



Graph-theoretic modeling reveals connectivity hotspots for herbivorous reef fishes in a restored tropical island system

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Abstract

Context Seascape connectivity refers to how the spatial configuration of marine habitats facilitates or hinders the movement of organisms, nutrients, materials or energy. Predicting and ranking potential connectivity among habitat patches for coral reef fishes helps to understand how reef fishes could utilize and

connect multiple habitat types through the flow of nutrients, energy and biomass across the wider seascape during foraging movements.

Objectives To advance a spatially explicit understanding of connectivity linkages within a tropical atoll system by modeling, mapping and quantifying potential seascape connectivity for two locally abundant herbivorous reef fish species, the parrotfish, *Chlorurus spilurus* (pahoro hohoni or pa'ati pa'apa'a auahi), and the surgeonfish, *Acanthurus triostegus* (manini).

Methods We applied a two-step modeling approach by first mapping habitat suitability for the focal species. A graph-theoretic modeling technique was then applied to model and measure the contribution of benthic habitat patches to species-specific potential connectivity within the seascape.

Results Habitat suitability was higher and less fragmented for *C. spilurus* than for *A. triostegus*. Potential ecological connectivity estimates for *C. spilurus* were higher across the entire seascape, with differences between species likely driven by local-scale benthic habitat patch configuration and species home ranges. Hotspots of ecological connectivity across the atoll were mapped for both species.

Conclusions Despite advances in the application of graph-theoretic techniques in the coastal environment, few marine conservation and restoration measures currently integrate spatial information on ecological connectivity. This two-step spatial modeling approach holds great potential for rapid application

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of connectivity modeling at multiple spatial scales, which may predict ecological responses to conservation actions including active habitat restoration.

Keywords Restoration ecology · Seascape connectivity · Ecological modeling · Remote sensing · MaxEnt

Introduction

Ecological connectivity is a central concept within landscape ecology that refers to the way that a landscape facilitates or hinders the movement of organisms, nutrients, materials and energy (Tischendorf and Fahrig 2000; Calabrese and Fagan 2004; Turner and Gardner 2015; Pittman et al. 2021). The ways in which marine organisms, materials and processes flow and interact among the structural elements of the seascape shapes biodiversity distributions, ecosystem integrity, resilience to disturbance and controls the quality and quantity of benefits to people (Olds et al. 2016; Carr et al. 2017). Evidence from tropical coastal ecosystems suggests that coastal seascape configuration and connectivity influence a wide range of ecosystem services (Pinsky et al. 2012; Guannel et al. 2016; Barbier 2017; Asplund et al. 2021; Bakker et al. 2023) and conservation outcomes including the resilience and fisheries replenishment function of marine reserves (Olds et al. 2012, 2016). The importance of ecological connectivity is further amplified within small, geographically isolated seascapes where suitable pathways between habitat patches are required to maintain local populations and the distribution of beneficial ecological processes supporting ecosystem integrity (e.g., flow of nutrients and energy) (Carr et al. 2017; Thompson et al. 2017; Friesen et al. 2019).

Oceanic island ecosystems are highly vulnerable to disturbance, particularly where coral reefs are tightly coupled to conditions and processes on land (Graham et al. 2018; Wedding et al. 2019; Strona et al. 2021; Sandin et al. 2022). Herbivory is a core ecosystem process on coral reefs where grazing by herbivores can have a dramatic influence on the structure and function of coral reef communities (Choat and Bellwood 1985; Tebbett et al. 2022). Herbivorous fishes influence benthic composition and coral reef resilience through their patterns of grazing, which can

alter coral-algal competition dynamics (Burkepile and Hay 2010; Rasher et al. 2012; Graham et al. 2013; Chung et al. 2019). Grazing patterns of reef fishes are species-specific (Chow et al. 2021) and influenced by the spatial configuration of the seascape (Pagès et al. 2014; Eggertsen et al. 2020). Although evidence is relatively sparse, it appears that some herbivorous fish exhibit high site fidelity to reefs (Welsh and Bellwood 2014; Ferguson et al. 2016; Pillans et al. 2017), use routine highly directional routes between consistent foraging areas (Fox and Bellwood 2014) and require sufficiently high connectivity across patches of reef to fulfill their need for grazing and refuge (Fox and Bellwood 2014; Kelly et al. 2016; Semmler et al. 2021). Hotspots of high connectivity in the seascape are therefore likely to experience greater ecological effects from interactions with fish (i.e., social, trophic and nutrient interactions) than low connectivity areas of the seascape (Olds et al. 2012; Dickson et al. 2019; Virtanen et al. 2020). At the Pacific Island of Mo'orea, for example, suitable connectivity pathways for herbivorous reef fish between lagoon nursery habitat and offshore coral reefs was considered to contribute to the maintenance of coral dominance after a major disturbance event (i.e., crown-of-thorns starfish outbreak) (Adam et al. 2011).

Ecological connectivity can be characterized using metrics of structural connectivity (i.e., the physical relationships among seascape elements) and functional connectivity (i.e., how structural patterns influence the movement of animals, as well as their energy, nutrients, genetic material and ecological functions) (Tischendorf and Fahrig 2000). Functional connectivity is typically an individual response to perceived costs and benefits of habitat structure and inter-patch movements that is constrained by unique combinations of species-specific traits (Nash et al. 2013; Catano et al. 2016; Lowerre-Barbieri et al. 2021). For example, coral reef fish will respond differently to crossing an expanse of sand between coral patch reefs which may present a barrier to some and not for others (Frederick 1997; Meyer et al. 2010; Turgeon et al. 2010; Pittman et al. 2014). In the absence of high-resolution geospatial data from acoustic telemetry, functional connectivity across heterogeneous seascapes is a difficult parameter to estimate. To address this data gap, spatial network graphs have been applied based on assumptions and indirect data on the potential for movement between patches

(e.g., home range estimates, habitat suitability and resistance surfaces) (Pittman et al. 2014; Engelhard et al. 2017; Stuart et al. 2023). Graph theoretic techniques from landscape ecology are increasingly being applied to marine environments to map and measure potential functional connectivity (hereafter, potential connectivity) (Kool et al. 2013; Engelhard et al. 2017; Stuart et al. 2023). In the patch-matrix model, low suitability or unsuitable patch types that are not directly utilized (i.e., no food or refuge from predators) are sometimes referred to as the matrix (Ricketts 2001; Tanner 2006). For species closely associated with coral reefs, the patches of coral reef are considered the focal habitat, and the surrounding sand is typically considered the matrix.

Coupling species-specific habitat suitability modeling and spatial network graph-based approaches offers a practical, cost-effective and quantitative analytical methodology to illuminate potential connectivity for focal fish species (Engelhard et al. 2017; Stuart et al. 2021, 2023). Management strategies that focus on restoring fish populations for coral reef resilience have been proposed (Williams et al. 2019), yet few marine protected areas (MPAs) (Balbar and Metaxas 2019) or coastal restoration projects (Gilby et al. 2019) have considered the species-specific movement patterns and resource needs of fishes and the influence of seascape composition and configuration on functional connectivity (Mumby et al. 2007; Engelhard et al. 2017). Where functional connectivity has been considered for coral reef fishes, the focus has most often been on larval connectivity across hundreds of kilometers of ocean (Kool et al. 2013), whereas the more localized movements of post-settlement (juvenile and adult) fishes have received less attention (Green et al. 2014). Moreover, functional connectivity research to date has focused primarily on reef fish movement and foraging behavior within localized daytime home ranges, while overlooking the often broad-scale (i.e., 10 s to 1000 s of m) movements of fishes to and from nighttime refuge areas and spawning sites. If management is to succeed in restoring and safeguarding healthy and resilient island-reef systems, these multi-scale fluxes of reef fishes and their nutrients, energy and ecological functions must be adequately considered.

Here, we broaden insights into multi-scaled habitat suitability and potential connectivity for key herbivorous fishes in tropical island-reef systems.

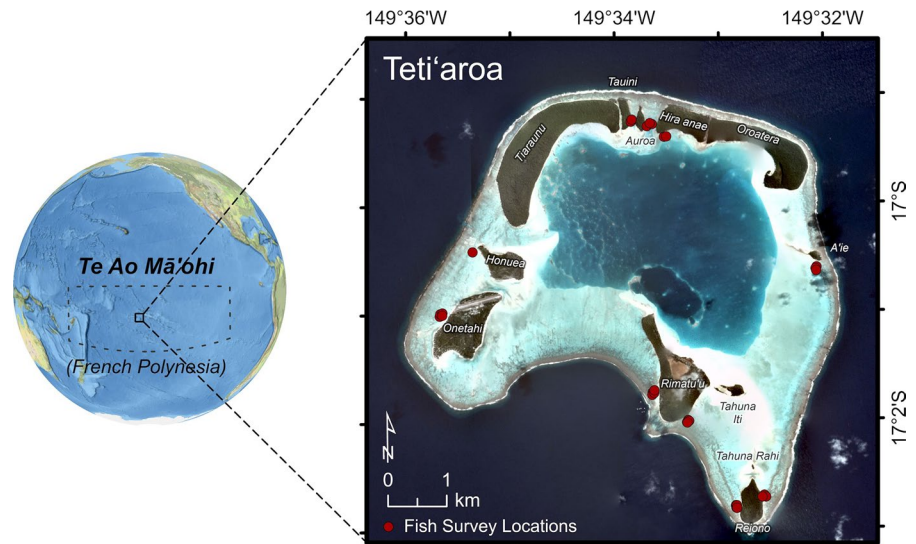
Specifically, we explore these patterns for the parrotfish *Chlorurus spilurus* (pahoro hohoni (initial phase) or pa'ati pa'apa'a auahi (terminal phase) in Tahitian) and the surgeonfish *Acanthurus triostegus* (manini in Tahitian) residing in the heterogeneous tropical seascape of Teti'aroa Atoll, French Polynesia. Our primary objective was to map and model habitat suitability throughout the seascape for the focal fishes and to pinpoint the key spatial-environmental variables driving these patterns. Our secondary objective was to then quantify species-specific potential connectivity across scales and to identify the benthic habitat patches contributing most to connectivity across the seascape. Given the crucial impact herbivores like *C. spilurus* and *A. triostegus* have on cross-ecosystem nutrient cycling, as well as the composition and resilience of coral reefs, the insights gathered from this study hold significant value for ongoing restoration initiatives in Teti'aroa.

Material and methods

Study area

Teti'aroa is a 33.8 km² atoll consisting of 12 coral islets (*motus*) located 55 km north of Tahiti within Te Ao Mā'ohi (French Polynesia; Fig. 1). Teti'aroa, once a special place for Tahitian royalty, is managed by the Tetiaroa Society through the Conservation and Sustainable Use Plan where urban development is prohibited to protect land-sea ecosystem integrity (Collin et al. 2014; Tetiaroa Society 2022). The land is privately owned, and the marine zone is in the public domain under the jurisdiction of the Government of French Polynesia. Although largely pristine, ecosystem dynamics have been impacted by introduced species including two species of rats that have consumed sea turtle hatchlings, land crabs, native vegetation and seabirds for many years. Seabird population suppression by rats can significantly disrupt the nutrient flow between land and sea and reduce the availability of nutrient-rich algae and corals for herbivorous fishes (Graham et al. 2018; Benkwitt et al. 2019). The Teti'aroa Atoll Restoration Program eliminated rats from all islets in 2021–22 to restore ecosystem dynamics across a land-sea gradient, with other activities such as partial removal of invasive coconut palms possible in the future. Monitoring of

Fig. 1 Location of Teti'aroa Atoll and the main islets (*motus*) in Te Ao Mā'ohi (French Polynesia). Satellite imagery: Pléiades © CNES 2022, Distribution AIRBUS DS, tous droits réservés. Usage commercial interdit



the ecological response to conservation action is presently taking place on land and in the sea. Teti'aroa's positioning as a remote tropical atoll with limited human influence enables the methodology used to be interpreted with a higher degree of confidence. This is due to the lack of confounding anthropogenic factors typically present in habitat suitability and connectivity models.

Coral reef fish surveys

While connectivity analyses have been conducted on mesopredatory fishes (Engelhard et al. 2017; Stuart et al. 2023), our study expands on previous literature by broadening connectivity modeling to herbivorous fishes. Specifically, our research focused on the widely occurring and functionally important herbivorous fish species, *Acanthurus triostegus* (convict surgeonfish) and *Chlorurus spilurus* (Pacific bullethead parrotfish). *C. spilurus* is one of the most abundant parrotfish in the tropical Indo-central Pacific and targets cyanobacteria on and within reef substrata across a variety of reef zones (Davis et al. 2017a, 2017b; Hamilton et al. 2017; Clements and Choat 2018). *C. spilurus* target epilithic and endolithic cyanobacteria as their primary food and, as excavators, remove both coral and algae during feeding (Clements et al. 2016; Clements and Choat 2018). *C. spilurus*—a protogynous species with females and primary phase males referred to locally as pahoro hohoni and terminal phase males referred to as pa'ati pa'apa'a auahi—has

very high reproductive output and high genetic diversity across its geographical range (Bay et al. 2004). The grazing behaviors of *C. spilurus* and other scraping and excavating parrotfishes play an important role in the distribution of sand, nutrients and microbes across the seascape and help to maintain surfaces suitable for coral recruitment (Ezzat et al. 2020). *C. spilurus* has a diverse movement and feeding ecology, as documented by regular outer reef excursions and herbivory in both fore, fringing and outer reef patches (Adam et al. 2011; Roff et al. 2019).

A. triostegus is also an abundant herbivore across the Indo-Pacific, often seen in mixed-species schools, and has a more taxonomically specialized diet than *C. spilurus*, consisting primarily of red filamentous algae, green macroalgae and turf algae (Abitia et al. 2011; Nalley et al. 2022). Feeding mostly on the epilithic algal matrix of coral reef ecosystems, *A. triostegus* influences coral reef productivity and reef substrate composition through their grazing behavior (Marshall and Mumby 2015; Wakwella et al. 2020; Pessarrodona et al. 2022).

Coral reef fish assemblages were surveyed at constant swimming speed by CEB along a 5 × 30 m (150 m²) belt transect at 13 locations with 2–5 transects per location, with each transect separated by at least 10 m (Fig. 1). Transect surveys were conducted during November 2021 across a 0.07–3.6 m depth range, 12 *motus* and 11 habitat patch types (back reef coral bommies, back reef coral framework, back reef rubble, back reef sediment, beach sand, lagoonal floor

barren, lagoonal floor coral bommies, lagoonal patch reef, lagoonal reef massive coral dominated, rock). Transects were placed to capture the major benthic habitat types in the atoll, including the hard-bottom habitats preferred by *C. spilurus*, *A. triostegus* and their conspecifics (Randall 1961; Davis et al. 2017a, 2017b). For our study, we isolated data on the locations of reef fish presence for *A. triostegus* and *C. spilurus* to represent key dominant herbivores. *A. triostegus* was present at 45 transects (total abundance of 414 individuals) and *C. spilurus* was present at 30 transects (total abundance of 131 individuals). Both *A. triostegus* and *C. spilurus* were associated with the same benthic habitat patch types (*Back reef*: coral bommies, reef coral framework, reef rubble and reef sediment; *Lagoonal*: barren floor, coral bommies, patch reefs, massive coral dominated reefs, and rock and beach sand).

Quantifying spatial environmental variables for habitat suitability modeling

Bathymetry and seafloor morphology

A complete high density LiDAR (Light detection and ranging) dataset, funded by the Island Digital Ecosystem Avatars (IDEA) program (Davies et al. 2016), was acquired in May 2017 (Gruen et al. 2017) over both the marine and terrestrial area of Teti'aroa. A helicopter-mounted Riegl LMS-VQ820G (Mallet and Bretar 2007) full wave green LiDAR was used to sample a 1.42 billion point cloud with 25 dot-per-square-meter density and 4.3 cm height accuracy. A very high-resolution (30 cm) digital terrain model (DTM) was processed from this point cloud (Ural et al. 2019) and used to model bathymetry and topographic complexity. Bathymetric slope and the slope-of-slope (a measure of surface complexity) were quantified across the seascape using ArcGIS Spatial Analyst software (Esri Inc.) (Fig. 2, Table 1 suppl.).

Benthic seascape patch-mosaics

A very high-resolution (2 m) remotely sensed map of habitat patch types was provided by the Khaled bin Sultan Living Oceans Foundation's Global Reef Expedition (Purkis et al. 2019) (Fig. 2, Table 1 Suppl.). This map was part of a larger mapping campaign using diver, vessel and satellite-based mapping

methods to provide high resolution habitat and bathymetric maps for 65,000 sq. km of the world's most remote coral reefs (Purkis et al. 2019). The map classified the study area into 21 discrete habitat classes which included reef, lagoonal and terrestrial habitats (Table 2 Suppl). As our focus was on the marine realm, areas classified as terrestrial were masked out of our model products.

The spatial-environmental variables for predicting coral reef fish habitat suitability included habitat patch types, topo-bathymetry, slope, and habitat complexity (Fig. 2). The spatial-environmental raster data layers (30×30 cm resolution pixels) were georeferenced in European Petroleum Survey Group (EPSG) coordinate system EPSG 4326 for habitat suitability modeling and projected into coordinate system EPSG 3857 for subsequent connectivity modeling in meters.

Modeling habitat suitability for herbivorous fishes

Maximum entropy (Phillips et al. 2017), a machine learning algorithm, was applied to model the relationship between fish presence and seascape conditions (benthic patch type, water depth, slope and topographic complexity) to predict habitat suitability for *A. triostegus* and *C. spilurus*. MaxEnt can produce robust results with sparse, irregularly sampled data, making it an excellent choice for modeling presence data collected using an unstandardized spatial approach (Elith et al. 2011; Wang et al. 2020). MaxEnt models are, however, influenced by spatial biases in sampling effort, requiring adequate management of unintentional biases to derive ecologically relevant models (Yackulic et al. 2013). In total, three distinct models were constructed for model validation and comparison before selecting one model to serve as the input into subsequent connectivity models. Using 80% of the available reef fish presence data, three distinct MaxEnt models were constructed for each species: 1) accounting only for spatial bias in the reef fish sampling design, 2) applying spatial filtering in addition to accounting for spatial bias and 3) applying an environmental variable trim in addition to accounting for spatial bias. To manage spatial bias, background manipulation and spatial filtering were utilized to compare and analyze model accuracy and overall fit (Kramer-Schadt et al. 2013; Fourcade et al. 2014). Background manipulation used the MaxEnt bias file with a Gaussian kernel density surface

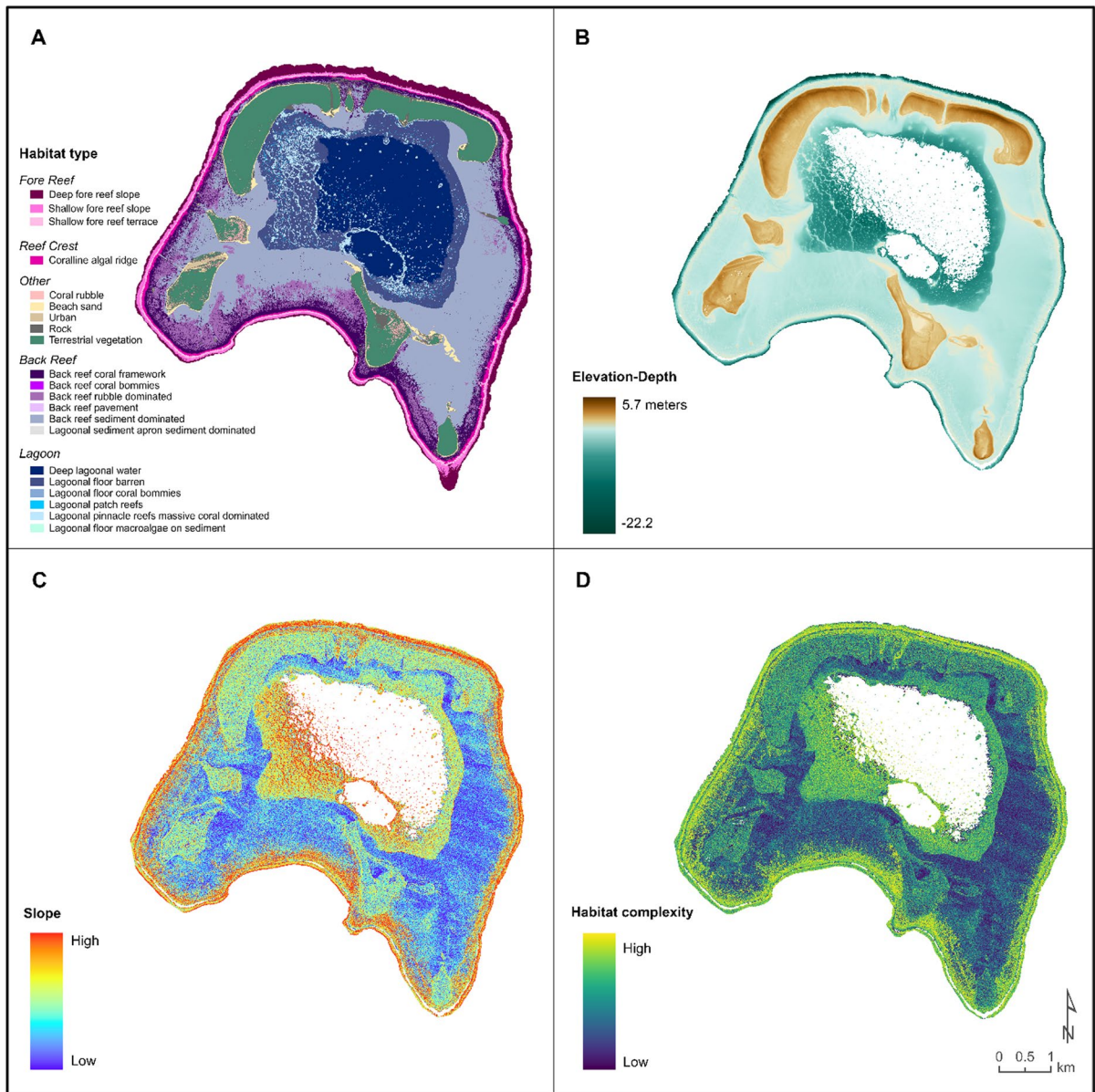


Fig. 2 Spatial-environmental variables for predicting fish habitat suitability using MaxEnt: **A** habitat patch types (Purkis et al. 2019), **B** topo-bathymetry, **C** slope, and **D** habitat complexity

capturing sampling intensity input into the MaxEnt model to consider the spatial bias during training algorithm development (Fourcade et al. 2014; Stuart et al. 2021). Spatial filtering was used to remove duplicate presence records within a single transect resulting in retention of 45 presence locations for *A. triostegus* and 30 presence locations for *C. spilurus*. The MaxEnt model iteration with trimmed

environmental variables considered only the spatial extent defined by the depth range and patch types within a 25 m radius buffer surrounding the sampled locations rather than predicting reef fish presence across the entire seascape.

The *A. triostegus* and *C. spilurus* MaxEnt models were calibrated using tenfold and fivefold cross-validation, respectively (Supplementary Material), due to

the greater availability of occurrence records for the former. Fitted models were then validated using the 20% of presence records withheld during model calibration. The area under the receiver-operating Curve (AUC) (Fawcett 2006) was used to measure MaxEnt model performance and select the optimal model for each species. AUC values range from 0 to 1, where a “rule of thumb” interpretation considers values >0.5 to indicate performance better than a random model, values >0.7 indicate acceptable performance and values >0.8 suggest excellent performance (Pearce and Ferrier 2000). MaxEnt’s built-in features of variable importance were examined for each reef fish species, with jack-knife resampling applied to assess the contributions each spatial predictor provided to the model.

Modeling and measuring potential seascape connectivity for fishes

The mapped continuous habitat suitability values were first converted into two binary classes derived from the maximum sensitivity plus specificity (Liu et al. 2013) suitability threshold calculated by MaxEnt: high suitability cells (values >0.5355 for *A. triostegus*; values >0.5627 for *C. spilurus*) and low suitability cells (≤ 0.5355 ; < 0.5627). Low suitability regions of the seascape are henceforth referred to as the matrix. High suitability patches were used to represent input nodes for subsequent potential connectivity modeling using Graphab software v2.8 (Foltête et al. 2021). Following Stuart et al. (2023), species-specific cost surfaces were calculated using negative exponential functions to transform the original continuous habitat suitability values to resistance values. Cost surfaces represent the degree to which seascape regions impede movement (Zeller et al. 2012). The spatial resolution of binary habitat maps and cost surfaces was reduced from 30×30 cm to 2×2 m for modeling in Graphab due to computational processing constraints. Network graphs were then used to construct and visualize linkages or corridors where fish movement could occur between suitable patches at different scales to investigate potential connectivity across the seascape (Urban and Keitt 2001; Urban et al. 2009; Engelhard et al. 2017).

Direct evidence of *C. spilurus* and *A. triostegus* movement in Teti’aroa is currently lacking; therefore, we relied on previous research from the Indian and

Pacific Oceans to select relevant movement thresholds for these species. As discussed in Davis et al. (2017a, b), parrotfishes display substantial plasticity in movement and foraging behaviors due to complex interactions between bottom-up, horizontal and top-down drivers. Indeed, tagging and tracking efforts in Palmyra Atoll revealed that *C. microrhinos* — a conspecific of *C. spilurus* — frequently moved several 100 s of m between daytime foraging areas and nighttime refuges (Davis et al. 2017b). Additionally, a tagged *C. microrhinos* individual repeatedly visited a spawning aggregation site located over 2 km from its core foraging grounds (Davis et al. 2017b). Likewise, *A. triostegus* movements are influenced by resource availability, biotic interactions and individual behavior. For example, Guerra et al. (2023) found that shoaling *A. triostegus* in Palmyra Atoll travel greater linear distances and cover larger areas than their solitary counterparts. Analogously, in the Tuamotu Archipelago, Randall (1961) recorded a large group of *A. triostegus* moving 100 s of m together in a just a few hours and, based on the recovery of tagged individuals in Hawai‘i, argued that *A. triostegus* may wander up to several miles if displaced from their home areas. Similarly, in Aldabra, large *A. triostegus* aggregations migrated from distances of up to at least 2 km to participate in group spawning (Robertson 1983). In light of these findings, it is essential to consider long-distance movements related to reproduction and crepuscular sheltering, in addition to concentrated foraging, when modeling and mapping potential connectivity for the focal species. As such, our models included potential connectivity linkages within a 3 km straight line distance to capture patterns of habitat use across multiple spatial scales.

Global (i.e., seascape-wide) potential connectivity for each reef fish species was measured using the probability of connectivity (PC) and equivalent connectivity (EC) metrics (Saura and Pascual-Hortal 2007). Probability of connectivity is the probability that two random nodes in the seascape network are connected given their areas and proximity and is measured as a value between 0 and 1 (Saura and Pascual-Hortal 2007; Keeley et al. 2021). As a probabilistic habitat availability metric, PC is straightforward to compute. However, it is sensitive to how the study area boundaries are defined and can overestimate the importance of large nodes (Saura et al. 2011). Equivalent connectivity offers a measure of both the quantity

and quality of connected nodes within the seascape network. Notably, EC remains unaffected by variations in the definition of the study area. Here, by prioritizing nodes based on habitat suitability rather than solely on their surface areas, EC more accurately represents the stepping-stone function of certain nodes, enhancing the calculation of overall connectivity (Saura et al. 2011). Individual nodes were also evaluated using the interaction flux (IF) local connectivity metric, which quantifies potential connectivity per node using quality-weighted areas and the probability of interaction between nodes (Foltête et al. 2014; Saharaoui et al. 2017). Thus, IF values represent the contribution of individual nodes to the global EC metric and provide a measure of their relative importance for maintaining connectivity across the seascape.

Results

Habitat suitability models

Ultimately, the species-specific habitat suitability models chosen for subsequent potential connectivity analyses were those that accounted for spatial bias in sampling effort using a bias file, without spatial filtering or environmental trim (Supplementary Material). MaxEnt model performance was considered excellent for both fish species with *A. triostegus* and *C. spilurus* models achieving AUC values of 0.929 and 0.917, respectively. Regardless of species, habitat suitability was most influenced by water depth and habitat patch type, with the variables of slope and habitat complexity contributing relatively little to the final models (Fig. 3). Suitable habitat for *A. triostegus* was characterized by a mean water depth of 0.9 m (2.3 to 11.6 m range), with 3.4 km² of the seascape predicted to be suitable. Suitable habitat for *C. spilurus* was characterized by a mean water depth of 1.7 m (2.4 to 9.6 m range), with 5.4 km² of the study area predicted to be suitable. All benthic habitat types were represented within suitable habitat for both species, though in different quantities (Fig. 4).

Potential connectivity models

Spatial graphs revealed species-specific potential connectivity networks within a 3 km movement threshold. *A. triostegus* nodes averaged 18 m² per node,

with movement pathways linking benthic habitats within an average distance of 191 m. *C. spilurus* nodes averaged 50 m² per node, with an average distance of 204 m for movement pathways. The probability of connectivity (PC) metric, defined here as the probability of two randomly chosen nodes being connected to one another, was used to understand the level of potential connectivity across the seascape as measured on a scale of 0 to 1. PC values, calculated using least-cost pathways, indicated low levels of connectivity for both species, with *C. spilurus* receiving a value of 0.0092 and *A. triostegus* faring worse with a value of 0.0034. Equivalent connectivity (EC), a measure of network-level connectivity taking into account node areas, relative suitability levels and inter-node distances, was also examined to provide additional insights. The EC results mirrored those of the PC analysis, demonstrating low connectivity across the seascape network, albeit suggesting higher values for *C. spilurus* relative to *A. triostegus* (5.37×10^7 and 3.24×10^7 , respectively). The interaction flux (IF) metric offered a per-node analysis to identify those contributing most to potential connectivity across the seascape. High ranking nodes for *A. triostegus* and *C. spilurus* consisted of lagoonal floor and back reef habitat types; however, *A. triostegus* connectivity was driven by shallower habitats (Fig. 4). Local connectivity hotspots for *A. triostegus* remained at shallow depths, whereas *C. spilurus* connectivity hotspots varied across a larger depth range. Global and local connectivity results suggest that, at present, *C. spilurus* experiences a higher level of potential connectivity across the Teti'aroa seascape.

Individual node assessment using the IF metric identified the *motus* facilitating the greatest potential connectivity for each species (Fig. 5). Of 12 *motus*, five ranked highly for both species: A'ie, Hira anae, Oroatera, Rimatu'u, and Tiaraunu. All lagoonal areas near these *motus* were shown to facilitate high levels of local connectivity for the focal species. These results indicated high connectivity within distinct, localized habitat networks, with shallow lagoonal areas facilitating the highest levels of connectivity for the focal species. Spatial graphs did, however, reveal inter-specific variation in connectivity estimates aligning with previous habitat suitability modeling results. Shallow, lagoonal areas off the northern Oroatera and Hira anae *motus* supported the highest levels of connectivity for *A. triostegus*, whereas a

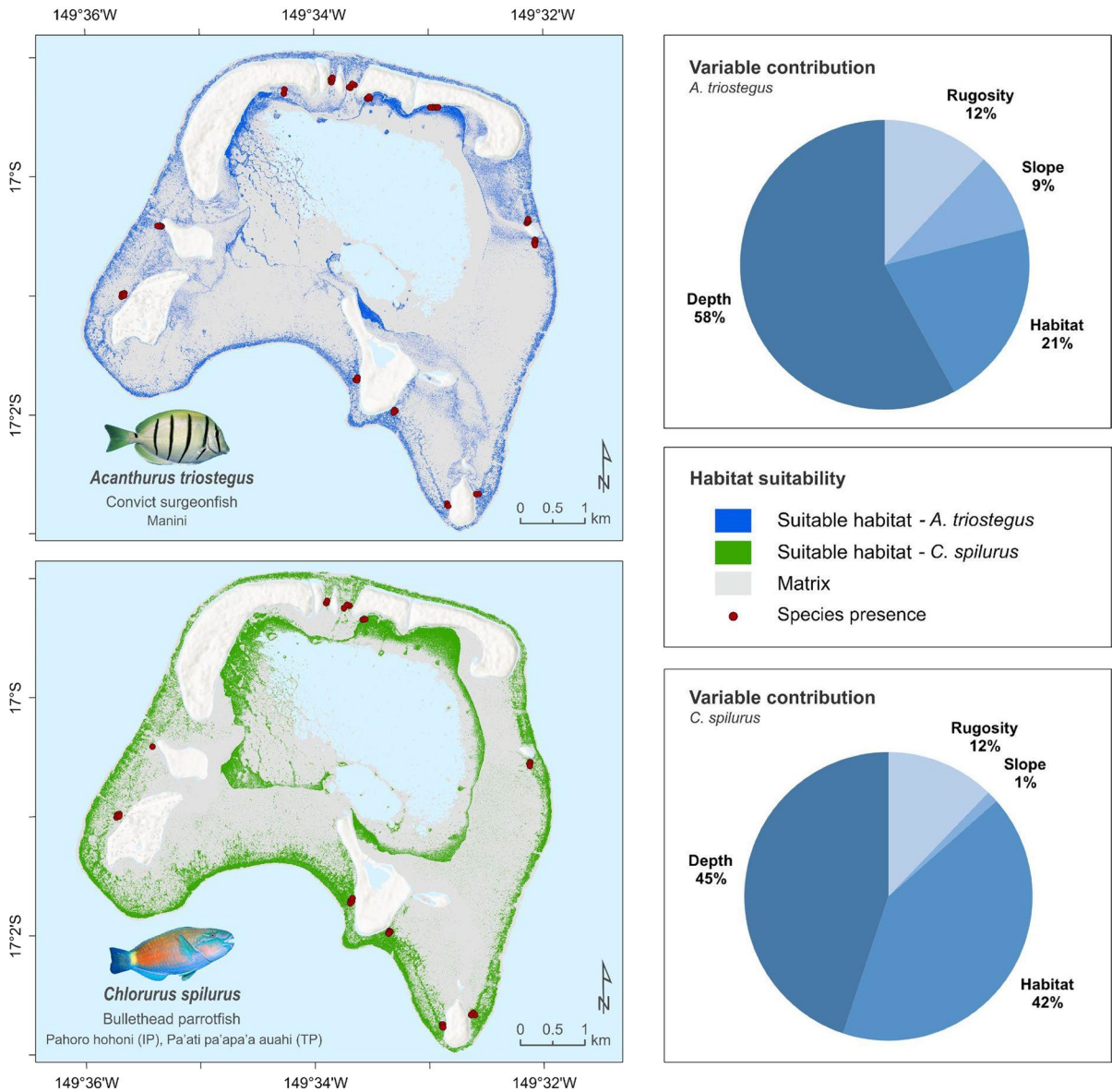


Fig. 3 MaxEnt predictions of habitat suitability and environmental predictor permutation importance for *Acanthurus triostegus* and *Chlorurus spilurus* across Teti’aroa, French

Polynesia. For the protogynous *C. spilurus*, *IP* initial phase (females or primary males) and *TP* terminal phase (supermales)

broader range of water depths and habitat types facilitated connectivity for *C. spilurus*, including portions of the outermost reef crest and a potential connectivity corridor linking Onetahi and Rimatu’u in the south. The 15 highest-scoring nodes for *C. spilurus* were more spatially connected and included a wider range of depths and habitat types relative to the *A. triostegus* nodes.

Discussion

Habitat suitability models

We aimed to map and model habitat suitability throughout the seascape for the focal fishes and to pinpoint the key spatial-environment variables driving these patterns. Our MaxEnt modeling approach

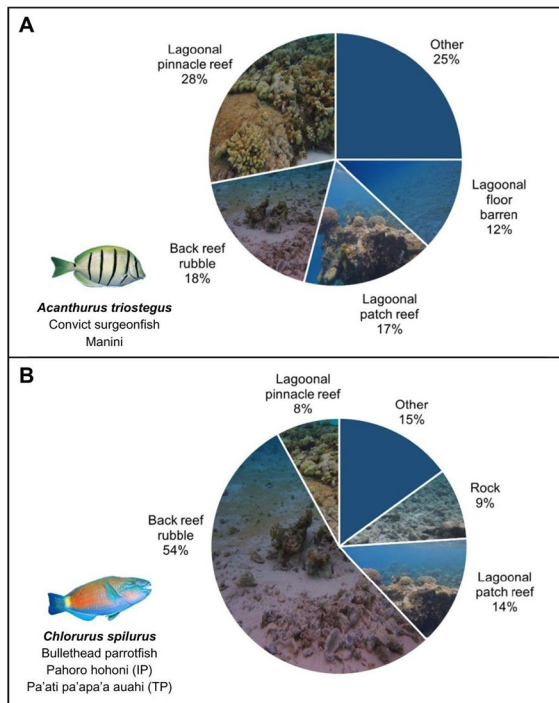


Fig. 4 Relative influence of benthic habitat types in determining potential connectivity for (A) *Acanthurus triostegus* and (B) *Chlorurus spilurus*. For the protogynous *C. spilurus*, IP initial phase (females or primary males) and TP terminal phase (supermales)

identified depth and benthic habitat patch type as the primary drivers of habitat suitability for two species of herbivorous coral reef fishes in Teti'aroa Atoll, French Polynesia. Furthermore, habitat suitability maps suggest that the Teti'aroa seascape provides a greater area of suitable habitat for *C. spilurus* than for *A. triostegus*. This is likely due to the differing ecologies of the species, as *A. triostegus* target algal turfs with higher nutritional content on shallow reef slopes where productivity is greatest, whereas *C. spilurus* is documented to utilize more diverse habitat along back reefs in French Polynesia (Adam et al. 2011; Hamilton et al. 2017; Roff et al. 2019).

In the northern lagoonal zones of Mo'orea, a high island neighboring Teti'aroa Atoll, patch reef configuration and the presence of macroalgae were both demonstrated to influence herbivory. The foraging behavior of *C. spilurus*, however, was influenced more strongly by macroalgal distributions than the structural characteristics of coral patch reefs (Eggertsen et al. 2020). Macroalgal presence associated

with mapped patch types in Teti'aroa was largely undocumented and no suitable proxies were available to map macroalgal distributions. Other studies in French Polynesia have found that *C. spilurus* is relatively resilient to disturbances that reduce live coral cover and structural complexity (Viviani et al. 2019), suggesting traits that may also explain the predicted broader extent of suitable habitat for this species. Little is known about the interplay between the extent of suitable foraging habitat and local population dynamics. The spatial availability and specificity of suitable foraging areas, however, is likely to influence the species-specific responses to disturbances or interventions that change the distribution, abundance and nutritional attributes of algae and cyanobacteria. It is important to note that species movement mechanisms, such as herbivorous grazing, influence the structure and functioning of coral reef communities. Our approach can be bolstered if combined with future studies on the rates of herbivory, as such behaviors influence functional connectivity for coral reef fishes.

MaxEnt modeling of habitat suitability was also applied successfully in a previous study focusing on coral reef fishes in the Florida Keys, USA (Stuart et al. 2021). Depth and habitat type were found to be key drivers of habitat suitability for the mesopredatory fishes examined in their study as well, with fine-scale variation in suitability predictions attributed to species-specific habitat and depth preferences along with motivations for movement (Stuart et al. 2021). Likewise, in an Australian study, MaxEnt outperformed nine other modeling approaches when calibrated using demersal fish occurrence records extracted from video transects and bathymetric variables derived from multibeam echosounders (Monk et al. 2010). Across the 5 demersal fish taxa examined, bathymetry and bathymetric derivatives consistently ranked amongst the most important seafloor variables for defining suitable habitat (Monk et al. 2010).

Potential connectivity

Our secondary aim was to then quantify species-specific potential connectivity across scales and to identify the benthic habitat patches contributing most to connectivity across the seascape. The habitat suitability modeling products allowed us to quantify potential

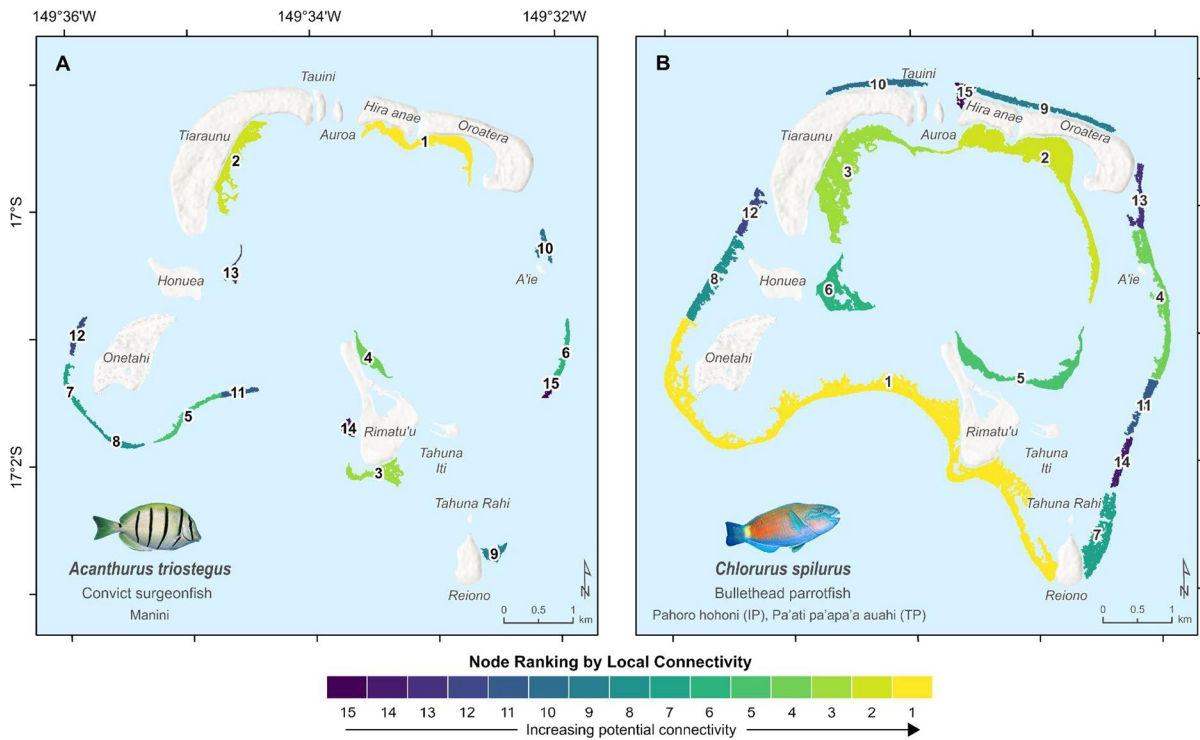


Fig. 5 Node-level contributions to potential connectivity across the Teti’aroa seascape as measured by the Interaction Flux (IF) local connectivity metric. For the protogynous *C. spilurus*, *IP* initial phase (females or primary males) and *TP* terminal phase (supermales)

connectivity for the abundant and functionally important herbivorous focal species. Herbivory is a key ecological process influencing the structure and function of coral reef communities (Steneck et al. 2017). Herbivorous fishes influence reef resilience with grazing behavior that exerts top-down control on coral-algal dynamics (Choat and Bellwood 1985; Tebbett et al. 2022). However, herbivorous fishes require a high degree of connectivity across structurally complex seascapes to access the critical resources in geographically discrete locations that enable them to fulfill their ecological role (Kelly et al. 2016; Semmler et al. 2021). Within the seascape ecology discipline, global connectivity is understood as the degree to which a seascape is connected and is thus heavily influenced by the geomorphology of the study area. Our analyses indicated relatively low global connectivity in Teti’aroa, which is likely due to numerous geomorphological characteristics of the atoll such as the deep central lagoon which may restrict movement between various *motus*. As such, local connectivity metrics are more useful in this instance as they indicate local

areas within a seascape that may facilitate much of the connectivity needed for groups of species to perform their ecological roles and maintain species assemblages.

Results from local connectivity analysis through the interaction flux metric, understood as the ranked importance of respective nodes to the facilitation of overall connectivity within the seascape, demonstrated unique potential connectivity patterning between the surgeonfish and parrotfish examined in our study. *C. spilurus* nodes facilitating high local connectivity were found near almost all *motus* in Teti’aroa apart from Honuea, whereas nodes facilitating high connectivity for *A. triostegus* were only found around a few key *motus*. Benthic habitat types driving potential connectivity aligned with the known ecologies of each species, as shallow depth and lagoonal habitats were the highest predictors in determining potential connectivity for *A. triostegus* and back reef habitat had more influence on potential connectivity for *C. spilurus*. The predicted connectivity hubs identified by our models, particularly those

catering to both focal species, hold significance for Teti'aroa's ongoing restoration efforts. These sites are anticipated to experience elevated social, trophic and nutrient interactions with *C. spilurus* and *A. triostegus*, underscoring their relevance to restoration.

Model assumptions and limitations

Our methodology for identifying suitable habitat patches and potential connectivity hotspots and coldspots for coral reef fishes demonstrates a way forward for linking structure and function in coral reef ecosystems at spatial scales relevant to management and restoration planning (Purkis and Kohler 2008; Welsh and Bellwood 2014; Gupta et al. 2019; Roberts et al. 2021). The success of this integrated modeling approach, however, hinges on the ecological realism of the habitat suitability models developed in the first phase. Moreover, these habitat suitability models are themselves contingent upon the availability and spatiotemporal resolution of input data. We had access to very high-resolution topographic, bathymetric and benthic habitat data, which is not always the case. Although the spatial-environmental predictors applied in our habitat suitability models resulted in satisfactory performance, the inclusion of additional predictors such as water quality and hydrological parameters may further improve model performance. At present, data sets of this nature are scarce for Teti'aroa, constrained by both availability and spatiotemporal extent and resolution. These limitations diminish their current utility and may restrict the generalizability of models including these data. Nonetheless, water quality and hydrological parameters play integral roles in this dynamic system, and we remain hopeful that they can be incorporated into future model iterations as more data become available. Biological factors also play key roles within the Teti'aroa seascape; however, our modeling approach is unable to account for factors such as intra- and inter-specific interactions experienced by the focal fishes as they move throughout the seascape. Such interactions were beyond the scope of this study and warrant further investigation.

We constructed habitat suitability models and connectivity networks using records of *C. spilurus* and *A. triostegus* from all size classes, yet patterns of habitat selection and movement are likely to vary among age and size classes. A previous study from Mo'orea

revealed life-stage specific responses of herbivorous reef fishes, including *C. spilurus*, to hard coral structure and the presence and density of macroalgae (Eggertsen et al. 2020). Therefore, additional research is needed to determine whether habitat suitability and connectivity predictions are transferable across different life stages, such as the pahoro hohoni and pa'ati pa'apa'a auahi stages of *C. spilurus*, as well as the smallest juveniles, locally referred to as ata. Confirmatory techniques such as acoustic telemetry (Hitt et al. 2011) could be used to validate habitat suitability models and construct movement pathways between day and night activity spaces to reveal more detailed habitat use patterns for the two focal species. Furthermore, our short duration daytime surveys represent only a snapshot of species-habitat associations, and these survey techniques may under-represent the presence of the highly mobile schooling species *A. triostegus* which exhibits a spatiotemporally patchy distribution (Han et al. 2016).

Implications for island restoration

More pertinent to conservation action are the areas of overlap where node rankings suggest critical connectivity facilitation for both species. Our models identified lagoonal patches in the north of the atoll adjacent to *motus* Tiaraunu, Hira anae and Oroatera as potential connectivity hotspots for both focal fish species. Similarly, in the south, multi-species connectivity hotspots appear to be concentrated around *motus* Rimatu'u and Onetahi. Data-driven connectivity quantification and hotspot identification for functionally important species can aid management practice by enabling closer examination of the relationships between seascape structure, community composition and ecosystem functioning (Grober-Dunsmore et al. 2009; Olds et al. 2012; Pittman et al. 2021). Through identifying overlapping connectivity hotspots for functionally important herbivorous fishes in Teti'aroa, French Polynesia, this work may inform ongoing restoration efforts within the island system to adequately consider ecological connectivity in a restoration context and serve as a baseline for analyzing future changes.

The spatially explicit areas identified within the seascape as connectivity hotspots may prove most influential for enhancing the resilience of the seascape as a whole, as herbivory is integral to nutrient

cycling and reef resilience. Our study provides spatially explicit findings to inform more nuanced monitoring of outcomes from recent conservation actions on French Polynesia's Teti'aroa Atoll. It is important to note that the connectivity results presented here serve as baseline estimates of ecological connectivity under the conditions at which the input environmental and species presence data were collected. Future restoration and anthropogenic action will alter the seascape, likely influencing habitat suitability and functional connectivity dynamics for herbivorous fishes, as well as other reef fish functional groups. Additionally, future research in this area may benefit from the consideration of other locally abundant and functionally important reef fish species that represent differing trophic groups or ecological functions (e.g., *Scarus psittacus*, *Lutjanus fulvus*, and *Acanthurus nigrofuscus*). Our approach that requires only fish presence locations and accurate benthic habitat and bathymetric maps offers high transferability to other coastal regions where information on seascape connectivity is integrated into conservation planning (MPA design and restoration and monitoring designs).

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Author contributions LMW and EAP conceived and designed the research. CEB, BS, and SJP contributed data inputs. CES contributed analytical expertise. CES, SJP and LMW provided theoretical background and supervision for the study. EAP conducted the analysis and led the writing team. All authors provided feedback on results and interpretation, read and approved the manuscript.

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Data availability Raw habitat and LiDAR data were generated by the Khaled bin Sultan Living Oceans Foundation and Island Digital Ecosystem Avatars (IDEA) program, respectively. The coral reef fish survey data collected by CEB and derived data products established in this study are available on the Open Science Data platform at https://osf.io/pgd8r/?view_only=b4e56cadafd048668f79f61346aa8af8.

Declarations

Ethical approval No animal testing was performed during this study.

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