ARTICLE

Broad-scale analysis of fish community data suggests critical need to support regional connectivity of coral reefs

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Abstract

Connectivity is vital for the biodiversity and functioning of marine ecosystems. It is known to be important for coral reefs, but the scales at which connectivity effects matter—and, correspondingly, the scales at which management responses are needed—are poorly understood in marine systems. We used 23 years of fish monitoring data collected from ~50 different coral reefs by the Australian Institute of Marine Science, together with a range of geographic data layers (including the Allen Coral Atlas) and additional network analysis, to explore the balance of local and regional influence on fish communities. Variance partitioning indicated that 42% of the variance in fish community composition could be explained by regional effects or their interaction with coarse-grained local influences (habitat). The variance explained by regional influences was divided evenly between measures that capture location on environmental gradients (e.g., proximity to coastal shelf, latitude) and cross-scale centrality measures of reef location within a broader reef network. A total of 11% of variance could be directly or indirectly attributed to management. Our results provide clear evidence that management and restoration of reefs across the globe must consider both local and regional influences on reef-associated organisms and highlight the potential benefits of improving connectivity in human-dominated coastal seascapes.

KEYWORDS
conservation, dispersal, fishes, fragmentation, marine, network analysis, scale

INTRODUCTION

Spatial connectivity is central to the persistence of almost all of the world's ecosystems, with transfers of energy or material between locations often being critically important for ecosystem function. The theory of island biogeography (MacArthur & Wilson, 1967) provided an initial entry point for understanding how connectivity might influence entire ecosystems. Subsequent research saw deep insights emerge into such topics as spatial subsidies (Polis et al., 1997), metapopulation dynamics (Hanski, 1999), and fragmentation impacts (Fahrig et al., 2019; Fletcher Jr et al., 2018; Kareiva, 1987; Miller-Rushing et al., 2019; Simberloff & Abele, 1982). Despite numerous advances, substantial gaps remain in our ability to quantify and manage broad-scale ecological connectivity.

Connectivity in the marine environment has long been recognized as important but hard to study

(Steele, 1989; Swanborn et al., 2022). Coral reef ecosystems are considered to be heavily influenced by connectivity (Munday et al., 2009). The relevance of connectivity for coral reefs ranges from detrimental impacts of terrestrial influences (Bainbridge et al., 2018; Tebbett et al., 2021) to the beneficial effects of oceanic currents boosting local productivity through the provision of pelagic subsidies (Morais & Bellwood, 2019). However, it is with the connectivity of populations that most coral reef research and management are concerned (Almany et al., 2017; Munday et al., 2009; Williamson et al., 2016).

Despite significant progress in understanding coral reef connectivity in the past three decades, one problem remains particularly challenging: the issue of scale. Coral reefs support populations that may be panmictic, with populations that are genetically connected across the Indo-Pacific spanning two thirds of the global tropics (Reece et al., 2010). Yet when it comes to the lives of individuals, they are remarkably restricted. Sedentary corals are a clear example of restricted dispersal capability, and many coral reef-associated fishes have home ranges that are in the order of a few square meters (Nash et al., 2015). This diversity of constraints, of different intensities and at different scales, raises critically important questions: which scales are most important in structuring reef populations? How are they manifested? And to what extent are they amenable to management and study?

In this paper, we address this issue using fishes. Reef fishes are both functionally important taxa in reef ecosystems (Bellwood et al., 2019) and important sources of value for reef users, whether via tourism, food production, or other benefits (Bartelet et al., 2022; Eddy et al., 2021; Laurans et al., 2013; Marre et al., 2015). Although there is a body of research on home range use by adult fishes, the relationship of fish home range to body size appears to be very strong (Nash et al., 2015). There is also a growing knowledge base on the seascape connectivity of reefs, with adult individuals moving from one habitat to another (Olds et al., 2012). However, by far the greatest attention has been paid to the role of larval connectivity, that is, the ability of larval fishes to disperse from or return to their natal reef. Indeed, the data from estimated dispersal kernels or maps of connectivity have been instrumental in planning, placing, and justifying networks of marine protected areas around the globe (Almany et al., 2017; Planes et al., 2009; Williamson et al., 2016).

Patterns of connectivity between coral reefs (driven by both geographic proximity and the directional flows of oceanic currents; Benthuysen et al., 2022) are set against a series of environmental and biogeographic gradients from depth and cross shelf to regional gradients, all of which are well known to correlate with significant variation in fish assemblages at almost every scale investigated

(Bellwood & Wainwright, 2001; Connolly et al., 2005). Given this overwhelming range of scale-dependent connectivity and constraints, teasing apart the relative contributions of the various components (specifically, the relative influence of local vs. regional drivers of community composition) is both challenging and important. Understanding the balance between local and regional influences is also critical for coral reef management actions from the setting of harvest limits in relation to the placement of protected areas and, in specific cases, restoration initiatives. Furthermore, if coral loss or reef degradation leads to fundamental changes in ecological parameters such as reproductive rates or dispersal capability, this may have far-reaching implications for reef fish connectivity. These details and possible outcomes are poorly understood (Hogan et al., 2012; Mora & Sale, 2002; Williamson et al., 2016).

To address the question of scale and connectivity in reef fish communities and better understand the likely ecological impacts of tradeoffs between investment in regional (e.g., creation of networks of no-take zones) versus local (e.g., local management) conservation management activities, we analyzed an extensive existing data set for coral reef fish communities of the Great Barrier Reef (GBR). We explicitly aimed to determine how much of the variance in fish community composition is driven by local and regional variables. Although many of these uncertainties will ultimately be best resolved by long-term research in postbleaching environments, existing data sets offer some valuable insights into the relative importance of local and regional influences and patterns of connectivity on fish community composition.

METHODS

Study area

The study focuses on the Great Barrier Reef Marine Park (GBRMP, henceforth "GBR"). The GBR is a long-standing and iconic marine protected area. It is an ideal location for this kind of study because of the number and geographic spread of potentially interconnected coral reefs. Its diversity of habitats and alternative habitat compositions (e.g., ranging from coral-dominated to rock-dominated coral reefs) mean that a single snapshot of local habitat variables in time covers a wide range of conditions and can provide a useful indicator of potential future outcomes when habitat composition changes. In addition, despite its overarching designation as a marine protected area, the area inside the official boundary of the GBR is zoned into different use areas that range from no-visit ("scientific research") zones through to commercial fisheries, providing a gradient of human impacts.

The oceanography of the GBR is dominated by the Pacific South Equatorial Current. As it reaches Australia, the current splits into northerly and southerly flows. The southerly flow forms the East Australia Current, which travels south along the coastal shelf between roughly 18° S and 32.5° S (Steinberg, 2007). Circulation patterns in the northern GBR are more complex, with additional influences from the Hiri Current (which flows along the shelf edge of the northern GBR into the Gulf of Papua) and the North Queensland Current, as well as a series of seasonally variable gyres (Steinberg, 2007). A high degree of local heterogeneity exists in water circulation patterns across the GBR, depending on specific climate conditions, thermoclines, and underlying bathymetry (Berkelmans et al., 2010). High rainfall on the Australian land mass can also lead to significant plumes of freshwater entering the GBR, often bearing substantial amounts of sediment, through the Burdekin and FitzRoy river systems. Although the direction of currents was not specifically included in this study, some additional variance in fish community composition is very likely to be explained by directionality in the connections between different reefs and the occurrence of potential sources of propagules to the north (i.e., from the Coral Sea) but not to the south of the GBR.

Fish data

We used the long-term monitoring data set produced by the Australian Institute of Marine Science (AIMS) for fish on the GBR to explore the relative influences of local and regional influences on fish community composition. The AIMS Long-Term Fish Visual Census of the Great Barrier Reef contains 147,466 individual records for a prescribed list of 212 species sampled periodically at ~50 different reefs from March 1992 to May 2015 (Figure 1). The data are freely and publicly available via the Global Biodiversity Information Facility (GBIF; https://www.gbif.org), from which they were downloaded on 15 February 2022.

According to the latest information provided by AIMS (see https://www.aims.gov.au/docs/research/monitoring/reef/sampling-methods.html, viewed 18 July 2022), the fish count data derive from intensive surveys at three sites per reef along five 50 m × 5 m belt transects. These are located 250 m or more apart (where possible) along "the first stretch of continuous reef (excluding vertical drop-offs) to be encountered when following the perimeter from the back reef zone towards the front reef in a clockwise direction, usually on the north-east flank of the reef" and a depth of 6–9 m. Once larger fish have been counted, the observer swims the transect again recording Pomacentridae (damselfishes). The fish species that are recorded include adults of 212 noncryptic species from 10 families. Reefs are visited on a rotation every 2–5 years. The precise protocols used for collecting the data, details of exactly which reefs are visited and when, and a full list of all observed fish species are available in other publications (Emslie et al., 2014; Jonker et al., 2008; Sweatman et al., 2008).

In the GBIF data set, transect data are combined to give abundance by species for each reef. We first screened these data for outliers, with data for one fish species (*Pomacentrus tripunctatus*, three-spot damsel) being removed. The final data set included 983 rows, with each row containing a different reef–year combination.

Local variables

Our goal was to explore the relative contributions of regional context and connectivity on fish community composition. This necessitated distinguishing true regional effects from the influence of localized, potentially ecologically relevant influences (e.g., areas of sand, rock, or rubble) in habitats where fish were not sampled. To quantify local habitat, we used the recently completed Allen Coral Atlas (ACA, see https://allencoralatlas.org; Lyons et al., 2020). Although more detailed coral cover data are available for the fish data collection sites from long-term AIMS coral surveys (Sweatman et al., 2011; Tsai et al., 2022), we deliberately used the ACA because it provides a single, highly standardized data layer that includes broader elements of coarse-grained structure and geomorphology for each individual reef.

Others have shown that the more detailed AIMS coral cover data set can explain around 40% of the local, fine-grained variance in fish abundance (Tsai et al., 2022). However, the selective focus of the AIMS data on a relatively small and ecologically similar area of each reef means that their description of coral community composition describes broader patch characteristics poorly. Our "local variables" were therefore measured at a grain of 5 × 5 m across an entire patch, rather than based on fine-grained ecological data that match the localized fish sampling locations precisely (as has been the case in previous analyses using the same data set).

The ACA provides the equivalent of a terrestrial land-cover map, consistently describing habitats in and around coral reefs at a resolution of 5 × 5 m. The atlas summarizes relevant habitats using a classification of six different benthic habitat categories (coral or algae, microalgal mat, seagrass, rock, rubble, sand) and 10 different kinds of reef (slope, crest, shallow lagoon, deep lagoon, inner reef flat, outer reef flat, terrestrial reef flat, shallow reef slope, back reef slope, plateau). Its primary weakness from an ecological perspective is the lumping together of
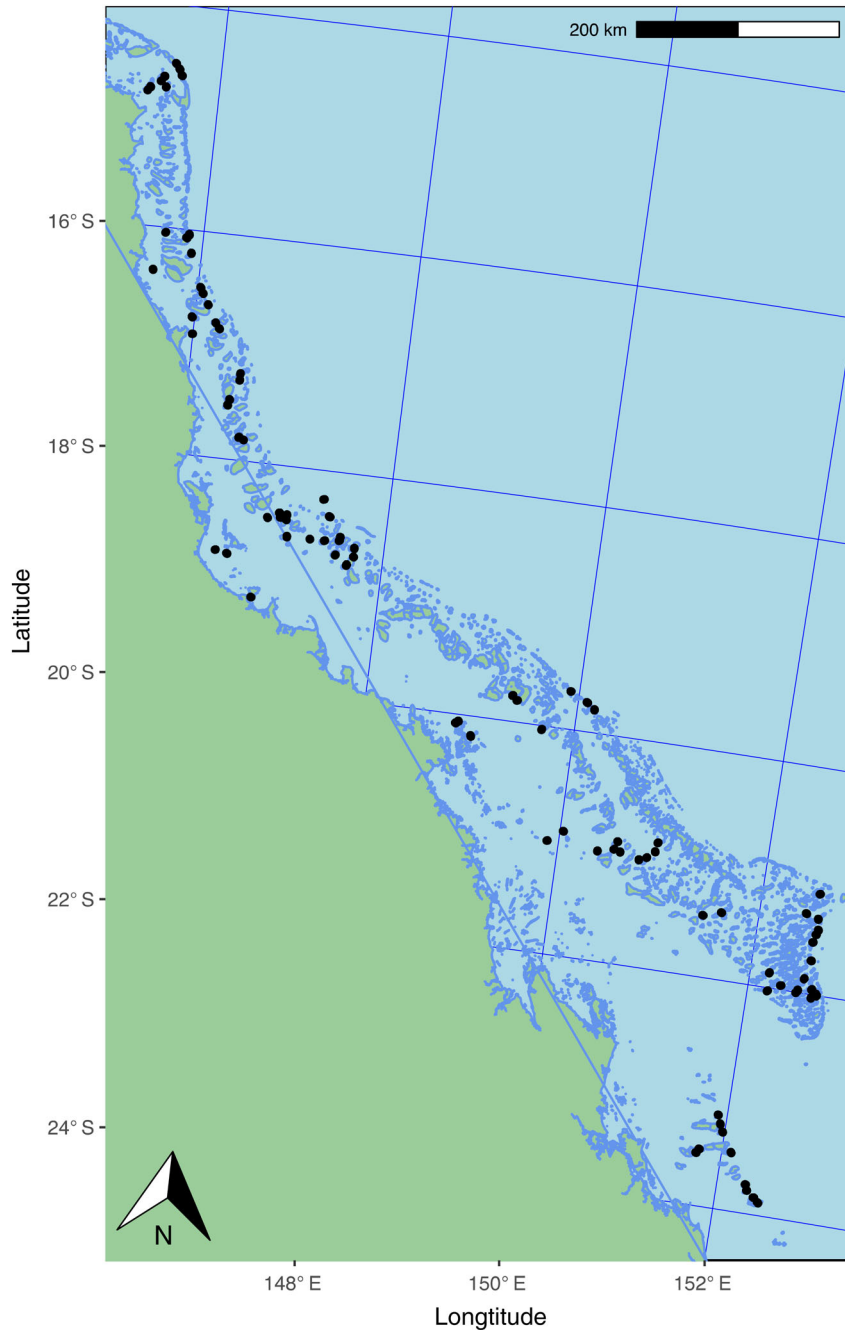
FIGURE 1 Map of Great Barrier Reef showing mainland northeastern Australia (green), boundaries of marine features including reefs, islands, and coastline (blue), and locations (black dots) from which fish data were collected by Australian Institute of Marine Science sampling team.

coral and algae into a single class, due to the challenges of separating their reflectance spectra. As explained earlier, the biggest advantages of the ACA are (1) its capacity for measuring characteristics at the extent of an entire reef in a directly standardized and comparable way and, because of its extensive coverage, (2) it sets the stage for interpolation to a much larger set of unsampled reefs.

We used the Google Earth Engine to clip the ACA data to the extent of the GBRMP and then overlaid the polygon outlines of each feature on the GBR

(GBR Features shapefile) and extracted the number of pixels of each cover type occurring within the boundaries attributed to each reef. Pixels were included if their centroid fell within the polygon boundaries.

Regional variables

The regional context of each individual reef was quantified using three different sets of measurements. The first

was the bounding box for each reef, defined as the smallest rectangle that could fully contain the reef boundary (as measured in the GBR features data layer). The northwest and southeast coordinates for the bounding box provide a precise and continuous measure of where each reef is located relative to both north–south and east–west gradients.

The second set of measurements included the nearest distance of the boundary of each reef to the edge of the coastal shelf, the eastern coast of Australia, and the proportion of distance to shelf relative to the width of the shelf (defined as shortest distance to coast + shortest distance to shelf) in that location. These variables described the reef's proximity to both deeper-water and coastal habitats, providing a surrogate for biogeographic patterns and some elements of dispersal and describing broad-scale differences in vulnerability to wave action and cyclone damage.

The third set of measurements included four different measures of cross-scale centrality for each reef: its degree centrality, betweenness centrality, eigenvalue centrality, and closeness centrality (explained in Table 1). Since the estimation of which reefs are connected is scale-dependent (e.g., reefs 50 m apart are likely to be connected by the direct movements of individual organisms, while those 1000 km apart are not), the estimation of centrality requires either selecting a single scale of connectivity or calculating a cumulative contribution across multiple scales. We adopted the second approach, which is more ecologically realistic given that organisms typically move at a wide range of scales. More detail on the estimation of cross-scale centrality and support for its ecological validity based on a simulation analysis using metapopulation models are provided by Cumming et al. (2022).

Working in an Australian Albers Equal-Area projection, we first calculated the geographic distance in meters between each individual reef pair, taking distance between the nearest edges of each polygon boundary using the *gDistance* command in the rgeos package (Bivand et al., 2017). Distances ranged from 0 m (where features were touching; note that the reef boundaries are coarsely measured, so this could involve the sandy area inside one reef polygon being adjacent to the rocky area of another) to 1964 km (the linear extent of the GBRMP). Distances of 0 m were set to 1 m so that network metrics could be validly calculated (centrality cannot be calculated for nodes that are not geographically distinct).

After calculating the distances between all reef pairs, we converted the paired data to a network in *igraph* format in R (Csardi & Nepusz, 2006) and added geographic distance as an attribute to each between-reef link. Using the network data set, we then estimated node centrality for each reef for each of the four metrics in Table 1. We used *igraph* to estimate all metrics, redefining node connectivity for each calculation using successive thresholds for connectivity. We calculated betweenness centrality

TABLE 1 Definitions and explanations of different centrality measures considered in the analysis.

Centrality measure	How it is measured	What it measures
Degree	No. direct links of each node	In our case, the number of neighboring reefs that can be reached at a given scale of movement without needing to pass through another "stepping stone" reef; simplest of four reef-level measures of connectivity
Betweenness	No. times a node lies on shortest path between other nodes, when all pairs of nodes are considered	Contribution of each reef to overall network connectivity; particularly relevant where some reefs are "stepping stones" or "bridges" that have low-degree centrality (i.e., few immediate neighbors) but play an ecologically important role by connecting two geographically distinct clusters of reefs
Eigenvector	No. connections to other nodes, weighted by how connected ("high-scoring") other nodes are; connections to other high-scoring nodes contribute more than equal connections to low-scoring nodes	Describes how connected each reef is to more highly connected reefs in data set; ecologically, being close to a single large, well-connected reef may have a greater influence on fish species composition than being close to several other less-connected reefs
Closeness	Average length of shortest geographic distance through network from focal node to every other node	How near in space reefs are, on average, to each other in network; goes beyond topology to explicitly consider how far an animal might have to move to get to another reef

Note: A node's centrality describes its importance for the overall connectivity of the network. The potential connections between reefs (nodes) are measured as straight-line distances between reefs (links). The distance of each reef from all other reefs is a rough surrogate measure of the potential for fish to act as mobile links that connect pairs of reefs. We did not attempt to include differences in matrix permeability (e.g., as influenced by benthic habitat type, predation, or water quality) or other possible barriers to movement (e.g., oceanic currents or human infrastructure, such as harbors or shipping lanes) in this analysis.

for 19 different networks with links defined as present at internode distance thresholds of 10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 km. Sampling intervals used two different step distances (1–100 in steps of 10 km and 100–1000 km in steps of 100) because network centrality measures change most rapidly, and nonlinearly, at smaller step distances; since the area under the curve is the parameter being measured, places where change relative to scale is gradual and effectively linear can be adequately approximated using points that are farther apart. We did not consider additional, greater distances because the greatest possible interreef distance was 1964 km. The range of scales considered was therefore up to approximately half the total possible distance. As expected, there was no significant change in network connectivity measures beyond this distance because even the two most-distant nodes can connect through a single central node.

The estimation of centrality measures produced four different centrality matrices, each with a structure in which each row represented a reef and each column a different geographic scale of centrality. Cumming et al. (2022) showed how this data set could be converted into a single variable by summing across its columns to produce a single estimate of cross-scale centrality (CSC) for each feature. In this particular instance, however, given no sample size limitations and a statistical approach that used matrices rather than single variables, we chose to work with each entire matrix rather than to reduce centrality matrices to single columns of data.

Human impact

Fishing activities in the GBR have been shown to impact fish community composition. To correct for this influence, we extracted data for each reef on their protection level, as estimated from GBRMPA's zoning map, noting that many reefs include several different use zones. We treated each zone as an individual variable and calculated the area by reef within each zone. Zones are described in Table 2 and on the GBRMPA's website at https://www.gbrmpa.gov.au/access-and-use/zoning (accessed 18 July 2022).

Statistical analyses

The procedures described produced a series of different variables, each with distinct properties resulting from the nature of the different data sets (Table 2). For example, different cover types and reef types are nonoverlapping areas calculated within a single polygon, so individual totals must add up to either 100% of the reef area or less (depending on whether the full extent of the polygon included any nonreef or deeper-water habitat types). It therefore did not make sense to explore correlations between individual variables.

Our research question asks how local and regional influences, and their interaction, affect fish community structure. Key predictor variables and the response variable were all multivariate. Reducing this kind of problem to a single response variable (e.g., fish species richness) and a set of intercorrelated predictor variables, as in a typical multiple regression model, risks the loss of a considerable amount of potentially important variance within the data and increases the potential for spurious conclusions. A better and widely used approach in community ecology is to compare entire matrices of data using variance partitioning and either canonical (constrained) correspondence analysis (CCA) or redundancy analysis (Borcard et al., 1992; Legendre & Legendre, 1998; Økland & Eilertsen, 1994; Truchy et al., 2019).

Variance partitioning estimates the variance that is explained by individual matrices using partial models. These are created using a subset of the predictor variables in the full model. The fractions of variance explained by each matrix or set of matrices are then grouped into three categories: variance explained purely by an individual variable, variance explained by an interaction effect of an individual variable with one more other variables, and unexplained variance (Borcard et al., 1992). We used an adjusted r^2 value to correct for overfitting. The approach describes the individual and combined influence of different predictor variables on the final model; results are presented as a visually intuitive Venn diagram-type figure, a bar chart that facilitates visual comparison of effect sizes, and in a table that provides more statistical detail about the candidate models.

As summarized in Table 2, we first merged the different local influences into a single matrix ("local") and the regional influences into another matrix ("regional"), keeping time (sampling year) separate as it represents a different kind of variable from the rest. Initial results indicated that time explained a negligible (less than 1%) amount of the variance in the fish community data at this grain and extent of analysis, so we dropped time as an individual variable from the analysis.

To explore the relative contributions of different data sets and the nuances associated with different variables, we used variance partitioning to test three different models of environmental influences (Table 3). All models included identical data, but we grouped the data in different ways to explore interactions between kinds of variable. Model 1 addressed our primary question of whether regional influences had a significant effect on fish

T A B L E 2   Variables considered in this study.

Usage in analysis	Variable(s)	Data source	Description
Response variable	Fish community composition	AIMS data set	Fish community composition over 15-year time period for 983 observations of 50 different reefs
Local variables: unless otherwise specified, all calculated as areas falling within bounds of feature polygon in reef feature data set	Areas of six benthic cover classes: coral or algae, microalgal mat, seagrass, rock, rubble, sand	Allen Coral Atlas	5 m resolution satellite-derived data for entire GBR.
	Areas of 10 reef type classes: slope, crest, shallow lagoon, deep lagoon, inner reef flat, outer reef flat, terrestrial reef flat, shallow reef slope, back reef slope, plateau	Allen Coral Atlas	5 m resolution satellite-derived data for entire GBR.
	zonation as eight different zones: (1) Buffer; (2) Commonwealth Island; (3) Conservation Park; (4) General Use; (5) Habitat Protection; (6) Marine National Park; (7) Preservation; (8) Scientific Research	GBR Marine Park Authority	Describes permissions and restrictions on human use of a given area; zones with higher no. offer more stringent levels of protection, as explained at https://www.gbrmpa.gov.au/access-and-use/zoning
Time	Year	AIMS data set	
Regional variables: describe geographic context of reef in relation to gradients, oceanography, and other reefs	X1, Y1, X2, and Y2	Calculated in R from GBR features data set	Northwest and southeast coordinates of corners of bounding box for each reef
	Cross-scale connectivity (CSC) estimated using betweenness centrality, degree centrality, eigenvalue centrality, and closeness centrality. Individual distances across 19 different scales as described above.	Calculated in R from GBR features data set; distances are nearest edge of each polygon to nearest edge of next polygon	Describes contribution of each reef to overall network connectivity
	Distance to edge of coastal shelf, distance to coast, and ratio of distances	Calculated in R using GBR features and coastal shelf data sets.	These three variables respectively describe reef distance to edge of continental slope, reef distance to coast, and proportion of reef distance to coast relative to total distance from coast to shelf for that reef; all distances were calculated as nearest distance between polygon edges

Note: Each variable consisted of a site (row) by variable (column) vector or matrix. For example, the site × species matrix for the fish community data contained each location–year combination as a row and the abundance of each fish species as columns, where each species corresponds to one column of data. Further details on data sources and how each variable was estimated are presented in the text.

Abbreviations: AIMS, Australian Institute of Marine Sciences; GBR, Great Barrier Reef.

communities on the GBR. Model 2 offered further insights into the variance in fish community composition explained by management impacts, and Model 3 provided complementary information about the relevance of network connectivity relative to location in space and along environmental gradients.

All models were run using the *varpart* command in the vegan R package. Note that changing model structure also influences the strengths of interaction effects, so changes in explained variance in Models 2 and 3 should not be interpreted as altering the primary conclusions provided by Model 1. We did not explicitly include additional interaction terms between variables in our models because there was no underlying reason to expect a multiplicative interaction. In considering spatial processes, note also that the coordinates of each location are

TABLE 3 Summary of different models for which results are presented.

Model summary	Explanatory data	Response data
Model 1: Local ALL + Regional ALL = Response	Regional ALL: X1, X2, Y1, Y2; distance to shelf, to coast, and ratio of shelf distance: coast–shelf distance; centrality (one of degree, betweenness eigenvector, or closeness) across 19 scales (27 variables in total)	Fish community matrix: 983 samples by 249 species
	Local ALL: Benthic classes ($n = 6$), reef type classes ($n = 10$), management zones ($n = 8$). (24 variables in total)	
Model 2: Local ENV + Regional ALL + Zonal = Response	Regional: X1, X2, Y1, Y2; distance to shelf, to coast, and ratio of shelf distance: coast–shelf distance; degree centrality across 19 scales (26 variables in total)	Fish community matrix: 983 samples by 249 species
	Local ENV: Benthic classes ($n = 6$), reef type classes ($n = 10$) (16 variables in total)	
	Zonal: management zones ($n = 8$) (8 variables in total)	
Model 3: Local ALL + Regional CSC + Regional GEO = Response	Regional GEO: X1, X2, Y1, Y2; distance to shelf, to coast, and ratio of shelf distance: coast–shelf distance (7 variables in total)	Fish community matrix: 983 samples by 249 species
	Regional CSC: degree centrality across 19 scales. (19 variables in total)	
	Local ALL: benthic classes ($n = 6$), reef type classes ($n = 10$), management zones ($n = 8$) (24 variables in total)	

Note: With 983 rows of data and 50 potential predictor variables, we had more than adequate statistical power with 19.6 observations per predictor variable. Since degree centrality emerged in Model 1 as the centrality metric with the highest explanatory power, we did not include additional centrality metrics in Model 2 or 3.

captured in the bounding box variables; these data capture variance that can be explained purely by geographic location and, hence, any direct influence of spatial autocorrelation (Legendre & Legendre, 1998). The variance explained separately by cross-scale metrics is therefore independent of spatial autocorrelation in fish community composition.

After completing the variance partitioning component of the analysis, we used CCA ordination plots and ANOVA tests to visualize the local and regional matrices relative to the fish community data as a way of obtaining further insights into which environmental variables were most heavily influencing the results.
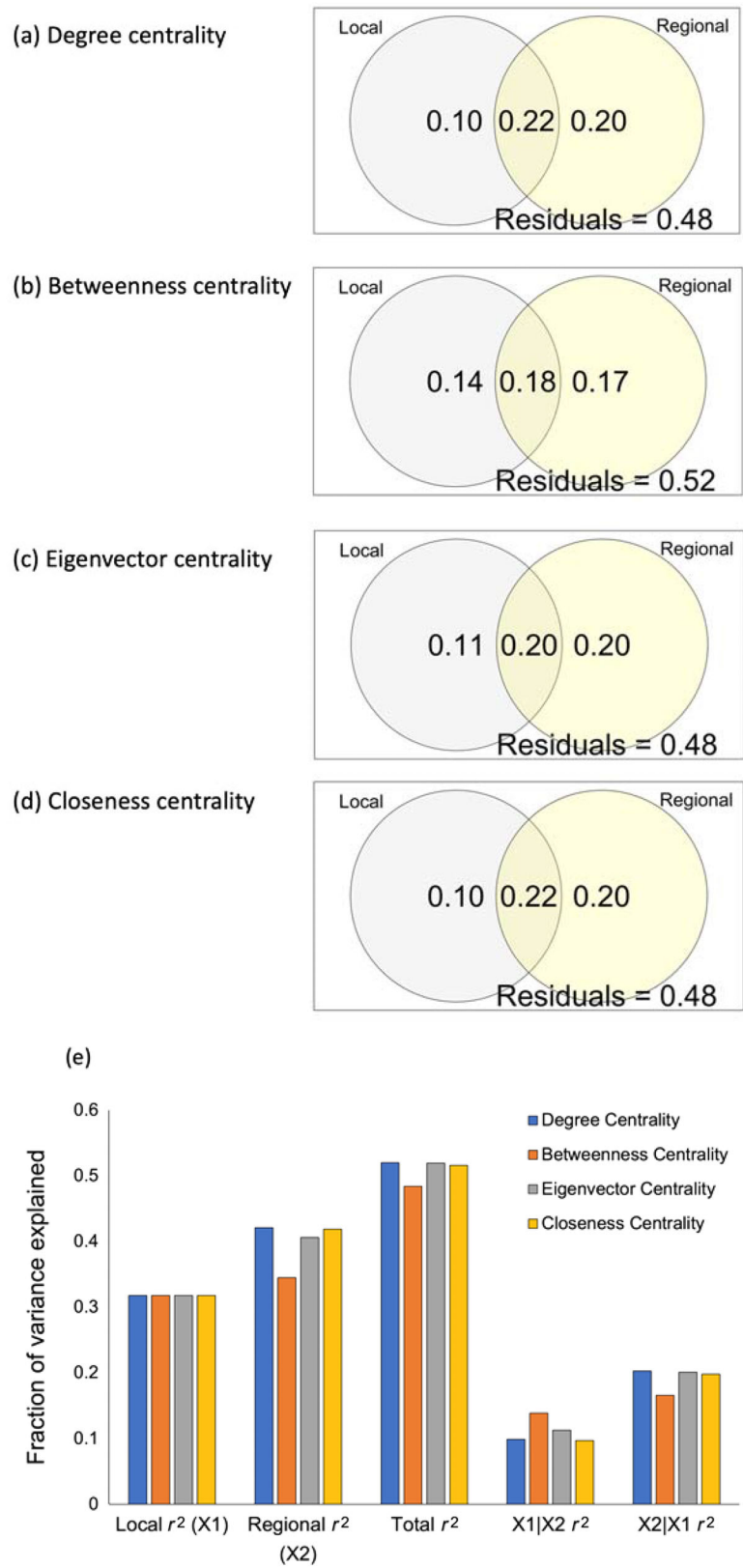
RESULTS

Model 1 showed that the predictor variables included in the analysis could explain just over half (52%) of the variance in the fish community data set. The four different measures of cross-scale connectivity produced similar results; the total variance explained by connectivity in Model 1 varied between 35% and 42% (Figure 2 and Table 4), with betweenness centrality performing worse than the other centrality metrics. Regardless of how it is measured, cross-scale centrality can explain significant amounts of variance in fish community composition. Of the four measures, degree centrality offered the

highest explanatory power (Table 4). Explained variance in Model 1 suggested that differences in fish community composition on the GBR derive from local factors (10%), regional factors (20%), and the interaction between regional and local factors (an additional 22%). The year of sampling did not significantly explain differences between fish communities, either directly or in interaction with other variables.

Model 2 used the same data as Model 1, with degree centrality as the connectivity metric, but separated out zonation from other local variables (Figure 3). This analysis indicated that, although zonation independently explained just 3% of the variance in local fish community composition, together with regional influences it explained 10% of the variance. Interaction effects that included zonation explained 8% of fish community variance, and zonation contributed in some way toward explaining 11% of all variance. Thus, there is clear evidence for a significant impact of management on fish communities across the GBR. The precise r^2 values associated with each matrix were local (0.225), regional (0.421), and zone (0.113) (Figure 3). Conditional r^2 values were (local|regional + zone) 0.057, (regional|local + zone) 0.202, and (zone|local + regional) 0.034.

Model 3, again using the same data partitioned differently and degree centrality as the measure of connectivity, suggested approximately equal contributions to regional variance from geographic and connectivity variables (Figure 4). Connectivity explained about 7%
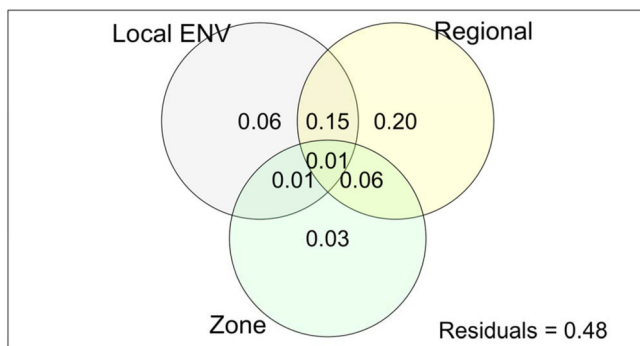
F I G U R E 2 Results of variance partitioning using (a) degree centrality, (b) betweenness centrality, (c) eigenvector centrality, and (d) closeness centrality; and (e) the same results summarized as a bar chart for easier comparison. In the partitioning diagrams, the gray circle describes variance in fish community composition explained by local variables; the yellow circle, variance explained by regional variables. The intersection of the two circles describes variance explained as a function of the interaction between local and regional variables. Analyses using degree centrality and closeness centrality both attribute 42% of variance in fish communities to regional factors (specifically, to the location of fish communities relative to those on other reefs and across environmental gradients, rather than local habitat types). Statistics in Table 4.

TABLE 4 Summary of statistical results from variance partitioning in Model 1 using different centrality measures to describe regional connectivity.

| Centrality metric	Local r^2 (X1)	Regional r^2 (X2)	Total r^2	X1|X2 r^2	X2|X1 r^2
Degree centrality	0.318	0.421	0.520	0.099	0.203
Betweenness centrality	0.318	0.345	0.484	0.139	0.166
Eigenvector centrality	0.318	0.406	0.519	0.113	0.201
Closeness centrality	0.318	0.419	0.516	0.097	0.198

Note: In all cases, total variation (SS) was 147,063 and variance 149.76; all reported r^2 values are adjusted. Columns are respectively for local (X1 r^2), regional (X2 r^2), and total variance explained (Total r^2), and conditional probabilities of local given regional (X1|X2 r^2) and regional given local (X2|X1 r^2) data.

FIGURE 3 Results of variance partitioning in Model 2 using local (gray) and regional (yellow) variables, with management variables (green) separated from other local variables. The regional variables remain the same as in Model 1. Local variables were divided into local environmental variables (Local ENV) and management zones (Zone).

($r^2 = 0.073$) of fish community variance independently, and reef location on the Earth's surface and relative to the continental shelf explained another 6% ($r^2 = 0.056$) of variance. The matrix of variables relating to location along gradients gave a cumulative r^2 of 0.285, and the degree centrality matrix gave a cumulative r^2 of 0.289. Thus, regional explanations for reef fish community composition appear evenly split between the influence of gradients and location (28.5%, including interaction effects) and the degree of connectivity to other reefs (28.9%, including interaction effects). About 20% of variance explained by regional variables was not due to interaction effects with local variables.

CCA of the fish community data projected on the regional data (as used in Model 1) indicated a significant relationship between the fish community and the regional environment ($\chi^2 = 0.69$, $F = 15.63$, df 26, $p < 0.001$; residual = 956, χ^2 of residual = 1.6). For the local data,
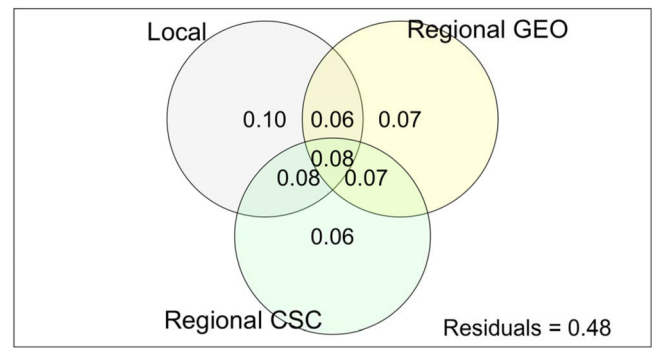
FIGURE 4 Results of variance partitioning in Model 3 using local (gray) and regional (yellow) variables, with management variables (green) separated from other local variables. Local variables in this model are the same as in Model 1 and include management zones. Regional variables are divided into regional geographic (GEO) variables that describe location and position along gradients and regional cross-scale centrality (CSC), which describes the network centrality of each reef as described in the text.

results were comparable but with slightly lower χ^2 statistic estimates ($\chi^2 = 0.50$, $F = 11.06$, df 24, $p < 0.001$; residual 958, χ^2 of residual = 1.8).

Visualization of site and species relationships for regional and local variables independently, using the first two axes identified by the CCA and degree centrality as the connectivity measure (Figures 5 and 6), provided some additional insights. First, for the regional variables (Figure 6), northing, easting, network centrality, and location relative to the continental shelf appeared to provide distinct axes of environmental variation.

Second, for the local variables, different variables included in the analysis provided a wide range of explanatory influences (i.e., arrows indicate that an environmental influence occurred over a wide range of different angles). The most influential variables, indicated by the lengths of the arrows in Figures 5 and 6 (full details in Appendix S1), were either those relating directly to reef characteristics (areas of reef crest, reef slope, reef flat) or particular use zones (notably Zones 1 [buffer], 5[habitat protection], and 8[scientific research only]). Clustering of the fish community based on the CCA axes (Appendix S2) produced no intuitively obvious patterns. These clusters could be explored for possible correlations with body size or ecological role, but this was not the objective of the paper.

DISCUSSION

The results showed that 42% of variance in coral reef fish community composition could be explained either by
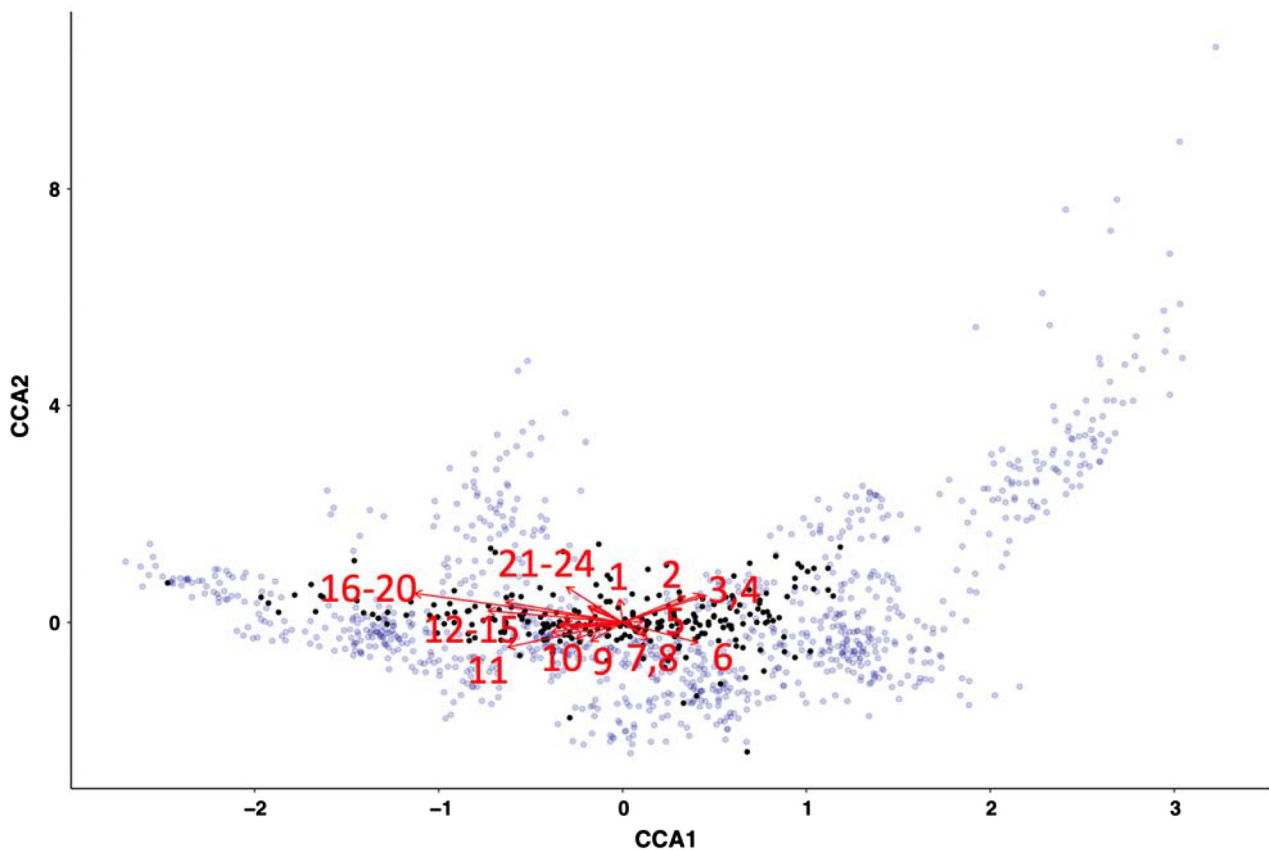
FIGURE 5 Canonical correspondence analysis and overlay of fish and reef data (black dots are fish species; blue dots are locations) over axes of local environmental variation (red arrows). The number of different environmental variables in this data set makes it difficult to see patterns in this figure, but the basic divide shown by the arrows appears to reflect reef flat (right-pointing arrow) and reef slope (left-pointing arrow) habitats. The coordinates of each arrow tip on this plot are given in Appendix S1. Numbers on arrows refer to variables (ordered longest to shortest arrow in cases of significant overlap): 1 = Great Barrier Reef Marine Park Authority (GBRMPA) Zone 8 (Scientific Research); 2 = GBRMPA Zone 2 (Commonwealth Island); 3 = rubble; 4 = terrestrial reef flat; 5 = plateau; 6 = GBRMPA Zone 5 (Habitat Protection); 7 = GBRMPA Zone 4 (General Use); 8 = back reef slope; 9 = shallow reef slope; 10 = deep lagoon; 11 = reef slope; 12–15 = inner reef flat, seagrass, shallow lagoon, macroalgal mats, corals/coralline algae; 16–20 = reef crest (longest arrow), GBRMPA Zone 1 (Buffer), rock, sand, GBRMPA Zone 6 (Marine National Park); 21–24 = outer reef flat (longest arrow), GBRMPA Zone 3 (Conservation Park), GBRMPA Zone 7 (Preservation).

regional context and potential connectivity or by the interaction of regional variables with local variables. The level of local protection and coarse-grained measures of the composition of the benthic surface and the areas of different reef habitat types explained another 11% of fish community variance. Although local habitat is important for reef fish communities, the results highlight what appear to be some highly significant ecological processes operating at and across regional scales. This finding supports and generalizes previous population-level research on large-scale connectivity in the GBR (Williamson et al., 2016). Connectivity, measured as nondirectional cross-scale degree centrality across the reef network, emerged as the single most important influence on reef fish communities from among the candidate variables.

The results must be interpreted in light of the strengths and weaknesses of the data that were used in this analysis. Given the coarse measures of both habitat and connectivity, the proportion of fish community variance explained here seems surprisingly high. We would expect that more precise and detailed measures of disturbance history and habitat quality, for example using coral species composition and structure (and reliably separating algae from coral), would explain a considerable proportion of the remaining 48% of community-level variance (Messmer et al., 2011, but see also Wismer et al., 2019). Indeed, Tsai et al. (2022) used fine-grained data on coral community composition to explain 40% of variance in fishes' long-term mean abundance as a consequence of volatility in coral cover. It is not possible to reconstruct the ACA for 2016; but, looking ahead and assuming that
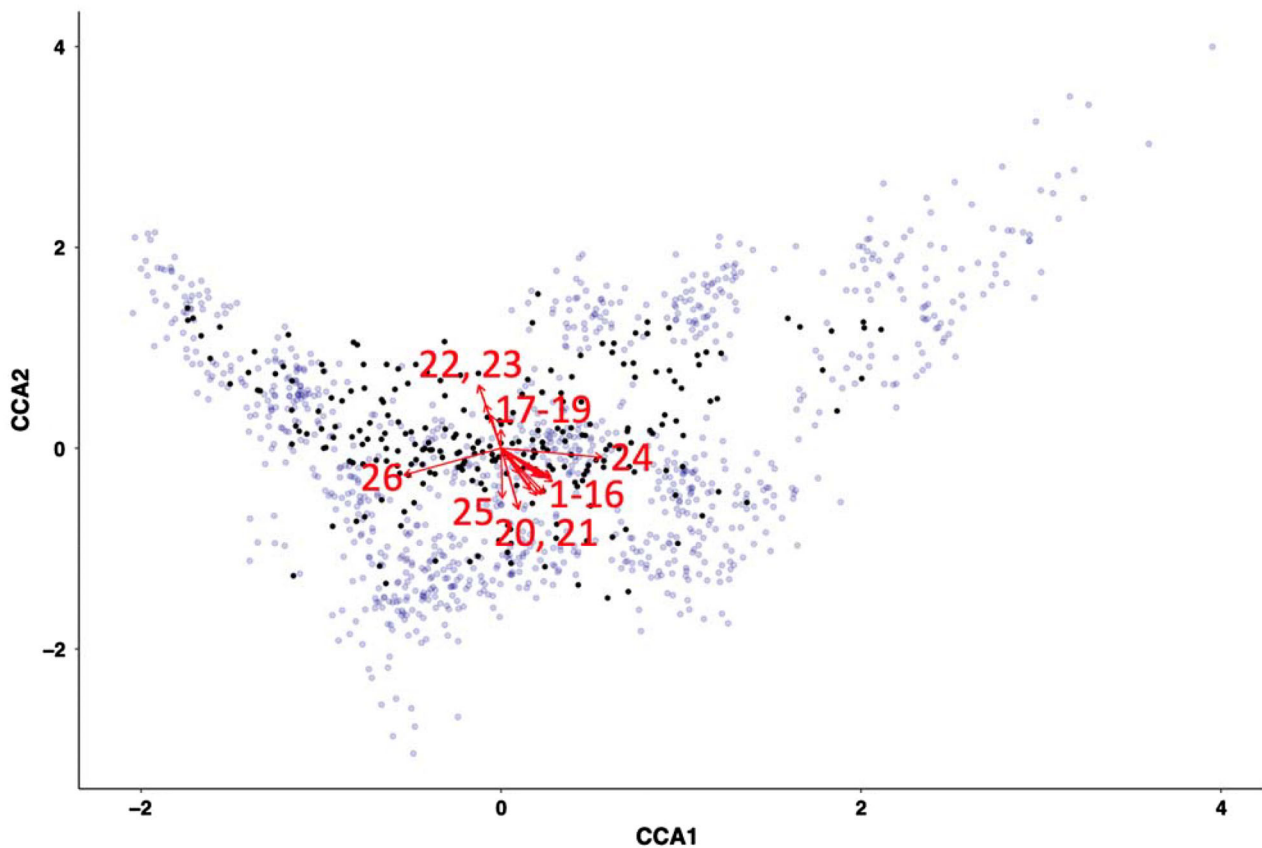
FIGURE 6 Canonical correspondence analysis projecting fish data (black dots) and reef data (blue dots) onto axes of regional environmental variation (red arrows). Network centrality (arrows mainly pointing to lower right quadrat of this plot) describes a subset of locations and species occurrences particularly well while being less directly relevant for some other locations and species. The coordinates of each arrow tip on this plot are given in Appendix S1. Numbers on arrows refer to variables (descriptions are ordered longest to shortest arrow in cases of significant overlap): 1–19 = cross-scale centrality measures; 20 = x-coordinate of bounding box, upper left corner; 21 = x-coordinate of bounding box, bottom right corner; 22 = y-coordinate of bounding box, upper left corner; 23 = y-coordinate of bounding box, bottom right corner; 24 = distance to shelf; 25 = distance to mainland; 26 = ratio of shelf: coast distance.

AIMS continues collecting fish community data, future iterations of the ACA will be able to use the current version of the ACA data set as a baseline and consider whether the balance of regional and local influences is shifting as the relative composition of reef habitats and the structure of the reef network change.

Several previous studies described and supported a role for connectivity as an important influence on reef fish communities at smaller geographic extents (Jones et al., 2020). The statistical interactions between reef connectivity and reef proximity to the continental slope reflect the density of reefs in different locations along an environmental gradient from the deep ocean to the land. Their nonrandom association means that teasing out the relative influences of connectivity and location relative to the reef slope will remain challenging. The inclusion of more detailed data on oceanic currents, and particularly on the potential influence of current velocity on the strength of connections between reefs (Benthuysen et al., 2022), offers

an obvious area for further refinement; the data set could also be improved by adding information about other relevant influences, such as water quality and fishing pressure. Regardless of potential improvements in the data set used in this analysis, however, the findings indicate a strong regional influence on fish communities in the GBR. Even if improved measurement of local variables were to explain substantially more variance in the fish community data (i.e., beyond the 10% explained here), regional effects and their interactions would still explain 42%. Including more or better local variables would have little impact on the overarching conclusions of this study. Consideration of the relationships of individual fish species to the measured variables would clarify which environment–fish community interactions are most responsible for the observed trends, and there is clear potential for the development of indicator species to capture both local and regional influences on the fish community. Our focus here is, however, on scale and the bigger-picture question of the relative

influences of local and regional drivers on fish community composition.

Our analysis emphasizes the role of interreef connectivity, as measured using cross-scale centrality. With the exception of *Bolbometopon* parrotfish (Bellwood & Choat, 2011), few benthic reef fishes are believed to move between reefs. The strong effect of connectivity is likely to be driven largely by pelagic larvae as the key link. There is strong evidence that the direction and speed of ocean currents can significantly affect fish larval dispersal and settlement (Harrison et al., 2012; Williamson et al., 2016); but there also appear to be some specific scale-dependent effects operating. Given an increasing emphasis on self-recruitment and closed population models in coral reef science, the concept of source–sink dynamics (i.e., dynamic interactions between locations that are net producers or net importers of individuals) has been less in favor in recent analyses (Gilroy & Edwards, 2017). Our centrality results, however, suggest that between-reef connectivity at a number of scales, including between reefs and among reefs within a region, is important in determining reef fish community composition.

These results have important implications for the conservation, restoration, and management of coral reefs, both in Australia and globally. In particular, they suggest ways in which the scales of management can be more appropriately aligned to the scale of ecological processes. To elaborate, in areas like the GBR where there is a relatively high density of reefs, connectivity across the network of reef habitats appears to be critical to maintaining reef fish community composition. As in terrestrial systems, shotgun approaches to local conservation or restoration of individual reefs will clearly be inadequate to sustain functionally and taxonomically diverse fish communities (McRae et al., 2012; Wintle et al., 2019). If the quality of coral reef habitats declines regionally, a network perspective on the conservation and management of coral reef fisheries (including the roles of both geographic proximity and the modifying influence of oceanic currents on the connections between reefs) will become increasingly important. This in turn suggests a strong need for increased attention to a set of concrete and feasible conservation actions: (1) removing potential anthropogenic barriers to fish connectivity, such as polluted, noisy, or sediment-laden environments, and managing those that qualify as ecological traps or sinks (Komyakova et al., 2021; Swearer et al., 2021); (2) focusing conservation efforts on reefs that contribute more to overall network connectivity (as quantified using cross-scale betweenness centrality); and (3) reducing fishing pressure and other stressors on reefs that act as sources of propagules for the entire network (e.g., those that host spawning aggregations or retain larger areas of intact coral).

The GBR already has an effective and well-implemented zonation plan in place to manage fishing and tourism impacts. Finer-scale, more-intensive analyses of fish populations have demonstrated the effectiveness of no-take zones in bolstering populations of fisheries species (Harrison et al., 2012; Russ et al., 2008). However, no-take zones as defined in the current management plan for the GBR were not located using estimates of their potential contribution to either adult or larval dispersal. Although the proportion of variance in pre-2016 reef fish communities that was explained either directly or indirectly by zonation was only 11%, this proportion is likely to increase substantially if fish populations are pushed toward local extinction by declines in coral reef habitat quality. Under a low-habitat scenario in which substantial areas of coral are removed or degraded by global heating, high-quality unfished reefs are likely to become increasingly important refugia. With the GBR under threat and clear evidence that connectivity matters for fish communities, affording greater protection to reefs that have a high cross-scale betweenness centrality offers a tangible management response.

It remains to be seen whether our results will be equally relevant for locations beyond the GBR, particularly those in which reef density is lower and reefs are more isolated. There is no obvious reason why broad-scale connectivity might be less important in areas of high reef density, such as the Coral Sea. Some additional insights into the long-term nature and implications of connectivity are provided by evolutionary biogeography and phylogenetics; given that cross-scale centrality appears to offer a useful approach for capturing regional elements of fish community composition, a possible next step following from this analysis would be to test whether cross-scale connectivity explains fish community composition better within as opposed to between biogeographic regions. In general, our results suggest that for ecosystems in which coral reefs have the potential to exchange fishes, the integrated management of habitat, environmental context, and human activities to maximize connectivity offers a potentially vital, feasible, but little-explored focus for the next generation of management approaches.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R code (Cumming & Bellwood, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.7739234. Fish data (Sweatman et al., 2008) were accessed via GBIF.org on 23 August 2022 at https://doi.org/10.15468/qzw2et. To quantify local habitat, we used the Allen Coral Atlas: Lyons et al. (2020), Kennedy et al. (2021); https://allencoralatlas.org (Allen Coral Atlas 2022, accessed 16 March 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.