

Marine population connectivity identifies ecological neighbors for conservation planning in the Coral Triangle

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Keywords

Connectivity; conservation; coral reef; Coral Triangle; ecoregions; network analysis.

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Received

31 January 2012

Accepted

7 May 2012

Editor

Leah Gerber

doi: 10.1111/j.1755-263X.2012.00260.x

Abstract

Robust conservation plans seek to accommodate functional connectivity by establishing regional priorities and through decisions regarding the size and placement of protected areas. In marine systems, connectivity refers to the ecological linkages (primarily larval dispersal) between populations and protected areas. Unfortunately, connectivity data for the majority of populations are unavailable, requiring managers to rely on expert knowledge and general "scale" and "distance" guidelines. We present a novel approach for integrating model-based connectivity estimates into the conservation planning framework. We quantify multispecies connectivity across the Indo-Pacific and demonstrate how this informs conservation planning in the Coral Triangle across three levels: countries, ecoregions, and priority seascapes. The emergent network structure of ecological linkages between planning regions complements the current bioregionalization across the Coral Triangle. This new ecological network perspective will help (re)define partnerships and assist in coordinating policy actions, ultimately leading to a more effective planning process.

Introduction

The coral reefs across the Indo-Pacific are characterized by exceptionally high levels of biodiversity (Roberts *et al.* 2002; Carpenter *et al.* 2011) and support the livelihoods of more than 138 million people (Burke *et al.* 2011). This region encompasses the Coral Triangle (Veron *et al.* 2009), a global center of marine biodiversity (Roberts *et al.* 2002; Hoeksema 2007). Unfortunately, these systems are under threat with an estimated 95% of the coral reefs at medium or higher threat by human activities (Burke *et al.* 2011). As a result, these threatened ecosystems have become an international priority for conservation and management, regionally organized as the Coral Triangle Initiative (CTI; CTI Secretariat 2009).

The approach implemented under the CTI calls for a coordinated and systematic action plan for improving the health of the marine ecosystems and well-being of the communities which depend on them (CTI Secre-

tiariat 2009). The CTI Action Plan prescribes an ecosystem based management strategy in which marine protected areas (MPAs) play a central role in balancing the broad objectives of biodiversity protection with resource use (Halpern *et al.* 2012). Because of the complex social and political structures, and the enormous extent of the Coral Triangle, defining ecologically meaningful planning regions (e.g., ecoregions, bioregions, or "priority seascapes") is critical for providing a framework in which managers can develop effective and representative conservation strategies (Lourie & Vincent 2004), ideally implemented through a systematic conservation planning framework (Margules & Pressey 2000; Mills *et al.* 2010). Within this framework, achieving the objectives of promoting species' persistence and ecosystem functions requires explicit information regarding the spatial scale and extent of biophysical and human attributes (Margules & Pressey 2000; Mills *et al.* 2010; Pressey & Bottrill 2009). Therefore, a key step involves identifying

ecologically meaningful planning regions in which local-scale actions can target biodiversity and population persistence objectives (Pressey & Bottrill 2009). This nested approach to management then reflects the ecological processes and biodiversity patterns it attempts to protect (e.g., evolutionary processes, ecological connectivity, endemism, etc.), a conservation planning framework urgently needed in the biologically and culturally diverse Coral Triangle (Mills *et al.* 2010).

Much progress has been made in delineating regions for marine conservation based on various criteria, including levels of endemism, unique thermal regimes, expert opinion, biogeographic breaks, and geopolitical boundaries (Spalding *et al.* 2007). There appears to be widespread support for a single global bioregionalization of coastal and marine areas: The marine ecoregions of the world classification (Spalding *et al.* 2007). This ecoregional framework is currently being used across the world by conservation organizations and governments, and has set the stage for conservation planning in the Coral Triangle (Green & Mous 2008). Because of the ecological complexity in this region, a finer scale regionalization has also been implemented to identify distinct subareas within which management measures can be developed more effectively. This effort produced thirty-two "functional seascapes" distributed across the Coral Triangle, where connectivity within seascapes is believed to be higher than connectivity with the surrounding regions, providing practical planning regions for conservation (Green & Mous 2008).

A central objective in the development and delineation of planning regions and MPA networks is the ability to incorporate "functional connectivity" within and between regions (West & Salm 2003; Green & Mous 2008). Connectivity is a key ecological process, which contributes to the development, maintenance, and spatial patterns in species abundance and biodiversity (Lester *et al.* 2007). Therefore, spatial estimates of larval dispersal neighborhoods (Palumbi 2004) should help define this scale and extent of conservation planning and the ecological context for the development of protected area networks. Quantifying the direction and strength of connectivity between marine populations, as well as planning regions, would identify ecological neighbors and important transboundary linkages where coordinated conservation planning would be beneficial (e.g., developing multicountry protected area networks, monitoring programs, fundraising efforts, etc.).

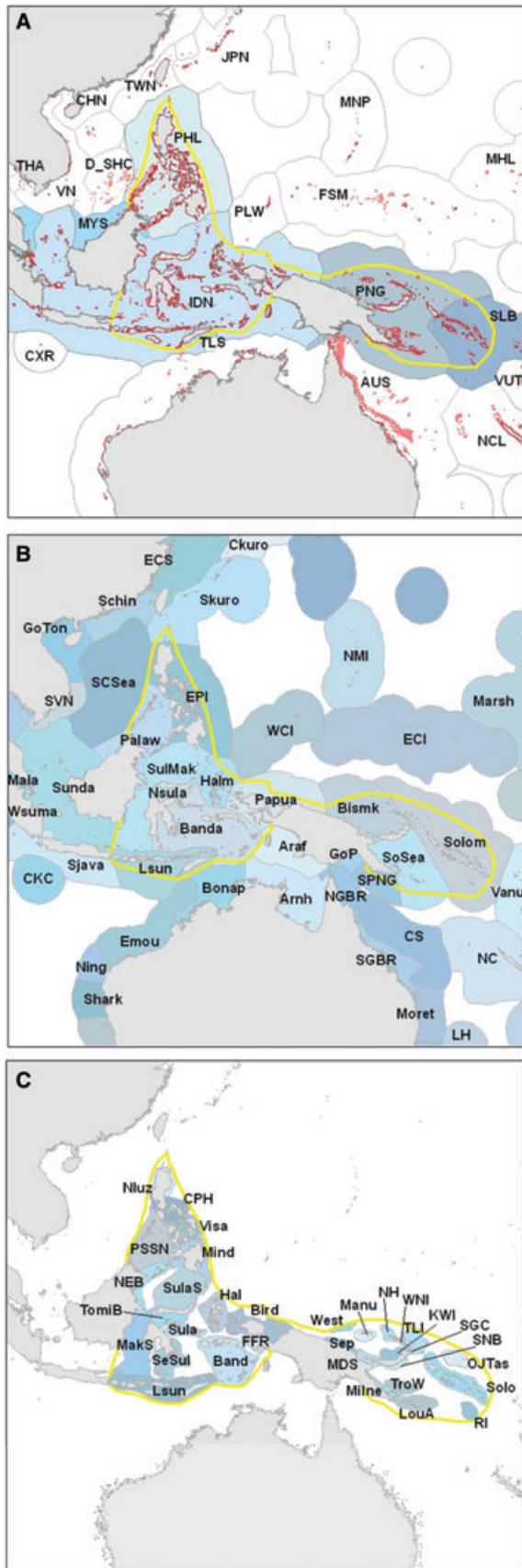
Currently, tracking individual larvae or comprehensively measuring realized connectivity is not feasible, so the only way to develop standardized regional estimates of population connectivity is through an ecological modeling approach. In general, these approaches integrate

ocean current data with a species' life history characteristics to simulate larval dispersal from discrete habitat patches distributed across a seascape (Cowen *et al.* 2006; Treml *et al.* 2008; Kool *et al.* 2011). These models produce a connectivity matrix, representing the discrete dispersal kernels, or the likelihood that larvae released from one population will recruit to some downstream population. Analyzing these marine population connectivity matrices as ecological networks is an intuitive way to visualize the connectivity structure and yields powerful insights into their emergent properties, such as network resilience, community clustering, and flow patterns (Urban *et al.* 2009; Cumming *et al.* 2010). Quantifying the marine population connectivity structure across the Coral Triangle with these network-based tools should provide a unique assessment of the bioregionalization and how well it meets multispecies connectivity objectives.

Here, we evaluate the population connectivity between coral reefs of the Coral Triangle region with the goal of assessing and integrating this functional connectivity into the regional conservation planning framework. We focus on coral reefs, in particular, as they represent an important marine ecosystem to the region's ecological and economic well-being. Marine population connectivity is quantified for three model species representing a range of life history parameters (dispersal capabilities, egg type, mortality, behavior, etc.) common to coral reef species. We combine high-resolution ocean circulation data with empirically based life history characteristics in an ecological marine connectivity model to quantify the multispecies larval neighborhoods for the Coral Triangle region. We use these predictions to identify and map the concordant dispersal corridors, barriers, and connectivity hotspots across the region. These connectivity estimates are then aggregated across three planning levels of the Coral Triangle (countries, ecoregions, and seascapes) to discover the network structure of ecological interactions among planning regions, effectively embedding connectivity into the established conservation planning framework.

Methods

A biophysical modeling approach (Treml *et al.* 2008, 2012) was used to estimate the larval dispersal between the reefs of the Coral Triangle (Figure 1) using the methods in the Marine Geospatial Ecology Tools software package (Roberts *et al.* 2010). The Coral Triangle model was parameterized using high-resolution shoreline data (Wessel & Smith 1996), coral reef habitat data (Spalding *et al.* 2001), and a well-validated oceanographic model, the Regional Ocean Modeling



System (Wang *et al.* 2005). The spatial resolution of the model (10 km) adequately captures the complex hydrodynamics of the region and multiple years (1997, 1999, and 2001) and all seasons were used to capture the temporal variability across multiple spawning periods. Individual species were represented by a unique suite of life history parameters, including spawning times, larval output (fecundity and adult density), pelagic larval duration (PLD), larval competency, larval behavior, and larval mortality. Three model species were used to explore a range in dispersal ability: a coral, damselfish, and anemonefish. The coral had high

Figure 1 The study area of the Indo-Pacific region, including the Coral Triangle center of marine biodiversity. Maps shows the coral reef habitat, land masses, the Coral Triangle boundary (yellow), and the three spatial scales of planning: (A) Exclusive Economic Zones of all countries (the Coral Triangle countries are in shades of blue) and all coral reefs shown in red, (B) Marine ecoregions (Spalding *et al.* 2007), and (C) Coral Triangle Priority Seascapes (Green & Mous 2008). (A) EEZ boundaries: JPN = Japan; CHN = China; TWN = Taiwan; THA = Thailand; IDN = Indonesia; VN = Vietnam; MYS = Malaysia; PHL = Philippines; D_SHC = Disputed; South China Sea; CXR = Cocos-Keeling/Christmas Island; MNP = Mariana Islands; FSM = Micronesia; PLW = Palau; AUS = Australia; TLS = East Timor; PNG = Papua New Guinea; SLB = Solomon Islands; VUT = Vanuatu; NCL = New Caledonia; MHL = Marshall Islands. (B) Marine Ecoregions: Araf = Arafura Sea; Arnh = Arnhem Coast to Gulf of Carpenteria; Banda = Banda Sea; Bismk = Bismarck Sea; Bonap = Bonaparte Coast; SGBR = Central and Southern Great Barrier Reef; Ckuro = Central Kuroshio Current; CKC = Cocos-Keeling/Christmas Island; CS = Coral Sea; ECI = East Caroline Islands; ECS = East China Sea; EPI = Eastern Philippines; Emou = Exmouth to Broome; GoP = Gulf of Papua; GoTh = Gulf of Thailand; GoTon = Gulf of Tonkin; Halm = Halmahera; Lsun = Lesser Sunda; LH = Lord Howe and Norfolk Islands; Mala = Malacca Strait; NMI = Mariana Islands; Marsh = Marshall Islands; NC = New Caledonia; Ning = Ningaloo; Nsula = North-east Sulawesi; Palaw = Palawan/North Borneo; Papua = Papua; Shark = Shark Bay; Solom = Solomon Archipelago; SoSea = Solomon Sea; SCSea = South China Sea Oceanic Islands; Skuro = South Kuroshio; SPNG = Southeast Papua New Guinea; Schin = Southern China; Sjava = Southern Java; SVN = Southern Vietnam; SulMak = Sulawesi Sea/Makassar Strait; Sunda = Sunda Shelf/Java Sea; NGBR = Torres Strait Northern Great Barrier Reef; Moret = Tweed-Moreton; Vanu = Vanuatu; WCI = West Caroline Islands; Wsuma = Western Sumatra. (C) Priority Seascapes: Band = Banda Sea; Bird = Birds Head; CPH = Central Philippines; FFR = Fak Fak Region; Hal = Halmahera; Milne = Huon Gulf and Coastal Milne Bay Islands; KWI = Kimbe-Witu Islands; Lsun = Lesser Sunda; LouA = Louisiade Archipelago; MDS = Madang-Dampier Strait; MakS = Makassar Strait/Flores Sea; Manu = Manus; Mind = Mindanao; NH = New Hanover-Mussau; Niluz = North Luzon; NEB = Northeast Borneo; OJTas = Ontong Java-Tasman Islands; PSSN = Palawan-Sulu-Sea-North Borneo; RI = Rennell Islands and Indispensable Reefs; Sep = Sepik; Solo = Solomon Archipelago; SeSul = Southeast Sulawesi; SNB = Southern New Britain; SGC = St George's Channel; Sula = Sula Spur Area; SulaS = Sulawesi Sea; TLI = Tbar-Lahir Islands; TomiB = Tomini Bay; TroW = Trobriand and Woodlark Islands; Visa = Visayas; West = Western Islands; WNI = West New Ireland.

fecundity and abundance, weak swimming capabilities and no homing ability, 20% daily larval mortality, a 60-day PLD, and an annual spawning periodicity. The damselfish was characterized by moderate fecundity and abundance, strong swimming and homing behavior, 35% daily larval mortality, seasonal spawning periodicity, and a 20-day PLD. The anemonefish had low fecundity and abundance, strong swimming and homing behavior, 25% daily larval mortality, a 10-day PLD, and seasonal spawning periodicity. Although the model species used in this study do not strictly represent specific coral reef taxa, they do capture a range of dispersal strategies characteristic of important reef-associated species, but may not be appropriate for nonreef or deep-water pelagic species such as tuna.

The dispersal model tracks a cloud of virtual larvae as it moves through the seascape, controlled by ocean currents and larval characteristics. As larvae encounter suitable habitat, the total concentration of larvae that settle per habitat patch is recorded through time. This two-dimensional dispersal kernel is tracked from every source patch resulting in a connectivity matrix quantifying the probability of dispersal between all habitat patches in the seascape. See the Supporting Information for the detailed model parameterization, assumptions, and numerical approach. The final connectivity matrices, along with the location of habitat, were used to build connectivity networks showing the geographic structure of marine population connectivity (Cowen *et al.* 2006; Trembl *et al.* 2008; Urban *et al.* 2009). The networks for the three model species were analyzed to quantify multi-species connectivity across the Coral Triangle.

To visualize the spatial structure of multispecies population connectivity, we merged then mapped the connectivity networks for the three model species. This composite connectivity network, containing all individual dispersal connections across all species, was used to map the relative density of connectivity across the region. This approach was used with two different connection strength thresholds: one to illustrate the spatial structure of demographically significant connectivity (using a probability threshold of 0.001), and a second to summarize all dispersal connections, including those, which may play a role in evolutionary processes (connection probability > 0.00001). The relative density maps are displayed using a linear stretch between the upper and lower 4th standard deviation to better illustrate the spatial structure of connectivity hotspots, and barriers.

To identify the ecological association among planning regions, we aggregated connections across species at the original coral reef habitat scale (1,002 individual reef patches) up to the spatial scale and structure of the planning regions: country boundaries defined by exclusive

economic zones (20 EEZ boundaries); marine ecoregions (Spalding *et al.* 2007) of the Indo-Pacific (43 regions), and the priority seascapes (Green & Mous 2008) of the Coral Triangle (32 seascapes). Connectivity within and among these planning regions was quantified by calculating the cumulative larval settlement to the reefs contained within each planning region for each species. The resultant ecological association networks explicitly show the structure of interactions between planning regions based on the population connectivity and identify all upstream and downstream ecological partners. The network metric, betweenness centrality (Freeman 1978), was used to calculate the degree to which individual planning regions maintain network-wide connectivity. This centrality measure uniquely captures this network property and has been used to identify critical patches for maintaining connectivity in complex landscapes (Estrada & Bodin 2008).

Finally, to compare the spatial structure in connectivity among species and to quantify the degree to which the ecoregion and seascape bioregionalization correspond to the species' connectivity, we used community structure algorithms and cluster similarity measures. The emergent clusters in the connectivity networks were identified by optimizing modularity (Newman & Girvan 2004), or the relative degree of connectivity within clusters to that between clusters, using the fast greedy algorithm (Clauset *et al.* 2004). This approach has been shown to be successful in similar marine population networks (Kininmonth *et al.* 2010). The species-specific clusters were combined to form a consensus matrix based on the consistency between individual clustering using resampling statistics (Monti *et al.* 2003; Simpson *et al.* 2010), effectively revealing the optimal clustering of reefs based on multispecies connectivity. Similarities between species-specific clusters, the consensus clustering, and bioregionalizations, were calculated using the Adjusted Rand Index (Hubert & Arabie 1985), as well as the Variation of Information metric which quantifies the amount of information lost and gained between two clusterings (Meila 2007).

Results

Relative density maps highlighting the spatial structure of multispecies connectivity are shown in Figure 2. The connectivity hotspots, shown in warm colors, are regions where the density of dispersal connections between coral reefs is greatest; regions where connectivity is rare or absent are blue. The spatial structure of demographically significant connectivity (levels above a probability of 0.001) clearly reveals hotspots where reef habitat is strongly connected by dispersal (Figure 2A). Conversely,

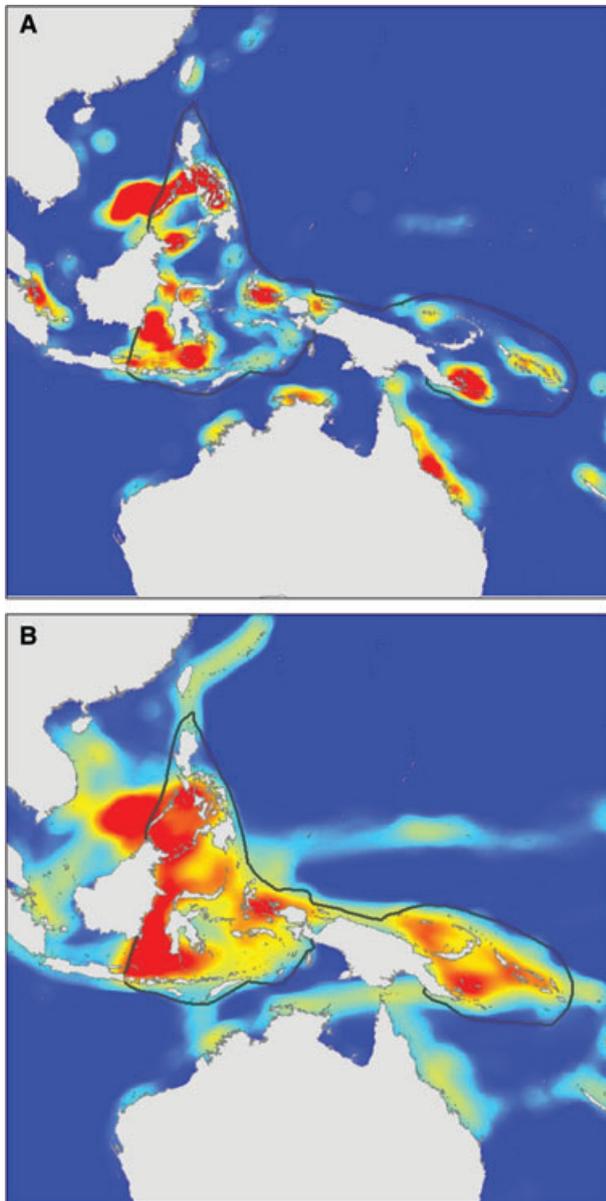


Figure 2 Connectivity density maps showing the multispecies population connectivity across the region. The boundary of the Coral Triangle is shown for reference. (A) Shows the density of only the strong, demographically significant connections (probability of connectivity > 0.001); (B) shows the density of all connections (demographically to evolutionarily significant, at probabilities > 0.00001). Connection densities are displayed using a linear stretch between the upper and lower 4th standard deviation; values beyond these limits are saturated (highest density is red, lowest density is blue).

the blue gaps between these hotspots identify the multispecies, and often semipermeable, dispersal barriers. Extending this probability threshold down to 0.00001 allows the spatial structure of all rare or weak, although possible, dispersal connections to be shown (Figure 2B). This map of evolutionary significant connectivity across

all model species shows where potential dispersal occurs along ocean currents.

The ecological association networks for the three scales of conservation planning are shown in Figure 3. Here, we show the dispersal connectivity among planning regions based on the dispersal potential of the damselfish model species (networks for the coral and anemonefish are shown in Figure S1). The marine population connectivity between planning regions is presented for: 20 countries (including the disputed zone in the South China Sea) which have a significant portion of their EEZ within the study area (Figure 3A); the 43 marine ecoregions (Spalding *et al.* 2007) of the Indo-Pacific (Figure 3B); and the 32 priority seascapes (Green & Mous 2008) within the Coral Triangle (Figure 3C). The size of the nodes represents the relative level of local retention within the planning region and the node color scales with the centrality value with the darkest nodes having the highest betweenness centrality.

The similarity matrix comparing the model species, the consensus clustering, and the two bioregionalizations are shown in Table 1. The species–species similarities varied by more than 40%, with the anemonefish clustering (threshold > 0.00001) having the highest mean similarity with all other species. The ecoregional and seascape groupings had mean similarities with the model species of 0.476 and 0.446, respectively, whereas the consensus groupings had a mean similarity of 0.558. In nearly all comparisons (and across both metrics), the consensus clustering was more similar to the model species than the ecoregion and seascape groupings.

The spatial structure of the consensus matrix is illustrated in Figure S2.

Discussion

Quantifying population connectivity is fundamental to understanding population dynamics (Hanski 1998), the effective management of marine communities (Roberts 1997; Cowen *et al.* 2000), the design of MPA networks (Roberts *et al.* 2003; Botsford *et al.* 2009), and is a key component in the development of systematic conservation planning strategies (Margules & Pressey 2000). We demonstrate a novel approach for integrating marine population connectivity estimates into the regional conservation planning framework. This spatially explicit and network-based approach uniquely identifies the location and strength of multispecies connectivity hotspots, dispersal barriers, and dispersal corridors. We show how these connectivity maps can be integrated within existing conservation planning schemes, enabling managers to discover relevant upstream and downstream linkages

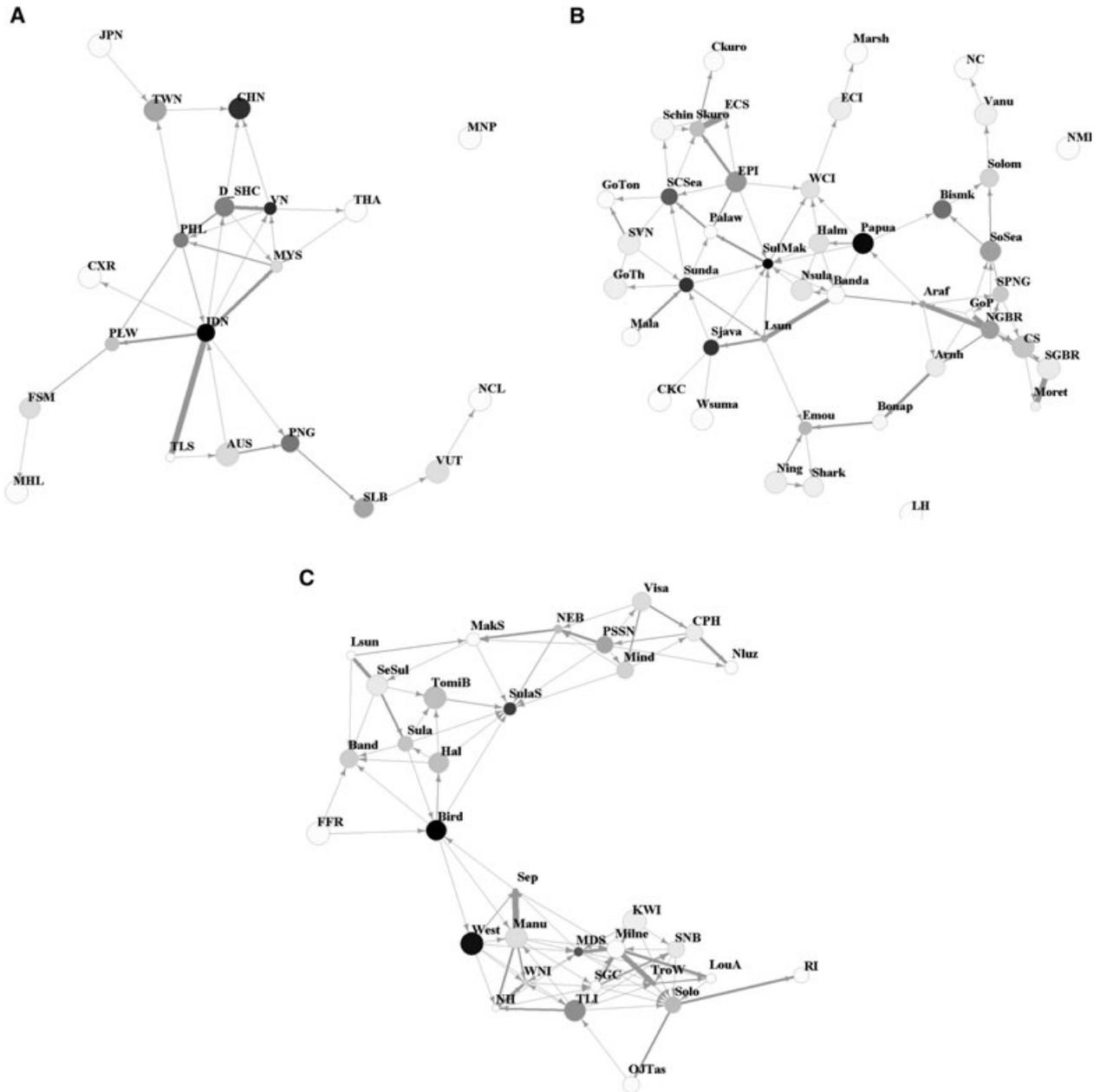


Figure 3 Ecological association networks based on the model species' population connectivity for (A) Countries of the Indo-Pacific (20 regions), (B) Marine Ecoregions of the Indo-Pacific (43 regions), and (C) Coral Triangle Initiative Priority Seascapes (32 regions). Networks are shown for the damselfish only, see the Supporting Information for the anemonefish and

coral networks. Darker nodes have higher betweenness centrality and the size is proportional to the level of local retention with the region. For clarity when connectivity existed in both directions between the same planning regions, only the strongest connection is shown. See Figure 1 for node names.

and gain new insights into the broader ecological relationships among planning regions. These ecological association networks explicitly represent the direction and strength of all transboundary corridors, highlighting important ecological relationships. To our knowledge, this is

the first example of quantifying and visualizing ecological associations among conservation planning regions, offering valuable insights into the regional structure.

The patterns in connectivity discovered here are broadly supported by a recent comparative

Table 1 The similarities between the model species' community structure (each at 0.001 and 0.00001 probability thresholds), the consensus matrix, and the bioregionalization schemes (ecoregions and priority seascapes) using the Adjusted Rand Index are shown above the diagonal and the Variation of Information (VI) metric below the diagonal. Adjusted Rand Index values closer to one are more similar whereas VI values closer to 0 are more similar

	Anenomefish (0.001)	Anenomefish (0.00001)	Damselfish (0.001)	Damselfish (0.00001)	Coral (0.001)	Coral (0.00001)	Consensus	Ecoregions	Seascapes
Anenomefish (0.001)	–	0.893	0.680	0.696	0.390	0.637	0.626	0.518	0.448
Anenomefish (0.00001)	0.450	–	0.636	0.781	0.396	0.648	0.665	0.509	0.437
Damselfish (0.001)	1.100	1.357	–	0.570	0.526	0.584	0.495	0.453	0.457
Damselfish (0.00001)	1.060	0.690	1.617	–	0.374	0.675	0.607	0.540	0.476
Coral (0.001)	2.380	2.469	1.858	2.728	–	0.481	0.340	0.322	0.373
Coral (0.00001)	1.300	1.282	1.632	1.306	2.254	–	0.617	0.516	0.485
Consensus	1.444	1.253	1.994	1.594	2.766	1.374	–	0.421	0.416
Ecoregions	2.043	2.069	2.242	1.939	2.932	2.096	2.666	–	0.611
Seascapes	2.146	2.226	2.080	2.034	2.454	2.053	2.362	1.299	–

phylogeography study (Carpenter *et al.* 2011). Many of the concordant breaks highlighted in this review were found in this study (Figures 2 and S2), including barriers in the vicinity of Cenderawasih Bay, near Halmahera, south of Luzon, and across the Sunda Shelf. Broad correspondence across fish and invertebrate taxa suggests that these common breaks function as persistent barriers to dispersal, forming ecologically and evolutionarily distinct units. We are currently extending this analysis to quantify the concordance between predicted dispersal barriers (Fig. 2) and the genetic barriers identified from population genetic and phylogeographic approaches.

In general, the spatial patterns we found were similar to the regional conservation planning boundaries at both the ecoregional and the priority seascape scale (Figures 1 and 2). This consistency was expected yet surprising. Consistent patterns were expected because of the explicit goal in the bioregionalization approach to identify regions based, in part, on connectivity characteristics (Spalding *et al.* 2007). It was also surprising because these schemes were developed with limited data regarding the spatial patterns in marine population connectivity per se and therefore relied heavily on expert knowledge. The broad spatial consistencies between the ecoregions and the connectivity hotspots (Figure 2) include the Solomon Archipelago, Bismark Sea, Solomon Sea, and Halmahera ecoregions. Concordant patterns with the priority seascapes are also apparent. Examples include the connectivity between Halmahera and the Bird's Head Seascape, the isolation of Tomini Bay, and the role Cenderawasih Bay plays in connecting the reefs of Papua New Guinea with those of the Bird's Head Seascape (Green & Mous 2008). Our results also add connectivity context where it is currently missing, such as around the Banda Sea seascape and throughout Papua New Guinea and the Solomon Islands. In general, the

consistent spatial patterns in connectivity along with the similarities between the species' community structure and the bioregionalizations (Table 1), lend strong support for the existing conservation planning framework in the Coral Triangle. Inconsistencies between the planning region boundaries (Figure 1) and the species' boundaries (Figure S2) may suggest areas where the influence of connectivity could warrant modifications or additions to the regionalizations.

The scale of on-the-ground conservation actions throughout much of this region is on the order of tens of meters to several kilometers and typically involves local protected areas (Weeks *et al.* 2010). The analysis presented here is based on larval connectivity estimates derived from a regional (10km) hydrodynamic model, and as a result, reef-scale decisions made below this resolution would not be appropriate. The modeling framework (Roberts *et al.* 2010; Trembl *et al.* 2012) and methodology are only constrained by the available hydrodynamic and biological data, and could be applied in regions where more local scale data are available. As we demonstrate here, these connectivity-based data and results can assist in the development of regional management strategies and identify regional priorities.

The network-based representation of the ecological linkages between planning regions (Figure 3) clearly identifies all transboundary corridors and strong ecological neighbors. Each linkage in these networks represents a strategic partnership where a coordinated effort in management, fund raising, and conservation prioritization would be beneficial. In addition, the centrality measures overlaid on these networks highlight those planning regions responsible for maintaining network-wide connectivity and cohesiveness. These core planning regions with high centrality, form the backbone of the ecological network and therefore have inherent regional

conservation value. The central role of Indonesia is apparent in all the connectivity networks and at all levels. The planning regions and reefs of Indonesia consistently have a high centrality quantifying their important role in defining and maintaining connectivity across the Coral Triangle. These new ecological network representations and spatial analysis should help add a more robust connectivity context to the conservation planning process, help build partnerships, and assist in coordinating policy actions, ultimately leading to a more cohesive regional conservation effort.

Acknowledgments

We thank H Possingham, M Beger, A Green, and M Knight for thoughtful discussions and critical feedback in the development of this analysis. Three anonymous referees provided constructive comments on an earlier draft. Funding for this work was provided by the Australian Research Council (DP0878306), the World Wildlife Fund (Kathryn Fuller Post-doctoral Research Fellowship to EAT), and the National Science Foundation (NSF OISE-0730256 to PNH).

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 (A) Ecological association networks based on the population connectivity of the anemonefish for the countries of the Indo-Pacific (20 regions). (B) Ecological association networks based on the population connectivity of the coral for the countries of the Indo-Pacific (20 regions). (C) Ecological association networks based on the population connectivity of the anemonefish for the Marine Ecoregions of the Indo-Pacific (43 regions). (D) Ecological association networks based on the population connectivity of the coral for Marine Ecoregions of the Indo-Pacific (43 regions). (E) Ecological association networks based on the population connectivity of the anemonefish Coral Triangle Initiative Priority Seascapes (32 regions). (F) Ecological association networks based on the population connectivity of the coral for Coral Triangle Initiative Priority Seascapes (32 regions).

Figure S2 Map illustrating the spatial structure of the consensus matrix showing the optimal 57 groups across the entire study region. Colors are assigned randomly.

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