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Extending networks of protected areas to optimize connectivity and population growth rate

Marco Andrello, Martin Nilsson Jacobi, Stéphanie Manel, Wilfried Thuiller and David Mouillot

M. Andrello (marco.andrello@gmail.com), Laboratoire d'Écologie Alpine, BP 53, 2233 Rue de la Piscine, FR-38041 Grenoble Cedex 9, France. – S. Manel and MA, UMR 151 – Aix Marseille Univ., IRD, LPED UMR 151, Marseille, France. SM also at: Centre de coopération internationale en recherche agronomique pour le développement, UMR AMAP, Montpellier, France. – W. Thuiller and MA, Univ. Grenoble Alpes, LECA, FR-38000 Grenoble, France, and CNRS, LECA, FR-38000 Grenoble, France. – M. Nilsson Jacobi, Complex Systems Group, Dept of Energy and Environment, Chalmers Univ. of Technology, SE-412 96 Göteborg, Sweden. – D. Mouillot, UMR 5119 – Écologie des Systèmes marins côtiers, Univ. Montpellier 2, Montpellier, France, and ARC Centre of Excellence for Coral Reef Studies, James Cook Univ., Townsville, Australia.

Protected areas (PAs) are recognized as the flagship tool to offset biodiversity loss on Earth. Spatial conservation planning seeks optimal designs of PAs that meet multiple targets such as biodiversity representation and population persistence. Since connectivity between PAs is a fundamental requirement for population persistence, several methods have been developed to include connectivity into PA design algorithms. Among these, the eigenvalue decomposition of the connectivity matrix allows for identifying clusters of strongly connected sites and selecting the sites contributing the most to population persistence. So far, this method was only suited to optimize an entire network of PAs without considering existing PAs in the new design. However, a more cost-effective and realistic approach is to optimize the design of an extended network to improve its connectivity and thus population persistence. Here, we develop a flexible algorithm based on eigenvalue decomposition of connectivity matrices to extend existing networks of PAs while optimizing connectivity and population growth rate. We also include a splitting algorithm to improve cluster identification. The new algorithm accounts for the change in connectivity due to the increased biological productivity often observed in existing PAs. We illustrate the potential of our algorithm by proposing an extension of the network of ~100 Mediterranean marine PAs to reach the targeted 10% surface area protection from the current 1.8%. We identify differences between the clean slate scenario, where all sites are available for protection, irrespective of their current protection status, and the scenario where existing PAs are forced to be included into the optimized solution. By integrating this algorithm to existing multi-objective and multi-specific algorithms of PA selection, the demographic effects of connectivity can be explicitly included into conservation planning.

Protected areas (PAs) are the most relevant tools to offset biodiversity loss (Spalding et al. 2008), and to ensure the long-term provisioning of ecosystem services essential for human wellbeing. The Convention on Biological Diversity (CBD) has set clear and ambitious targets to be reached by 2020: to protect at least 17% of land ecosystems and 10% of marine and costal habitats (COP10; <www.cbd.int/cop10>). Since the current protected fraction of the world is extremely small and unevenly distributed (Spalding et al. 2008, Marinesque et al. 2012), the need to expand existing PA networks has stimulated vigorous debates about their future design (location, size, spacing, and configuration), efficiency (maximizing the gain for a given cost) and effectiveness (ensuring that targets and objectives are met) (Rodrigues et al. 2004). This increasing demand has triggered the development of conservation planning which, for the last two decades, has provided criteria and tools for PA network design and for guiding policy decisions (Margules and Pressey 2000, Pressey et al. 2007).

Spatial conservation planning seeks optimal designs of PAs that meet multiple targets while minimizing costs (Margules and Pressey 2000). Biodiversity representation and species persistence are the key targets of conservation planning (Cabeza and Moilanen 2001). If the former target has received much attention, the latter is still overlooked partly due to a lack of theoretical framework and appropriate tools. Landscape connectivity affects population persistence through the effects of dispersal on colonization, recruitment and gene flow (Baguette et al. 2013, Kool et al. 2013) and as such is crucial to develop effective conservation planning (Noss and Daly 2006). For example, Moilanen et al. (2005) use 'population connectivity surfaces' as a way to integrate connectivity into spatial conservation planning. Similarly, incidence functions have been used to include the effect of dispersal on species occurrence probability and rank habitat patches (Cabeza et al. 2003, van Teeffelen et al. 2006). However, these approaches do not explicitly frame the optimization function in terms of population persistence, which is still largely missing in the PA selection process.

This is even more surprising, because metapopulation theory offers a valid framework to include the population persistence target into PA selection methods (Nicholson and Ovaskainen 2009) through the development of metrics such as the probability of population persistence (Moilanen and Cabeza 2002), the mean time to extinction (Nicholson et al. 2006, Kininmonth et al. 2011), the number of occupied habitat patches (Ovaskainen 2002) or the metapopulation capacity (Hanski and Ovaskainen 2000, Nilsson Jacobi and Jonsson 2011). All these metrics depend on dispersal, which in turn depends on the structure of the landscape. PA selection algorithms would thus need to optimize at least one of these metrics to allow population persistence becoming an operational target of conservation planning (Moilanen and Cabeza 2002, Nicholson et al. 2006).

The development of PA selection algorithms including connectivity as a driver of population persistence has been paralleled by the continuous improvement of methods for assessing organism movement, dispersal and functional connectivity through the use of satellite tags, genetic parentage analyses and biophysical models (Baguette et al. 2013, Kool et al. 2013). Taking advantage of this increasing quantification of connectivity and the availability connectivity matrices among habitat patches, Nilsson Jacobi and Jonsson (2011) developed an algorithm based on the metapopulation theory to rank sites according to their contribution to population growth rate. The population growth rate is calculated as the largest eigenvalue of the connectivity matrix (Hanski and Ovaskainen 2000) while the contributions of individual sites are calculated using eigenvector analysis. The eigenvalue perturbation theory (EPT) algorithm was specifically designed to use the whole information contained in the connectivity matrix (Nilsson Jacobi and Jonsson 2011). The main distinctiveness of the EPT algorithm from the other PA selection methods is the use of the full eigenvalue spectrum, instead of the largest eigenvalue only, as a metric of population viability. This methodological improvement produces spatially balanced configurations of PAs when the metapopulation is weakly connected and composed of subpopulations or clusters.

However, the EPT algorithm was only designed for the clean slate scenario (no pre-existing PAs), whereas in most real-world cases PAs are already present in the region where more conservation effort is needed. PAs are still classically established on the basis of local socio-political considerations instead of a regional strategy. However, removing some PAs to select new ones is rarely implemented even if it can be cost-effective (Fuller et al. 2010, Alagador et al. 2014). Instead, a more realistic and appropriate objective of conservation planning is to optimize the future network by adding new PAs to the existing ones. The optimal extended network may substantially deviate from the clean slate scenario (Malcolm et al. 2012). The aim of our study is therefore to develop a flexible algorithm, based on EPT, to extend existing networks of PAs while optimizing connectivity and population growth rate. We then illustrate the applicability of the algorithm with the network of Mediterranean marine PAs which is currently extending but still lagging behind CBD targets (Gabrié et al. 2012).

Methods

Eigenvalue perturbation theory (EPT)

We first explain how the eigenvalue perturbation theory (EPT) can be used to optimize a network of PAs based on the importance of local sites for population growth rate and persistence. Protecting a site has positive effects on population dynamics enhancing survival, growth and fecundity rates (Claudet et al. 2008). Higher vital rates promote higher production of propagules and biomass in this given site but the effect on the global population persistence, i.e. across sites, is largely modulated by the ability of sites to exchange propagules (e.g. seeds or larvae) (Hastings and Botsford 2006, Artzy-Randrup and Stone 2010). For instance, if a given site is isolated and cannot supply propagules to any other site but itself, increasing its productivity would not benefit the metapopulation. Conversely, the protection of a site that is highly connected to many others by dispersal would enhance population persistence beyond its boundaries. We can thus rank sites according to their contribution to population growth rate by analyzing connectivity patterns.

To this aim, the EPT considers a geographically structured population made up by n local sites connected by propagule dispersal. Generations are discrete and the production of propagules is set equal among sites. The square connectivity matrix **C** of size n contains probabilities of propagule dispersal between sites. We focus on propagule dispersal (larvae or seeds for example) but the demographic model could be formulated to describe adult dispersal without loss of generality.

The **C** matrix has eigenvalues $[\lambda_1, \lambda_2, \ldots\lambda_n]$ with the largest, $\lambda_{\max}$, termed metapopulation capacity (Hanski and Ovaskainen 2000), corresponding to population growth rate. The contributions of sites to $\lambda_{\max}$ can be obtained by multiplying **C** by a diagonal matrix **E** whose elements, E_{ii}, represent the productivity of site i relative to the unprotected case, i.e. $E_{ii} = 1$ means an unprotected site while $E_{ii} = 1.1$ means a 10% productivity increase and thus can be used to represent a protected site. Increasing a diagonal element of **E** mimics a productivity increase at a single site i: the effect of such an increase on $\lambda_{\max}$ can be found by calculating the new eigenvalues of the product of the two matrices **C** and **E**. The contribution of site i to $\lambda_{\max}$ is defined as the resulting increase in $\lambda_{\max}$ due to the increase in site productivity. Numerical methods can be used to calculate the eigenvalues of **CE** but a linear approximation was proposed by Nilsson Jacobi and Jonsson (2011). It offers a fast, efficient and precise approximation for the computationally intensive calculations of eigenvalues and eigenvectors. A productivity increase δ in a site is considered as a perturbation of the **C** matrix. Simultaneous perturbations of multiple elements of **E** can be considered independently and their effects calculated separately.

When connectivity is low, the largest eigenvalue $\lambda_{\max}$ cannot solely describe accurately the whole population dynamic since clusters of connected sites have their own dynamics. In such case, detecting clusters of sites before calculating the site contribution to population growth is required to avoid spatially unbalanced site prioritization (Supplementary material Appendix 1).

There are various methods to define clusters of connected sites. We used sequentially two of them to improve our algorithm efficiency. The first method is an iterative splitting of the connectivity matrix aiming at minimizing connectivity among clusters and maximizing connectivity within clusters (Nilsson Jacobi et al. 2012). The iterative split can however lead to the trivial solution where the entire population belongs to a single cluster because this maximizes connectivity within a large cluster. To avoid this, Nilsson Jacobi et al. (2012) penalize splits that assign pairs of sites with weak connectivity to the same cluster. They define a threshold $1/\beta$ (where $\beta > 0$ is defined by the user) to penalize solutions that assign to the same cluster pairs of sites i, j with $C_{ij} < 1/\beta$. The optimal clustering thus depends on β. Since there is no objective method to set the value of β, we recommend using different values and merging the different final configurations. The second method is based on the spectral decomposition of the connectivity matrix (Nilsson Jacobi and Jonsson 2011). Different clusters can be associated to different eigenvalues of the spectrum even if sites are not assigned explicitly and univocally to a single cluster. We can thus calculate the contribution of site productivity increase to each eigenvalue. It represents the contribution to population growth rate in the cluster associated to that eigenvalue.

Here, we propose to use the two methods sequentially (Fig. 1a). In the first step, we split the connectivity matrix into clusters by minimizing connectivity among clusters. This produces a set of connectivity submatrices, one for each cluster. Then, in a second step, we calculate, for each submatrix, the contributions of each site to all the dominating eigenvalues of the submatrix, i.e. the eigenvalues whose corresponding eigenvectors have only positive (or only negative) elements. This produces a number of ranks equal to the number of dominating eigenvalues of the submatrix. After calculating site contributions for all dominating eigenvalues and clusters (submatrices), a ranking of sites is created according to their highest contributions across all eigenvalues and clusters. The final rank of each site is obtained by taking its highest contribution across eigenvalues, clusters and values of β. In the clean slate scenario, the final configuration of PAs corresponds to the first n_t sites (total number of sites to be protected) of the final ranking. The splitting of the population in the first step may seem redundant but our calculations showed that using the eigenvalue decomposition alone led to many degenerate eigenvalues. Eigenvalues are degenerate when their values are too similar to be unequivocally associated to a single cluster; more formally, an eigenvalue is degenerate when it is associated to two or more linearly independent eigenvectors. Especially, if a subpopulation has a low growth rate, its dominating eigenvalues can become mixed within a set of subdominant eigenvalues of subpopulations with higher growth rates. Using the two methods sequentially reduces the probability of having degenerate eigenvalues and therefore produces more reliable results.

Extending networks of PAs

The original EPT method was not designed to include already protected sites, and existing PAs may modify total population growth thanks to their higher productivity compared to unprotected sites. Higher productivity in protected vs. unprotected sites has been widely documented for marine species (Halpern 2003, Sala et al. 2012) and is beneficial for exploited species for which PAs can act as sources of larvae and adults for fished areas (Christie et al. 2010, Pelc et al. 2010, Harrison et al. 2012). Productivity increase in terrestrial PA is less documented but examples show that dispersal from PAs allows the recolonization of areas where the species was eradicated (Ahlering et al. 2012).

Including existing PAs in the final configuration is therefore a crucial step forward for the ETP algorithm. For doing so, we estimated a new connectivity matrix $\mathbf{C}'$ that takes into account higher productivity in protected sites. $\mathbf{C}'$ is obtained by multiplying the connectivity matrix $\mathbf{C}$ by a productivity matrix $\mathbf{P}$: $\mathbf{C}' = \mathbf{CP}$. $\mathbf{P}$ is a diagonal matrix whose elements are the site-specific productivities. The elements of $\mathbf{C}$, $c(i,j)$, are the probabilities that a propagule produced in site j will reach site i. Matrix $\mathbf{P}$ scales these probabilities by site productivity, i.e. by the number of offspring produced by an individual during its lifetime. The elements of $\mathbf{C}'$, $c'(i,j)$, can be seen as the probabilities that offspring from an individual in site j will reach site i. $\mathbf{P}$ mimics that existing PAs have higher productivity than unprotected sites. For example, by setting $p(i,i)_{i \in PAs} = 1.1 * p(j,j)_{j \notin \mathrm{PAs}}$, we assume that existing PAs have a 10% higher propagule productivity than unprotected sites. The ranking of the remaining unprotected sites is then calculated by applying the EPT algorithm to the $\mathbf{C}'$ matrix. The new approach thus accounts for productivity increase in PAs and its effect on connectivity is similar to that of Berglund et al. (2012) accounting for varying habitat quality among sites. The whole framework for extending networks of PAs to maximize connectivity is summarized in Fig. 1b.

If the number of existing PAs is n_e, the final configuration is found by taking the n_e existing PAs and the first $(n_t - n_e)$ sites in the ranking of unprotected sites calculated with the EPT algorithm. Such final configuration including existing PAs will likely be suboptimal relative to the configuration of the clean slate scenario, except in the very unlikely case where all n_e PAs are in the top ranking of the clean slate scenario (i.e. the existing PAs network was indeed selected to optimize connectivity).

Evaluation of optimality

A final configuration of sites is optimal if population growth rate is maximized relative to other solutions. Since the objective is to increase population growth rate at low population size, one criterion to evaluate the final configuration is to calculate population size after disturbance using a simple model of population dynamics (Nilsson Jacobi and Jonsson 2011). For the clean slate scenario, the model is:

$$x_{i,t} = \chi(t) E_{ii} \sum_{j} \left[C_{ij} x_{j,t-1} \left(\frac{\alpha}{1 + \frac{\alpha}{R_{\max}} x_{\mathrm{j,t-1}}} \right) \right] \tag{1}$$

where $x_{i,t}$ is population size in site i at time t. C_{ij} is the ij-th element of the connectivity matrix. E_{ii} is the ii-th element of the diagonal matrix defining which areas are protected:

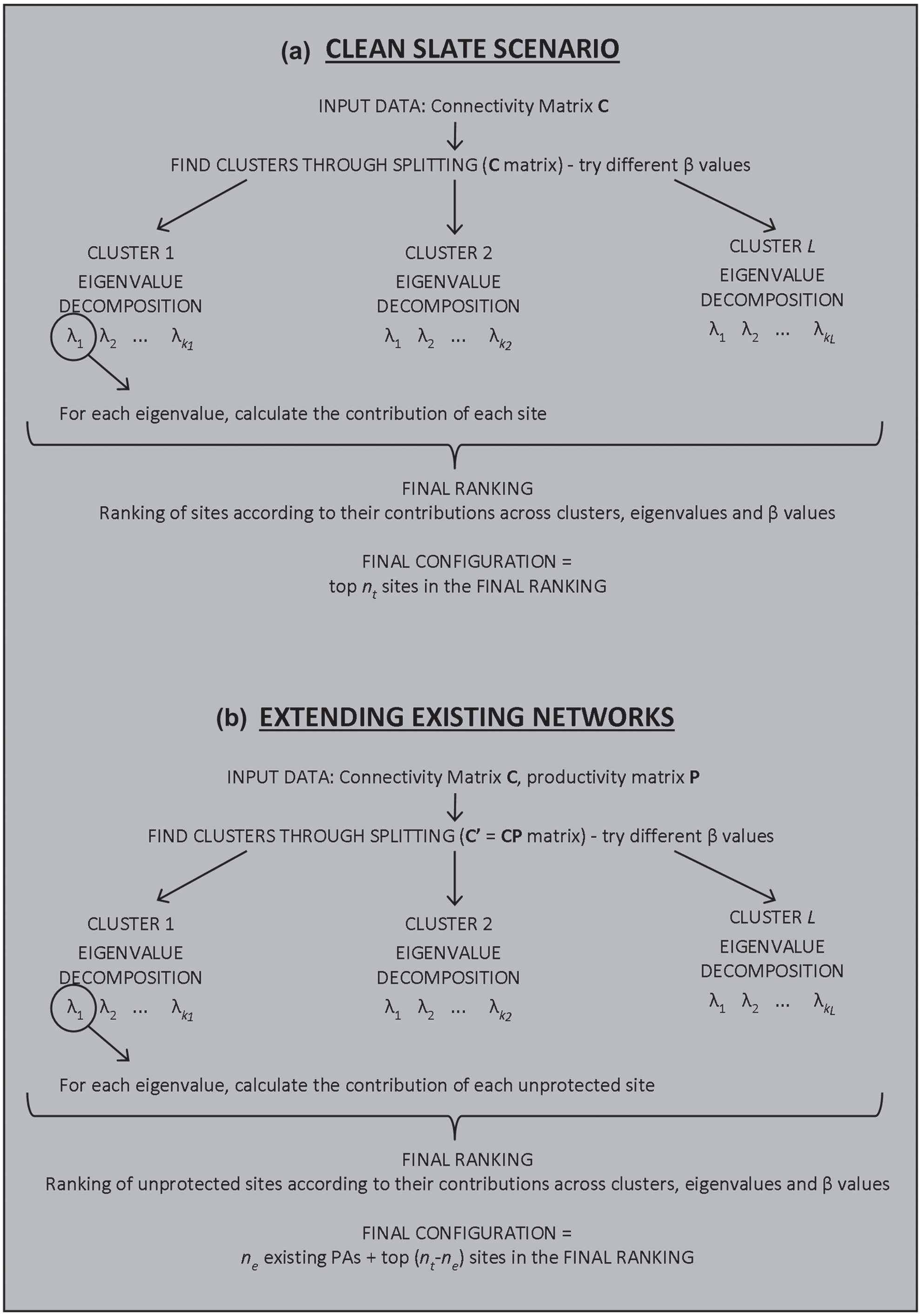

Figure 1. Workflow of the algorithm for selecting sites in the clean slate scenario (a) and in the extending network scenario (b). Clusters are found through iterative splitting of the connectivity matrix using different values for the parameter β. L denotes the number of clusters and k_i the number of dominating eigenvalues of cluster i. The final ranking is obtained by merging sites across clusters, eigenvalues and β values.

$E_{ii} = 1 + \delta$ if i is protected and 1 otherwise. $\chi(t)$ is a stochastic variable that is set to $\varepsilon < 1$, where ε is typically a small number, with probability $1/\tau$ in every time-step, and 1 otherwise. $\chi(t)$ simulates a random reduction by ε of recruitment that happens on average every τ years. The quantity in parentheses is a Beverton–Holt recruitment function with parameters α and $R_{\max}$. Equation (1) is iterated for a large number of years and the demographic performance, d, of the configuration is measured as the mean population size for the years with the smallest total population sizes.

For the extension of an existing network, the population dynamic model is similar as in Eq. (1), except that C_{ij} is replaced by C'_{ij}. In addition, $E_{ii} = 1 + \delta$ only for sites chosen for protection that are not already protected since the increase in productivity in existing PAs is already accounted for in the $\mathbf{C}'$ matrix.

The demographic performance of the final configuration can be compared with that of alternative configurations obtained by choosing sites at random. If the final configuration has consistently a higher performance than random configurations, it can be considered close to optimal.

Application: the Mediterranean Sea

To illustrate the method, we applied the EPT algorithm to the case of marine PAs (MPAs) in the Mediterranean Sea. The Mediterranean Sea harbors more than 600 fish species with a high fraction of endemism (Coll et al. 2010) and experiences unprecedented levels of human pressure from fishing, exotic species, and pollution (Coll et al. 2012). The Mediterranean Sea benefits from the presence of approximately a hundred of MPAs, mainly concentrated in its northern coast (Abdulla et al. 2009, Coll et al. 2012). Overall, the protected surface covers around 1% of the sea (Garcia-Charton et al. 2008, Gabrié et al. 2012). Therefore, more effort is required to reach the 10% target set by the Convention on the Biological Diversity by 2020 (COP10; <www.cbd.int/cop10>; Micheli et al. (2013)). Moreover, the Mediterranean Sea is the archetypal situation where the persistence criterion needs to be included in the conservation planning since 1) the network of MPAs already covers most of fish biodiversity fulfilling the representation criteria (Mouillot et al. 2011); and 2) many fish species are overexploited and are conservation-dependent to maintain viable populations.

All marine areas shallower than 200 m (continental shelf) were considered. This area was subdivided into sites on a latitude–longitude grid with a 1/10th degree resolution. The boundaries of the sites followed this grid and the coast trait. The coast trait was smooth because polygons were used. Therefore, some sites were square while others had more complex shapes. This produced a set of 7703 sites covering the continental shelf (Lasram et al. 2010, Mouillot et al. 2011, Albouy et al. 2012). Sites that overlap with a MPA for at least 50% of their surface were considered protected, otherwise they were classified as unprotected. According to this criterion, we classified 142 sites out of 7703 as protected (1.8%; Fig. 2a).

The connectivity matrix was calculated using a biophysical model to simulate dispersal of fish larvae by sea currents among all sites. Further details on the parameterization of larval simulations can be found in Andrello et al. (2013) and in Supplementary material Appendix 2. The connectivity matrix **C** was then analyzed using our algorithm for both the clean slate scenario and the extension of existing network case. We used a productivity increase $\delta = 0.1$ (10% increase in protected vs unprotected areas), i.e. $E_{ii} = 1.1$ for sites chosen for protection and 1 otherwise. To split the matrix, we set β to values ranging from $n/5$ (1540.6) to $2n$ (15406).

For extending the existing network, we built the productivity matrix **P** by setting its diagonal elements to $1 + \delta$ in the 142 sites classified as existing MPAs and 1 otherwise. The value of δ was set equal to the one used to build the **E** matrix and constant across sites but various δ values could be used with more information on site productivity and protection effectiveness. The final configuration was created by taking the 142 protected sites and the first 628 sites in the final ranking of unprotected sites obtained with the algorithm to obtain a total of 770 sites for protection.

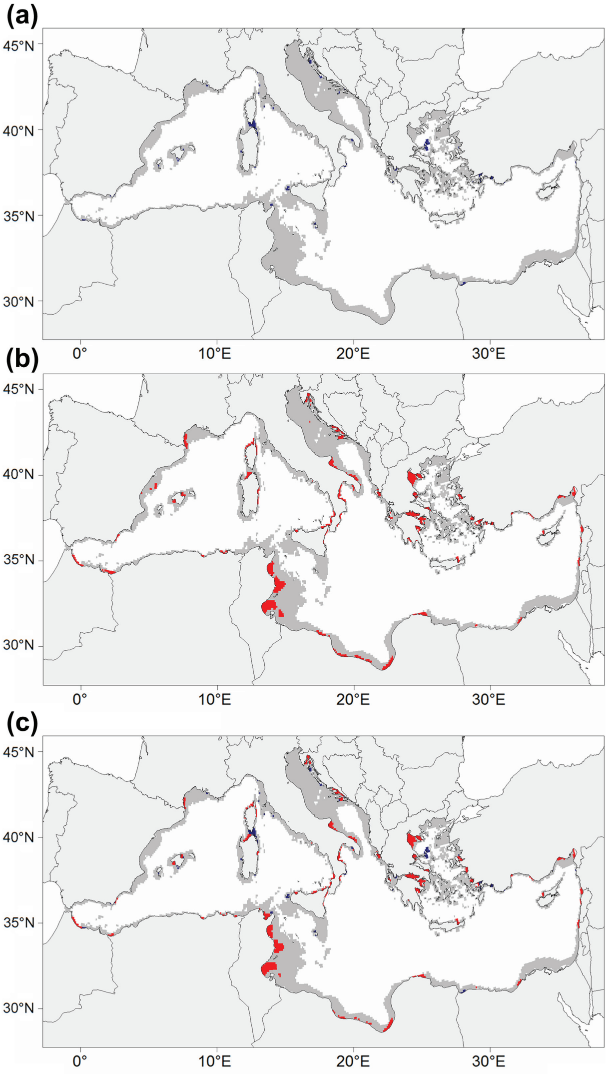

Figure 2. (a) The current system of MPAs in the Mediterranean Sea. Coastal areas are colored in gray and existing MPAs in blue. (b) Final configuration of selected sites (in red) for the clean slate scenario. The original connectivity matrix **C** was analyzed, without accounting for the increased productivity in existing MPAs. (c) Final configuration for the extension of existing network scenario. The matrix $\mathbf{C'} = \mathbf{CP}$ corrected for increased productivity in MPAs was analyzed and existing MPAs (blue) are plotted with new proposed sites (red). The total protected area is 10% of sites in both cases and corresponds to the sum of red sites in (b) and of red and blue sites in (c).

To evaluate the final configuration using equation (1), we used $\varepsilon = 0.1$, $\tau = 10$ (i.e. a decimation of population size every ten years on average), $\alpha = 10$ and $R_{\max} = 6$. Equation (1) was iterated for 250 yr and performance was measured as the mean population size for the five years with the smallest total population sizes. We also evaluated how incremental extension of the network from the current 142 sites to the targeted 770 sites improves the demographic performance. We tested whether adding sites at random results in lower performance than adding sites according to the final configuration. More precisely, the network was extended from the current 142 sites (1.8% surface protection) to the targeted 770 sites (10% protection) by sequentially adding unprotected sites following the ranking calculated with the EPT algorithm, starting from the site with the highest contribution. The performance of this extended network was compared to an interval of performances (minimum and maximum over 30 replicates) obtained from a network extended with sites chosen randomly.

The linear approximation at the basis of the EPT algorithm is appropriate even for rather large values of δ (up to 5 in Nilsson Jacobi and Jonsson 2011). As a matter of fact, MPAs have positive effects on fish density, biomass, fecundity and egg production according to empirical evaluation showing that productivity in Mediterranean MPAs can reach levels up to 20-fold the productivity of unprotected areas (Garcia-Charton et al. 2008, Afonso et al. 2011). We then checked the accuracy of the linear approximation when the increase in productivity in MPAs was very high (20-fold increase, $\delta = 19$).

Results

The biophysical model simulates low connectivity among sites, except for neighboring sites that are connected by high larval dispersal probabilities (Fig. 3). The number of realized connections was 2 341 730 out of 59 336 209 potential connections, giving a connectance of 3.9%. The median number of connections was 275 per site (interquartile range 183–394.5); for protected sites, the median number of connections was 249 (interquartile range 171–398) and was not significantly different from that of unprotected sites (median: 275; interquartile range 184–394; Wilcoxon rank sum test: W = 514387.5, p-value = 0.3926).

Clean slate scenario

We applied the splitting algorithm to find clusters. Depending on the value of β, the number of identified clusters ranged from 9 ($\beta = n/5$, Fig. 4a) to 33 ($\beta = 2n$, Fig. 4b). We then applied the EPT algorithm within each cluster to rank sites according to their contribution to eigenvalues, and merged the rankings across eigenvalues, clusters and values of β to create the final configuration (Fig. 2b). Selected sites were often located along curvilinear coasts, gulfs, bays and small sea inlets. Greece and Tunisia hosted many selected sites (the Gulf of Corinth, the Saronic Gulf and the Thermaic Gulf in Greece; the Gulf of Gabès and the Gulf of Hammamet in Tunisia). Due to their high connectivity, these sites contributed more than others to population growth. Altogether, selected sites were quite evenly distributed all over the region and were not concentrated in a single place: the final configuration was spatially balanced. The final configuration contained only 18 sites out of 770 that are already protected (2.3% of the final configuration and 12.7% of existing PAs).

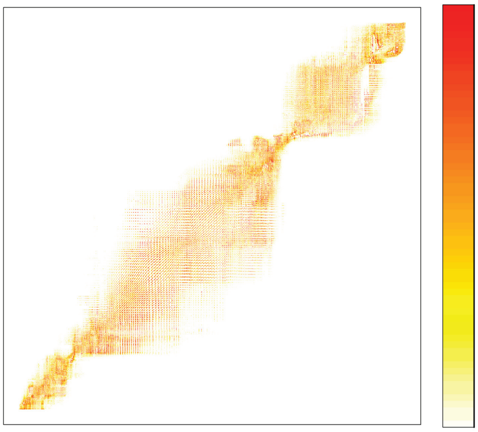

Figure 3. Connectivity matrix for the Mediterranean Sea. Colors represent probability of larval dispersal between the 7703 sites.

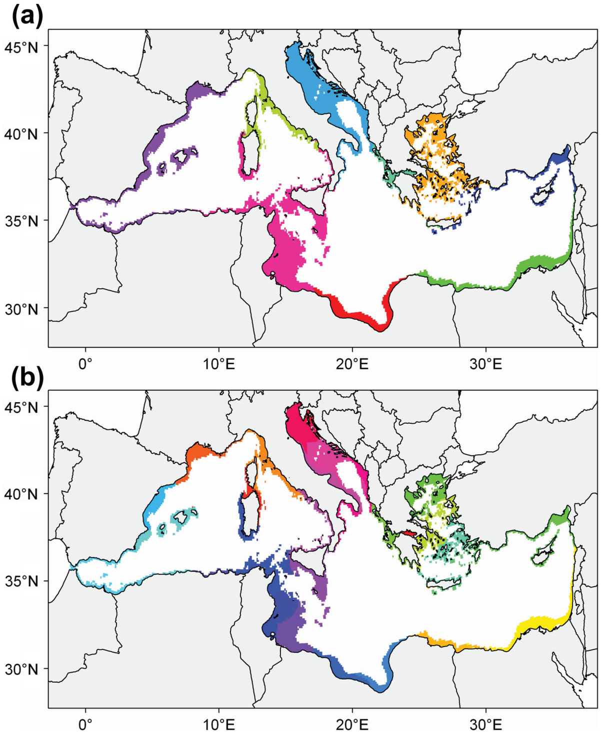

Figure 4. Clusters identified with the splitting algorithm. (a) $\beta = n/5$, 9 clusters; (b) $\beta = 2n$, 33 clusters.

We compared the performance of this final configuration to those obtained with networks where sites were randomly selected (Fig. 5a). The final configuration found with the EPT algorithm was always superior to random networks.

Extending the existing network

We ran our algorithm on the corrected $\mathbf{C}'$ matrix to account for the effects of existing PAs on connectivity with a productivity increase of $\delta = 10\%$. The final configuration was set by taking the 142 existing PAs and the top 628 sites in the final ranking of unprotected sites. Comparison between this final configuration and that of the clean slate scenario showed that most sites (79.2%) were common to both scenarios (Fig. 2c).

We compared the demographic performance of the final configurations between the clean slate scenario and

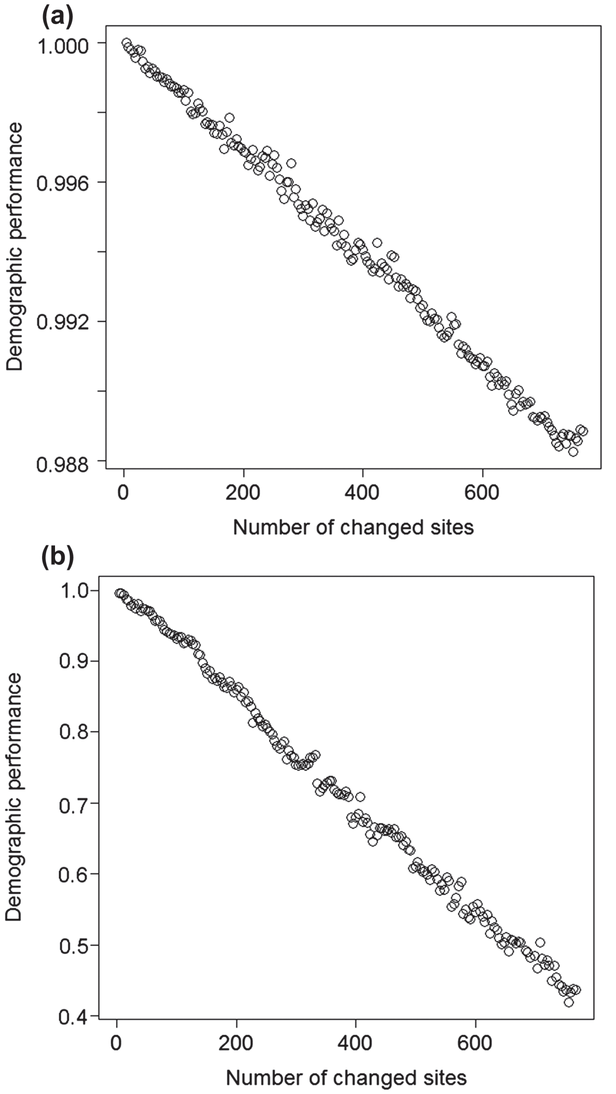

Figure 5. Comparison of the final configuration of sites selected by the EPT algorithm with random networks. The demographic performance is calculated as the mean total population size at low abundance and is normalized against the demographic performance of the final configuration, i.e. the region below 1 means that changing the sites in the configuration leads to a decreased overall population size. Demographic performance is plotted as a function of the number of sites that are changed in the final configuration obtained with the EPT algorithm (the 0 on the horizontal axis corresponds to the final configuration obtained with the EPT). (a) Final configuration obtained in the clean slate scenario, for productivity in protected areas being 1.1 × that in unprotected areas ($\delta = 0.1$). (b) Final configuration obtained in the extending network scenario, for productivity in protected areas being 20 × that of unprotected areas ($\delta = 19$).

the network extension scenario. We iterated Eq. (1) using the $\mathbf{C}'$ matrix in both cases to assess whether the solutions differ when increased productivity is considered in the population dynamics: the clean slate scenario performed slightly better ($d = 956.99$) than the extending network scenario ($d = 951.96$).

We evaluated the demographic performance of networks obtained by sequentially adding sites to the existing network made of 142 PAs. Adding sites at random resulted in considerably poorer performances than adding sites according to their ranking in the final configuration (Fig. 6).

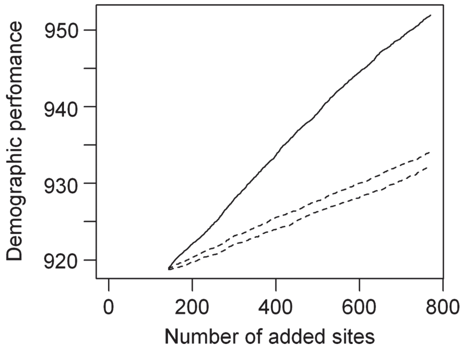

Figure 6. Demographic performance of the protected areas network as a function of the number of sites added to the existing network. The demographic performance is calculated as the mean total population size at low abundance. The network is extended from the current 142 sites (1.8% surface protection) to the targeted 770 sites (10% protection) by sequentially adding sites. The solid line represents the performance when sites are chosen on the basis of the final configuration calculated with the EPT algorithm in the extending network scenario, starting from the site with highest contribution in decreasing order. Dotted lines represent the interval of performance (minimum and maximum over 30 replicates) when sites are chosen randomly .

Robustness to the small perturbation assumption

We then checked the accuracy of the linear approximation when the increase of productivity in MPAs was very high (20-fold increase). The final list consistently showed a higher performance than random networks (Fig. 5b), confirming that the linear approximation was accurate enough to obtain a solution close to optimal.

Discussion

Planning for conservation aims at preserving not only the extant patterns of biodiversity but also the processes maintaining them and the persistence of species (Pressey et al. 2007). Landscape connectivity is affecting species persistence through a variety of processes, e.g. migration, gene flow, source-sink dynamics and transfer of matter and energy among habitats (Baguette et al. 2013, Kool et al. 2013). More specifically, migration of individuals between habitat patches is an essential component of the metapopulation dynamics for species distributed in fragmented landscapes. Many PA design algorithms were grounded into the metapopulation theory to optimize species persistence with networks (Nicholson and Ovaskainen 2009). We have extended one of these methods, the EPT algorithm (Nilsson Jacobi and Jonsson 2011) which optimizes the connectivity within networks of PAs, by spatially balancing the choice of sites to be protected and allowing its application to regions where PAs are already in place. These two properties appear essential to make the EPT framework applicable on realistic scenarios where PA networks are already set but need to be reinforced. The Mediterranean network represents such an archetypal case where an urgent extension is needed to counteract ever increasing pressures (Coll et al. 2012). We show that the final optimized configuration to place future MPAs has a considerably higher demographic performance than other solutions based on a random choice of sites. This demonstrates that, beyond covering most of biodiversity, including connectivity into conservation planning is essential to ensure population persistence and to decrease the risk of extinction of exploited or vulnerable species (van Teeffelen et al. 2006, Berglund et al. 2012, Blowes and Connolly 2012).

Various approaches have been developed to integrate connectivity in PA selection. Popular planning software products such as Marxan and Zonation implement habitat continuity as a measure of landscape connectivity using distribution smoothing and boundary quality penalty (Ball et al. 2009, Lehtomäki and Moilanen 2013). Graph-theory has also been used to calculate the importance of single habitat patches as a function of their connectivity within the network of sites (Rothley and Rae 2005, Fuller and Sarkar 2006, Minor and Urban 2008). Network metrics such as betweenness centrality have been used to rank sites in a network (Treml and Halpin 2012). Node removal approaches, where single sites are sequentially removed from the network, can inform on the value of single habitat patches for network connectivity (Watson et al. 2011). However, these approaches can be limited if they consider connectivity as a stand-alone entity without accounting for population dynamics (Moilanen 2011). The persistence objective requires translating the effects of connectivity into a target metric of population viability. Metapopulation theory thus offers a valid framework to integrate connectivity into conservation planning via the specific objective of population persistence (Nicholson and Ovaskainen 2009). Several studies have improved PA selection algorithms to include population persistence of single (Moilanen and Cabeza 2002) or multiple species (Moilanen et al. 2005, Nicholson et al. 2006) using a variety of viability metrics (Nicholson and Ovaskainen 2009). Our method aims at increasing metapopulation growth rate for a single species through an analytical approach that allows considering multiple population clusters. In doing so, the algorithm maximizes not only the global metapopulation growth rate but also the cluster-specific population growth rates. This is achieved by considering the full eigenvalue spectrum and not only the highest eigenvalue, thus avoiding the trivial solution where only the sites of the most productive cluster are protected (Supplementary material Appendix 1). In addition, the identification of clusters is improved by applying a splitting algorithm that maximizes intra cluster connectivity while minimizing between clusters connectivity before performing the eigenvalue analysis and running the EPT algorithm.

Beyond combining the original EPT algorithm (Nilsson Jacobi and Jonsson 2011) with the population splitting algorithm (Nilsson Jacobi et al. 2012), we developed a framework for realistic scenarios where existing network of PAs are extended. This requires modifying the original algorithm to account for two key features: the increased site productivity of existing PAs and their forced inclusion in the final configuration. The assumption of the original EPT method is that sites are equally productive. However, variation in site productivity caused, for example, by differential habitat qualities, can result in different prioritization solutions (Berglund et al. 2012). Since protection from human disturbance often leads to higher fecundity and productivity (Claudet et al. 2008, Afonso et al. 2011), the protection status of some sites may modify the final selection of sites via changes in site productivity. We took into account this effect in the productivity matrix **P** that modifies the probabilities of successful propagule dispersal. The formulation is equivalent to the one used by Berglund et al. (2012) to represent variation in habitat quality among sites and could be used to weight sites according to habitat suitability and patch size.

The second key feature is the forced inclusion of existing PAs in the final configuration. This alters the demographic performance of the final configuration relative to solutions that are not constrained by the inclusion of existing PAs. Existing PAs may not be in the top contributors to connectivity and therefore may lower the demographic performance of the network when included. Malcolm et al. (2012) show that extending a network of existing PAs results in lower effectiveness in terms of biodiversity representation relative to the clean slate scenario. In our case, including existing PAs in the final configuration lowered the demographic performance of the network, albeit weakly since current MPAs represent only a small subset of MPAs required to meet the 10% surface requirement. Forcing the inclusion of existing PAs in the final configuration is expected to have higher impacts when there are more existing PAs, when the conservation target is almost reached with few new PAs being created, or when these existing PAs make low contributions to eigenvalues.

The main assumption of the EPT algorithm is that productivity increases in PAs relative to unprotected areas is small, so that it can be considered as a small perturbation of the connectivity matrix and the first-order approximation is justified. However, productivity in PAs can increase up to 20-fold compared to unprotected areas (Afonso et al. 2011). However, the algorithm proves to be robust to this assumption and the final configuration is still close to optimal when such large increases are considered. This was a surprising result and the reason underlying the robustness is unknown. Possibly, the sparseness of the connectivity matrix (many connections are not realized) may explain this robustness and deserves further theoretical investigations.

The main limitations of our approach are the applicability to only one species and the focus on a single objective, namely population growth rate. Standard practices in conservation planning are multi-specific and multi-objective, often achieved through optimization of biodiversity representation. The ultimate goal would be to integrate, into a single benefit function, both the representation of species and habitats and the persistence of population by using an explicit model of persistence accounting for dispersal between sites. To our knowledge, such a model has not yet been developed, but some attempts towards multi-specific and multi-objective optimization have been made. For instance, Nicholson et al. (2006) developed a model for multi-species persistence that accounts for dispersal between sites that could be parameterized using species-specific connectivity matrices. However, for highly fragmented populations with a modular structure, such an approach may favor the maximization of growth rate for the largest cluster, disregarding smaller clusters and producing a spatially unbalanced solution. An alternative could be using directly the site contributions calculated with the EPT algorithm as 'connectivity scores' into a multi-objective function. This would preserve the importance of smaller clusters and allow for a multi-specific optimization by calculating scores for multiple species.

The demographic model assumed by our algorithm is density-independent and, even if the evaluation of optimality was introduced with temporal stochasticity, the connectivity matrix was constant in time. Introducing density dependence may alter the demography of the system, although previous analyses show that some features of density-independent metapopulation models are retained in the density-dependent case (Armsworth 2002). The demographic framework used in our study could be extended to consider environmental stochasticity in connectivity through the analysis of stochastic population growth rate (Watson et al. 2012, Williams and Hastings 2013). Such a framework could accommodate for long term temporal changes in connectivity, as the ones expected under climate change (Travis et al. 2013, Magris et al. 2014).

The results obtained for spatial prioritization of MPAs in the Mediterranean Sea are to be interpreted with caution. The connectivity matrix was obtained over a limited temporal extent of oceanographic data (2004–2008) and the spatial resolution of the oceanographic model may be too coarse to resolve small-scale current dynamics associated with coastal and shallow environments (Largier 2003, Werner et al. 2007). We estimated the connectivity matrix for a generic benthic species that spawn in the summer and has a planktonic duration of 30 d, but disregarded other life-history traits important for connectivity such as larval growth and behavior, mortality, and juvenile movements (Leis 2007, Di Franco et al. 2012, Treml et al. 2012). We had to operate a compromise between biological realism and the need for a multi-species perspective on PA design.

Ongoing efforts aiming to increase the surface of PAs to 10% of marine areas and to 17% of terrestrial habitats (COP10; <www.cbd.int/cop10>) face the challenge of optimally placing the next PAs given a multitude of constraints. Targeting highly connected sites for protection will decrease the risk of population collapse and increase the sustainability of vulnerable populations. In particular, the method developed in this study focuses on the eigenvalue spectrum of the connectivity matrix as a quantity to maximize and can be applied to extend existing network of PAs to optimize population persistence. By integrating this crucial component to existing multi-objective and multi-specific algorithms of PA selection, it becomes possible to explicitly include the demographic effects of connectivity into conservation planning.

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Supplementary material (Appendix ECOG-00975 at <www.ecography.org/readers/appendix>). Appendix 1–2.