Received: 15 November 2022 | Revised: 30 March 2023 | Accepted: 19 April 2023
DOI: 10.1002/eap.2867

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

β-diversity reveals ecological connectivity patterns underlying marine community recovery: Implications for conservation

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Funding information
European Community 7th Framework Programme (FP7/2007–2013), Grant/Award Number: 287844

Handling Editor: Marissa L. Baskett

Abstract

As β-diversity can be seen as a proxy of ecological connections among species assemblages, modeling the decay of similarity in species composition at increasing distance may help elucidate spatial patterns of connectivity and local- to large-scale processes driving community assembly within a marine region. This, in turn, may provide invaluable information for setting ecologically coherent networks of marine protected areas (MPAs) in which protected communities are potentially interrelated and can mutually sustain against environmental perturbations. However, field studies investigating changes in β-diversity patterns at a range of spatial scales and in relation to disturbance are scant, limiting our understanding of how spatial ecological connections among marine communities may affect their recovery dynamics. We carried out a manipulative experiment simulating a strong physical disturbance on subtidal rocky reefs at several locations spanning >1000 km of coast in the Adriatic Sea (Mediterranean Sea) and compared β-diversity patterns and decay of similarity with distance and time by current transport between undisturbed and experimentally disturbed macrobenthic assemblages to shed light on connectivity processes and scales involved in recovery. In contrast to the expectation that very local-scale processes, such as vegetative regrowth and larval supply from neighboring undisturbed assemblages, might be the major determinants of recovery in disturbed patches, we found that connectivity mediated by currents at larger spatial scales strongly contributed to shape community reassembly after disturbance. Across our study sites in the Adriatic Sea, β-diversity patterns suggested that additional protected sites that matched hotspots of propagule exchange could increase the complementarity and strengthen the ecological connectivity throughout the MPA network. More generally, conditional to habitat distribution and selection of sites of high conservation priority (e.g., biodiversity hotspots), setting network internode distance within 100–150 km, along with sizing no-take zones to cover at least 5 km of coast, would help enhance the potential connectivity of Mediterranean subtidal rocky reef assemblages from local to large scale. These results can help improve conservation planning to achieve the goals of promoting ecological connectivity within MPA networks and enhancing their effectiveness in protecting marine communities against rapidly increasing natural and anthropogenic disturbances.

KEYWORDS
distance–decay similarity, experimental marine ecology, marine protected areas, Mediterranean Sea, reserve networks, resilience, rocky reef communities

INTRODUCTION

While prioritizing areas to protect a representative portion of marine biodiversity at a regional scale can be relatively feasible (Asaad et al., 2018; Coll et al., 2012; Micheli et al., 2013), siting and spacing of marine protected areas (MPAs) to match ecological connections among protected communities is far more challenging (Balbar & Metaxas, 2019; Gaines et al., 2010; Gouhier et al., 2013). Yet, ecological spatial connectivity enables a collection of MPAs to function as a network that can bolster the persistence of marine communities at a larger spatial scale given local-scale natural and anthropogenic disturbances and environmental changes (Carr et al., 2017; Robert et al., 2021). Although MPAs have been recognized to promote the resilience (here referred to as the ability of a system to maintain and/or restore its structure and functions in the face of disturbance; Côté & Darling, 2010; Hodgson et al., 2015) of protected communities by either increasing their resistance to environmental instability or enhancing their recovery after disturbance (e.g., Aller et al., 2017; Babcock et al., 2010; Baskett & Barnett, 2015; Bevilacqua et al., 2006; Bevilacqua, Vellani, et al., 2022; Fraschetti et al., 2013; Roberts et al., 2017), the potential of these effects to extend beyond the reserve boundaries might, indeed, strongly depend on their spatial arrangement (Boero et al., 2016; Steneck et al., 2009). The spatial architecture and connectivity patterns among spatial units underlie the vulnerability of ecosystems in the face of external sources of perturbation (Scheffer et al., 2012), and our understanding of these dynamics is essential to inform conservation and mitigation strategies (Grorud-Colvert et al., 2014).

β-diversity is a primary descriptor of spatial variation in community structure, quantifying how species composition differs among spatial units within the landscape (Whittaker, 1972) and, ultimately, how local- and regional-scale diversity are related (Witman et al., 2004). A complex interplay among environmental factors and biological processes, including historical and biogeographic constraints, may influence the spatial distribution of species and metacommunity assembly (Soininen, Lennon, & Hillebrand, 2007). However, larval dispersal, supply of asexual propagules (e.g., viable fragments), adult movements, and all aspects concerning the flux of matter and energy among patches can strongly affect the outcome of recruitment, species interactions, and other processes (Lewin, 1986; Mouquet & Loreau, 2003; Underwood & Fairweather, 1989), thereby significantly contributing to the generation of β-diversity patterns. In this view, β-diversity can be seen as a proxy of ecological connectivity, as the similarity in species composition among different places not only indicates shared environmental features or common local-scale biological interactions but also the potential for the exchange of individuals among populations and communities (Chiantore et al., 2018; Hewitt et al., 2005; Thrush et al., 2013).

The analysis of the two additive components of β-diversity, which account for the two mechanisms causing changes in species composition from one place to another, namely, turnover (species replacement) and nestedness (species gain or loss), could also help to distinguish processes generating β-diversity (Baselga, 2010). β-diversity is due to nestedness when differences in species composition between two assemblages depend on differences in species richness, and the poorer assemblage is a subset of the richer one; turnover occurs when differences in species composition depend on the replacement of species (Figure 1a). When differences in species composition are due to both species replacement and change in species richness, both components contribute to the overall β-diversity (Figure 1a). Directional changes in conditions, resources, and/or habitat availability, for instance, often influence ordered patterns of species gain or loss along environmental gradients leading to nested communities (Bender et al., 2017; Stuart et al., 2017). Species turnover, instead, may arise from species sorting due to environmental filtering or limits to dispersal (Victorero et al., 2018).

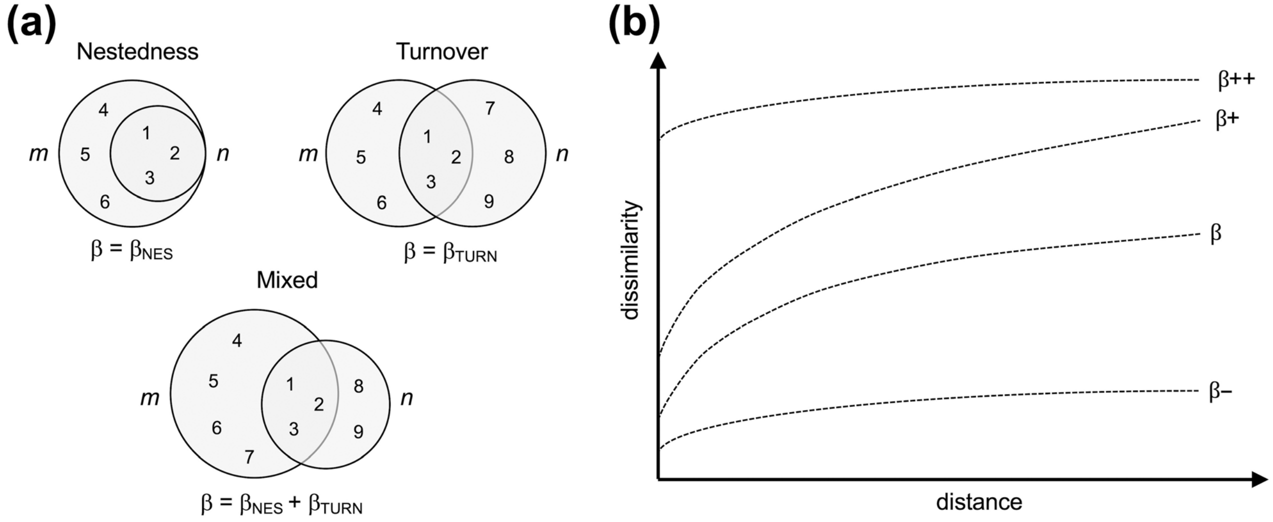

FIGURE 1 (a) Venn diagrams showing contribution of nestedness (β_{NES}) and turnover (β_{TURN}) to total dissimilarity (β) between two hypothetical assemblages *m* and *n* (numbers represent different species). $\beta = \beta_{NES}$: species richness in *m* (α_m) is higher than in *n* (α_n), *n* has no distinctive species and is a subset of *m*; $\beta = \beta_{TURN}$: $\alpha_m = \alpha_n$, distinctive species of *m* (4, 5, 6) are replaced by the same number of distinctive species in *n* (7,8,9); $\beta = \beta_{NES} + \beta_{TURN}$: $\alpha_m > \alpha_n$, *m* has more distinctive species than *n*, therefore a portion of distinctive species is replaced between the two assemblages (turnover) and the remaining portion represents species gain/loss (nestedness). (b) Hypothetical distance–dissimilarity relationships of marine assemblages in a region. (−β) Dissimilarity is low from local to large scale, local-scale environmental conditions and processes (e.g., species interactions) are similar over the whole region, dispersal is not limited (e.g., absence of strong geographic and/or environmental barriers, intense current transport), and the potential connectivity is high. (β) Dissimilarity is scale-dependent, increasing with distance, local-scale environmental conditions and processes change across the region, dispersal is limited; increasing slope and intercept (+β) reflect increasing β-diversity from local to large scale: The potential connectivity is mid/low. (++β) Environmental conditions and processes are highly heterogeneous from local to large scale and the potential connectivity is very low.

The relative contribution of the two components to differences between local- and large-scale species pools, moreover, provides further insights on the connectivity and resilience potential of marine communities in a given region (Chiantore et al., 2018; Thrush et al., 2013).

A well-known macroecological pattern reflecting changes in β-diversity across multiple spatial scales is the decay of similarity in community composition at increasing distance. The distance–decay of similarity depicts how biodiversity is distributed over a given spatial extent, its spatial heterogeneity, and discontinuities in β-diversity patterns, thereby assisting the identification of the scale of ecological connectivity to inform interreserve distance in MPA networks (Nekola & White, 1999). Typically, distance–decay relationships can be represented by fitting an exponential or power model of (dis)similarity against geographic distance. Changes in shape, slope, and intercept of the model may spotlight mechanisms behind the observed patterns of increasing dissimilarity at increasing distance (Figure 1b).

The slope of the curve represents the rate at which β-diversity changes with distance, which is a measure of the scale dependency of β-diversity (Soininen, McDonald, & Hillebrand, 2007). Smoothed slopes indicate that the rate of species change varies slowly with increasing spatial scale, suggesting habitat and/or environmental homogeneity across the investigated spatial extent, lack of strong barriers to dispersal, and, therefore, high potential for connectivity (Figure 1b). In contrast, sharp slopes imply that species change is highly scale dependent, indicating habitat heterogeneity, changes in the environmental features, or limits to dispersal, which suggest a low potential for connectivity. Also, the average initial value of β-diversity, identified by the intercept of the model, provides indications about small-scale dissimilarity, potential small-scale connectivity, and habitat patchiness (Figure 1b).

In the last two decades, research in marine conservation has increasingly focused on the importance of β-diversity in the setup and implementation of effective networks of MPAs (Bevilacqua & Terlizzi, 2020; Carlos-Júnior et al., 2019; Socolar et al., 2016; Winberg et al., 2007). However, field experiments investigating β-diversity patterns are scarce and limited to spatial extents of tens of kilometers at best (e.g., Thrush et al., 2013). To our knowledge, models of distance–decay of similarity have never been applied to the exploration of the spatial and temporal patterns of β-diversity among recovering communities, the elucidation of mechanisms actually contributing to community reassembly following a disturbance, and the assessment of the relative importance of self-repair processes against connectivity potential at local or even large spatial scales.

In the Mediterranean Sea, efforts in marine conservation have greatly increased over the last 20 years, leading to the establishment of over a thousand MPAs throughout the basin, with a total protected surface of about 12% (MAPAMED, 2022). However, a general low level of enforcement and governance of MPAs and the lack of systematic approaches to conservation planning and shared management strategies have raised broad general concerns on the effectiveness of MPAs in protecting marine biodiversity and representing ecologically coherent networks across the basin (Claudet et al., 2020; Fraschetti et al., 2018). This fragmentation is even more problematic for subbasins involving strict transnational cooperation (Manea et al., 2021) and are more vulnerable to global changes due their ecological peculiarities, such as the Adriatic Sea, requiring further efforts devoted to implementing uniform conservation planning and management practices among coastal countries and to improving the understanding of patterns and processes underlying ecological connectivity among the existing and prospective MPAs (Bastari et al., 2016; Manea et al., 2021).

Here, we used data from a large-scale manipulative experiment simulating a severe physical disturbance on shallow rocky habitats at several sites spanning over >1000 km of coastline in the Adriatic Sea to (1) quantify the overall β-diversity of sessile assemblages under undisturbed conditions, partitioning its nestedness and turnover components, and (2) model increasing dissimilarity with distance and current transport. We also (3) compared distance–dissimilarity relationships of undisturbed versus disturbed assemblages throughout the recovery process and (4) assessed the relative contribution of nestedness and turnover to dissimilarity between undisturbed and disturbed assemblages at different times since a disturbance and at varying spatial scales.

Specifically, we examined three non-mutually exclusive hypotheses about the main processes shaping community reassembly: (1) Local-scale, nonrandom processes (e.g., niche-based community dynamics) could affect primarily recolonization, leading to steeper distance–dissimilarity relationships and high nestedness in disturbed assemblages at early stages of recovery; (2) large-scale, neutral processes (e.g., random dispersion) could mostly drive early stages of recovery, leading to contrasting patterns (i.e., smoothed distance–dissimilarity relationships and high species replacement); (3) colonizers from the local species pool are expected to dominate all successional stages since the experimental treatment opened relatively small patches embedded within a background of undisturbed assemblages, leading to overlapping distance–dissimilarity models and high nestedness at all the investigated times since disturbance. In the event that the multiple processes invoked by Hypotheses 1–3 operated simultaneously, a substantial overlap of distance–dissimilarity models coupled with a mixed contribution of nestedness and turnover to the total dissimilarity between disturbed and undisturbed assemblages during recovery could be envisaged.

MATERIALS AND METHODS

Experimental design and sampling

The experiment was carried out at seven locations representative of shallow subtidal rocky reefs in the Adriatic Sea (Figure 2a,b). In most cases, locations were selected within MPAs, natural parks or reserves, or other areas included in current and future conservation plans, in order to assess the connectivity potential of the existing and projected network of protected areas in the basin.

For each location, we identified three random sites (1–5 km apart) characterized by comparable conditions, in terms of type and slope of the substrate and exposure. At each site, we randomly selected six square patches (a few meters apart, each approximately 2 m^2) on subhorizontal rocky bottoms at 5–7 m depth and permanently marked at the four corners with screws and epoxy putty. Three of the six patches were randomly chosen and experimentally disturbed by removing the resident assemblages from the substrate (Figure 2c). We conceived this treatment to simulate the effect of strong physical or biological disturbance (e.g., destructive fishing practices, overgrazing), which could lead to almost complete desertification of the substrate in subtidal rocky habitats (Fanelli et al., 1994; Guarnieri et al., 2020; Steneck et al., 2004). Epibenthic assemblages in treatment patches were scraped off with chisels and hammers. Steel brushes were used to remove organism remains after treatment. The other three patches were left untouched and used as reference during the experiment.

The experimental setup started in June 2013 and treatments in all locations were performed within 1 month. Sessile assemblages were sampled in five sampling occasions, one at the beginning of the experiment (July–August 2013, undisturbed patches only) and then at 3 (October–November 2013), 9 (April–May 2014), 12 (July–August 2014), and 24 (July–August 2015) months since disturbance. Three random 400-cm^2 photographic samples were taken in each patch for each time of sampling using a digital underwater camera equipped with strobes.

A total of 1701 photographic samples were collected and analyzed to identify epibenthic organisms. Vagile organisms were not considered in the analysis. A total of 101 taxa were identified with the help of voucher specimens collected for fine taxonomic identification (Appendix S1: Table S1); however, due to the intrinsic

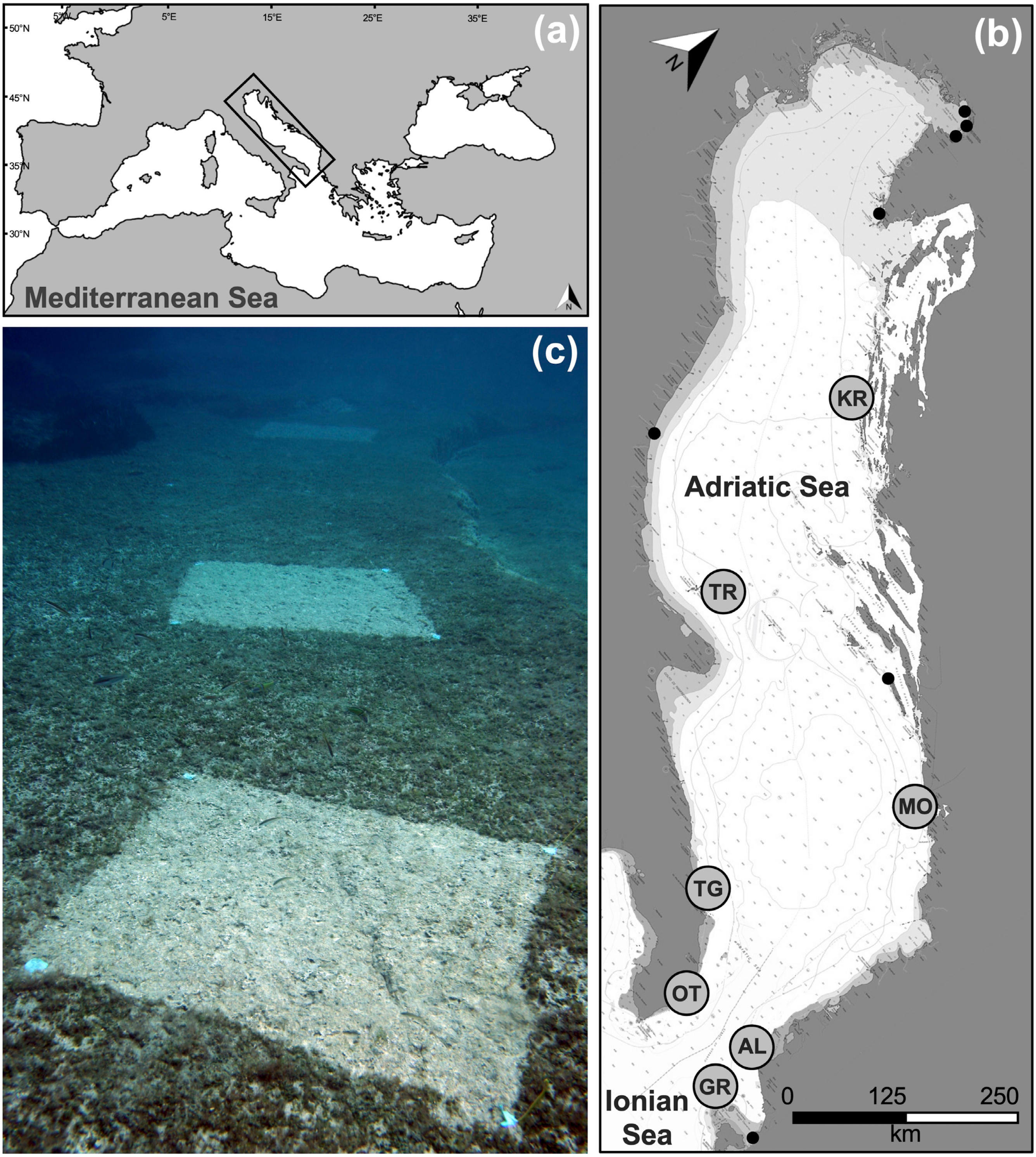

FIGURE 2 (a, b) Study area and locations. Italy: Marine protected area (MPA) of Tremiti Islands (TR), MPA of Torre Guaceto (TG), EU Special Area of Conservation, Otranto (OT); Croatia: Kornati Islands National Park (KR); Montenegro: Herceg Novi (MO); Albania: Karaburun-Sazan National Park (AL); Greece: EU proposed Site of Community Importance, Othonoi Island (GR); black points indicate other MPAs established with national statute and internal zonation. (c) Example of experimental site with disturbed and undisturbed patches (photo credits: Giuseppe Guarnieri).

difficulties of taxonomic discrimination from images, we collapsed some taxa into morphological groups or taxonomic levels higher than species obtaining a set of 70 taxa/groups, most of them (~80%) at the level of species or genus, which were retained for further analysis.

Quantifying the overall β-diversity in the region

We used data from undisturbed patches to assess the overall β-diversity of sessile assemblages in the region. The total species pool in each site was assumed to include all taxa found in that site across all times of sampling, and β-diversity between sites was calculated as pairwise Jaccard dissimilarity in species composition (Jost, 2007). The separate contributions of species turnover and nestedness to β-diversity were determined following the approach proposed by Baselga (2012), which formulated the additive partitioning of the Jaccard dissimilarity into these two components (Baselga & Orme, 2012). A heat map of total dissimilarities in species composition between sites was created and associated with a group average cluster analysis in order to depict site clustering and highlight patterns of nestedness and turnover in the region.

Modeling changes in β-diversity against geographic distance and current transport

Several spatial and environmental factors could drive changes in species composition from one place to another (Borcard & Legendre, 2002; Dray et al., 2006; Rattray et al., 2016). In this study, we considered two of the main aspects virtually generating patterns of variation in assemblage dissimilarity, namely, their spatial (geographic) distance and their potential connections by currents. Pairwise geographic distances between sites were calculated using the least-cost distance by sea. Distance by currents was calculated as the minimum transit time of particles between pairs of sites determined by a Lagrangian particle movement simulation of dispersal based on the modeling framework developed by Treml et al. (2012), using the Marine Geospatial Ecology Tools (MGET) (Roberts et al., 2010).

Significant numbers of connections were obtained by simulating particle dispersion models over a period of 3 years (2013–2015), with four different seasonal periods considered for each year. The pelagic duration of the released particles was set to 30 days, assumed to be the maximum larval duration for sessile species characterizing Mediterranean shallow rocky reefs (see Bevilacqua and Terlizzi [2020] for a collection of data on pelagic larval duration for these organisms). The model did not include any other biological parameterizations, such as presettlement period, postsettlement period, or mortality, since this information is unavailable for most taxa. Simulations referred to the movement of particles of water between sites, and therefore, distance by currents represented the minimum particle transit time (days) between pairs of sites. Sea current velocities and directions were derived from AVISO+ altimetry data (SSALTO/DUACS, 2022).

The separate contribution of geographic distance and distance by currents in explaining the β-diversity of undisturbed assemblages between sites was determined through an analysis of principal coordinates of neighbor matrices (PCNM) (Borcard & Legendre, 2002), followed by a distance-based redundancy analysis (db-RDA) (Dray et al., 2006). PCNM is based on a principal coordinate analysis of a truncated distance matrix, generating a set of positive eigenvectors representing predictors of the local- to large-scale spatial relationships among sites in the response data matrix (Bellier et al., 2007; Borcard & Legendre, 2002). PCNM was used to generate predictors for spatial distance and distance by currents, with a truncation distance (here defined as the longest distance to keep data connected) at $t = 241.5$ km for least-cost distance and $t = 29$ days for distance by currents.

A forward selection by permutation of residuals ($n = 999$) was used to select predictors significantly related to the response data matrix (i.e., the site × taxa presence/absence matrix). Specifically, the procedure was used to select only those predictors that (1) significantly (at $\alpha = 0.05$) contributed to the explained total variation and (2) whose inclusion in the model did not lead to the exceedance of the adjusted R^2 obtained using all predictors (Blanchet et al., 2008). The selected predictors were then used as explanatory variables in the db-RDA to determine the independent and combined contributions of geographic distance and distance by currents (connectivity time) in explaining the total variation (adjusted R^2) in the species dissimilarity matrix and the residual unexplained variation (Dray et al., 2006).

Dissimilarity in species composition between sites was modeled against the corresponding geographic distance and distance by currents. In equivalence to distance–decay of similarity (Nekola & White, 1999), the relationships of pairwise species dissimilarity between sites against the corresponding pairwise distance were assessed by fitting a power model through GLMs and a log-link function (Baselga, 2010). A Mantel test based on Monte Carlo simulations ($n = 5000$) was used to test for correlations between the triangular matrices of distances and the species dissimilarity matrix.

Comparing distance–dissimilarity relationships between disturbed and undisturbed assemblages

Power models of increasing dissimilarity of sites at increasing geographic distance and distance by currents for both disturbed and undisturbed assemblages were also fitted separately at 3, 9, 12, and 24 months since disturbance. This made it possible to test whether distance–dissimilarity relationships converged or diverged between disturbed and undisturbed assemblages during recolonization. Distance–dissimilarity power models were compared through a bootstrapping procedure (Baselga et al., 2018), which allowed for constructing a frequency distribution ($n = 1000$) of estimated coefficients (intercepts and slopes). The probability that a given coefficient would be different between undisturbed and disturbed assemblages was then empirically calculated by comparing the respective frequency distributions.

Nestedness and turnover between disturbed and undisturbed assemblages

To quantify the relative importance of nestedness (species gain/loss) and turnover (species replacement) for β-diversity between disturbed and undisturbed assemblages at different stages of recovery, we calculated the percentage of dissimilarity in species composition imputable to the two components (Baselga, 2012) at the scale of patches (i.e., within sites) separately for each time. This made it possible to quantify the relative contribution to the recolonization of disturbed patches provided by the species pool from undisturbed assemblages within sites (i.e., colonizers that represented a subset of the species pool of the site) and by species from farther away (i.e., colonizers that represented a set of replaced species). Analogously, we also compared the species pool in each time of sampling between undisturbed and disturbed assemblages at the scale of sites (i.e., within locations).

All analyses were done in R version 4.2.0 (R Development Core Team, 2022) using the packages betapart (Baselga & Orme, 2012) and vegan (Oksanen et al., 2022).

RESULTS

Overall patterns of β-diversity of undisturbed assemblages

The total number of taxa was largest at AL (Karaburun-Sazan National Park, Albania) and OT (European Special Area of Conservation, Otranto, Italy), followed by TG (MPA of Torre Guaceto, Italy) and TR (MPA of Tremiti Islands, Italy), whereas KR (Kornati Islands National Park, Croatia), MO (Herceg Novi, Montenegro), and GR (European proposed Site of Community Importance, Othonoi Island, Greece) had the lowest values of taxon richness (Figure 2). The average dissimilarity of undisturbed assemblages between sites across the basin was 47% (±0.01) and was mostly due to species turnover rather than nestedness (36% ± 0.01 and 11% ± 0.01, respectively). Assemblages at AL and GR were quite distinct from those at the other locations, with a large proportion of total dissimilarity determined by species turnover; two distinct clusters included sites from MO and KR and those from TR, TG, and OT, with the species pool of the former appearing as a nested subset of the species pool of the latter (Figure 3).

Relationships with geographic distance and distance by currents

The cumulative influence of geographic distance and connectivity by currents explained two-thirds of the total variation in β-diversity among sites (Table 1). The effects of both factors were significant, although the fraction of the total variation explained by geographic predictors was greater than the fraction explained by current-based predictors, with a relatively large intersection between the two. This shared fraction can be seen as the portion of variation explained by overlapping patterns of geographic distance and current transport. After removing the reciprocal influence, the effect of geographic distance still explained a major fraction of variation with respect to distance by currents (Table 1).

The average pairwise dissimilarity of undisturbed assemblages between the closest sites was relatively low (29% ± 0.02) and sharply increased up to 100 km for geographic distance and 10 days for transport time (Figure 4). Correlation with pairwise dissimilarity was significant in both cases, although weaker for distance by currents than for geographic distance (Table 2).

Distance-dissimilarity patterns between disturbed and undisturbed assemblages

Pairwise dissimilarity between disturbed assemblages was significantly correlated with geographic distance for all sampling times except at 9 months since disturbance (Table 3). Comparisons of fitted models did not detect significant differences between treatments and controls at 3, 9, 12, and 24 months, indicating comparable distance–dissimilarity relationships between disturbed and undisturbed assemblages across the basin during the recolonization process (Table 4, Figure 5). The same patterns were found for distance by currents, although correlations with dissimilarity were weaker compared to geographic distance and not significant at 9 and 12 months for both undisturbed and disturbed assemblages (Appendix S1: Table S2, Figure S1).

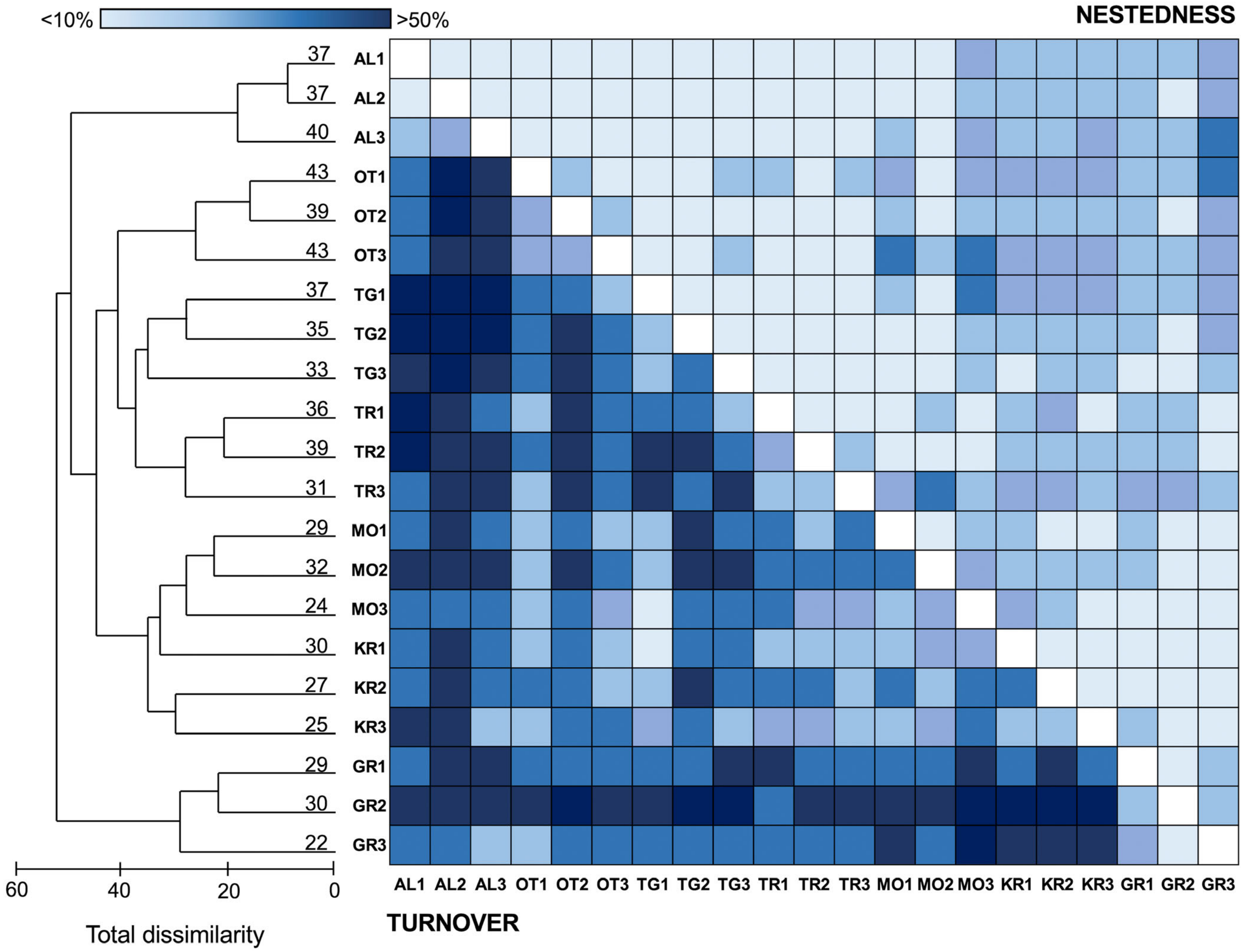

FIGURE 3 Heat map of pairwise contributions of species turnover and nestedness to total dissimilarity between sites from each location (undisturbed assemblages across times). Color gradient indicates dissimilarity values ranging between <10% (light blue) and >50% (dark blue). A cluster analysis of sites based on the total dissimilarity (turnover + nestedness) is also provided on the left side of the map. Numbers in the dendrogram indicate the total number of taxa in each site. Acronyms of locations as in Figure 1 (1, 2, 3 indicate the three sites).

Nestedness and turnover between disturbed and undisturbed assemblages

At the scale of patches within sites (i.e., tens of meters), nestedness and turnover evenly contributed to differentiating the recovering assemblages from the undisturbed neighboring assemblages during recolonization (Figure 6a). After 24 months since disturbance, species replacement (turnover) still represented a considerable portion of the overall dissimilarity between disturbed and undisturbed assemblages in most of the experimental sites (Figure 6a).

At larger spatial scales (i.e., thousands of meters, sites within locations), nestedness was the dominant component of β-diversity between disturbed and undisturbed assemblages in some locations at early (AL), late (MO, KR), or even all stages of recovery (TG) (Figure 6b). Nonetheless, species turnover often represented a large portion of dissimilarity between disturbed and undisturbed assemblages across sites within locations, underlining a clear contribution to the recovery of colonizers from areas farther away (Figure 6b).

DISCUSSION

None of the three hypotheses originally formulated individually explained the experimental results. We observed a substantial overlap of distance–dissimilarity patterns and comparable contributions of nestedness and turnover to local-scale dissimilarities between disturbed and undisturbed assemblages, suggesting that neither very local (e.g., vegetative regrowth from neighbors) nor larger-scale processes (e.g., neutral dispersal) dominated recovery dynamics. Instead, the different processes structuring and maintaining β-diversity patterns in the region, including multiscale (i.e., tens and thousands of meters and >100 km) ecological connections, likely co-participated in shaping the recolonization of disturbed patches during all stages of recovery, leading distance–dissimilarity relationships between undisturbed and disturbed conditions to overlap. Local- to large-scale sink–source effects and habitat distribution and homogeneity in the region probably counterbalance the influence of species sorting and small-scale biological interactions on metacommunity dynamics (Mouquet & Loreau, 2002; Pinsky et al., 2012; Suzuki & Economo, 2021), so that the rate of distance decay, in both disturbed and undisturbed conditions, was the result of contrasting but not mutually exclusive processes (Soininen, McDonald, & Hillebrand, 2007).

TABLE 1 Variance partitioning of site dissimilarity matrix for undisturbed assemblages.

Variance partitioning	Adjusted R^2	p
Total variance		
[a + c] = total geographic	0.50	0.001
[b + c] = total currents	0.30	0.001
[a + b + c] = total variation explained	0.64	0.001
Individual fractions		
[a] = geographic	0.34	0.002
[b] = currents	0.14	0.002
[c] = geographic + currents	0.16	…
[d] = residual unexplained	0.36	…

Note: The total variation was partitioned into four portions, representing the independent fractions of variation explained by geographic (least-cost) distance [a] and distance by currents [b], the nonseparable fraction of variation explained by the two factors in combination [c], and the residual unexplained variation [d].

β-diversity patterns of undisturbed assemblages at regional scale

Sessile assemblages on shallow subtidal rocky reefs were quite similar across the study area, with the average dissimilarity in species composition being lower than 50% even for sites ~400 km apart, or ~60 days away if considering the

TABLE 2 Summary of coefficient estimates of power models fitted to dissimilarity in overall species pool of undisturbed assemblages at increasing geographic distance and distance by currents.

Model type	Intercept	Slope	r	p
Least-cost distance	0.308	0.055	0.249	0.007
Distance by currents	0.408	0.041	0.164	0.038

Note: Pearson product–moment correlation coefficient r and results of Mantel test were also reported.

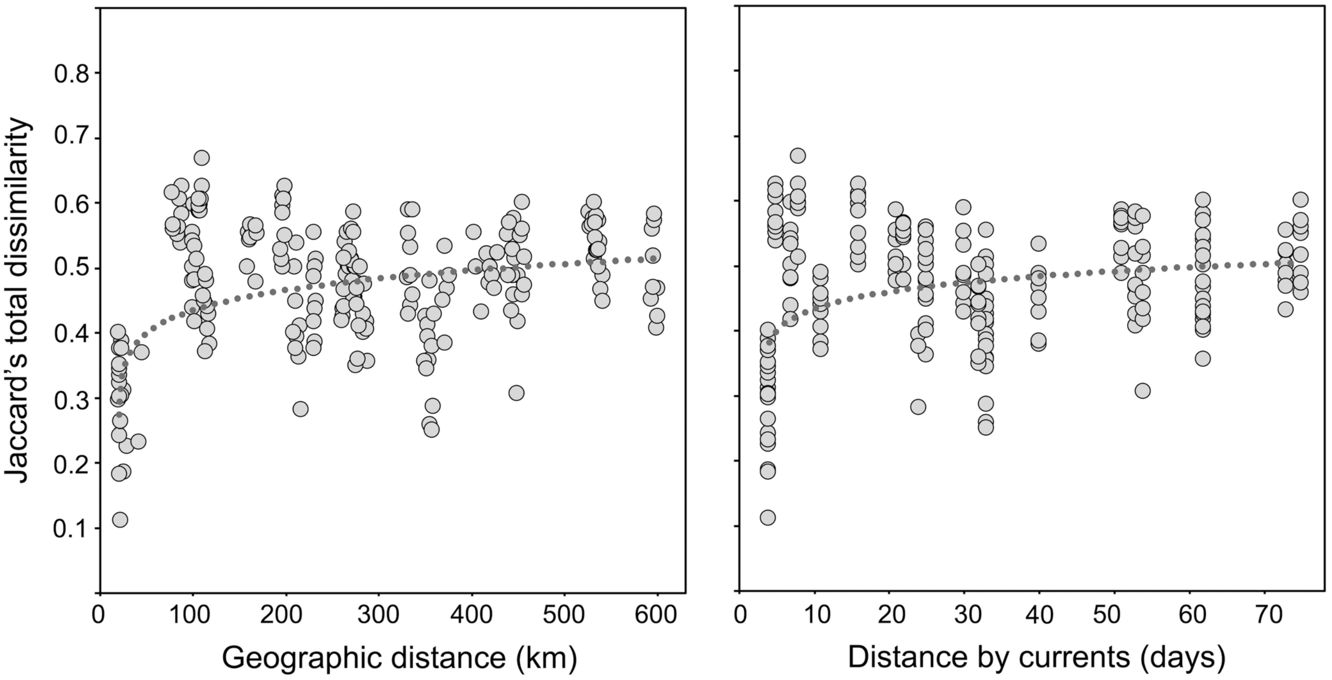

FIGURE 4 Total dissimilarity between sites against geographic distance (left panel) and distance by currents (right panel) for undisturbed assemblages (across times). Dotted lines indicate the model fitted to the data. Coefficients of models and correlation values are given in Table 2.

TABLE 3 Summary of coefficient estimates of power models fitted to dissimilarity in overall species pool of disturbed and undisturbed assemblages at increasing geographic distance, separately for each time of sampling.

Assemblages	Intercept	Slope	*r*	*p*
Undisturbed 3 months (U3)	0.411	0.067	0.293	0.002
Undisturbed 9 months (U9)	0.451	0.047	0.093	0.143
Undisturbed 12 months (U12)	0.351	0.065	0.227	0.020
Undisturbed 24 months (U24)	0.241	0.083	0.349	0.001
Disturbed 3 months (D3)	0.438	0.068	0.295	0.001
Disturbed 9 months (D9)	0.446	0.069	0.157	0.057
Disturbed 12 months (D12)	0.354	0.050	0.212	0.021
Disturbed 24 months (D24)	0.189	0.094	0.403	0.000

Note: The Pearson product–moment correlation coefficient *r* and results of Mantel test were also reported.

TABLE 4 Comparison of distance–dissimilarity power models between undisturbed (U) and disturbed (D) assemblages 3, 9, 12, and 24 months since disturbance.

Model coefficients	U3–D3	U9–D9	U12–D12	U24–D24
Intercept[a]	0.266	0.248	0.506	0.135
Slope[a]	0.461	0.063	0.079	0.163

[a] Numbers are *p*-values of tests comparing coefficient estimates (intercept and slope) of the fitted model between disturbed and undisturbed assemblages.

time of transport by currents. This was probably due to a relatively low heterogeneity of habitat features, which the selection of standard experimental conditions (in terms of, e.g., substrate orientation, exposure, and depth) could have further reduced, and to the lack of sharp environmental changes (with the exception of the northern Adriatic Sea) or strong geographic barriers in the basin (Berline et al., 2014; Rattray et al., 2016). Nevertheless, a clear pattern of variation in dissimilarity among locations emerged. Assemblages at AL and GR on the southeast coast were characterized by high species turnover, with more distinct species composition with respect to the other locations. This distinctiveness may depend on their position at the boundary between the Adriatic and Ionian marine ecoregions and on the fact that the absence of consistent circulation structures connecting the southeast to the southwest coast probably makes AL and GR more isolated from the other areas (Andrello et al., 2013; Berline et al., 2014; Bray et al., 2017). Locations on the west coast (TR, TG, and OT) of the Adriatic Sea generally had more taxa, possibly representing a hotspot of diversity in the basin, whereas assemblages from the two locations on the north-central east coast (MO and KR) appeared as nested subsets of the western species pools.

Such findings largely overlap with evidence from studies investigating genetic connectivity in fish and invertebrate species across the Adriatic Sea (e.g., Paterno et al., 2017; Pujolar et al., 2013; Schiavina et al., 2014), supporting a strong relationship between the potential connectivity inferred from β-diversity patterns and the realized connectivity owing to dispersion and the exchange of propagules. Simulations of invertebrate larval dispersal in the region provided insights on the potential pathways of larval export underlying the observed pattern of connectivity, highlighting a typical transport route from east to west associated with high propagule retention along the western coast, and especially in the southwest, which seemed to act as a sink for larvae from benthic populations (Bray et al., 2017). The exception to this almost unidirectional transport concerned areas near mid-Adriatic gyres, here represented by the location TR, which may perform an important function as nodes for bidirectional (eastward and westward) larval interchange.

Least-cost distance and current transport in combination explained a large amount of the observed variation among sites, confirming that other factors, such as local-scale environmental features, could be less important in shaping community dissimilarities in the basin (Rattray et al., 2016) or might be aligned with geographic factors. Although spatial predictors were of primary importance, the independent contribution of transport time in explaining β-diversity patterns was remarkable, suggesting that connectivity by currents is critical in shaping similarities and discontinuities in community structure and composition by affecting the immigration and export of propagules and, therefore, colonization and recolonization of habitat patches.

The Mediterranean Sea is particularly vulnerable to climate change, and future projections suggest substantial modifications of atmospheric and oceanographic circulation (Adloff et al., 2015; Juza & Tintoré, 2021; Kim et al., 2019). Besides direct effects (e.g., mass mortalities, increased vulnerability to invasion) of climate-related

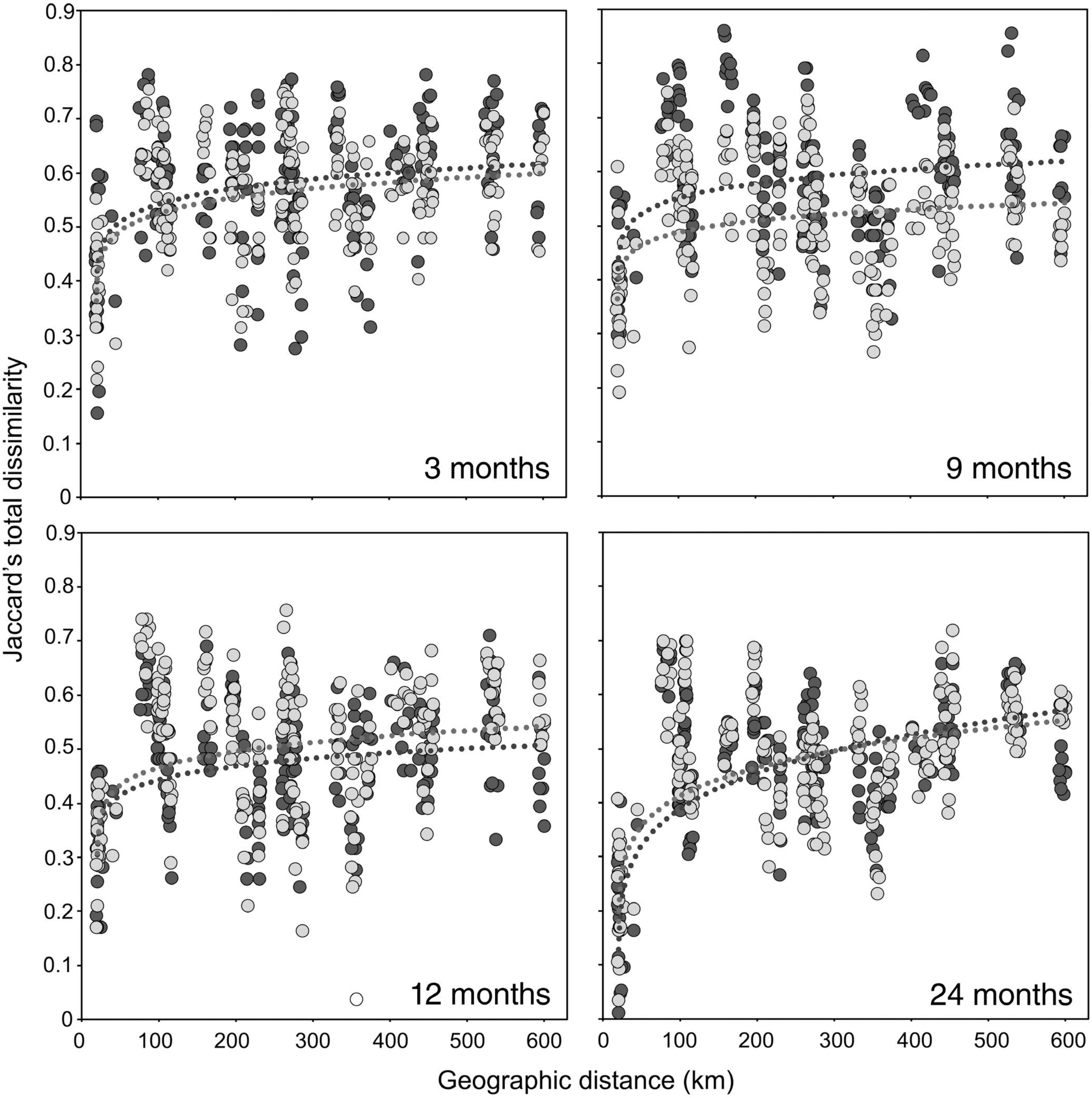

FIGURE 5 Total dissimilarity between sites against geographic distance at 3, 9, 12, and 24 months since disturbance for undisturbed (light gray) and disturbed (dark gray) assemblages. Dotted lines indicate the model fitted to the data. Coefficients of models and correlation values, along with tests for differences in the fitted models between disturbed and undisturbed assemblages, are given in Table 3.

disturbances (e.g., heatwaves, increased sea surface temperature, storms), indirect impacts of climate change on marine communities through the alteration of current transport and connectivity potential can be hypothesized. Although increasing energy in the atmosphere and wind forcing could intensify superficial currents (Juza & Tintoré, 2021) and reinforce local-scale connections, the projected increase in sea water temperature and salinity will probably affect deep water formation, thus weakening the thermohaline circulation in the basin (Somot et al., 2006) and, therefore, connectivity by currents over large spatial scales. From this perspective, a better understanding of the processes and scales underlying ecological connectivity among marine communities could help the adaptation of conservation strategies to future climate change scenarios.

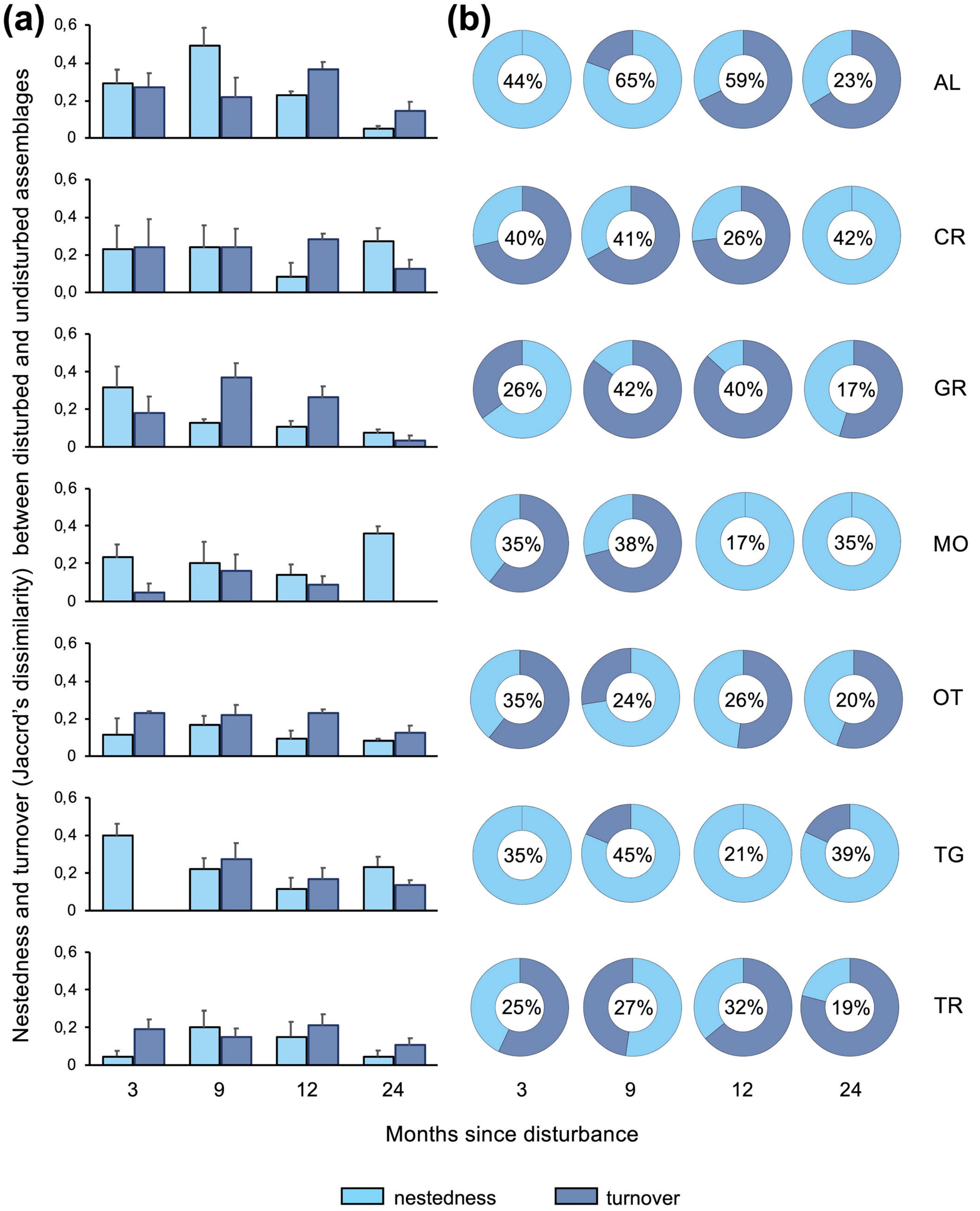

FIGURE 6 Nestedness (light blue) and turnover (blue) contribution to overall dissimilarity between species pool of undisturbed assemblages and species pool of recovering assemblages at each time of sampling at scale of (a) sites (mean ± SE; $n = 3$) and (b) locations. For (b), numbers in pie charts are the total dissimilarity between the species pool of disturbed and undisturbed assemblages at the scale of locations.

β-diversity patterns of disturbed assemblages and processes driving recovery

Distance–dissimilarity patterns were comparable between disturbed and undisturbed conditions at each time of sampling. This could occur because in nonisolated patches, and especially for clonal organisms, recovery strongly depends on vegetative regrowth or propagule supply from neighboring undisturbed assemblages (Keough, 1984). Thus, the pool of species in disturbed patches at each time of sampling is expected to be a subset of the species pool from undisturbed neighboring assemblages, leading distance–dissimilarity patterns between disturbed and undisturbed conditions to overlap, on average, during recovery (Hypothesis 3). However, under this hypothesis, we should have observed nestedness as the dominant component of the dissimilarity between disturbed and undisturbed assemblages at a very local scale (i.e., among patches within sites, tens of meters) since the early stages of recovery. In contrast, what we found was that both nestedness and turnover contributed to dissimilarity in the first 12 months since disturbance and even at late stages of recovery, demonstrating that the recolonization of disturbed patches was not limited to regrowth from boundaries and/or larval supply from neighbors but that there was also considerable species replacement due to colonizers from sources farther away. At the scale of sites (thousands of meters), partitioning the contribution of nestedness and turnover to the dissimilarity between undisturbed and disturbed assemblages indicated that the pool of species within 1–5 km was fundamental for recovery. The species pools from disturbed and undisturbed assemblages were quite similar (dissimilarity <30%) since the early stages of recolonization (e.g., TR), or they were characterized by high nestedness (e.g., MO, TG). Nevertheless, species replacement was important in many cases and still persisted at 2 years since disturbance, underlining the substantial contribution to recolonization of sources located more than a few kilometers apart.

The increased scale dependence of distance–dissimilarity relationships (i.e., increased slopes and/or decreased intercept), coupled with high nestedness between disturbed and undisturbed assemblages (Hypothesis 1), should have occurred if recovery had been initially driven by local-scale, nonrandom processes (e.g., recolonization by local sets of early colonizers). This would also suggest impediments to the dispersal of species that may fit local environmental conditions coming from more distant sites (Nekola & White, 1999). The recruitment of these species, therefore, could be delayed in the succession, leading distance–dissimilarity relationships to converge between disturbed and undisturbed conditions only in the late stages of recovery.

On the other hand, if random colonization from a common larval pool had been driving early stages of recovery, then we should have observed an increase in dissimilarities from local to large scales (i.e., increased intercept and decreased slope of distance–dissimilarity curves, Hypothesis 2). This is because random dispersion would have reduced the scale dependence of the distance–dissimilarity relationships (Soininen, McDonald, & Hillebrand, 2007), and the "lottery model" of colonization would have led to an increase in variability among sites (Greene & Schoener, 1982). As recovery proceeded, species sorting (i.e., selection of those species that best fit local environmental conditions) would have reduced the stochastic effects of succession (Nekola & White, 1999), reconducting the distance–dissimilarity patterns of disturbed assemblages to reflect those observed for undisturbed ones. A reduced scale dependence of distance–dissimilarity relationships could also emerge if recovery was initially driven by colonization from a certain regional pool of good dispersers and/or early colonizers. In this case, a decreased dissimilarity should have characterized the recovering assemblages over the whole region (i.e., decreased intercept and slope of distance–dissimilarity curve) due to the "mass effect" of these regionally successful species homogenizing assemblages at early stages of recovery (Leibold et al., 2004; Suzuki & Economo, 2021). The return to distance–dissimilarity relationships typical of undisturbed assemblages will then occur as the colonization from the local species pool, but also postsettlement and recruitment processes (e.g., competition and predation), reestablishes the original distinctiveness in species composition among sites. In both cases, the turnover between disturbed and undisturbed assemblages should be relatively high due to the initial presence of several species that will be replaced or excluded at later successional stages.

Implications for conservation

Networks of MPAs can sustain resident populations via both local replenishment and larval dispersal from other reserves (Burgess et al., 2014; Cowen et al., 2000; Planes et al., 2009). Modeling of species dispersal and genetic analysis are powerful tools to reconstruct connectivity patterns (Andrello et al., 2015; Friesen et al., 2019; Pujolar et al., 2013; Schiavina et al., 2014), thereby supporting the process of network design. However, assessments of β-diversity can complement these approaches by quantifying the spatial structure of communities, highlighting their ecological and functional linkages in space and time and providing indications on their potential resilience (Bevilacqua & Terlizzi, 2020; Hewitt et al., 2005; Shackell et al., 2012). The comparison

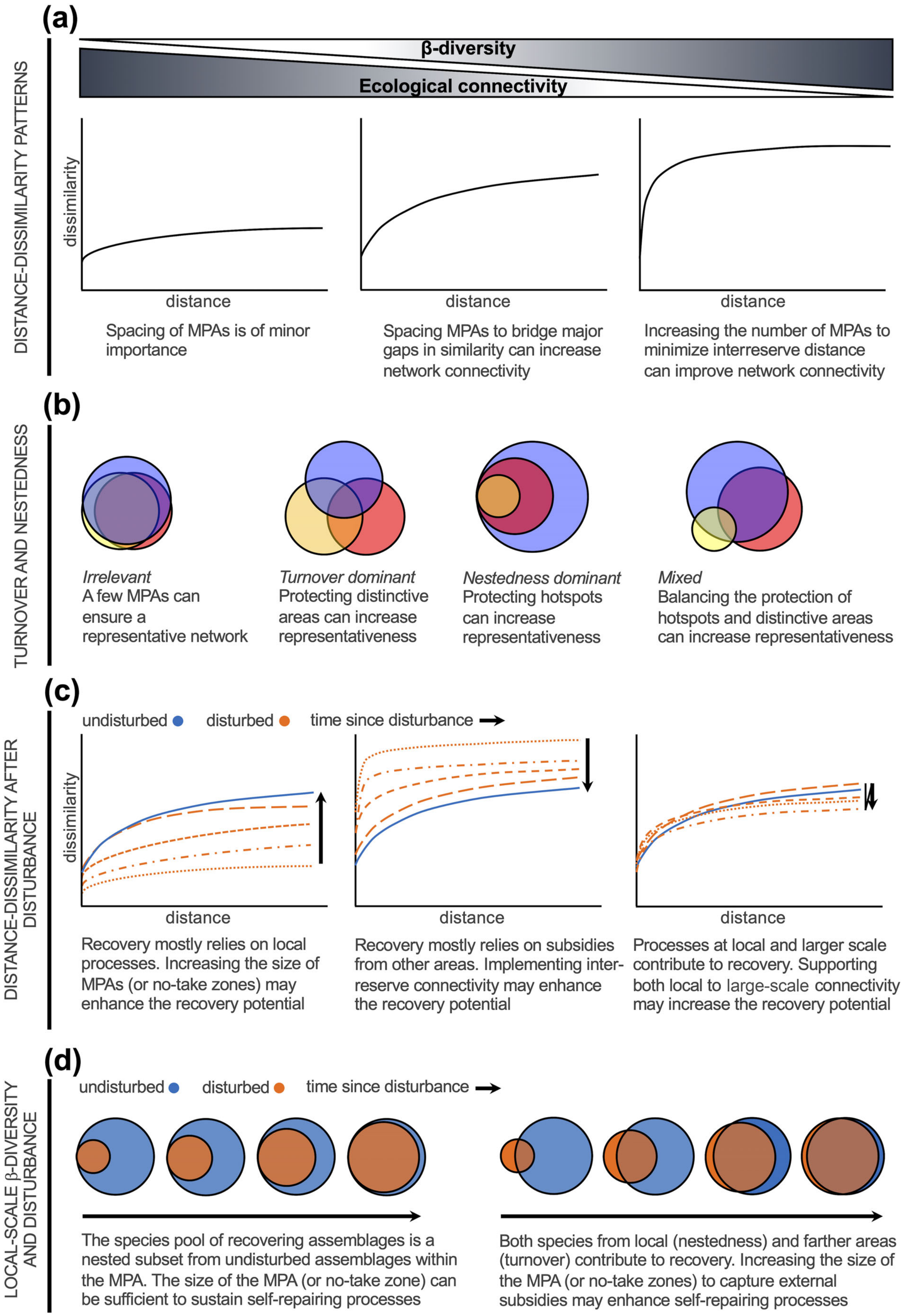

FIGURE 7 Legend on next page.

of distance–decay relationships, the partitioning of β-diversity into its nestedness and turnover, and the relative contributions of these two components to the dissimilarity between disturbed and undisturbed assemblages may shed light on the nature and scales of the main processes driving community assembly in regions of interest, thereby providing guidance for conservation planning and management of existing networks from a local to a large scale (Figure 7).

Complex connectivity patterns characterize the Adriatic Sea, with a common local-scale propagule retention coexisting with intense movement of propagules across the basin (Melià et al., 2016). Our experiment demonstrated that this complexity may influence the recovery of marine communities and that the recolonization process in disturbed rocky habitats may depend on the connectivity potential at different spatial scales, even when very local processes, such as vegetative regrowth or larval supply from neighbors, are expected to be the major determinants of recovery. The observed spatial patterns of dissimilarity suggest that the architecture of sessile assemblages on rocky reefs in the Adriatic Sea may be arranged in a modular way, with small- and meso-scale clusters of relatively strong connectivity bound together by weaker, but consistent, connections by currents at larger spatial scales (Bray et al., 2017; Marino et al., 2022; Melià et al., 2016; Paterno et al., 2017; Pujolar et al., 2013; Schiavina et al., 2014). Systematic conservation strategies at the basin scale that consider this modularity could lead to intensification of the interconnectivity of more isolated spatial subunits, which could then be sustained by subsidies from other subunits when facing perturbations (Scheffer & Carpenter, 2003). From this perspective, an increase in the number of MPAs to include areas of high diversity and distinctiveness (e.g., AL) could sustain local resilience by increasing their capacity for self-replenishment (Cecino & Treml, 2021), while the implementation of new MPAs in the central Adriatic could reinforce exchanges between the east and the west coast (Assis et al., 2021).

Our analysis of β-diversity patterns after disturbance provided some practical insights that might increase the effectiveness of MPA networks in protecting subtidal rocky assemblages. For example, if the decline in similarity mostly occurred in the first 100–150 km, spacing MPAs farther than this distance would reduce the potential of connectivity for these assemblages. Also, concerning the size of MPAs, and especially of fully protected areas, ~5 km of coast (i.e., the spatial scale of sites within locations in our experiment) appeared as the smallest linear extension that would protect self-sustaining in resident assemblages, as their recovery capacity relies not only on close neighbors but also on the supply of propagules from sources within that distance and beyond. Since most of the world's fully protected areas cover less than 5 km^2, with a median of 1.7 km^2 (Thomas et al., 2014), their size is likely less than local-scale connectivity patterns for shallow subtidal reefs in many cases. It is worth stressing that our experiment focused on a single habitat (shallow rocky subtidal) and a specific component of marine communities (sessile macrobenthos), whereas MPAs are generally implemented to protect several marine habitats and the associated biodiversity. Indeed, our guidelines might also be extended to other habitats/assemblages as we provided experimental evidence supporting previous theoretical expectations for the sizing and spacing of MPAs based on dispersal abilities of different marine organisms, from marine plants and macroalgae to invertebrate and fish species (Cowen et al., 2006; Grantham et al., 2003; Hogan et al., 2010; Moffitt et al., 2011; Shackell et al., 2012; Shank et al., 2003). However, because different habitats can exhibit heterogeneous distributions within a marine region, which in turn could reflect different levels of ecological connectivity, assessments that integrate β-diversity patterns across habitats and ecological compartments could identify idiosyncrasies and commonalities and help optimize conservation strategies for a more comprehensive protection of marine ecosystems.

Spatial ecological connectivity and conservation of rocky reef communities

So far, most research on connectivity in the marine realm has focused on fish species through genetic assessments and dispersal simulations to inform on the size and spacing of MPAs and, ultimately, to enhance spillover effects and benefits for fisheries

FIGURE 7 Conceptual framework integrating main β-diversity patterns within a marine region (or within a network of marine protected areas [MPAs]) and their implications for conservation planning and management from local to large scale. (a) Distance–dissimilarity scenarios for natural assemblages and spacing of MPAs. (b) Relative contribution of turnover and nestedness to overall β-diversity and siting of MPAs to increase network representativeness; circles of different colors are Venn diagrams representing assemblages from different MPAs in a hypothetical network (intersections are the shared portions of species and the size of circles is proportional to species richness). (c) Temporal changes in distance–decay patterns between disturbed and undisturbed assemblages and sizing/spacing of MPAs. (d) Changes in β-diversity components between recovering assemblages and neighboring undisturbed assemblages within a MPA and sizing (as in panel [b], circles are Venn diagrams representing disturbed and undisturbed assemblages during recovery).

(Harrison et al., 2020; Hogan et al., 2010; Krueck et al., 2017), largely neglecting macroinvertebrates and, above all, macrobenthic assemblages. This is probably because, despite their ecological importance for marine ecosystems, the consequences of human activities on these assemblages are often overlooked (Chen, 2021). Sessile macrozoobenthos and macroalgal forests play a major ecological role in structuring rocky habitats and sustaining the associated biota, and evidence of the increasing degradation of these systems is mounting worldwide, which has motivated calls for developing effective strategies to protect their integrity (Bevilacqua et al., 2021; Hughes et al., 2010; Krumhansl et al., 2016). Even though MPAs may be effective tools for the protection of marine biodiversity and benthic habitats, their spatial arrangement into cohesive systems can enable scaling-up of their ecological benefits, and incisive efforts to mitigate anthropogenic pressures over and beyond their boundaries can complement the effect of protection in improving wide-scale ecological processes and environmental conditions (Boero, 2021; Hawkins, 2012; Lubchenco et al., 2003). While taking into account the spatial distribution of the habitats being protected and sites deserving conservation priority when designing MPA networks may increase their representativeness of regional marine biodiversity, tailoring the siting, spacing, and sizing of MPAs to match the complexity of connectivity patterns may sustain the persistence of protected populations and communities (Boero, 2017; Magris et al., 2018). Planning MPA networks to maximize spatial ecological connectivity could support the maintenance of viable populations and the recovery of protected communities by ensuring self-repair (e.g., self-recruitment) and adequate supply of propagules from areas farther away (Carr et al., 2017). Our experiment suggested that sizing fully protected areas to extend more than 5 km along the coast and siting MPAs less than 150 km apart could enhance the recovery potential of benthic assemblages by improving both local- and large-scale connectivity processes. Such findings could help to guide marine conservation planning for effective protection of rocky reef communities and to inspire further experimental research aimed at improving the design of MPA networks in the Mediterranean Sea and elsewhere.

AUTHOR CONTRIBUTIONS

Stanislao Bevilacqua: conceptualization, methodology, sampling and field works, data curation, formal analysis, writing—original draft, writing—review and editing. **Simonetta Fraschetti**: conceptualization, methodology, sampling and field works, data curation, writing—review and editing, supervision. **Ferdinando Boero**: project coordination and funding, writing—review and editing. **Giuseppe Guarnieri**: sampling and field works, data curation, writing—review and editing. **Vesna Mačić** and **Antonio Terlizzi**: sampling and fieldwork, writing—review and editing. **Francesco De Leo**: methodology, formal analysis, writing—review and editing. **Lisandro Benedetti-Cecchi**: writing—review and editing.

ACKNOWLEDGMENTS

This work was supported by the European Community's 7th Framework Programme (FP7/2007–2013) for the project Towards COast to COast NETworks of Marine Protected Areas (from the shore to the high and deep sea), coupled with sea-based wind energy potential (CoCoNet), Grant Agreement 287844. C. Vaglio, I. Dalle Mura, C. Kruschel, and D. Petricioli provided invaluable assistance during fieldwork. We greatly appreciate the support of the MPAs of Torre Guaceto and Tremiti Islands to this research, granting special permission for clearings in the no-take zone and logistic support. We are grateful to the editor and two anonymous reviewers for their fruitful comments, which greatly improved this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Bevilacqua, Fraschetti, et al., 2022) are available in Mendeley Data at https://doi.org/10.17632/fn3p3st69b.2.

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SUPPORTING INFORMATION

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

How to cite this article: Bevilacqua, Stanislao, Ferdinando Boero, Francesco De Leo, Giuseppe Guarnieri, Vesna Mačić, Lisandro Benedetti-Cecchi, Antonio Terlizzi, and Simonetta Fraschetti. 2023. "β-Diversity Reveals Ecological Connectivity Patterns Underlying Marine Community Recovery: Implications for Conservation." *Ecological Applications* e2867. https://doi.org/10.1002/eap.2867