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Comparing spatial conservation prioritization methods with site- versus spatial dependency-based connectivity

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Abstract

Larval dispersal is an important component of marine reserve networks. Two conceptually different approaches to incorporate dispersal connectivity into spatial planning of these networks exist, and it is an open question as to when either is most appropriate. Candidate reserve sites can be selected individually based on local properties of connectivity or on a spatial dependency-based approach of selecting clusters of strongly connected habitat patches. The first acts on individual sites, whereas the second acts on linked pairs of sites. We used a combination of larval dispersal simulations representing different seascapes and case studies of biophysical larval dispersal models in the Coral Triangle region and the province of Southeast Sulawesi, Indonesia, to compare the performance of these 2 methods in the spatial planning software Marxan. We explored the reserve design performance implications of different dispersal distances and patterns based on the equilibrium settlement of larvae in protected and unprotected areas. We further assessed different assumptions about metapopulation contributions from unprotected areas, including the case of 100% depletion and more moderate scenarios. The spatial dependency method was suitable when dispersal was limited, a high proportion of the area of interest was substantially degraded, or the target amount of habitat protected was low. Conversely, when subpopulations were well connected, the 100% depletion was relaxed, or more habitat was protected, protecting individual sites with high scores in metrics of connectivity was a better strategy. Spatial dependency methods generally produced more spatially clustered solutions with more benefits inside than outside reserves compared with site-based methods. Therefore, spatial dependency methods potentially provide better results for ecological persistence objectives over enhancing fisheries objectives, and vice versa. Different spatial prioritization methods of using connectivity are appropriate for different contexts, depending on dispersal characteristics, unprotected area contributions, habitat protection targets, and specific management objectives.

Comparación entre los métodos de priorización de la conservación espacial con sitio y la conectividad espacial basada en la dependencia

KEYWORDS
connectivity, graph theory, larval dispersal, marine reserve design, Marxan, systematic conservation planning

Resumen

La dispersión larval es un componente importante de las redes de reservas marinas. Existen dos estrategias conceptualmente distintas para incorporar la conectividad de la dispersión en la planeación espacial de estas redes y es una pregunta abierta cuándo alguna de las dos es la más apropiada. Los sitios candidatos a reserva pueden ser seleccionados individualmente con base en las propiedades locales de la conectividad o en la estrategia espacial basada en la dependencia que consiste en seleccionar grupos de fragmentos de hábitat con un vínculo fuerte. La primera estrategia actúa sobre sitios individuales, mientras que la segunda actúa sobre pares de sitios vinculados. Usamos una combinación de simulaciones de dispersión larval que representaban a diferentes paisajes marinos y estudios de caso de modelos biofísicos de dispersión larval en la región del Triángulo de Coral y en la provincia de Sulawesi Sudoriental, Indonesia, para comparar el desempeño de estos dos métodos en el software de planeación espacial Marxan. Exploramos las implicaciones del desempeño del diseño de la reserva de diferentes distancias y patrones de dispersión basados en el establecimiento del equilibrio de larvas en las áreas protegidas y sin protección. Además, analizamos las suposiciones sobre las contribuciones metapoblacionales de las áreas sin protección, incluyendo el caso de la reducción al 100% y escenarios más moderados. El método de la dependencia espacial fue adecuado cuando la dispersión estuvo limitada, una proporción elevada del área de interés estaba sustancialmente degradada o era baja la cantidad meta de hábitat protegido. Al contrario, cuando las subpoblaciones estaban bien conectadas, la reducción al 100% estuvo relajada, o si una mayor parte del hábitat estaba protegido, la protección de los sitios individuales con altos puntajes en las medidas de conectividad fue una mejor estrategia. Los métodos de dependencia espacial generalmente produjeron soluciones con una agrupación más espacial y con más beneficios dentro que fuera de las reservas en comparación con los métodos basados sitios. Por lo tanto, los métodos de dependencia espacial tienen el potencial de proporcionar mejores resultados para los objetivos de persistencia ecológica por encima de los objetivos de mejora de las pesquerías, y viceversa. Los diferentes métodos de priorización espacial que usan la conectividad son apropiados para contextos diferentes, dependiendo de las características de dispersión, las contribuciones del área sin protección, las metas de protección del hábitat y los objetivos específicos del manejo.

PALABRAS CLAVE

conectividad, diseño de reservas marinas, dispersión larval, Marxan, planeación sistemática de la conservación, teoría de gráficos

【摘要】

幼体扩散是海洋保护区网络的一个重要组成部分。有两种基于不同概念的方法可以将扩散连接度纳入保护区网络的空间规划中, 而它们的适用情境仍存有争议。这两种方法包括根据连接度的局部属性来独立地选择候选保护区, 以及用基于空间依赖性的方法选择一片紧密连接的栖息地斑块。前者作用于单个位点, 而后者作用于相连的一对位点。我们利用代表不同海洋景观的幼体扩散模拟和珊瑚三角区及印度尼西亚东南苏拉威西的幼体扩散生物物理模型的案例研究, 比较了这两种方法在空间规划软件Marxan中的表现。研究根据幼体在保护区和非保护区的平衡定殖情况, 探讨了不同扩散距离和模式对保护区设计效果的影响。我们进一步评估了对来自非保护区的集合种群贡献的不同假设, 包括100%枯竭和更适中的情况。空间依赖性方法适用于以下情况:扩散受到限制, 感兴趣的地区有很大一部分严重退化, 或者受保护的栖息地目标数量较低。相反, 当亚种群相互连接, 100%枯竭的假设被放宽, 或是更多栖息地得到保护时, 保护连接度指标得分高的单个位点则会成为较好的策略。与基于位点的方法相比, 空间依赖性方法通常会产生更多空间上聚集的解决方案, 且在保护区内比在保护区外有更多益处。因此, 空间依赖性方法可能为生态续存目标提供更好的结果, 而非有利于渔业目标, 反之亦然。根据扩散特征、未受保护地区的贡献、栖息地保护目标和具

体的管理目标, 基于连接度的不同空间优先保护方法也适合于不同的情况。【翻译:胡怡思;审校:聂永刚】

INTRODUCTION

Ecological connectivity, defined here as the movement of larvae between spatially fragmented habitats, is a key element in designing successful marine reserve systems (Álvarez-Romero et al., 2018; Balbar & Metaxas, 2019; Magris et al., 2014). Because many marine life histories involve a mobile pelagic larval and relatively sedentary adult stage (Cowen & Sponaugle, 2009), ecologically relevant larval dispersal needs to be sustained between protected marine habitats for long-term population persistence (Andrello et al., 2015; Engelhard et al., 2017; Schill et al., 2015). Metapopulations have greater stability when connective pathways permit rescue effects of new colonists following local disturbances (Schnell et al., 2013), whereas more broadly, gene flow can reduce the chance of patch extinctions resulting from genetic drift or inbreeding (Almany et al., 2009).

Networks of well-connected marine reserves are routinely designed using spatial conservation prioritization techniques, a biogeographic–economic analysis in which conservation actions are allocated to important areas for biodiversity (Kukkala & Moilanen, 2013). Spatial data are collected across a planning region of important conservation features, such as species, habitats, or ecosystem services, and of socioeconomic variables, such as opportunity cost or acquisition cost (Ban & Klein, 2009). Algorithms are then used to identify efficient reserve systems that minimize cost while maximizing the amount of biodiversity features allocated for protection (Margules & Pressey, 2000). In early implementations, connectivity was incorporated via generic guidelines (McCook et al., 2009), such as setting minimum reserve sizes (Green et al., 2009) or determining optimal reserve spacing (Moffitt et al., 2011). Various reserve design software also provided functionalities to create spatially compact reserves by minimizing the ratio of outer boundary edge length to area (Game et al., 2008; Lehtomäki & Moilanen, 2013), which may help protect movements between physically adjacent habitat patches (e.g., through ontogenetic migration) (Edwards et al., 2010). However, as advances were made in genetic, hydrodynamic, and ecological methods, allowing quantitative measurements and simulations of connectivity between subpopulations (White et al., 2019), more sophisticated approaches were developed to incorporate these new data.

There are 3 broad ways by which larval connectivity can be incorporated in spatial conservation prioritization tools for biodiversity protection (Daigle et al., 2020). In the first method (hereafter the spatial dependency method), a measure of connectivity between all pairwise adjacent and nonadjacent habitat patches creates a penalty for protecting only 1 of a pair of strongly connected patches (Beger et al., 2010). In the second (hereafter the connectivity-based features method), metrics describing properties of connectivity are calculated for each habitat patch and given targets (Magris et al., 2016; White, Schroeger, et al., 2014). Both approaches are applied to represent larval connectivity alongside conventional features such as species abundance and cost while giving the user a degree of control over the relative weighting of different components (Beger et al., 2015; Magris et al., 2016; White, Schroeger, et al., 2014). In the third approach, the cost layer to be minimized is replaced by an inverse measure of connectivity (Krueck et al., 2017; Weeks, 2017). Because this final method precludes the use of real socioeconomic costs and limits the applicability for real-world planning, we consider it a distinct application and focus on the former 2 (Figure 1).

The spatial dependency and connectivity-based methods take 2 conceptually different approaches to connectivity, which has implications for their applicability in certain contexts. The former selects clusters of multiple, highly connected sites at a time and uses strength of connection between pairwise sites to identify important linkages to protect (Beger et al., 2010). This is a potentially better strategy in a worst-case scenario in which unprotected areas are highly degraded with no larval output (Edwards et al., 2010). If persistence of individual subpopulations depends on larval supply from outside sources, then protecting upstream sources and downstream destinations together can help ensure sufficient larval exchange to avoid localized collapses. In contrast, the latter takes a site-based approach in which individual high-ranking sites are selected for reserve designation based on local properties of connectivity. Because this does not guarantee protection of upstream larval sources supplying these sites, the supply of incoming larvae may be severely reduced under a worst-case scenario (White, Schroeger, et al., 2014) (Figure 1). A cursory comparison of the 2 along the northern Californian (U.S.A.) coast revealed that the connectivity-based features method generally achieves greater total population biomass, except for species with relatively widespread larval dispersal, for which performance was similar (White, Schroeger, et al., 2014). The Californian boundary current system has linear, relatively simple oceanographic patterns that result in directional flow of larvae along the coastline. However, optimal strategies for reserve site configurations may differ under more complex dispersal patterns (Kininmonth et al., 2011). Additionally, assumptions about contributions of unreserved areas to the wider metapopulation matter. Most unprotected patches contribute to overall larval supply, but worst-case assumptions are often made (Cabral et al., 2016; Edwards et al., 2010; Hastings & Botsford, 2003; Mumby et al., 2011).

We compared the spatial dependency and connectivity-based features methods to incorporate larval connectivity in the conservation planning software Marxan (Ball et al., 2009).
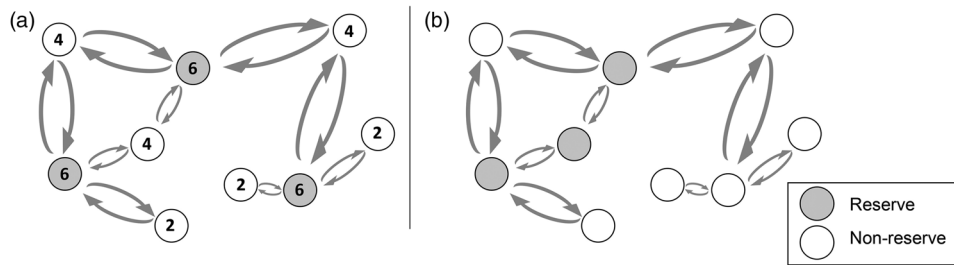
FIGURE 1 Network of hypothetical reefs (circles) connected by incoming and outgoing larval dispersal (arrows): (a) example of the connectivity-based features method where reefs having the highest degree (values inside circles), defined as the cumulative number of incoming and outgoing connections, are selected for reserve solutions and (b) example of the spatial dependency method that selects for reserve a cluster of strongly connected reefs

We compared the performance of these 2 approaches under alternative assumptions about larval dispersal patterns and metapopulation contributions from unprotected sites. Reserve networks were designed for a number of representative simulated seascapes and 2 case studies in the Coral Triangle region and the province of Southeast Sulawesi, Indonesia. Different spatial reserve configurations were assessed by calculating equilibrium settlement inside and outside reserves as an approximate proxy for conservation and fishery benefits, respectively. To help inform the feasibility of implementing different methods, we also evaluated the degree of spatial clustering of reserve networks. Our findings are intended to help researchers incorporate connectivity data into reserve network design. Although our assessment is based on marine systems, our findings are relevant to terrestrial landscapes and reserve design as well.

METHODS

Simulated seascapes

To test the spatial dependency and connectivity-based features methods on a range of different larval dispersal conditions, we created a graph-theoretic seascape representation in which nodes represent habitat patches and weighted edges connecting nodes give the probability of dispersal between patches. Graph theory is increasingly used in marine spatial planning and connectivity research due to its minimal data requirements and efficient algorithms (Minor & Urban, 2007; Moilanen, 2011; Ospina-Alvarez et al., 2020). Similarly, graph theory has informed planning for connectivity in coral reef ecosystems (Kininmonth et al., 2011; Magris et al., 2016; Treml et al., 2008).

Patches of equal size ($n = 100$) were randomly placed in 2-dimensional cartesian space (5000 × 5000). A Euclidean distance matrix $\mathbf{D}_{ij}$ giving interpatch distance was passed through the function $P_{ij} = e^{-1\theta \times \mathbf{D}_{ij}}$ to obtain the probability of dispersal from patch i to j assuming a negative exponential larval dispersal kernel (Urban & Keitt, 2001). We tested a range of values for the exponential decay rate parameter (θ), which gives the mean dispersal distance, from 50 to 250 by intervals of 50 chosen from a preliminary set of runs. Connections smaller than 1×10^{-6} were removed, such that networks were not fully connected.

Local retention, the probability of larvae originating from a patch retained in that same patch, was assigned values similar to dispersal to close neighboring patches.

In this basic near-neighbor seascape pattern, connections were strongest between close neighbors and weakened with increasing distance. However, in some marine environments, strong currents may carry larvae over long distances and increase the probability of dispersal to distant habitat patches (Bode et al., 2006). These long-distance connections can form a small-world network, whereby any 2 distant habitat patches are connected by relatively few steps (Watts & Strogatz, 1998), a pattern that occurs in the Great Barrier Reef (Kininmonth et al., 2010). To examine the effects of these patterns, we simulated a second seascape with small-world links in which a certain proportion of edges were randomly rewired to create new dispersal pathways that had high dispersal probabilities over long distances.

Because each iteration of seascape generation involved random patch placement, 100 replications were generated for each of the 10 different configurations (5 mean dispersal distances and 2 patterns of near-neighbor and small-world links) to avoid potential artifacts and determine average reserve design method performance for all different seascape scenarios. All seascapes were generated with the igraph package (Csárdi & Nepusz, 2006) in R (R Core Team, 2021).

Coral Triangle region and Southeast Sulawesi, Indonesia, case studies

In addition to the simulated seascapes, we compared the 2 methods of incorporating connectivity in 2 case studies for which we had coupled biophysical models describing larval dispersal of different marine species over different spatial scales (Figure 2; Appendix S1). In contrast to the simulated seascapes, these dispersal models quantified asymmetric flow between patches based on realistic currents and larval traits, mortality in the pelagic stage, and complex spatial distribution of habitat patches.

Model outputs were available for larval dispersal of coral trout (*Plectropomus leopardus*) and a sea cucumber (*Holothuria whitmaei*) for the Coral Triangle region (Beger et al., 2015).
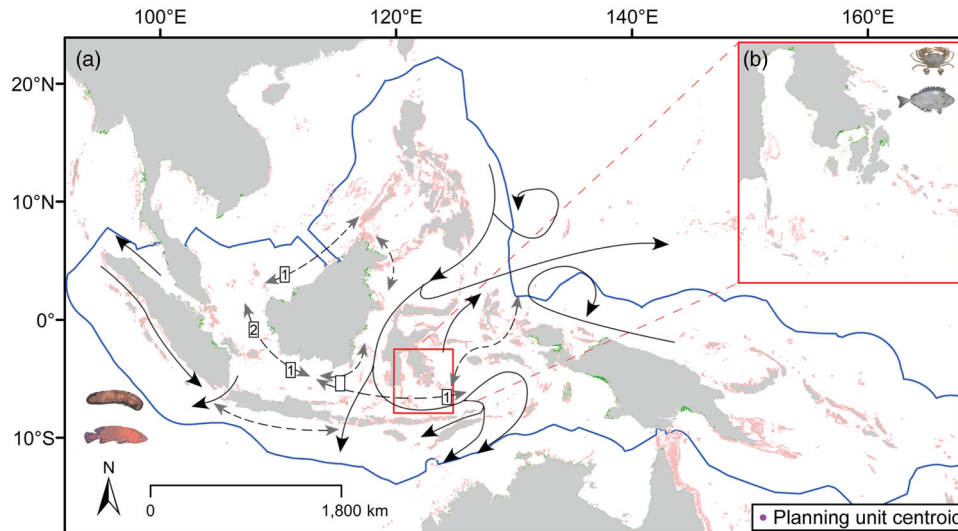
FIGURE 2   (a) The Coral Triangle region (blue) with larval dispersal models for coral trout and sea cucumber and (b) the province of Southeast Sulawesi, Indonesia (red), with larval dispersal models for rabbitfish and mud crab (solid arrows, permanent, major ocean currents, including the Indonesian throughflow (ITF); dashed arrows, dominant current direction during the November–February southwest monsoon [1]) and May–August northeast monsoon [2]; currents adapted from van der Ven et al. [2021]; pink, coral reef; green, mangroves)

The dispersal models simulated larval transport from 425 reef patches by advection and diffusion in surface ocean currents. Larval biological traits and larval behavior were obtained from the literature. Maximum pelagic larval duration of these 2 species is 35 days and 15 days, respectively. Models were also available for the commercially important mud crab (*Scylla serrata*) and rabbitfish (*Siganus canaliculatus*) for the province of Southeast Sulawesi, Indonesia. Larval dispersal was modeled for 487 reef patches for rabbitfish and 216 mangrove patches for mud crab. Life-history parameters were taken from the literature (Appendix S2). Maximum pelagic larval duration of these 2 species is 38 days and 19 days, respectively.

Marxan prioritization

Habitat patches were used as spatial planning units and assigned the same, uniform habitat area and cost to eliminate the effects of these components on solutions, ensuring that any differences could be solely attributed to the method by which Marxan used connectivity. We ran a range of protection targets from 5% to 30% of the habitat feature by 5% increments. Marxan runs were first performed without any connectivity to establish a baseline of effectiveness that may incidentally be capturing some amount of connectivity, followed by runs using the spatial dependency method (Beger et al., 2010) and the connectivity-based features method (White et al., 2014). Following standard practice (Game et al., 2008), we used 100 Marxan repeat runs for each uniquely generated seascape or species to account for flexibility in solutions generated by the simulated annealing algorithm. We then chose the top 10 solutions given by the lowest Marxan score to assess performance of methods.

The spatial dependency method was implemented following Beger et al. (2010). The physical boundary file in Marxan was replaced with an edge list of interpatch larval dispersal probabilities. The value of the connectivity strength modifier, a parameter that weighs the connectivity component against the cost and biodiversity targets in the objective function, was set as the maximum possible value while keeping total costs similar to baseline runs without connectivity.

The connectivity-based features method was implemented following White et al. (2014). We calculated a number of patch-specific metrics of connectivity used in previous studies (Jacobi & Jonsson, 2011; Magris et al., 2015, 2016; Roberts et al., 2021) (Table 1; Schill et al., 2015). Metrics were converted into quartiles to create discrete conservation features (Daigle et al., 2020), and targets were set at the highest possible value while keeping costs similar to baseline runs. Because the simulated seascapes had symmetric dispersal, the metrics for incoming and outgoing degree and flow were identical and combined into flow and degree.

Assessment of protected area networks

We compared the effectiveness of different spatial reserve solutions by applying the dispersal-per-recruit model implemented in the R package ConnMatTools (Kaplan et al., 2017) to calculate equilibrium settlement inside and outside reserves as well as cumulatively across the total system. This model is a simplified discrete-time metapopulation model assuming sedentary adults, dispersive larvae, and a density-dependent settler–recruit relationship, relevant for many benthic invertebrates and reef fishes (Kaplan et al., 2006). All habitat patches were initially saturated at the maximum recruitment carrying capacity, and the consequent equilibrium settlement at each patch was calculated by dispersing larvae according to interpatch dispersal probability (Kaplan et al., 2006). We used a hockey-stick settler–recruit

TABLE 1   Summary of graph-theoretic metrics used in the site-based connectivity-based features method in Marxan spatial planning software

Name	Description
Betweenness centrality	measure of the number of shortest paths across the network that pass through a patch (Minor & Urban, 2007); can highlight important stepping stones in a network
Eigenvector centrality	measure of the contribution of a patch to the growth rate of a linear metapopulation; calculated using number and strength of connections (D'Aloia et al., 2017)
Google PageRank	similar to eigenvector centrality; measures importance of a patch in the wider network based on number and local density of connections (Kininmonth et al., 2019); originally derived from internet web pages ranking; has been used to assess species extinction risk (Allesina & Pascual, 2009)
Local retention	measure of how self-sustaining a patch is; calculated as the proportion of individuals originating from a patch retained in that patch (Burgess et al., 2014)
In or out degree	number of connections when ignoring connection strength; measures the involvement of the node in the network (Opsahl et al., 2010); can be divided further into in degree and out degree for incoming and outgoing connections to describe properties of sinkness and sourceness, respectively
In or out flow	cumulative weight of incoming and outgoing connections from a habitat patch to neighboring patches (Urban & Keitt, 2001); can be divided further into in flow and out flow for incoming and outgoing connections to describe properties of sinkness and sourceness, respectively

relationship that increases linearly until a maximum is reached (Barrowman & Myers, 2000), with the slope at low egg production chosen to correspond to 35% of natural egg production (White, 2010), a threshold for persistence commonly assumed in fishery management (Kaplan et al., 2006).

The parameter of lifetime egg production (LEP) in the dispersal-per-recruit model, which gives the relative reproductive output of habitat patches, was set as 1 for reserves and at 0.00, 0.25, 0.50, or 0.75 for nonreserves. This represents a range of assumptions regarding nonreserve contribution from a worst-case condition of 100% reduction in LEP (LEP = 0) in which nonreserves were highly degraded or overexploited and made no contribution to more benign scenarios of 75%, 50%, and 25% LEP reduction.

We used Bayesian linear models implemented in the R package rstanarm (Goodrich et al., 2020) to quantify the fixed effects of the Marxan connectivity method on reserve system performance. Bayesian tests are considered more appropriate for analyzing simulation model results, given that p values in frequentist statistical hypothesis tests can be artificially decreased as greater computational power permits a larger sample size of simulations (White, Rassweiler, et al., 2014). We chose the median of the posterior distribution to represent a point estimate of effects and calculated 89% credible intervals in the R package bayestestR based on the highest density interval (Makowski et al., 2019).

RESULTS

Simulated seascapes

Mean dispersal distance, pattern of dispersal, and conditions outside reserves affected the performance of reserve networks designed using different Marxan methods (Figure 3). In the near-neighbor pattern, for which dispersal probability declined exponentially with increasing distance, more methods performed similarly well if nonreserves were less degraded (LEP = 0.75). Spatial dependency tended to perform better under worse assumptions (LEP = 0 and 0.25) or at lower mean dispersal distances, whereas the converse was true for connectivity-based features methods. Of all metrics, protecting patches that scored highly in Google PageRank performed well most often, although eigenvector centrality also performed well for seascapes with high mean dispersal distances. In the small-world links pattern, in which strong dispersal events were emulated between distant patches, spatial dependency performed comparatively worse; it performed well only when there was very little protected habitat (5%) or when seascapes had low mean dispersal distances. Protecting patches with high Google PageRank performed well for all combinations of habitat protection and nonreserve contributions. Eigenvector centrality and flow also performed well for seascapes with high and low dispersal distances, respectively.

In general, the gain in conservation benefits from incorporating connectivity compared with baseline scenarios was higher when nonreserves were more degraded (Appendix S3). In the worst-case scenario, the best connectivity method produced up to a 30-fold higher total equilibrium settlement compared with baseline runs with no connectivity. This difference was only 1.3-fold in the most benign assumption (LEP = 0.75). There were also differences in the relative proportion of equilibrium settlement inside versus outside reserves depending on which method was used (Appendix S3). If nonreserves made little or no larval contributions (LEP = 0 and 0.25), spatial dependency methods generally produced reserve networks with a greater proportion of settlement inside than outside reserves compared with connectivity-based features methods, even when cumulative settlement was similar between the 2. However, under more benign assumptions (LEP = 0.5 and 0.75), the relative proportion inside and outside reserves was similar across methods.
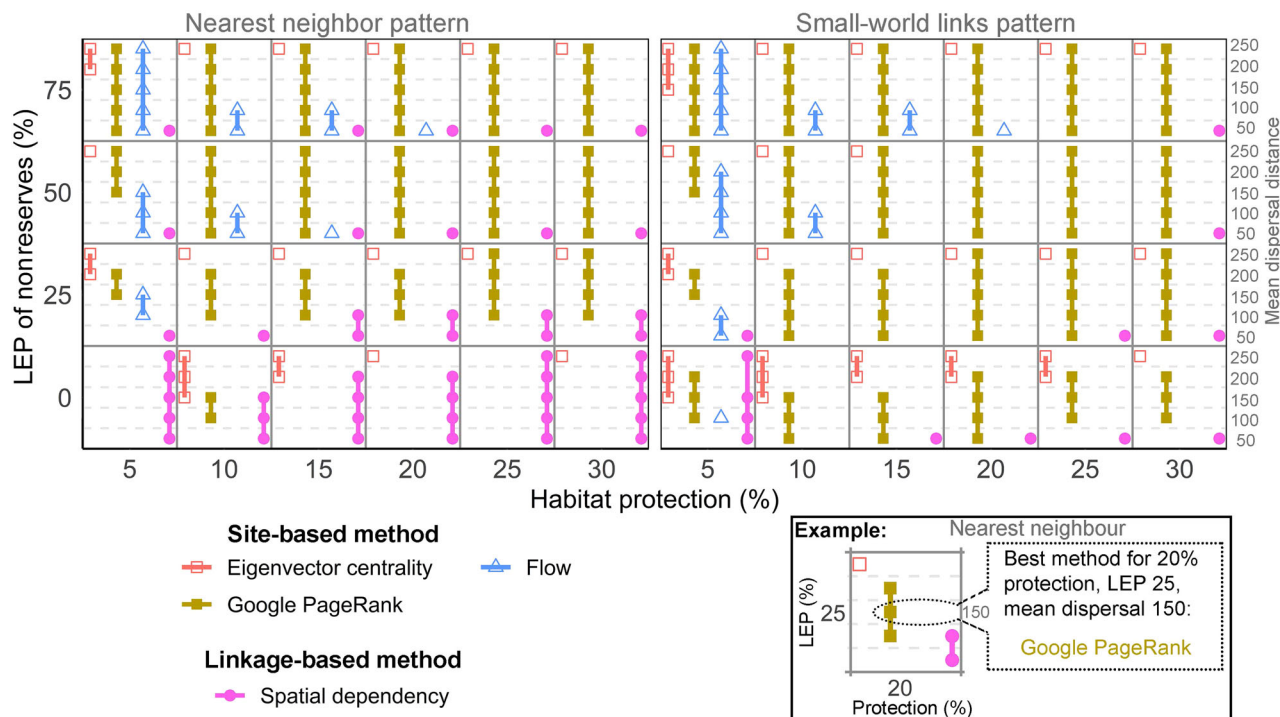
FIGURE 3 Marxan methods achieving highest total equilibrium settlement in simulated seascapes. Each cell is a different combination of habitat target and lifetime egg production (LEP) assumption. In each cell, the position of the point indicates for which of the 5 dispersal distances (50, 100, 150, 200, and 250) the method performed best (lowest dispersal at bottom, greatest at the top). Where multiple symbols occur in a row, these methods performed equally well. A 100% depletion of the species is at LEP = 0.

Case studies

The 2 case studies corroborated the observation from simulated seascapes that the spatial dependency method performed comparatively better when nonreserves made little or no larval contributions or the total amount of habitat protected was low (Figure 4). For coral trout and sea cucumber in the Coral Triangle region under a worst-case scenario, reserve networks designed with the spatial dependency method achieved the highest equilibrium settlement. As the amount of habitat protected increased or assumptions were relaxed (LEP = 0.25, 0.5, and 0.75), connectivity-based features methods performed equally well or better. Protecting patches scoring high in Google PageRank consistently achieved good outcomes, whereas in flow, local retention, and eigenvector centrality occasionally performed equally well. Outcomes for Southeast Sulawesi were markedly different. Here, the connectivity-based features method with targets set for local retention achieved greatest equilibrium settlement compared with all other methods; in flow, Google PageRank, and spatial dependency occasionally performed equally well for certain habitat targets and nonreserve assumptions.

As in the simulated seascapes, the performance gain from incorporating connectivity was lower when nonreserves were less degraded and made greater contributions. The relative proportion of settlement inside and outside reserves in the case studies also showed similar trends to the simulated seascapes (Appendix S3). Spatial dependency produced higher proportions inside reserves compared with connectivity-based features

methods, particularly when nonreserves made little or no contributions. However, this trend was more evident in the Coral Triangle species than in the Southeast Sulawesi species.

The degree to which reserve solutions were spatially clustered differed depending on which method was used (Appendix S4). As expected, the spatial dependency method tended to create clusters of reserves concentrated in certain parts of the region, although more than 1 distinct cluster could be selected if habitat targets were sufficiently high. For example, 2 spatially distinct clusters of reserves were identified for coral trout if 20% of habitat was protected, explained by the presence of 2 succinct subnetworks in the eastern and western parts of the Coral Triangle region, and there was little larval flow past the island of Papua. Use of certain metrics, including eigenvector centrality, in degree, and out degree, also created more spatially clustered solutions. In contrast, use of other metrics resulted in individual reserves being more evenly distributed across the region.

To understand why setting targets for local retention performed substantially better in the Southeast Sulawesi species compared with the Coral Triangle species (Figure 4), we investigated the distribution of local retention of habitat patches and the effect on within-patch equilibrium settlement (Appendix S5). The Coral Triangle species showed a left-skewed distribution of local retention (many patches retained a high proportion of larvae), whereas the inverse was observed in the Southeast Sulawesi species, for which most patches retained few larvae and only a small number of patches had high retention. The consequence of this relationship was that Marxan selected all the best patches for retention with highest prereserve settlement in both
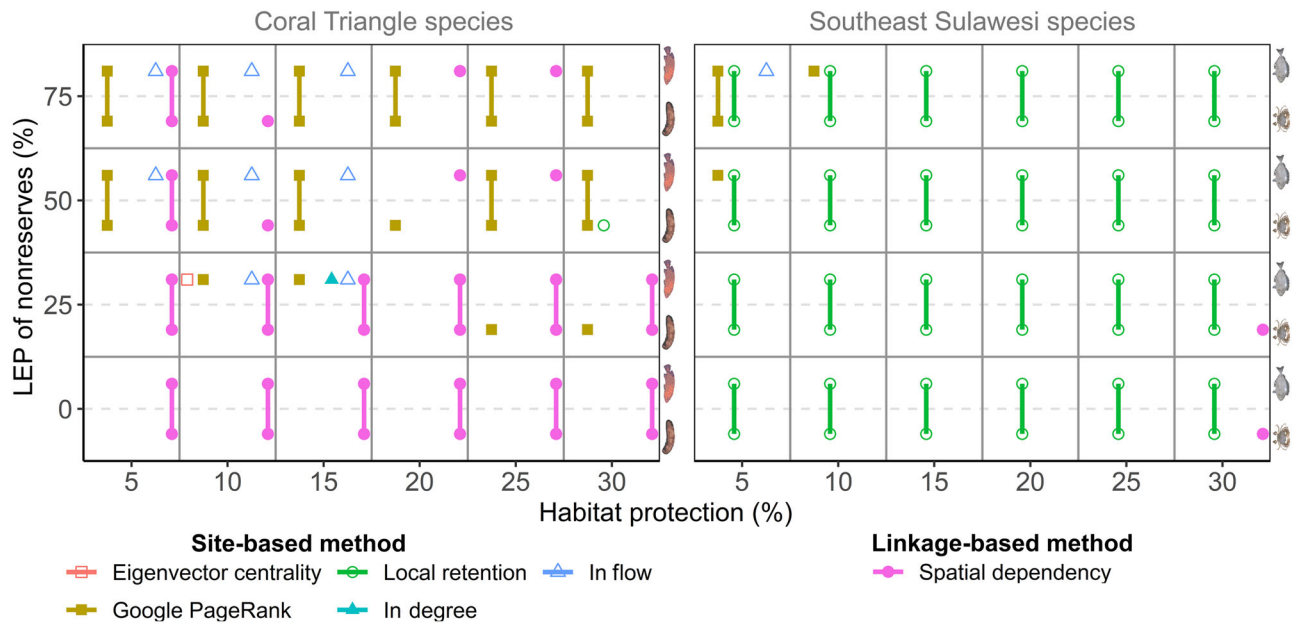
FIGURE 4 Marxan methods achieving highest total equilibrium settlement in 2 case studies. Each cell is a different combination of habitat target and lifetime egg production (LEP) assumption. In each cell, the position of the point indicates for which of the 2 species the method performed best (coral trout and rabbitfish at the top, sea cucumber and mud crab at the bottom). Where multiple symbols occur in a row, these methods performed equally well. A 100% depletion of the species outside reserves is at LEP = 0.

regions. Remaining sites had very low retention and significantly lower prereserve settlement in Southeast Sulawesi, but remaining sites had higher retention and similar or greater prereserve settlement in the Coral Triangle.

DISCUSSION

No single method consistently performed best. Assumptions about metapopulation contributions of unprotected areas, larval dispersal ability, and the proportion of habitat protected determined how well either method performed. In general, spatial dependency performed better when dispersal distance was limited, a high proportion of the area of interest was substantially degraded, or the target amount of habitat protected was low. Instead, the connectivity-based features method achieved higher equilibrium settlement when dispersal was greater, areas were less degraded, or more habitat was protected. However, choice of method will depend on whether management objectives are focused more on prioritizing settlement within reserves to rebuild populations that are severely depleted or on prioritizing settlement outside reserves to support fisheries and whether spatial clustering of reserves is a desirable characteristic. The spatial dependency-based methods created more spatially clustered solutions and generally produced more benefits inside reserves, with a trade-off of benefits outside reserves, as compared with the site-based methods.

As expected, a key determinant in performance of methods was the assumption regarding the contribution of nonreserves. In classical reserve theory and conservation planning, a conservative worst-case assumption is often taken where larvae from nonreserves make no contribution (Cabral et al., 2016; Edwards et al., 2010; Hastings & Botsford, 2003; Mumby et al., 2011). This often applies to terrestrial systems where habitat is destroyed in unprotected areas (Almany et al., 2009). However, this strict premise may not always be true in marine ecosystems where spillover and adult movements can sustain biodiversity outside reserves (Russ & Alcala, 2011; Sale et al., 2005). However, for naturally patchy and increasingly degraded reef systems this assumption may be justified to explore worst-case scenarios under ongoing habitat loss given the ongoing deterioration of reefs worldwide (Burke et al., 2011). Overfishing and removal of key functional groups such as grazing herbivores are common in many tropical coastal fisheries, which, combined with declining water quality and other stressors, have caused widespread phase shifts to algal-dominated reefs supporting fewer fish (Hughes et al., 2007; Roth et al., 2018). The precautionary assumption of a worst-case scenario may therefore be permitted unless unprotected habitat can confidently be expected to host relatively healthy populations, when, for example, pressures such as fishing and coastal run-off are well regulated and policies are enforced (MacNeil et al., 2015; Richmond et al., 2019).

Larval dispersal characteristics were also key determinants in the relative performance of the 2 connectivity methods. At lower dispersal distances in the simulated seascapes where habitat patches were only connected to a few near neighbors, the spatial dependency method achieved greater equilibrium settlement. Instead, when the network conditions became better connected, through either small-world links, a greater dispersal distance, or unprotected patches acting as stepping stones by relaxing assumptions of degradation, the connectivity-based features methods performed as well or better. More specifically,

metrics describing properties of network centrality, defined as the importance of a node in a wider network, such as Google PageRank and eigenvector centrality, performed well in this context. This result is supported by previous findings suggesting that species with short dispersal distances tend to benefit from denser networks of marine protected areas, whereas those with long dispersal distances can benefit from more distributed networks (Shanks et al., 2003; Treml et al., 2012).

The case studies showed that performance of connectivity methods also depended on how dispersal strength was distributed across patches. Highest equilibrium settlement was achieved in Southeast Sulawesi by designating habitat patches with high local retention as reserves. White, Schroeger, et al. (2014) also found that protecting reefs with high local retention achieves greater biomass in reserve systems for 4 out of 5 reef species in the northern California coast compared with protecting reefs with high network centrality. Similarly, Burgess et al. (2014) recommend that protecting local retention, and thereby self-persistence, is generally an advantageous strategy. However, this strategy did not perform better than the spatial dependency method for the Coral Triangle species, for which many habitat patches had similarly high levels of local retention, indicating different performances when local retention had either left- or right-skewed distributions. The larger size of planning units in the Coral Triangle, where mean size was roughly 350 times bigger compared with Southeast Sulawesi planning units, is likely why local retention was overall much higher because most short-dispersing larvae were retained within planning units. Because the size of planning units relative to the scale of dispersal processes influences the value of connectivity metrics, this in turn affects the performance of different connectivity-based features methods.

Our results presented require some important caveats to be considered. First, the performance metric of equilibrium settlement relates to an objective of designing reserves with high maximum spawning potential across both protected and unprotected areas. However, other performance indicators may be more appropriate for different management objectives. Second, the oceanographic models in each of the case studies are resolved at different spatial scales, and dispersal simulations are known to accurately quantify local retention. Currents close to the shoreline were more accurately predicted in the 500-m resolution Southeast Sulawesi models compared with the coarser 10-km resolution Coral Triangle models. Correctly accounting for these coastal boundary layers, where current velocities are reduced, can substantially change the prediction of larval local retention (Nickols et al., 2015). This highlights the ongoing need for validation of dispersal models (Bode et al., 2019) and the use of cross-validating studies employing different methods (McCook et al., 2009) as the use of dispersal estimates in conservation planning becomes more widespread.

Apart from the conditions outside reserves and characteristics of larval dispersal, choice of method will also be informed by some of the practical benefits and drawbacks associated with either method. The connectivity-based features method has no theoretical limit on how many different metrics of connectivity can be added as conservation features in the same prioritiza-

tion problem, meaning that connectivity can be incorporated for multiple species having contrasting dispersal abilities (Magris et al., 2016, 2018). In contrast, the spatial dependency method can only use 1 connectivity data set per prioritization problem. Connectivity of multiple species could be aggregated into a single matrix to allow the use of this method, but there is no guarantee that this will be an appropriate surrogate for each species (Magris et al., 2018). Regardless of which method is selected, post hoc population viability analyses or real-world evidence of conservation impacts is required because neither method explicitly links connectivity to demographic processes (Bode et al., 2016). This will be especially important when multiple species are used to evaluate whether contrasts are correctly captured for each species or lost if effects are averaged out.

Although we used Marxan in our analyses, our results are likely to apply to other similarly functioning tools. The R package prioritizr has a nearly identical framing of an objective function containing objectives, constraints, and penalties, but it uses an integer linear programming algorithm to identify exact optimal solutions (Hanson et al., 2021). As with Marxan, asymmetric connectivity can be incorporated as a boundary penalty between planning units or as a conservation feature. Zonation is another commonly used tool in which a priority ranking of the entire landscape is performed and sites most valuable for biodiversity have the highest ranks (Lehtomäki & Moilanen, 2013). Ways to incorporate connectivity include boundary length penalties and conservation features. Additional options are available, such as including interactions between different environment types and data layers (Lehtomäki & Moilanen, 2013). Although different tools will undoubtedly generate different solutions, these approaches broadly fall into either spatial dependency-based or site-based categories because connectivity is used either between sites or for a single site and similar considerations as we have discussed here will apply.

Our comparative analyses showed that different methods of using connectivity in spatial conservation prioritization are appropriate under different contexts. When a high proportion of habitat in the area of interest is heavily degraded or the metapopulation is not widely connected, the spatial dependency method of protecting clusters of highly connected habitat patches could be a desirable prioritization approach to rebuild and sustain populations. In other instances, protecting sites that have high Google PageRank scores, measuring patch importance in the wider network based on weight and number of connections, or local retention scores, measuring the proportion of larvae retained in each patch, could be more advantageous. As the use of connectivity in marine spatial planning becomes more widely adopted, these results highlight the importance of post hoc evaluations and the need to understand assumptions and possible limitations associated with dispersal estimates.

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