et al. 2010), we hypothesized that coral restoration sites neighboring nursery habitats would support the highest levels of functional connectivity for sub-adult *L. griseus* and *H. sciurus*, and would therefore be most likely to benefit from nutrient enrichment and other fish-mediated ecological processes in the future.

2. MATERIALS AND METHODS

2.1. Study area

Our study focused on the subtropical coastal seascape of the Florida Keys, USA (Fig. 1), comprising a mosaic of mangroves, seagrasses, patch reefs, and the third-largest barrier reef in the world. The Florida Reef Tract is a system of important natural capital in the local economy with diverse benefits for people (Brander & van Beukering 2013), yet it has experienced significant ecological degradation in recent decades (Ogden et al. 1994, Lirman et al. 2019). Topographic flattening and coral loss have been severe across the Florida Reef Tract due to thermal stress, disease, and poor water quality, reducing coral cover to 2% in many areas (Palandro et al. 2008, Alvarez-Filip et al. 2009, NOAA Fisheries 2019). In 2019, the US National Oceanic and Atmospheric Administration (NOAA) and interdisciplinary partners launched the 'Mission: Iconic Reefs' project to recover the diversity and cover of living corals in the Florida Reef Tract system over the next 30 yr. To address this challenge, coral restoration practitioners and coral reef managers ranked a set of priority areas based on criteria including ecosystem services, community interest, and logistical practicality, leading to the selection of 7 final 'Iconic Reefs' (NOAA Fisheries 2019; Fig. 1, Table S1 in the Supplement at www.int-res.com/articles/suppl/m14321_supp.pdf). Although ranked highly as a criterion during the initial site-selection process, connectivity was assessed qualitatively using expert knowledge and available oceanographic data sets; specific taxonomic or functional groups, however, were not considered. 'Mission: Iconic Reefs', therefore, offers the opportunity to apply spatial graph analyses to quantify relative potential connectivity across sites (5 of the selected 'Iconic Reefs' and 10 alternates; Fig. 1, Table S1) for 2 representative mesopredatory reef fish species relevant to coral restoration and to compare graph models to conventional site selection approaches.

2.2. Focal species

We modeled potential connectivity for sub-adult gray snapper *Lutjanus griseus* (9.51–24.71 cm total length [TL]) and bluestriped grunt *Haemulon sciurus*

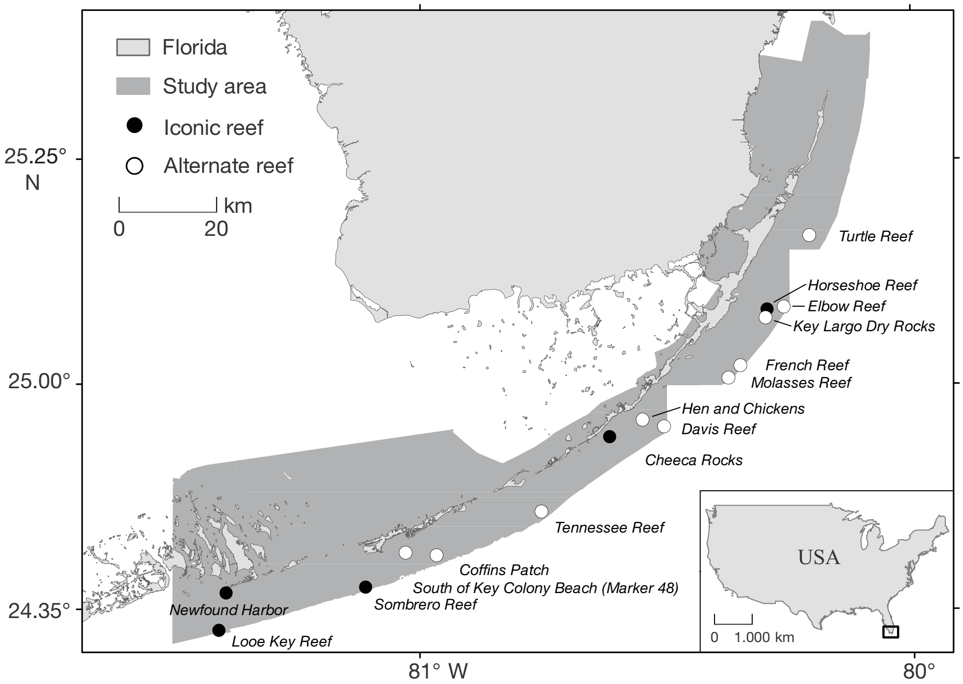

Fig. 1. Study area in the Florida Keys, USA. Potential connectivity for sub-adult gray snapper *Lutjanus griseus* and bluestriped grunt *Haemulon sciurus* was assessed across the seascape as well as at 15 sites considered under the 'Mission: Iconic Reefs' coral restoration program (black circles: selected 'Iconic Reefs'; white circles: alternate reefs). Please note that the linear cutouts between Turtle and Horseshoe Reefs, Molasses and Hen and Chickens Reefs are artefacts of the spatial coverage of the high-resolution input data and that the true geography of the study area does include these regions

(11.90–25.33 cm TL) (Faunce & Serafy 2007). Subadult *L. griseus* and *H. sciurus* undertake ontogenetic habitat shifts from nearshore mangrove and seagrass nurseries to adult habitats on offshore reefs (Christensen et al. 2003, Luo et al. 2009, Appeldoorn & Bouwmeester 2022), supporting the formation of fish-derived nutrient hotspots (Shantz et al. 2015, Ladd et al. 2018). The geographical pathways traveled, however, remain unclear, as tagging studies have typically focused on finer-scale movement patterns for adult fishes (e.g. Luo et al. 2009). Thus, potential connectivity models are a first step in predicting the connectivity corridors that may maintain metapopulation persistence for these commercially and recreationally valuable species ahead of restoration and identifying future restoration locations that are likely to benefit from ecological interactions with these migrating fishes (Ault et al. 2005).

2.3. Model construction

Applying a spatial graph-theoretic approach (Urban & Keitt 2001, Fall et al. 2007), we modeled the Florida Keys seascape as a spatial graph constructed of suitable habitat patches (i.e. nodes) connected by a series of dispersal links (i.e. edges). Rather than extracting nodes from thematic habitat maps, we leveraged previously constructed (Stuart et al. 2021) species-specific habitat suitability models (HSMs) that related fish occurrence records from daytime underwater visual surveys to spatially explicit environmental data, including seasonal water temperature and salinity, benthic habitat composition and configuration, and bathymetry and metrics of seascape surface geomorphology, including slope and rugosity. Stuart et al. (2021) applied 3 distinct habitat suitability modeling techniques, (1) maximum entropy modeling (MaxEnt), (2) lasso-penalized logistic regression, and (3) ridge-penalized logistic regression, to identify the optimal modeling approach. The ecological realism of HSMs was evaluated using visual inspection and qualitative comparisons to available literature on species–environment relationships. Discriminatory ability was quantified using the area under the receiver-operator curve (AUC), a threshold-independent, ranked-based statistic used to indicate a model's ability to discriminate between a random presence point and a random absence or background point, where performance increases on a scale of 0 to 1, and a value of 0.5 denotes random performance (Phillips et al. 2006). Finally, to quantify predictive performance, Stuart et al. (2021) used species-specific data sets of known presence locations withheld during model construction to assemble confusion matrices and calculate sensitivity (i.e. the percentage of correctly predicted presences) and specificity (i.e. the percentage of correctly predicted absences).

We selected the MaxEnt-derived HSM for each species because they displayed the highest discriminatory ability according to AUC (0.88 and 0.86 for *L. griseus* and *H. sciurus*, respectively), struck an appropriate balance between sensitivity and specificity, and, aligning with known species–environment relationships for the focal species, revealed patchy distributions of suitable habitat driven primarily by habitat patch type, depth, and broad-scale seafloor features (Stuart et al. 2021). We converted the continuous, species-specific MaxEnt HSMs to a binary scale (i.e. suitable seascape patches vs. low-suitability matrix) using the threshold whereby each model achieved a maximum sum of sensitivity and specificity (Max SSS; Liu et al. 2013). Max SSS is an objective method that optimizes discriminatory ability, operates consistently across modeling techniques, performs well even when species prevalence is low, and outperforms other threshold options in terms of the true skill statistic (i.e. a well-accepted and widely applied accuracy measure) (Liu et al. 2013). The Max SSS suitability threshold was used to identify and extract species-specific suitable seascape patches for use as nodes in spatial graph models of potential connectivity.

Although acoustic tagging data suggest that adult fishes in the Florida Keys can make nursery-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 m^2 to retain only those that were large enough to support the daily activity spaces of sub-adults. The 100 m^2 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 (Beets et al. 2003, Verweij & Nagelkerken 2007, Hitt et al. 2011b) and also ensured that the resulting spatial graphs included both small stepping stones and larger patches of long-term use.

We calculated edges between node pairs using least-cost paths, which integrate information about the spatial configuration of habitats and the resistance of the surrounding matrix to movement (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 original habitat suitability indices (HSIs) of Stuart et al. (2021) to resistance values. The transformation function (Keeley et al. 2016, Duflot et al. 2018) was as follows:

$$\begin{gathered}\text{If HSI} \geq \text{Max SSS threshold}\\ \rightarrow \text{species habitat} \rightarrow \text{resistance} = 1\\[6pt] \text{If HSI} < \text{Max SSS threshold} \rightarrow \text{matrix} \rightarrow \text{resistance} =\\ e^{\frac{\ln(0.001)}{\text{Max SSS threshold}}} \times \text{HSI} \times 10^3\end{gathered} \tag{1}$$

This function assigns a resistance value of 1 when HSI equals or exceeds the species-specific Max SSS threshold, 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, instead allowing resistance to increase slowly as suitability first departs from its maximum, then dramatically at lower suitability values (Keeley et al. 2016). Negative exponential transformation functions have been supported in related terrestrial research on red-cockaded woodpeckers (Trainor et al. 2013), desert bighorn sheep (Keeley et al. 2016), and woodlark (Duflot et al. 2018). We expected this method to accurately predict the movements of sub-adult *L. griseus* and *H. sciurus* as well, which 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, Duflot et al. 2018). The resulting unitless resistance surfaces provide a measure of the relative cost of movement through sections of the seascape as determined by their underlying habitat suitability.

We developed spatial graphs using Graphab 2.6, a free software built for modeling, analyzing, and visualizing connectivity networks (Foltête et al. 2012, 2021; https://sourcesup.renater.fr/www/graphab/en/home.html). We constructed graphs using planar topology with a cell resolution of 10 × 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). We then pruned the resulting graphs to retain only paths with metric distances equal to or shorter than the estimated maximum dispersal distance (10 km) of sub-adult *L. griseus* and *H. sciurus*. Acoustic telemetry studies provided direct evidence that *H. sciurus* (30 cm TL) and *L. synagris* (30.4 cm TL), a congener of *L. griseus* of similar body shape and size, can move 11.7 km and 10.6 km, respectively, in a single day (Pittman et al. 2014). Luo et al. (2009) also documented reefdirected movements of roughly 10 km, with a maximum distance of 15 km, for acoustically tagged *L. griseus* adults in the upper Florida Keys. The 10 km estimated maximum dispersal distance was converted to a unitless cost value for graph pruning via Graphab's distance conversion function.

2.4. Model evaluation

2.4.1. Global connectivity metrics

We first calculated species-specific potential connectivity across the entire seascape network using the probability of connectivity (PC) (Saura & Pascual-Hortal 2007) and equivalent connectivity (EC) (Saura et al. 2011) global connectivity metrics (see Section S1 in the Supplement). The PC index — which incorporates information on the surface areas of nodes (an indicator of their capacity to support populations), inter-node distances, and the total surface area of the study region — is the probability that 2 fishes placed randomly in the seascape fall into habitat patches that are connected. The PC index takes on values of 0 to 1, with larger values suggesting higher connectivity across the seascape network.

Graphab's global PC metric considers only node areas and inter-node distances as drivers of potential connectivity; however, connectivity for reef fishes 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 value in the original HSMs of Stuart et al. (2021). Using these quality-weighted areas, we then calculated the EC index, which measures the availability and quality of connected nodes across the seascape considering estimated inter-node dispersal fluxes and overall network topology (Saura et al. 2011). The EC index increases with improved connectivity.

2.4.2. Local connectivity metrics

To evaluate the connectivity contributions of individual nodes, including those considered for restoration under 'Mission: Iconic Reefs', we calculated the interaction flux (IF) local connectivity metric (see Section S2 in the Supplement). IF quantifies potential connectivity at the node scale, considering the probability of interaction between nodes and each node's quality-weighted area as an indicator of their capacity to support populations (Foltête et al. 2014, Sahraoui et al. 2017). IF values represent the contribution of individual nodes to the global EC metric; thus, the geographic coordinates of candidate 'Mission: Iconic Reefs' sites (n = 15; Fig. 1) were used to extract IF values from each species' spatial graph, provided they fell on or within 10 m (i.e. a one-cell distance) of an existing node. Finally, to evaluate model- and field-based approaches to connectivity estimation, we compared site rankings based on the IF metric to those derived from the empirical reef fish survey data used by Stuart et al. (2021) (i.e. site rankings based on the proportion of surveys with sub-adults of the focal species present; Tables S2 & S3).

2.4.3. Node composition and nursery habitat proximity

Here, nodes represent a mosaic of suitable habitats extracted from HSM maps, rather than single patch types in isolation. Therefore, we evaluated the percent cover of unique habitat patch types within node boundaries by intersecting them with an existing benthic habitat map — the Florida Unified Reef Map (v2.0; FWRI 2016). Similarly, we examined whether mean Euclidean distances to the nearest potential mangrove and seagrass nursery habitats were correlated with node- and species-specific IF values by calculating Pearson pairwise correlation coefficients (r) using the 'cor()' function in base R (v4.0.2; R Core Team 2020). Under the nursery hypothesis, we would expect node-specific IF estimates of local connectivity to reduce substantially as distance away from mangroves and seagrasses increases, resulting in a significant negative correlation between nursery distances and IF. These correlative analyses may also help to discern whether one nursery habitat type is perhaps more influential over local connectivity than the other in our focal system. Together, these assessments allowed us to identify potential connectivity-enhancing restoration sites and evaluate how seascape composition and nursery proximity influence potential connectivity for sub-adult *L. griseus* and *H. sciurus.*

2.4.4. Sensitivity analyses

Although the 10 km maximum dispersal distance was estimated based on evidence from previous studies of *L. griseus*, *H. sciurus*, and congeners, sub-adult dispersal capacity may vary within and between species. To examine the sensitivity of our global potential connectivity estimates to assumptions regarding dispersal ability, we used batch processing to calculate species-specific PC and EC values along a cumulative cost dispersal gradient of 0 to 250 000. Similarly, to determine whether node-scale connectivity contributions fluctuated with dispersal distance, we recalculated local IF values and coral restoration site rankings using the cost-distance equivalencies of 3 distinct Euclidean dispersal thresholds: a lower estimate of 5 km, the original estimate of 10 km, and a higher estimate of 15 km. Finally, to compare the connectivity contributions of the 15 prospective coral restoration sites to the remaining nodes in the network, we ranked all nodes by their IF values at these 3 dispersal thresholds and examined whether any of the selected or alternate restoration sites ranked in the top 100 according to their contributions to seascape-wide potential connectivity.

3. RESULTS

3.1. Spatial graph structure

Minimum planar graphs revealed species-specific connectivity networks. The sub-adult *Lutjanus griseus* graph consisted of 36 339 least-cost edges connecting 21 166 nodes, which together covered approximately 7 % of the seascape (Fig. 2). The sub-adult *Haemulon sciurus* graph contained a larger number of least-cost edges and nodes, with 47 427 and 27 271, respectively, the latter of which covered approximately 10 % of the seascape (Fig. 3). Overall, 48 % spatial overlap occurred between nodes in the 2 connectivity networks.

Node suitability levels were essentially identical between species, averaging 0.75 ± 0.10 for *L. griseus* and 0.74 ± 0.09 for *H. sciurus* (mean ± SD). Node size, however, varied substantially within and between

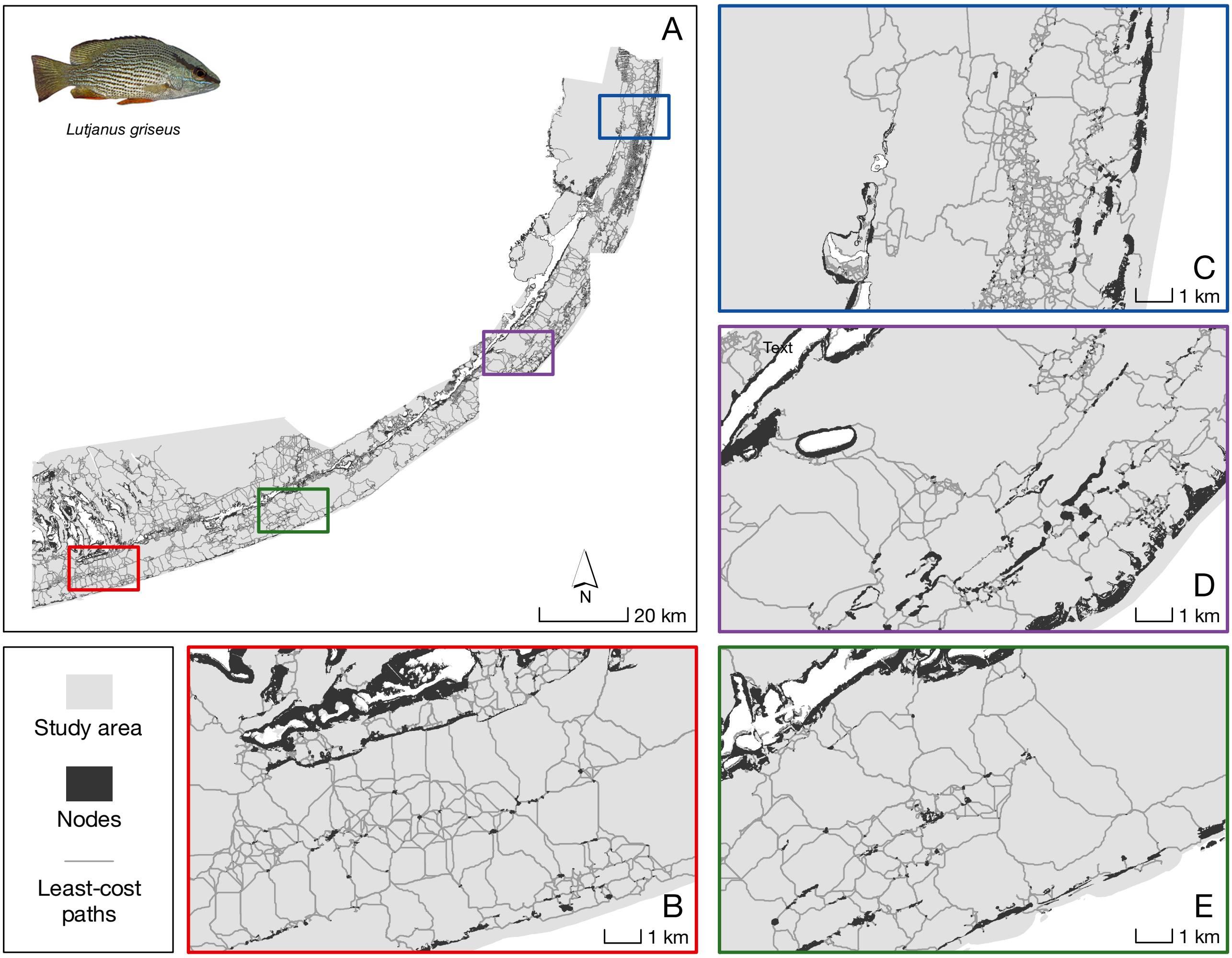

Fig. 2. (A) Minimum planar graph representing the potential connectivity network for sub-adult gray snapper *Lutjanus griseus* across the Florida Keys study seascape assuming a 10 km dispersal threshold. (B–E) Examples demonstrating the detail of nodes and least-cost edges derived from MaxEnt habitat suitability models

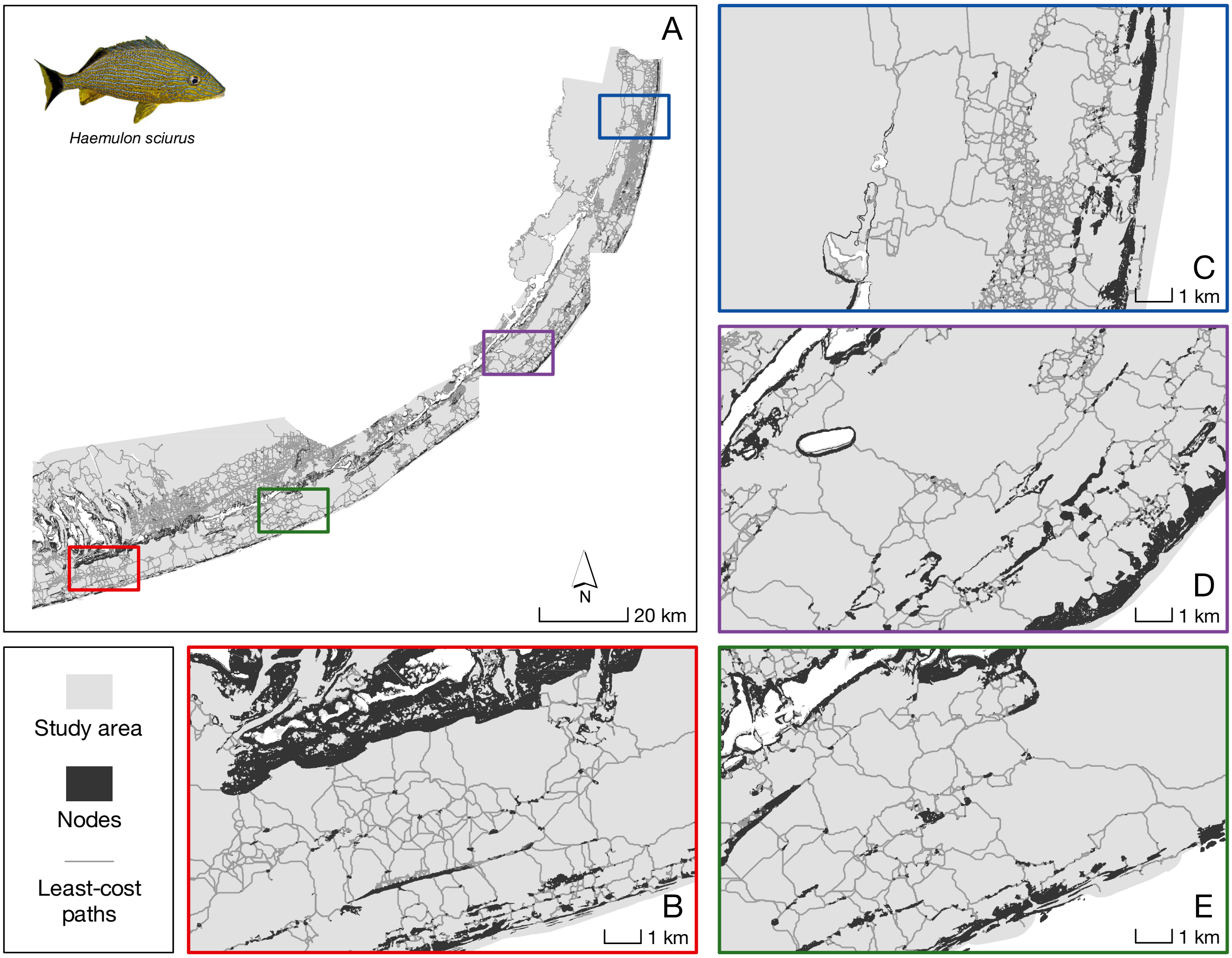

Fig. 3. (A) Minimum planar graph representing the connectivity network for sub-adult bluestriped grunt *Haemulon sciurus* across the Florida Keys study seascape assuming a 10 km dispersal threshold. (B–E) Examples demonstrating the detail of nodes and least-cost edges derived from MaxEnt habitat suitability models

species, ranging from small, isolated patch reefs to mosaics of seagrass and hard bottom habitats (*L. griseus*, median: 500 m^2, range: 100–1.85 × 10^7 m^2; *H. sciurus*, median: 500 m^2, range: 100–7.05 × 10^7 m^2). Metric edge distances varied considerably as well, with median lengths of 68.28 m (range: 20.00–7.20 × 10^3 m) and 64.14 m (range: 20.00–1.04 × 10^4 m) for *L. griseus* and *H. sciurus*, respectively. Cumulative cost distances followed the same pattern (*L. griseus* median cumulative cost: 23.77, range: 2.00–7.51 × 10^4; *H. sciurus* median cumulative cost: 18.42, range: 2.00–3.52 × 10^4); however, the 50 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.

3.2. Global connectivity metrics

When a maximum dispersal distance of 10 km was applied, 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 for *H. sciurus*. Similarly, the *H. sciurus* graph produced a higher EC estimate than the *L. griseus* graph when assuming a 10 km dispersal threshold, with values of 2.20 × 10^8 and 1.62 × 10^8, respectively.

To examine the sensitivity of PC and EC estimates to assumptions about species' movement ability, we recalculated these metrics across a dispersal gradient. Regardless of the dispersal threshold applied, the PC (Fig. 4A) and EC (Fig. 4B) metrics indicated higher levels of global connectivity for sub-adult *H. sciurus* relative to *L. griseus*. Furthermore, the sensitivity results displayed a clear pattern whereby Euclid-

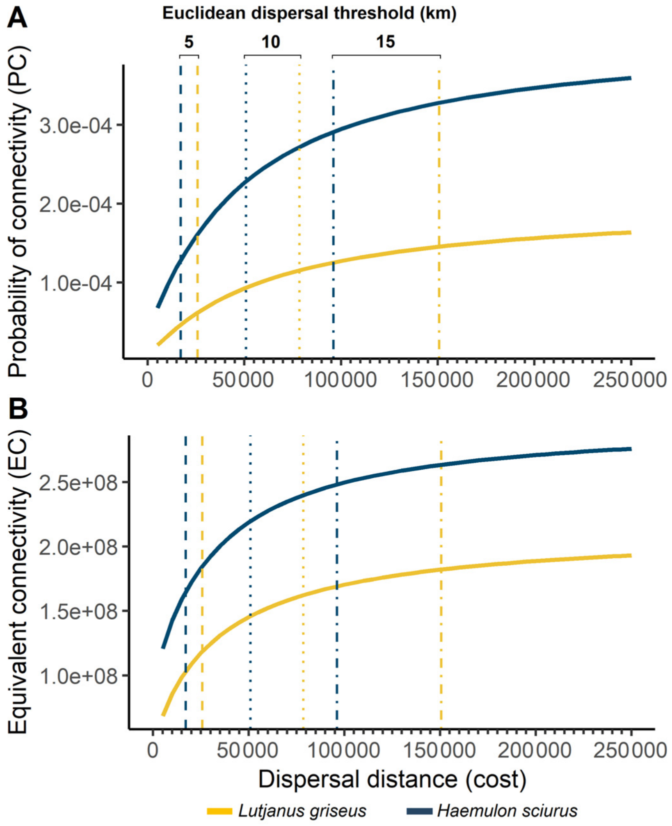

Fig. 4. Relationships between dispersal distance (cumulative cost) and the (A) probability of connectivity and (B) equivalent connectivity global metrics. The cumulative cost equivalents of 5, 10, and 15 km Euclidean dispersal thresholds are displayed by the dashed, dotted, and dot-dashed lines, respectively

ean dispersal distances were associated with higher cumulative costs for sub-adult *L. griseus* compared to *H. sciurus*, with this trend being especially apparent at higher Euclidean distances (Fig. 4).

3.3. Local connectivity metrics

3.3.1. L. griseus

At a 10 km dispersal threshold, spatial graph analysis identified Newfound Harbor, Sombrero, French, Turtle, and Molasses Reefs as being, in decreasing order, the 5 restoration sites with the highest levels of potential connectivity for sub-adult *L. griseus* under current conditions (Fig. 5A). These top-5 ranked sites represented 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 S1). Contrary to our hypothesis, we found no evidence of a statistically significant correlation between IF estimates of relative connectivity for *L. griseus* and mean distances from nodes to potential nurseries ($r_{\text{mangrove}} = -2.24 \times 10^{-2}$, $r_{\text{seagrass}} = -3.60 \times 10^{-3}$).

The 5 highest-ranking restoration sites in the *L. griseus* network did, however, coincide spatially with nodes of varying 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 patch types (Turtle Reef) (Fig. 6A). Of these, only Newfound Harbor and Sombrero Reef were sites selected for active restoration by the 'Mission: Iconic Reefs' advisory panel (Table S1, Fig. 5A). The remaining 3 selected 'Iconic Reefs' in our study area — Looe Key Reef, Horseshoe Reef, and Cheeca Rocks — ranked sixth, ninth, and fifteenth, respectively, in terms of supporting potential connectivity for sub-adult *L. griseus* (Table S1, Fig. 5A). IF-based site rankings remained highly consistent when re-examined at dispersal thresholds of 5 and 15 km (Table 1). Newfound Harbor, Sombrero, French, Turtle, and Molasses Reefs routinely ranked among the top 5 potential restoration sites within the *L. griseus* graph, with their rankings changing only slightly (Table 1). Conversely, Key Largo Dry Rocks, Davis Reef, and South of Key Colony Beach consistently ranked among the lowest potential coral restoration sites based solely on their relative connectivity contributions for *L. griseus* (Table 1). Despite high levels of consistency across spatial graph runs, site rankings based on the local IF connectivity metric were not correlated with empirical reef fish survey data (Table S2).

When all nodes in the *L. griseus* graph were considered, the number of coral restoration sites ranking among the top 100 according to the IF metric varied depending on the dispersal threshold applied. At a 5 km threshold, only one restoration site ranked among the top 100 nodes ('Iconic Reef' Newfound Harbor). The 10 km dispersal threshold resulted in 4 restoration sites ranking among the top 100 nodes — 2 selected 'Iconic Reefs' (Newfound Harbor and Sombrero Reef) and 2 alternates (Turtle and French Reefs). Finally, at a dispersal threshold of 15 km, 5 candidate sites ranked among the top 100 nodes — 2 selected 'Iconic Reefs' (Newfound Harbor and Sombrero Reef) and 3 alternates (Turtle, French, and Molasses Reefs).

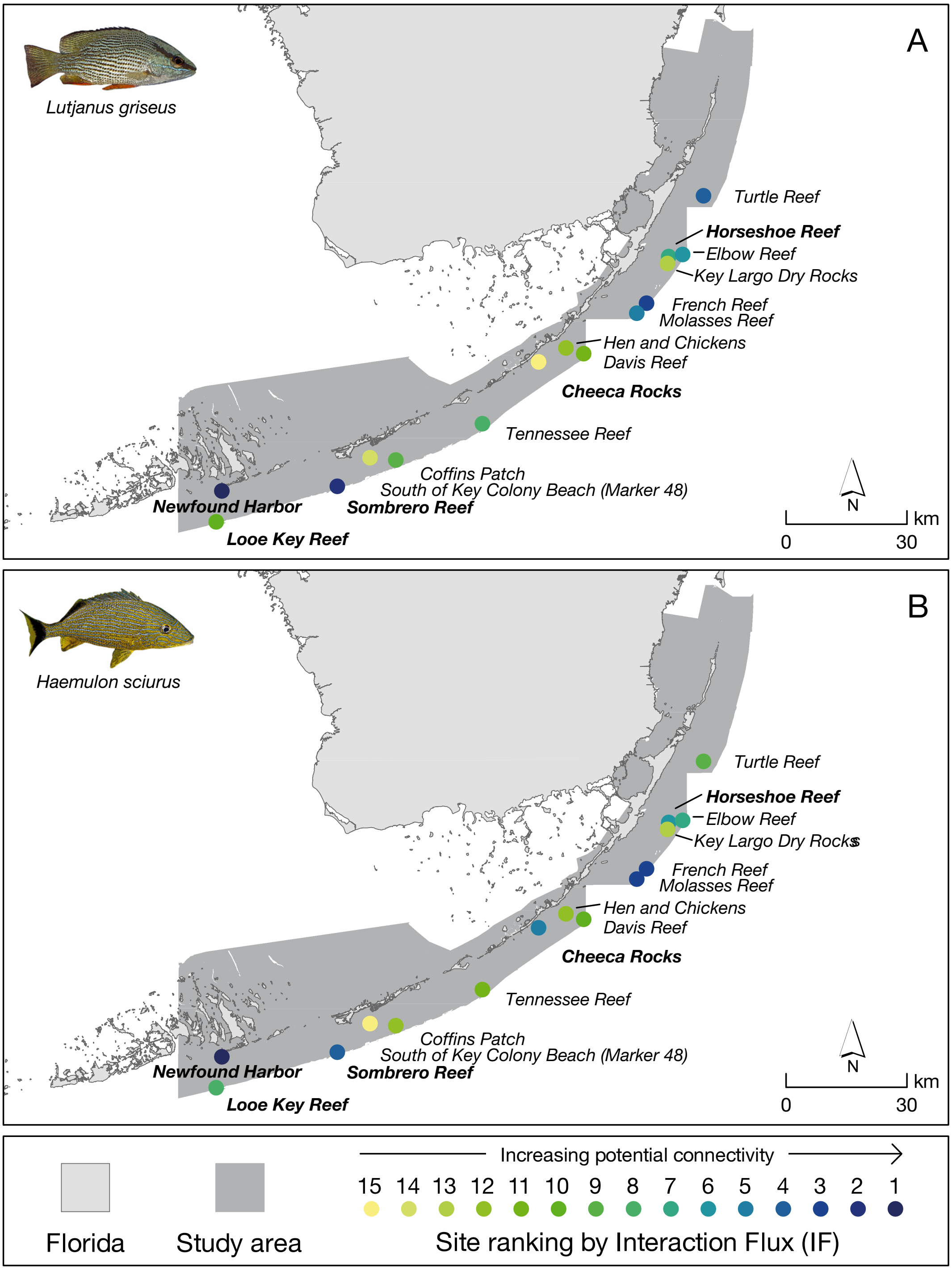

Fig. 5. Sites considered for coral restoration under the 'Mission: Iconic Reefs' program, where sites are colored based on their potential connectivity contributions for (A) sub-adult gray snapper *Lutjanus griseus* and (B) bluestriped grunt *Haemulon sciurus* according to the local interaction flux (IF) metric, assuming a 10 km dispersal threshold. Sites highlighted in **bold** were selected for restoration by the 'Mission: Iconic Reefs' advisory panel

3.3.2. *H. sciurus*

At a 10 km dispersal threshold, spatial graph analysis identified Newfound Harbor, French Reef, Molasses Reef, Sombrero Reef, and Cheeca Rocks as the 5 coral restoration sites with the highest levels of potential connectivity for sub-adult *H. sciurus*, in decreasing order, according to the IF metric (Table 1,

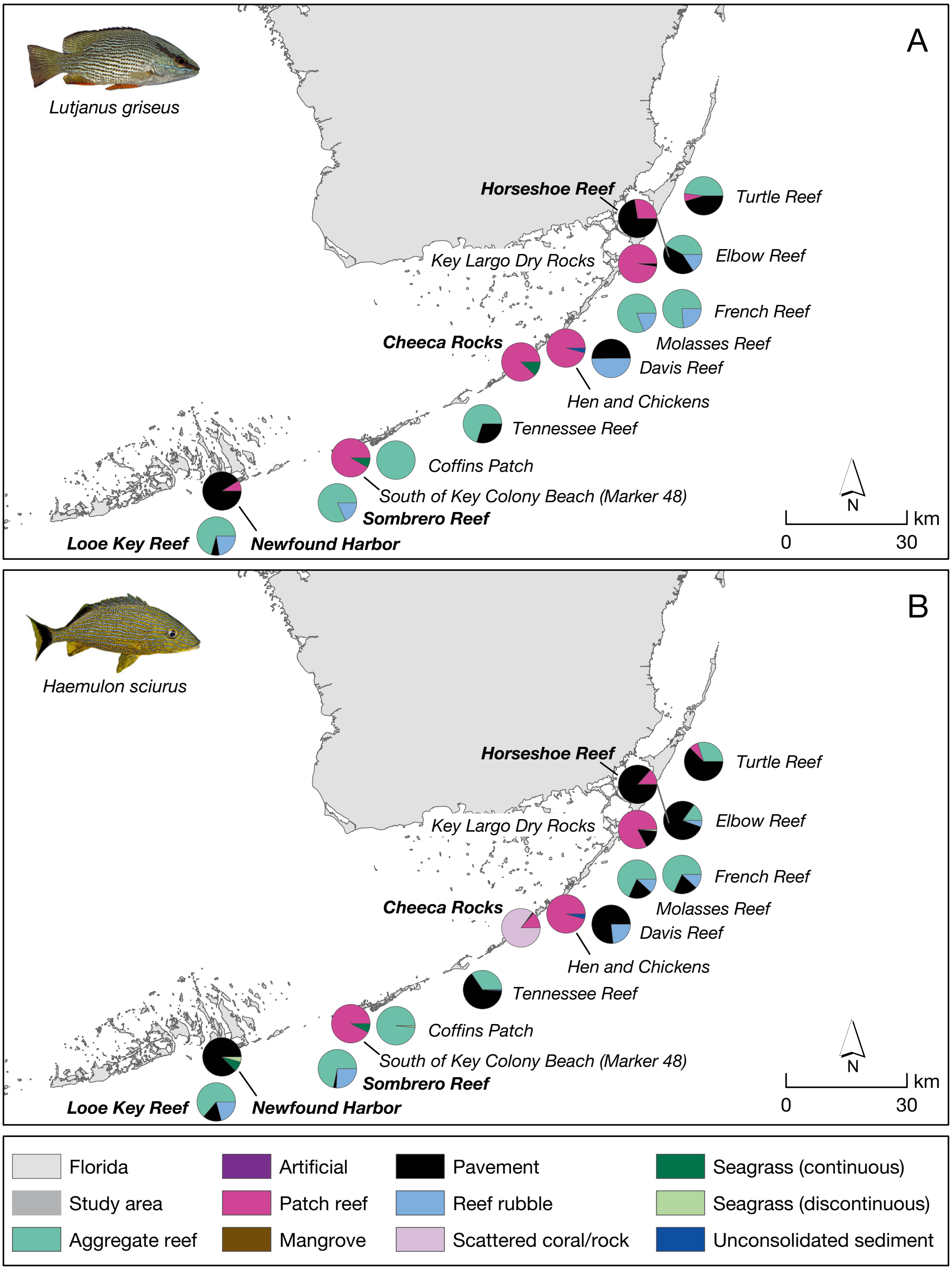

Fig. 6. Habitat composition of species-specific nodes spatially coinciding with 15 sites considered for coral reef restoration under the 'Mission: Iconic Reefs' program. Pie charts represent the contributions (proportion) of individual habitat types to the total surface area of (A) sub-adult gray snapper *Lutjanus griseus* and (B) bluestriped grunt *Haemulon sciurus* nodes. Sites highlighted in **bold** were selected for restoration by the 'Mission: Iconic Reefs' advisory panel

Fig. 5B). Similar to the findings of the *L. griseus* graph, the top 5 connectivity-contributing sites for *H. sciurus* varied substantially with respect to their surrounding node 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) (Fig. 6B). Of these,

Table 1. Site-specific connectivity contributions according to the local interaction flux (IF) metric, evaluated at 15 coral restoration sites considered under the 'Mission: Iconic Reefs' initiative using dispersal thresholds of 5, 10, and 15 km for sub-adult gray snapper *Lutjanus griseus* and bluestriped grunt *Haemulon sciurus*

Site	Iconic Reef	IF (ranking by IF)					
		L. griseus			*H. sciurus*		
		5 km	10 km	15 km	5 km	10 km	15 km
Turtle Reef	No	3.66×10^{12} (5)	2.93×10^{13} (4)	5.22×10^{13} (4)	9.89×10^{12} (9)	6.44×10^{13} (8)	1.19×10^{14} (8)
Horseshoe Reef	Yes	1.83×10^{12} (7)	1.41×10^{13} (7)	2.58×10^{13} (7)	2.35×10^{13} (5)	1.22×10^{14} (5)	2.44×10^{14} (3)
Elbow Reef	No	1.77×10^{12} (8)	1.67×10^{13} (6)	3.46×10^{13} (6)	1.94×10^{13} (6)	8.92×10^{13} (6)	1.66×10^{14} (5)
Key Largo Dry Rocks	No	2.73×10^{11} (15)	2.44×10^{12} (13)	4.68×10^{12} (13)	5.36×10^{11} (14)	3.13×10^{12} (13)	6.42×10^{12} (13)
French Reef	No	5.54×10^{12} (3)	3.70×10^{13} (3)	6.89×10^{13} (2)	6.31×10^{13} (3)	2.84×10^{14} (2)	5.12×10^{14} (2)
Molasses Reef	No	3.92×10^{12} (4)	2.66×10^{13} (5)	5.00×10^{13} (5)	6.31×10^{13} (3)	2.84×10^{14} (2)	5.12×10^{14} (2)
Hen and Chickens	No	2.12×10^{12} (6)	4.51×10^{12} (12)	5.62×10^{12} (12)	2.47×10^{12} (11)	5.73×10^{12} (12)	7.45×10^{12} (12)
Davis Reef	No	7.46×10^{11} (11)	5.57×10^{12} (11)	9.44×10^{12} (11)	1.07×10^{13} (8)	4.20×10^{13} (9)	6.33×10^{13} (9)
Cheeca Rocks	Yes	1.01×10^{12} (9)	1.86×10^{12} (15)	2.24×10^{12} (15)	6.93×10^{13} (2)	1.31×10^{14} (4)	1.62×10^{14} (6)
Tennessee Reef	No	6.27×10^{11} (13)	7.44×10^{12} (8)	1.40×10^{13} (9)	5.07×10^{12} (10)	2.97×10^{13} (10)	4.86×10^{13} (10)
Coffins Patch	No	7.30×10^{11} (12)	6.78×10^{12} (9)	1.21×10^{13} (10)	1.62×10^{12} (12)	1.06×10^{13} (11)	1.77×10^{13} (11)
South of Key Colony Beach	No	9.18×10^{11} (10)	2.18×10^{12} (14)	2.78×10^{12} (14)	1.26×10^{12} (13)	2.86×10^{12} (14)	3.68×10^{12} (14)
Sombrero Reef	Yes	5.74×10^{12} (2)	4.28×10^{13} (2)	7.56×10^{13} (1)	4.79×10^{13} (4)	1.64×10^{14} (3)	2.37×10^{14} (4)
Newfound Harbor	Yes	3.13×10^{13} (1)	4.99×10^{13} (1)	5.93×10^{13} (3)	8.80×10^{15} (1)	1.19×10^{16} (1)	1.37×10^{16} (1)
Looe Key Reef	Yes	4.81×10^{11} (14)	6.37×10^{12} (10)	2.06×10^{13} (8)	1.59×10^{13} (7)	7.37×10^{13} (7)	1.22×10^{14} (7)

Newfound Harbor, Sombrero Reef, and Cheeca Rocks were sites selected as 'Iconic Reefs' by the original advisory panel. Furthermore, Newfound Harbor, Sombrero Reef, and French Reef were among the top-5 ranked potential restoration sites in the sub-adult *L. griseus* spatial graph, with the first-mentioned site taking the top spot for both species. In fact, the Newfound Harbor IF value calculated from the *H. sciurus* spatial graph exceeded that of the other 14 sites under consideration by roughly 1 to 3 orders of magnitude (Table 1). The remaining 2 selected 'Iconic Reefs' in our study area, Horseshoe and Looe Key Reefs, ranked sixth and eighth, respectively, in terms of their ability to support seascape-wide potential connectivity for *H. sciurus*, assuming a 10 km maximum dispersal distance.

As with *L. griseus,* we found no statistically significant correlation between node-specific IF values for sub-adult *H. sciurus* and mean distances to potential nursery habitats ($r_{\text{mangrove}} = -7.70 \times 10^{-3}$, $r_{\text{seagrass}} = -1.70 \times 10^{-3}$). IF-based site rankings for *H. sciurus* were also relatively insensitive to changes in assumed dispersal thresholds (i.e. 5, 10, 15 km), with Newfound Harbor, French, Molasses, Sombrero, and Horseshoe Reefs consistently ranking in the top 5 and Tennessee Reef, Coffins Patch, Hen and Chickens, Key Largo Dry Rocks, and South of Key Colony Beach regularly receiving low rankings (Table 1). However, IF-based site rankings assuming a 10 km dispersal threshold differed from those estimated based on *in situ* observations (i.e. based on the proportion of surveys on which a sub-adult *H. sciurus* was present; Table S3).

Once again, the number of coral restoration sites ranking among the top 100 connectivity-contributing nodes in the *H. sciurus* graph varied depending on the dispersal threshold applied. At 5 km, 7 potential restoration sites ranked among the top 100 nodes — 4 'Iconic Reefs' (Cheeca Rocks, Newfound Harbor, Sombrero Reef, and Horseshoe Reef) and 3 alternates (Elbow, French, and Molasses Reefs). At thresholds of 10 and 15 km, 10 restoration sites ranked among the top 100 nodes — 5 'Iconic Reefs' (Cheeca Rocks, Newfound Harbor, Sombrero Reef, Horseshoe Reef, and Looe Key) and 5 alternates (Elbow, French, Molasses, Turtle, and Davis Reefs).

4. DISCUSSION

4.1. Spatial graph performance and global connectivity

Minimum planar graphs have emerged as a helpful analytical tool for informing landscape conservation efforts, as they represent the key characteristics of connectivity networks while being more efficient to construct, analyze, and communicate than the complete graphs that they approximate (Fall et al. 2007). Here, minimum planar graphs permitted the visualization and quantification of potential connectivity for sub-adult *Lutjanus griseus* and *Haemulon sciurus* occupying a spatially heterogeneous nearshore seascape in the Florida Keys, USA. Our spatial graphs pinpointed suitable seascape locations and pathways that may play fundamental roles in supporting these economically and ecologically valuable species during their ontogenetic migrations across the mangrove–seagrass–reef continuum. Furthermore, our findings demonstrate a desirable property of spatial graphs that has been primarily illustrated in terrestrial systems: their ability to represent potential connectivity as an emergent property of seascapes arising from unique interactions among species and the spatial patterns that they encounter. For example, potential connectivity appraisals suggest that, overall, our focal seascape supports a higher level of potential connectivity for sub-adult *H. sciurus* relative to *L. griseus* under pre-restoration conditions. This pattern remained consistent during sensitivity analyses (Fig. 4) and aligns with previous work by Faunce & Serafy (2007), who suggested that *H. sciurus* undertake longer circular forays between offshore reefs and inshore mangrove and seagrass nurseries relative to the more coastal movements of *L. griseus*, likely resulting in higher levels of functional connectivity across the seascape for the former species.

Differences in spatial graph estimates of global connectivity for *L. griseus* and *H. sciurus* were likely driven in part by variation in species-specific patterns of habitat suitability across the seascape. Previous research from the greater Caribbean region has revealed strong associations between mangroves and *L. griseus* of all size classes (Nagelkerken et al. 2000, Cocheret de la Morinière et al. 2002), and although diel movements between daytime mangrove resting sites and nocturnal seagrass foraging grounds are frequent, long-distance migrations to offshore reefs may be shorter in frequency and duration for this species (Luo et al. 2009). Furthermore, Stuart et al. (2021) found that patches of pavement, reef rubble, and unconsolidated sediments along with deeper waters in the same Florida Keys seascape offered higher levels of habitat suitability for sub-adult *H. sciurus* compared to *L. griseus*. These selective patterns of habitat use may explain the larger quantity and surface area of accessible, suitable habitat patches, and thus higher estimates of seascape-wide potential connectivity, for sub-adult *H. sciurus* in our study area.

4.2. 'Mission: Iconic Reefs' and local connectivity

The IF metric, which estimates species-specific potential connectivity at a local scale, allowed us to compare 15 sites considered under the 'Mission: Iconic Reefs' program — a newly established habitat restoration initiative seeking to recover the diversity and health of Florida's reef-building coral communities (NOAA Fisheries 2019). IF values suggest that the 5 'Iconic Reefs' selected for 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 — vary considerably in their ability to support and benefit from positive interactions with the focal fish species.

Assuming a likely dispersal limit of 10 km, the top 5 highest-ranking coral restoration sites supporting connectivity for sub-adult *L. griseus* included 2 selected 'Iconic Reefs' (Newfound Harbor and Sombrero Reef) and 3 alternates (Molasses, French, and Turtle Reefs). For sub-adult *H. sciurus*, the 5 highest-ranking sites included 3 selected 'Iconic Reefs' (Newfound Harbor, Sombrero Reef, and Cheeca Rocks) and 2 alternates (Molasses and French Reefs). The selected 'Mission: Iconic Reefs' coral restoration sites in our study area are therefore more likely to facilitate ecological interactions (e.g. nutrient provisioning) with migrating sub-adult *H. sciurus* relative to *L. griseus*. In the present study, local connectivity estimates were relatively insensitive to fluctuations in assumed species' dispersal ability (Table 1); however, multi-scaled approaches and sensitivity analyses should still be explored in future studies, as they may help to reveal the various scales of movement (e.g. diel, tidal, seasonal, ontogenetic) taken by fishes of different life stages (e.g. juvenile, sub-adult, adult), thereby providing a more holistic picture of potential connectivity.

Newfound Harbor and Sombrero Reef sites were potential connectivity hotspots for both species across various dispersal thresholds, which is especially promising for the success of restored corals at these 'Iconic Reefs' (Table 1). Aggregating grunts 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, sub-adult *L. griseus* and *H. sciurus* aggregating on and around the Newfound Harbor and Sombrero Reef restoration sites may be greatly beneficial to the survival and growth of out-planted corals 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). Considering their substantial local connectivity contributions and proximities 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 at this time (Table 1).

4.3. Node composition and nursery habitat proximity

Potential connectivity hotspots were characterized by a higher proportion of pavement, reef rubble, and scattered coral and rock for *H. sciurus* relative to *L. griseus*. These differences likely stem from interspecific variation in the suitability levels of benthic habitat types (Borland et al. 2021, Stuart et al. 2021). For instance, the selected Cheeca Rocks restoration site is a patch reef surrounded by scattered coral and rock and, to a lesser extent, seagrass. This translated to a larger, more suitable node for *H. sciurus*, as the suitability level of scattered coral and rock is much higher for *H. sciurus* than *L. griseus* (Stuart et al. 2021), the latter of which is likely more restricted to the patch reef itself and the small beds of seagrass nearby. This probably explains why the Cheeca Rocks 'Iconic Reef' site ranked highly for *H. sciurus* but last for *L. griseus.* Importantly, however, the IF values presented here serve as only a baseline estimate of node-level potential connectivity under present conditions. Future coral restoration efforts, if successful, will increase the proportion and architectural complexity of coral habitats around selected restoration sites, thereby enhancing sheltering and foraging opportunities, habitat suitability, and levels of functional connectivity (Huntington et al. 2017).

Beyond habitat composition, we examined whether distances to mangrove and seagrass nursery habitats (attributes that will remain unchanged by coral restoration) influenced node-scale potential connectivity estimates for the focal fishes. Contrary to our expectations under the nursery hypothesis, mangrove and seagrass nursery proximities were neither positively nor negatively correlated with spatial graph estimates of node-level connectivity for either species. This is despite the fact that 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. This finding is also at odds with that of Nagelkerken et al. (2017), who 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, Faunce & Serafy (2008) found that several Florida reef fish species, 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. Moreover, the sizes and suitability levels of nurseries, along with the identities and densities of their occupants, may play larger roles in determining functional connectivity with offshore coral reefs relative to simple Euclidean measures of inter-habitat distances (Huijbers et al. 2013, Nagelkerken et al. 2017). Together, these factors 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 system.

4.4. Model limitations and assumptions

The transmission of reliable information from HSMs to spatial graph models of potential connectivity relies on several assumptions. The first key assumption is that the input HSMs, which were constructed using records of species presence on daytime surveys conducted in various geomorphic zones and habitat types (Stuart et al. 2021), accurately reflect the suitability of the seascape. Although these HSMs performed well with respect to discriminatory ability, predictive accuracy, and ecological realism according to multiple metrics of model performance, they may be further improved by using species abundance or density records rather than occurrence data. Additionally, our models did not include anthropogenic disturbances such as fishing pressure, vessel traffic, and ecotourism activity that interact with the underlying suitability and structural connectivity of habitat patches to drive species distributions. Initial HSMs that incorporate species abundance or density data, as well as anthropogenic stressors alongside biogeophysical predictors, may provide more ecologically realistic spatial mapping of habitat suitability, translating to a more comprehensive picture of cross-scale functional connectivity.

Our application of least-cost paths derived from HSMs depended on 2 additional assumptions: (1) that species' movements are driven by similar spatial–environmental factors as habitat selection, and (2) that ontogenetic migrations faithfully follow least-cost paths (Zeller et al. 2012). Although GPS telemetry or genetic data may help to minimize uncertainty around these assumptions in the future (Zeller et al. 2018), we are currently reliant upon limited or indirect knowledge of species' dispersal ability. Our application of minimum planar graphs also necessitated the use of only non-crossing, direct edges (Fall et al. 2007). These restrictions are justified in the present study, as it is unlikely that fishes migrating at the vulnerable sub-adult life stage would cross over suitable nodes without stopping for rest, foraging opportunities, protection from predators, or other potential benefits (Krumme 2009).

These model assumptions and limitations, coupled with uncertainties surrounding the behaviors and intra- and inter-specific interactions of sub-adult *L. griseus* and *H. sciurus* as they migrate, may help to explain the discrepancies that arose when ranking candidate 'Mission: Iconic Reefs' sites based on connectivity model outputs and empirical observations (Tables S2 & S3). However, comparison between model results and observation-derived rankings should be considered in the context of several limiting factors. In particular, *in situ* survey data and subsequent HSMs represent snapshots of fish presence and abundance in time and space that are the outcome of complex ecological processes. Issues such as sampling inadequacy, accounting for interference in fish behavior (and thus detectability) from processes such as fishing pressure and observer bias, and other limitations can affect inferences made from patterns in these observational data. The reef fish surveys used in this research were also heterogeneous with respect to sampling effort across the 15 candidate restoration sites, thereby contributing to further uncertainty in observation-derived rankings (Tables S2 & S3). Likewise, some mismatch between broad-scale model results and empirical observations is to be expected when the former is applied to the local level. In future studies, it may be valuable to compare model-based site rankings to those derived from density or abundance maxima using quantile regression to provide a more nuanced understanding of the relationships between fish habitat use, habitat suitability, and functional connectivity.

4.5. Implications and recommendations for coral reef restoration

Due to the persistence of interacting stressors and the rapid rates of decline in reef health and complexity in the Florida Keys, 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 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 (Huntington et al. 2017, Gilby et al. 2018, Ladd et al. 2018). As demonstrated here for sub-adult *L. griseus* and *H. sciurus*, spatial graphs of potential connectivity informed by habitat suitability modeling aid in the identification of these priority restoration sites. Florida practitioners can further enhance the probability of coral reef restoration success by overlaying maps of habitat suitability or functional connectivity for targeted coral species with graph models of potential connectivity for functionally important community members. This would enable the identification of 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-environmental contexts. These multi-scale and multi-species efforts will help to revitalize and protect the culturally and economically important reefs of the Florida Keys that support thousands of jobs and a multi-billion dollar fisheries- and tourism-based economy annually (Ault et al. 2005)

Restoration programs 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, Pittman et al. 2021). Previously, challenges in quantifying and representing multi-species and multi-scale connectivity precluded their integration into marine habitat restoration planning (Gilby et al. 2018). Although opportunities for improvement remain, spatial graphs offer much-needed baseline estimates of potential connectivity across species and spatial scales and are particularly relevant as foresight tools for guiding restoration in fragmented and degraded seascapes, as has been previously demonstrated in freshwater (e.g. Stewart-Koster et al. 2015) and terrestrial (e.g. Saura & Pascual-Hortal 2007, Duflot et al. 2018, Préau et al. 2020) environments. Critically, however, spatial graph estimates of potential connectivity should serve as only one component of a larger, interdisciplinary site selection framework to ensure that desired restoration outcomes are met. We recommend that multi-species spatial graphs be constructed early in the project timeline to identify potential restoration sites, which can then be reviewed and refined using information on available resources for conducting restoration (e.g. funding, time, personnel), as well as the locations of other valued natural resources. Potential connectivity models offer a practical tool for informing the restoration and conservation of coastal seascapes across spatial scales in the face of ongoing ocean change, and their products can be considered alongside other criteria and constraints using existing decision support tools (e.g. Marxan Connect, Zonation) to identify the restoration sites that offer the greatest socio-ecological value.

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