CORAL REEFS

Protecting connectivity promotes successful biodiversity and fisheries conservation

Luisa Fontoura[1], Stephanie D'Agata[1,2,3], Majambo Gamoyo[4], Diego R. Barneche[5,6], Osmar J. Luiz[7], Elizabeth M. P. Madin[8], Linda Eggertsen[9], Joseph M. Maina[1,10]*

The global decline of coral reefs has led to calls for strategies that reconcile biodiversity conservation and fisheries benefits. Still, considerable gaps in our understanding of the spatial ecology of ecosystem services remain. We combined spatial information on larval dispersal networks and estimates of human pressure to test the importance of connectivity for ecosystem service provision. We found that reefs receiving larvae from highly connected dispersal corridors were associated with high fish species richness. Generally, larval "sinks" contained twice as much fish biomass as "sources" and exhibited greater resilience to human pressure when protected. Despite their potential to support biodiversity persistence and sustainable fisheries, up to 70% of important dispersal corridors, sinks, and source reefs remain unprotected, emphasizing the need for increased protection of networks of well-connected reefs.

Ecological networks of larval dispersal support the long-term resilience of marine assemblages through population replenishment and gene flow [1, 2]. The spatially asymmetric nature of larval dispersal driven by species-specific life history traits and oceanographic conditions shapes coral reef connectivity patterns [3]. Reefs acting as "sources" of fish larval export can help stabilize and restore fisheries in connected "sinks" [4]. Dispersal corridors connect populations between sources and sinks, thus promoting gene flow and supporting biodiversity persistence [5, 6]. Discerning functionally important connectivity attributes on coral reefs is vital for maximizing biodiversity and fisheries benefits that largely contribute to the well-being of human populations [7, 8]. We address three fundamental gaps concerning protection of ecological connectivity on coral reefs: (i) the relative importance of distinct larval connectivity attributes in supporting reef fish species richness (biodiversity persistence) and biomass (sustainable fisheries); (ii) fish community responses along gradients of larval connectivity, human pressure, and fisheries management; and (iii) the state of connectivity conservation for coral reefs.

We applied a Bayesian hierarchical modeling framework to test the association between fish larval connectivity and ecosystem services provision, quantified with fish species richness and fish standing biomass across a gradient of human pressure and fisheries restrictions [9]. To account for variation in species' reproductive and larval traits [10], we calibrated larval dispersal models with biological parameters describing four fish groups with different ecological roles (fig. S1). We estimated a suite of connectivity attributes for each and across fish groups. We collated five socioenvironmental factors associated with 272 coral reefs as predictors of total fish biomass and species richness (Fig. 1A). Connectivity attributes describe the relative probability of reefs to export, receive, and retain larval subsidies. Endogenous connectivity attributes are based on reefs' direct connections, whereas exogenous connectivity attributes are based on reefs' indirect connections (table S1).

Biogeographic patterns of reef fish biodiversity are partly shaped by reef connectivity [11]. Likewise, we found that higher fish species richness was associated with highly connected dispersal corridors, particularly of small-bodied species with short pelagic larval durations (Fig. 1, B and D, and table S3). Small-bodied reef fishes contribute disproportionately to coral reef species richness relative to larger fish species [12]. Thus, protecting dispersal corridors that are functionally important in maintaining larval connectivity—particularly connectivity of small-bodied fish populations—is likely to disproportionately benefit biodiversity conservation. Notably, reefs with several incoming connections are embedded in a complex network of well-connected reefs through larval dispersal (fig. S2). This emphasizes the need to identify and protect exogenous connections.

In addition to the known effects of species richness, temperature, and human pressure on fish biomass [13, 14], we found that connectivity was influential, as suggested by recent evidence [15] (Fig. 1C). Adding connectivity attributes as covariates in the hierarchical model increased the explained variance from 33 to ~51% and the model's predictive accuracy (table S2). Overall, fish biomass was higher for reefs with a greater probability of accumulating larval subsidies from adjacent, connected reefs. Net larval flow (i.e., netflow), defined as the gradient between absolute larval sinks and absolute larval sources, was associated more strongly with fish biomass (table S4). Fish biomass in absolute sink reefs was approximately twice as high as in absolute source reefs (Fig. 1E). This finding over such a large spatial scale corroborates the long-held understanding that the accumulation of larvae subsidies favors fish population replenishment and long-term resilience of sink locations [2]. By contrast, reefs with the greatest potential for exporting larvae may be more sensitive to fishing pressure and require higher fishing restrictions to maintain high biomass and support sustainable fisheries in connected sink reefs [16].

The positive association between larval sinks and fish biomass was more evident when accounting for connectivity patterns of species that reproduce year-round, namely cryptobenthic fish and resident spawners (Fig. 1C). Resident spawners often include species targeted by fishing (e.g., surgeonfish, small snappers). By contrast, short–lifespan cryptobenthic fish are not a target but constitute up to 60% of biomass consumed by piscivorous fish [17]. Therefore, our results suggest that constant larval inflow at sink locations may support fishery benefits by promoting year-round population replenishment of fisheries-targeted species and key piscivorous prey species.

The association between fish biomass and human pressure varied with the sink-source gradient and management categories (Fig. 2 and fig. S3). Fish biomass was relatively lower in larval sources than sinks in no-take and restricted reefs (Fig. 2, A to B). However, fished larval sinks demonstrated higher sensitivity to human pressure above an apparent human pressure threshold (Fig. 2C). Unsustainable harvest and higher fishing pressure on sink reefs undermines the potentially positive impacts of larvae inflow on fish biomass [18]. Therefore, managing fisheries (e.g., area- or gear-based regulations) in larval sinks may facilitate the persistence of fish biomass and provide ecosystem goods and services for human coastal populations that depend on local fisheries [19]. The extent to which larval sinks can contribute to local food security may also depend on the management status of connected reefs that serve as their larval sources [16]. These contrasting associations between fish biomass and human pressure under different connectivity and fisheries management

[1]Department of Earth and Environmental Sciences, Macquarie University, Sydney, NSW 2109, Australia. [2]Marine Programs, Wildlife Conservation Society, Bronx, NY, USA. [3]ENTROPIE (IRD, University of La Reunion, CNRS, University of New Caledonia, Ifremer), 97400 Saint-Denis, La Reunion c/o IUEM, 29280 Plouzané, France. [4]Coastal and Marine Resources Development, Mombasa, Kenya. [5]Australian Institute of Marine Science, Crawley, WA 6009, Australia. [6]Oceans Institute, The University of Western Australia, Crawley, WA 6009, Australia. [7]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, NT, Australia. [8]Hawai'i Institute of Marine Biology, School of Ocean and Earth Science and Technology, University of Hawai'i at Mānoa, Kāne'ohe, HI 96744, USA. [9]Department of Earth Sciences, Uppsala University, SE-621 67 Visby, Sweden. [10]Centre for Environmental Law, Macquarie University, Sydney, NSW 2019, Australia.
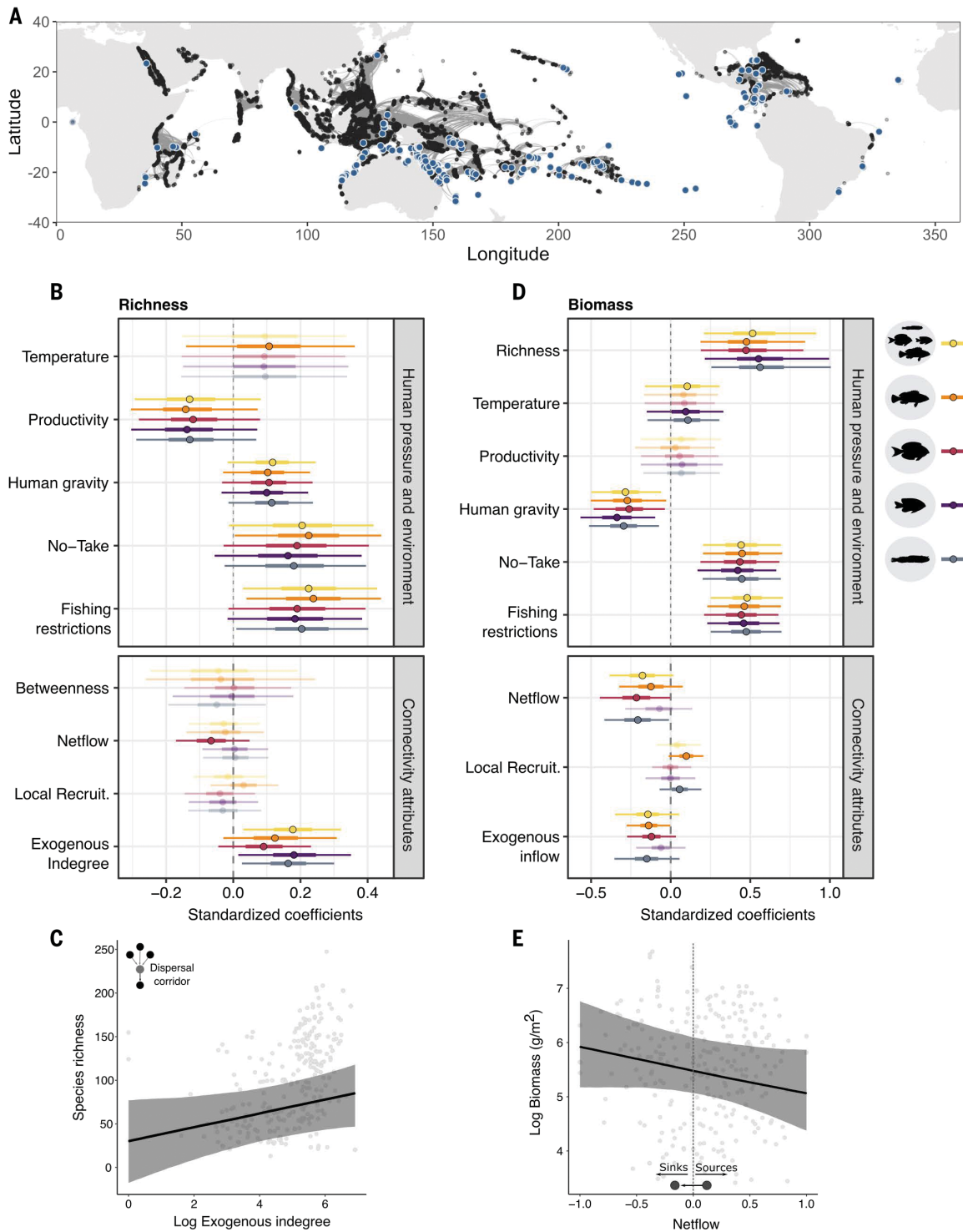*Corresponding author. Email: joseph.mbui@mq.edu.au

Fig. 1. Global patterns of fish larval connectivity on coral reefs and association with total fish biomass and species richness. (**A**) Fish larval dispersal simulated for coral reefs globally with ocean data from 2000 to 2005. Connectivity attributes and human pressure were estimated for 272 reef sites (blue points) to determine the role of connectivity in promoting fish biomass and species richness. (**B**) Bayesian models with fish species richness and (**D**) biomass as response variables, and the estimated standardized effect sizes for human, environmental, and connectivity covariates. Horizontal error bars represent 95% Bayesian credible intervals, with the inner, thicker lines defining the 50% credible intervals. In (B) and (D), the *y* axes are the model covariates of total connectivity—average connectivity across the four fish groups—and connectivity based on individual fish groups. Model-predicted relationships between the number of inward connections of dispersal corridors (**C**) and species richness and net larval flow and fish biomass (**E**). Models were fitted with both random slopes and intercepts across provinces (fig. S4).
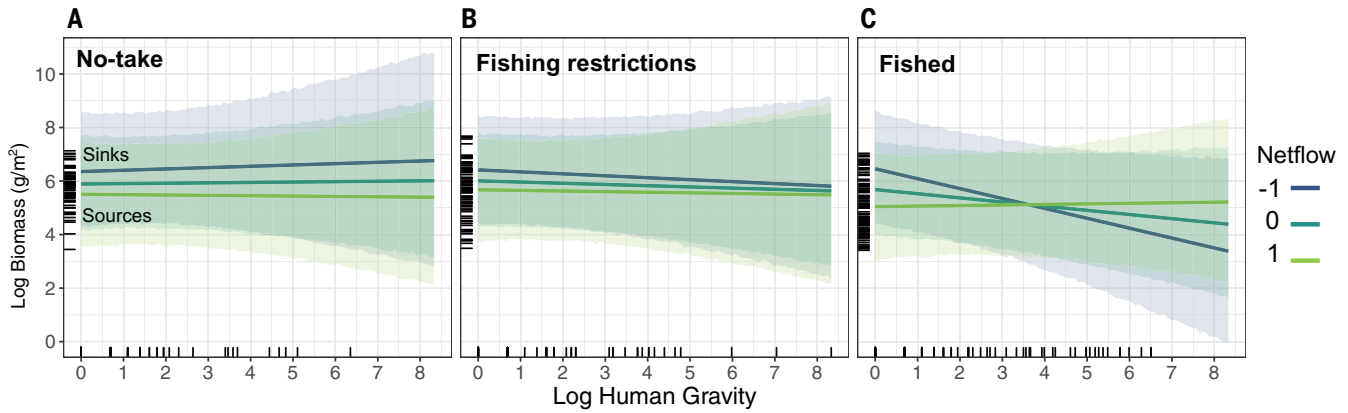
Fig. 2. Model-predicted relationships between fish biomass and human pressure on reefs along the net larval flow gradient in three management categories. Management levels represent (**A**) no-take marine reserves, (**B**) areas with fishing restrictions (e.g., marine parks), and (**C**) fished areas. Lines represent three levels of net larval flow (netflow): −1 (absolute larval sinks), 0, and 1 (absolute larval sources). Uncertainty bands represent 95% confidence intervals.

Fig. 3. A conceptual framework for applying connectivity to optimal placement of MPAs and OECMs for biodiversity and fisheries management and the global status of connectivity conservation on coral reefs. (**A**) Illustration of sweet spot locations for no-take and restricted fishing zones. The color gradient illustrates the potential of sources, sinks, and dispersal corridors to support sustainable fisheries and biodiversity persistence relative to the strength of their connectivity attributes. Dispersal corridors, when protected, can promote biodiversity persistence through gene flow and population resilience. No-take source areas support sustainable fisheries in sink areas through fish larval export. Fishing restrictions in sink areas can sustain fisheries benefits through larval subsidies from source areas. Dispersal corridors that function as strong sinks can be fished with restrictions to support local fisheries. In all other reef areas, a portfolio of fisheries management approaches can be applied. (**B**) Reef locations (*n* = 14,804) within the 90th and 10th percentile of net larval flow are considered critical larval sources and sinks, respectively. Those within the 90th percentile along the inward connections gradient are regarded as essential dispersal corridors. The proportion of currently protected sources, sinks, and dispersal corridors are represented by colored bars.
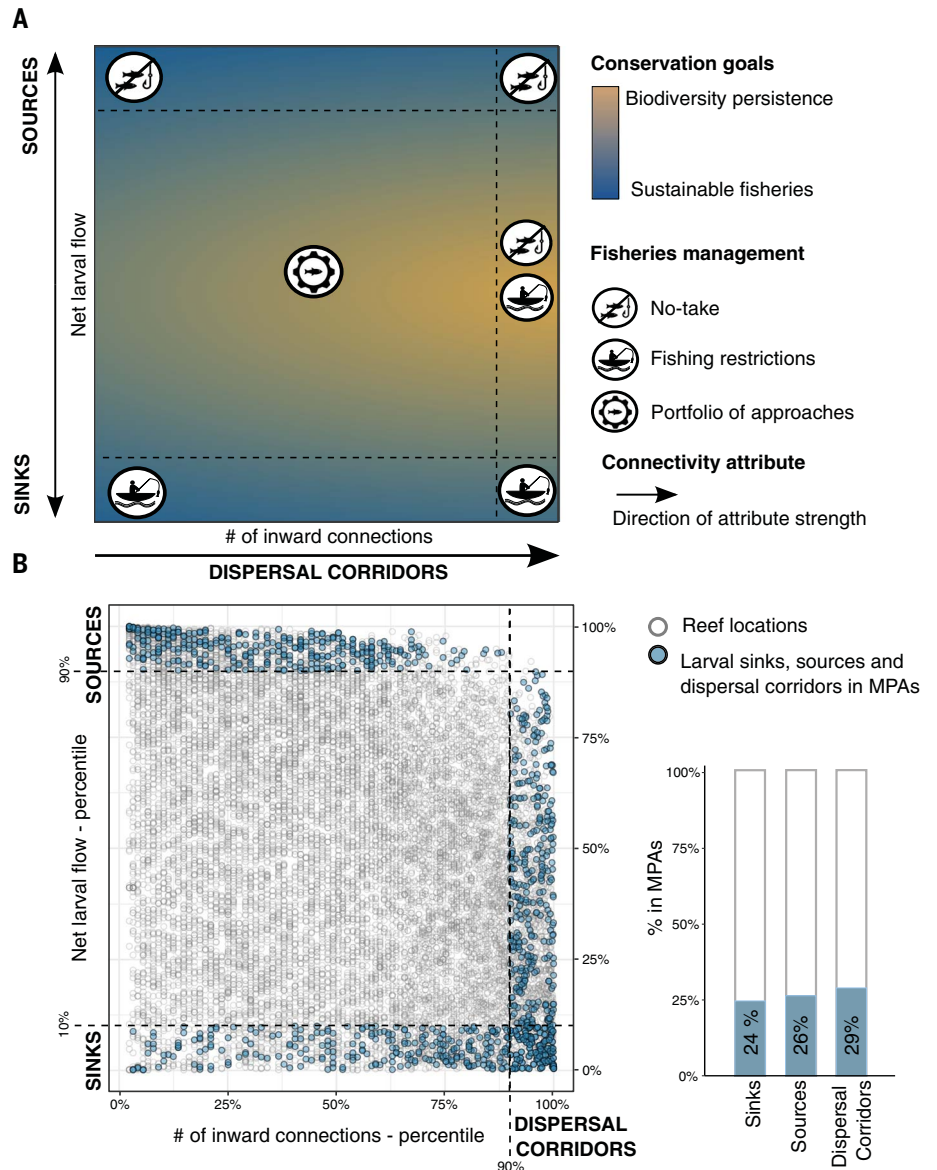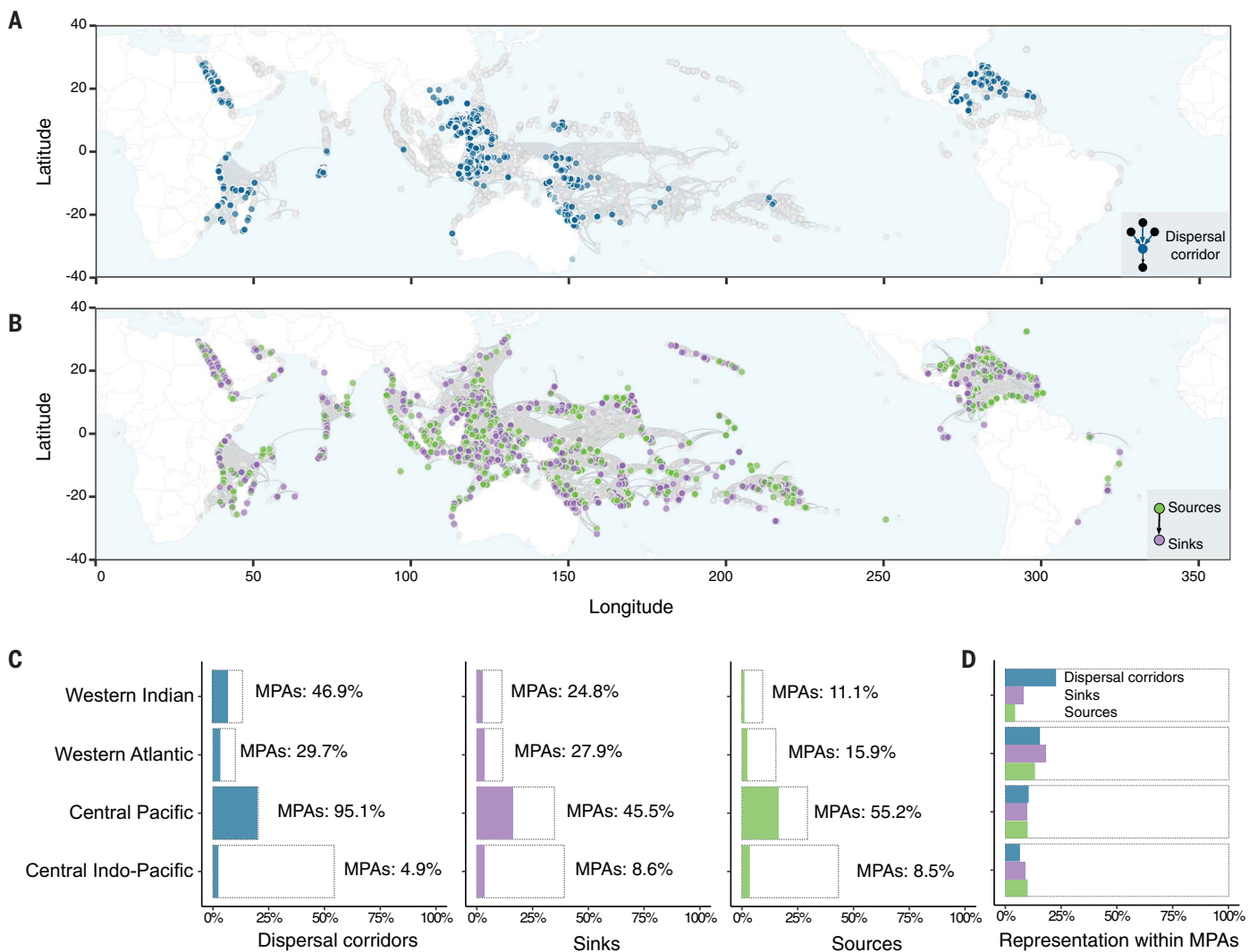
Fig. 4. Geographical representation of critical dispersal corridors, larval sources and sinks, and their conservation status across four biogeographical regions. Darker points represent critical dispersal corridors (**A**) in addition to sources and sinks (**B**), as defined in Fig. 3. (**C**) Dotted lines indicate the percentage of functionally important reefs across the four biogeographical regions and colored bars indicate the percentage of these reef cells within MPAs. (**D**) Bars indicate the representation of critical dispersal corridors, sinks, and sources within regional MPA networks.

scenarios underscore the importance of assessing a reef's inherent connectivity attributes and the local socioecological context.

Linking distinct connectivity attributes with marine protected area (MPA) goals is critical for making informed management decisions, particularly for coral reefs where sustainability goals of biodiversity conservation and fisheries sustainability compete (7, 20). Findings on distinct yet complementary roles of sinks, sources, and dispersal corridors in predicting species richness and fish biomass can inform placement of MPAs and other effective area-based conservation measures (OECMs) for optimizing biodiversity persistence and fisheries benefits (Fig. 3A).

Despite the expansion of MPAs over the past decade (21), we found considerable shortfalls in implementing connectivity conservation and poor placement of MPAs. Approximately 70% of the most critical dispersal corridors, larval sources, and sinks are unprotected (Fig. 3B and table S5). Furthermore, we found low representation of these functionally important reefs within the current spatial arrangement of the MPAs (~11% globally; table S5). Globally, 29% of dispersal corridors, 26% of larval sinks, and 24% of sources are currently within MPAs, but large disparities exist between biogeographical regions (Fig. 4). Conservation efforts to protect connectivity were lowest in the Indo-Pacific region, which has the largest proportion of functionally important reefs. In this global biodiversity hotspot where more than 40% of human populations depend on local fisheries (22), only 5 to 8.5% of key dispersal corridors, larval sinks, and sources are currently protected (Fig. 4C). Implementing connectivity conservation in these regions may have a disproportionately large, positive effect on the persistence of biodiversity and ecosystem services.

Despite limitations in biophysical models at large spatial scales (9), we found that connectivity attributes differed in their relative roles and importance for biodiversity maintenance and fisheries. Well-connected dispersal corridors were associated with species richness, whereas source-sink systems were more strongly associated with fish biomass. Given that ~70% of functionally important coral reefs are currently unprotected globally, these gaps highlight opportunities for implementation of connectivity conservation by strategic placement of MPAs and OECMs as part of the expansion proposed

by the post-2020 biodiversity conservation policy (*23*).

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Science

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Luisa FontouraStephanie D'AgataMajambo GamoyoDiego R. BarnecheOsmar J. LuizElizabeth M. P. MadinLinda EggertsenJoseph M. Maina

Protecting connectivity

Coral reefs are highly threatened by climate change and human pressure. Recent research has focused extensively on how to protect reefs from these impacts, but a fact that is often missed is that reefs are not isolated systems. Fish and coral larvae are actively exchanged across regions, and some reefs supply more whereas others receive more. Fontoura *et al.* looked at the source/sink dynamics of reefs globally and found that maintaining these networks, including dispersal corridors, is essential for biodiversity conservation and sustainable fisheries. Furthermore, they found that the majority of key source reefs and corridors remain unprotected. —SNV

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