Identifying critical regions in small-world marine metapopulations

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The precarious state of many nearshore marine ecosystems has prompted the use of marine protected areas as a tool for management and conservation. However, there remains substantial debate over their design and, in particular, how to best account for the spatial dynamics of nearshore marine species. Many commercially important nearshore marine species are sedentary as adults, with limited home ranges. It is as larvae that they disperse greater distances, traveling with ocean currents sometimes hundreds of kilometers. As a result, these species exist in spatially complex systems of connected subpopulations. Here, we explicitly account for the mutual dependence of subpopulations and approached protected area design in terms of network robustness. Our goal is to characterize the topology of nearshore metapopulation networks and their response to perturbation, and to identify critical subpopulations whose removal would reduce the risk for stock collapse. We define metapopulation networks using realistic estimates of larval dispersal generated from ocean circulation simulations and spatially explicit metapopulation models, and we then explore their robustness using node-removal simulation experiments. Nearshore metapopulations show small-world network properties, and we identify a set of highly connected hub subpopulations whose removal maximally disrupts the metapopulation network. Protecting these subpopulations reduces the risk for systemic failure and stock collapse. Our focus on catastrophe avoidance provides a unique perspective for spatial marine planning and the design of marine protected areas.

Nearshore marine ecosystems are some of the most productive and diverse environments on earth, maintaining a wide variety of organisms and providing essential food and services to the global population. Unfortunately, they are also under increasing stress from perturbations, such as oil spills, climate change, and overfishing, and are at risk for losing their productive output (1, 2). Mitigating the impacts of these perturbations is difficult because most nearshore marine species exist in a spatially complex system of connected subpopulations; stress placed at one location may detrimentally reduce stock levels at many others (3, 4). Quantifying patterns of connectivity is crucial to our ability to manage these systems effectively. For example, marine protected areas (MPAs) have emerged as an important tool for conservation and fisheries managers tasked with maintaining nearshore systems and accounting for the mutual demographic dependence of populations (3–9). Current approaches to their design center on either protecting essential habitats (5, 6, 9) or maximizing economic goals (10, 11). We provide an alternative and consider the design of MPAs as a problem of metapopulation network robustness, here defined as the ability of a system to withstand perturbation (12). Our goal is to account for patterns of connectivity and identify key regions whose protection from perturbation safeguards against systemic failure and stock collapse (12–14).

Many nearshore marine species are sedentary as adults, with home ranges on the order of 0.1–10 km (15). Longer distances are traveled as newly spawned larvae (15). During this larval stage, larvae advect primarily by means of ocean currents, potentially traveling distances orders of magnitude greater than those traveled as adults (i.e., ~100 km) (15–18). As a direct consequence of this larval dispersal stage, nearshore marine species exist in systems of interconnected subpopulations (3, 4). Typically, larval connectivity has been estimated using simple statistics of ocean circulation and Euclidean distance (e.g., 3, 4, 19). This approach has been used extensively to gauge criteria for metapopulation persistence and in the design of protected areas (3, 4), but it ignores several important details (17, 18). For instance, theoretical studies have shown that heterogeneity, asymmetry, and temporal variability in larval connectivity patterns are key properties that affect the persistence of metapopulations (20–23). To a large degree, these properties are not captured by standard empirical methods and remain elusive in realistic settings.

To capture the complexity of larval connectivity patterns, we combine ocean circulation simulations with realistic metapopulation modeling. Over the past decade, simulation approaches to quantifying larval connectivity have grown in prominence and have been used to investigate the scales of larval dispersal (16–18, 24), the population genetic structure of nearshore species (25, 26), and processes affecting the composition of nearshore communities (27), to name a few examples. Here, our goal is to use ocean circulation simulations to explore how nearshore metapopulations respond to perturbation and to identify specific nearshore regions that are key to metapopulation robustness. We focus our attention on the dynamics of several commonly fished species in the Southern California Bight (Fig. L4): kelp bass (Paralabrax clathratus), kelp rockfish (Sebastes atrovirens), ocean whitefish (Cataloquitlantis princeps), red sea urchin (Stronglylocentrotus franciscanus), opaleye (Girella nigricans), California halibut (Paralichthys californicus), and California sheephead (Semicossyphus pulcher), whose life history characteristics span a broad range. These species were used as part of a recent MPA planning program in the Southern California Region (9), and our methods use the numerical models developed for this process.

Patterns of larval connectivity for each study species are quantified in a two-step process. First, Lagrangian probability
density functions (PDFs), which summarize water parcel trajectories derived from high-resolution ocean circulation simulations (28), were used to quantify the probability of a larva, of a given species, traveling from one subpopulation to another. This quantity is termed “potential connectivity” (17, 18). An example of a Lagrangian PDF for a particular production site on San Nicolas Island in the center of the domain, consistent with the spawning season of kelp bass, is shown in Fig. 1B (larval life history parameters are provided in Table S1). Determinations of potential connectivity were then used in realistic metapopulation models to estimate the number of larvae spawned at a given source that subsequently recruit to a certain destination subpopulation. Because this quantity accounts for such demographic processes as larval production and mortality, it is termed “realized connectivity” (18). Network metrics were then used to analyze these estimates of realized connectivity, guiding node-removal simulation experiments (29, 30). These simulate a series of catastrophic events at particular nearshore locations and assess metapopulation robustness, answering the question of which nodes (subpopulations) should be protected in order to fortify the entire network (metapopulation) against systemic failure (stock collapse) (12, 29–32).

Results
The potential connectivity for all species in the Southern California Bight (Fig. 2A for kelp bass and Fig. S1 for all other species) is heterogeneous and asymmetric, with differences in dispersal parameters (spawning season, spawning period, and pelagic larval duration) creating differences among species. This interspecific variation is also evident in the realized connectivity (Fig. 2B for kelp bass and Fig. S2 for all other species), where the metapopulation models and parameters (fecundity, natural mortality, and density-dependent larval mortality) transform the potential connectivity. Among species, potential and realized connectivity show stark differences, emphasizing the importance of these demographic processes in spatially structuring metapopulation networks. For example, for kelp bass, there are strong potential connections from southern mainland subpopulations to those on the northern islands (Fig. 2A, source indexes 1–63, destination indexes 63–96). However, because these subpopulations are characterized by areas of low suitable habitat, and hence low larval production, realized connectivity is relatively weak (Fig. 2B). Equilibrium spatial distributions of biomass also reflect these differences in dispersal and demographic parameters (contrast Fig. 2C for kelp bass and Fig. S3 for all other species).

Plotted on a log-log axis, the frequency distributions for realized connectivity across all nonzero i,j pairs are reasonably linear, albeit with slight curvature (Fig. 3A for kelp bass and Fig. S4 for all other species), indicating that metapopulations are characterized by many weak and few strong larval connections (33). In this way, nearshore metapopulations resemble small-world networks, which typically have long-tailed degree distributions (31, 33, 34). Further, across all species investigated, only a small fraction of the coast (10–23%) accounted for 50% of the total number of recruits in the metapopulation (Fig. 3B, this metric is henceforth termed $R^{0.5}$). Together, these two properties of realized connectivity indicate that “hub” subpopulations exist. These are the most connected subpopulations in the metapopulation. Interestingly, we found that $R^{0.5}$ was smaller for species with summer spawning months (Fig. 3B, colors). This variation reflects the seasonality found in patterns of ocean circulation in the Southern California Bight (17, 18, 28).

For all species, sequentially removing subpopulations following the network metric, eigenvector centrality, produced the most rapid declines in metapopulation biomass (35–37) (Fig. 4A and Fig. S5, red line), collapsing metapopulations after 40–65% of the coast was removed. In contrast, the expectation of removing subpopulations randomly was shallower, even though the set of random removal curves theoretically includes the eigenvector centrality curve itself (Fig. 4A and Fig. S5, light blue lines are 100 random realizations, and the dark blue line is the mean over 2,000 realizations). The difference between the central mean random removal curves reveals that these nearshore metapopulations are, in general, robust to random perturbations yet vulnerable to directed disturbances.

A greedy search algorithm was also used to identify critical subpopulations and for comparison with the eigenvector centrality results. At each removal stage, the locally optimal solution, the subpopulation that would create the largest decline in metapopulation biomass when removed, was found numerically. The greedy algorithm removal curves were matched by eigenvector centrality in the rate at which the metapopulation biomass declined to collapse (Fig. 4A and Fig. S5, compare the black circles and red lines). However, the exact order in which subpopulations were removed was not the same, revealing that there is redundancy in the importance of subpopulations; it is not necessarily the order in which important subpopulations are removed, merely that they are (note the initial mismatch in the red line and black circles for kelp rockfish; Fig. S5F). Removing subpopulations following the area of suitable habitat created removal curves that were slightly shallower than both the greedy and eigenvector centrality curves (green lines) but steeper than the mean random removal curve.

We defined a small-world metric as the difference between the eigenvector centrality and the mean of the random removal

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**Fig. 1.** (A) Southern California Bight with bathymetry and 135 subpopulations (red circles). (B) Example Lagrangian PDF for kelp bass. Lagrangian particles are released from the pink subpopulation during the kelp bass spawning period and are transported with ocean velocities, produced from a regional ocean model, for a given pelagic duration (Table S1). Given these time constraints, Lagrangian PDFs quantify the probability of a Lagrangian particle reaching other locations (color scaling; ref. 17).
curves in the fraction of removed coastline required to reduce the metapopulation biomass by 50%. This was termed $C^{0.5}$. When $C^{0.5}$ is high, there is a large difference between the random and central removal curves, indicating that the studied metapopulation resembles a small-world network whose robustness is reliant on a few key hub subpopulations. This metric shows a significant negative linear relationship with $F^{0.5}$, the fraction of the metapopulation responsible for 50% of the total number of recruits (reference to this second metric in Fig. 3A). (C) Spatial distribution of equilibrium biomass for kelp bass. Subpopulation biomasses are fractions of the total metapopulation biomass. Sites with zero biomass are those with little or no suitable habitat. The potential connectivity, realized connectivity, and distributions of biomass for the six other species can be found in Figs. S1–S3, respectively. Isl, island; N., north; S., south.

Discussion

We have found that patterns of larval connectivity in nearshore marine metapopulations have small-world network properties (14, 33, 34). The most important characteristic is the existence of hub subpopulations (21, 29, 35, 36). These are the most
connected subpopulations, and they produce the majority of larval recruits in the metapopulation. We used realistic metapopulation models to estimate patterns of realized connectivity and eigenvector centrality to identify the locations of hub subpopulations for a range of species in the Southern California Bight. Across species, we found that the hub subpopulations are spatially aggregated (Fig. 5 and Fig. S6), suggesting that a localized catastrophe, such as an oil spill, has the potential to affect multiple sites and species. If these sites are already challenged by ongoing perturbations (e.g., from fishing), this additional event could effectively “remove” these subpopulations and increase the risk for domain-wide metapopulation collapse. With regard to spatial management, MPAs designed to cover these key subpopulations would be an important step in avoiding this worst-case scenario. This perspective reflects the fortification of key nodes in other network systems, such as keystone species in food webs (37) or server machines in computer networks (32).

The metapopulation models can be thought to balance the demographic influence of the amount of habitat and potential connectivity. The amount of habitat determines a given subpopulation’s carrying capacity, but it alone does not guarantee that a subpopulation will be important to the robustness of the metapopulation. For that to happen, the subpopulation must also have high potential connectivity, with the larvae that it produces dispersing to other subpopulations. Thus, although the habitat removal curves tracked those of eigenvector centrality (Fig. 4A and Fig. S5), they were never precisely the same and always shallower. Indeed in a direct comparison of the removal curves, the areas of suitable habitat and eigenvector centrality do not show strong correspondence (Pearson’s r, range: 0.44–0.81; Table S2). On its own, the area of suitable habitat cannot account for patterns of larval connectivity; hence, it identifies not only subpopulations that are highly central but also those that are sinks of larval connectivity. These sinks do not contribute to the overall robustness of the metapopulations (22).

A long-held tenet of spatial management is that the number of recruits produced from a given subpopulation or “source strength” identifies areas that are important to metapopulation persistence (3, 4, 6, 8, 11, 22). In the Southern California Bight, source strength removal curves show extremely high correspondence with those of eigenvector centrality (Pearson’s r, range: 0.92–0.99 across species; Table S2). The strong correlations reveal that the key hub subpopulations are exactly the major sources of recruits. In the Southern California Bight, the spatial...
scales of the domain and of potential connectivity overlap. The result is that a larva spawned anywhere has the potential to disperse to all other subpopulations in one step. The overlap in spatial scales results in the first-order connections being the most important; hence, the strong correspondence between eigenvector centrality and source strength. However, being a good source is not necessarily the same as being a central hub. Source strength only captures the influence of first order larval connections, whereas eigenvector centrality is designed to take into account higher order “stepping-stone” connections. If a larger domain were considered, for example, the whole western coast of the United States, larvae would not be able to reach every subpopulation in one step. Potential connectivity would be more sparse, and the importance of higher order connections would increase, resulting in greater differences between source strength and eigenvector centrality.

The area of suitable habitat deserves further consideration because it controls the intensity of density-dependent larval mortality and the carrying capacity of a given subpopulation (38, 39) (Eq. 3 and Methods). Theoretically, at some extremely high level of density dependence, spatial heterogeneity in larval connectivity, which creates differences in the importance of subpopulations, will diminish (40). We tested the effect of different levels of larval density dependence by altering demographic parameters (Methods) and found that the robustness of metapopulations to subpopulation removal was indeed affected by these changes; removal curves were steeper at lower compensation ratios (CRs) and less intense larval density dependence (Fig. S7B). However, the location of the hub subpopulations did not change greatly, suggesting that the location of key subpopulations is robust to this demographic uncertainty (Fig. S7 C and D).

A network perspective is extremely useful for understanding metapopulation structure and dynamics (14, 21, 29, 33, 35, 41–44). However, there are several caveats to its application. Although both the potential and realized larval connectivity show large degrees of structure, with asymmetry and heterogeneity in connections, it is the edge weights that hold all the information. Both the potential and realized connectivity matrices have no zero elements, with all nodes in the metapopulation network connected to each other. Thus, it is not the lack of connections that defines metapopulation networks but the strength of the connections. This is in contrast to most studied networks (e.g., 31, 32, 37, 41, 44), which do not show such extreme connectivity. Thus, caution should be applied when using network metrics that were originally designed for binary (i.e., networks where pairs of nodes are simply connected or not) and more sparse networks. For example, betweenness centrality has been used previously to identify critical subpopulations in metapopulation networks (21). However, in the node removal experiments, betweenness centrality did not match the greedy algorithm as closely as eigenvector centrality and produced shallower removal curves (Pearson’s r; range: 0.65–0.95; Table S2). Thus, it did not identify the most critical nodes in the nearshore metapopulation networks.

We must note that eigenvector centrality is a metric designed for linear systems (36, 37), whereas models of metapopulation dynamics, like ours, are typically nonlinear (45). As a result, eigenvector centrality is only a heuristic metric for identifying critical subpopulations. It does not identify the exact solution to the problem of finding the smallest set of subpopulations whose removal maximally reduces metapopulation biomass. However, the close match-up with the greedy algorithm indicates that eigenvector centrality performs well, allowing us to conclude that it is indeed hub subpopulations that are critical to metapopulation robustness. Another caveat is that our analysis focuses on the dynamics of one species at a time. An important development will be to understand how perturbations, occurring as a result of overfishing or climate change, affect the trophic linkages between species as well as their spatial dynamics [i.e., meta-community dynamics (46)]. Needless to say, our analysis also depends on the accuracy of the Lagrangian particle simulations in capturing the spatial patterns in larval dispersal. Going forward, it will be important to gauge the impact of known computational issues, such as domain edge effects (17, 18), and biological processes, such as larval behavior (47), mortality (48), and environmental stochasticity (23, 49).

In summary, coupling high-resolution oceanographic simulations products with realistic metapopulation modeling is a powerful tool for understanding the spatial dynamics of nearshore marine species. We have found that nearshore marine metapopulations exhibit small-world characteristics, being robust to random perturbations yet highly vulnerable to directed disturbances. Numerous complex systems exhibit this “robust yet fragile” property (12, 50), and we have shown that by knowing metapopulation network quantities, such as realized connectivity and eigenvector centrality, critical subpopulations can be identified. These subpopulations are hubs of larval connectivity and are key to the robustness of metapopulation networks. Hence, they are ideal candidates for MPAs placed with the aim of reducing the risk of stock collapse.

Methods

Potential Connectivity. Potential connectivity (Dij) is defined as the probability of a larva, spawned at a given source subpopulation (i), traveling to a destination subpopulation (j). Estimates of potential connectivity were produced using Lagrangian particle simulations (17). Over the model integration period, 1996–2002, ~400,000 Lagrangian particles were released from a number of discrete patches (5-km radius; Fig. 1A, red circles) during each annual spawning season of a given species (a total of over 50 million particles). The size of these patches reflects limitations in both the numerical simulations of larval dispersal and the node removal experiments. Particles then advect passively for a specified pelagic larval duration (Table S1), being moved by ocean velocities produced from a high-resolution (1 km horizontally, 40 layers vertically) regional ocean modeling system solution for the Southern California Bight (28).

Lagrangian PFDs were then used to calculate the site-to-site transition probabilities that define potential connectivity (17). Potential connectivities were calculated for the spawning periods of each case-study species and for each of the 7 y of modeled Lagrangian particle data. These data were then averaged across years. Potential connectivity values between all pairs of nearshore patches were then stored in a matrix (Fig. 2A and Fig. S1). This method is described in detail by Mitarai et al. (17), and the reader is referred to that study for further information on Lagrangian PFDs.

Metapopulation Model and Larval Connectivity. Dynamic and spatially realistic models for several nearshore species were developed from models created as part of the State of California’s Marine Life Protection Act (MLPA) (9). For all species, the model domain was the Southern California Bight and the 5-km patches used to calculate potential connectivity were utilized to define the spatial extent of the subpopulations (Fig. 1A, red circles). The state variable is biomass (kg), and the models are deterministic with equilibrium values insensitive to initial conditions. The model is general to all species, and it is the parameterization that leads to species-specific dynamics. Species parameters were estimated as part of the MLPA process (9) and can be found in Table S1. Population dynamics are iterated forward in discrete yearly intervals until equilibrium biomass values are reached (examples of spatial distributions of biomass are shown in Fig. 2C and Fig. S3):

\[
A^{t+1}_{n+1} = \begin{cases} 
A^n_{j+1} & \text{if } n \geq 1 \\
\frac{R^n_{j}}{1 + m} & \text{if } n = 0 
\end{cases}
\]

where \(A^n_{j+1}\) is the number of adults of age \(n+1\), at subpopulation \(j\), at time \(t+1\) (next year). \(A^n_{j}\) is the number of adults of age \(n\), at subpopulation \(j\), at time \(t\). \(m\) is the natural mortality and, with the exception of kelp rockfish, is constant across patches and through time. The kelp rockfish is a northern species, and we modeled its natural mortality as a negative linear function of the long-term average sea-surface temperature, where the warmest subpopulation has \(m = 0.4\) and the coolest has \(m = 0.2\) (9, 18, 51). The long-term mean sea surface temperature for each subpopulation was...
where \( W_{ij} \) is the biomass of adults of age \( n \) (kg), at subpopulation \( i \), at time \( t \), \( j \) is the fecundity (number of larvae produced per kilogram of adult biomass) of age group \( n \), and \( D_{ij} \) is the potential connectivity described previously (i.e., the probability of a larva traveling from a source subpopulation \( i \) to a destination subpopulation \( j \)). Fecundity is zero if \( n < \) age at maturity (Table S1). The number of larvae arriving at a given destination patch \( j \) is a result of larvae produced by all age groups (summation over \( n \)) and from all source patches (summation over \( i \)). \( \sigma_{ij} \) is the postsettlement, density-dependent, recruitment probability of a larva arriving at patch \( j \), modeled using a Beverton–Holt function:

\[
\sigma_{ij} = \frac{1}{1 + H_{ij}^{\beta}}
\]

where \( H_{ij} \) is the area of suitable habitat in the spatial extent of a given subpopulation, \( \beta \) is a constant, and \( H_{ij}^{\beta} \) is the number of larvae arriving at patch \( j \) at time \( t \). \( \beta \) is simply the double-summation term in Eq. 2. \( \sigma_{ij} \) describes larvae-on-larvae competition and is used widely in fisheries science (e.g., 9, 38, 45); adult-on-larvae competition was assumed to be negligible. For halibut, suitable habitat \( H \) was defined as nonrocky substrate, whereas suitable habitat was defined as rocky habitat for all other species (9, 18, 51) (Fig. S7A). \( \beta \) is a nondimensional parameter that, along with fecundity, controls the strength of density dependence. It also accounts for larval mortality as larvae disperse, which is assumed to be constant. We measured \( \beta \) using the settler-recruit curve, where the slope at the origin can be described as a nondimensional CR (9, 38, 39). This is the ratio of the per capita settler survival rate at very low densities to the per capita settler survival rates at the highest possible density of settlers. We chose \( \beta \) and fecundity values to create a range of CRs (3, 4, and 5) for all species. The figures presented in the main text and SI Text are from simulations using a CR of 4; this is a commonly chosen strength of density dependence, reflecting the recent MLPA process (9). The affect of varying CR is presented in the Discussion and in Fig. S7.

We further calculated realized connectivity \( (R^*_j) \), which is defined as the number of larvae that travel from a source subpopulation \( i \) and subsequently recruit to a destination location \( j \) (18). Hence, it takes into account larval production and density-dependent larval mortality. Realized connectivity is found by knowing both the number of larvae dispersing between patches and the density-dependent larval mortality rate:

\[
R^*_j = \sum_i W_{ij} j \sigma_{ij} D_{ij}
\]

Like potential connectivities, realized connectivities between all pairs of nearshore patches are stored as a matrix.

The lengths of adults of each age were found using the von Bertalanffy equation:

\[
K^n = K_0 \left(1 - e^{-k(n-n_0)}\right)
\]

where \( K^n \) is the length of an individual at age \( n \) at time \( t \) for a given subpopulation. \( K_0, A, \) and \( n_0 \) are constants related to asymptotic length, size at settlement, and growth rate, respectively (each specific value is presented in Table S1). The mass of individuals of age \( n \) at each subpopulation was then found through the following allometric relationship:

\[
W_{ij} = a \left(K^n\right)^b
\]

where \( W_{ij} \) is the mass of an individual (kg) of age \( n \), at time \( t \), at patch \( i \). The terms \( a \) and \( b \) are constants (Table S1). The total biomass \( (B^*_i) \) at a given patch \( i \) at given time \( t \) was then found by multiplying the number of fish of each age by their mass and summing over all ages \( n \):

\[
B^*_i = \sum_n A^n_i W^n_{ij}
\]

### Node Removal Experiments

Node removal experiments were used to explore metapopulation network robustness and to identify key subpopulations. For each modeled species, subpopulations were sequentially removed, allowing a new equilibrium to be obtained at each iteration. This was achieved by changing the appropriate value of \( H_{ij} \), the area of suitable habitat at the target subpopulation \( j \), to zero, essentially creating 100% larval mortality at a particular patch. Removal continues until the total metapopulation biomass is less than an arbitrary “collapsed” state, which we define as 1% of the virgin, before node removal, metapopulation biomass.

Subpopulations were chosen for removal using metrics of subpopulation importance. In age-structured models, the “reproductive value” quantifies the contribution of individual age classes to future generation (53). This metric has been generalized to metapopulations by Ovaskainen and Hanski (35) and Jacobi and Jonsson (36), and it identifies the contribution of an individual subpopulation to the growth rate of the entire metapopulation. This metric is otherwise known as “eigenvector centrality” in network theory and has been used to identify keystone species in food webs (36) and important Web pages by the Google search algorithm (54). Here, eigenvector centrality is calculated as the left eigenvector associated with the leading eigenvalue of the realized connectivity matrix \( (R^*_j) \) and identifies subpopulations that are hubs of realized connectivity. We present eigenvector centrality as a dimensionless metric by normalizing values to the interval \([0, 1]\). In this way, this metric is used simply to rank patches by their importance. More details on eigenvector centrality and its ecological applications are provided elsewhere (35–37).

A greedy search algorithm was also used to identify critical subpopulations and for comparison with the eigenvector centrality results. At each removal stage, the locally optimal solution (i.e., the subpopulation that would create the largest decline in metapopulation biomass when removed) was found numerically. This is a heuristic approach and does not necessarily find the globally optimal solution (i.e., the smallest set of subpopulations that, if removed, collapses the metapopulation). This, however, is not our goal. By implementing the greedy algorithm, we simply create a numerical solution that we know to be near optimal. This provides an objective measure with which to compare the eigenvector centrality removal experiments. Subpopulations were also removed in descending order of the area of suitable habitat, source strength [defined as the number of recruits produced from a given patch (18)], and betweenness centrality (21, 55); as a null case, subpopulations were also removed at random, with 2,000 replicates to generate measures of variance. For source strength and betweenness centrality, the order in which subpopulations were removed was compared directly (using Pearson’s correlation coefficient); results are presented in the Discussion and Table S2.

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