Optimal networks of nature reserves can be found through eigenvalue perturbation theory of the connectivity matrix

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Abstract. Conservation and management of natural resources and biodiversity need improved criteria to select functional networks of protected areas. The connectivity within networks due to dispersal is rarely considered, partly because it is unclear how connectivity information can be included in the selection of protected areas. We present a novel and general method that applies eigenvalue perturbation theory (EPT) to select optimum networks of protected areas based on connectivity. At low population densities, characteristic of threatened populations, this procedure selects networks that maximize the growth rate of the overall network. This method offers an improved link between connectivity and metapopulation dynamics. Our framework is applied to connectivities estimated for marine larvae and demonstrates that, for open populations, the best strategy is to protect areas acting as both strong donors and recipients of recruits. It should be possible to implement an EPT framework for connectivity analysis into existing holistic tools for design of protected areas.

Key words: connectivity; conservation; dispersal; eigenvalue perturbation theory; networks; protected areas.

INTRODUCTION

The conditions determining dynamics and persistence of spatially structured populations, i.e., metapopulations, are of major interest in contemporary ecology (Levin 1992, Hanski 1999, Revilla and Wiegand 2008). One key process is the dispersal of gametes, juveniles, and adults influencing population dynamics in space and time (Gaines and Roughgarden 1985, Hughes 1990, Levin et al. 2003). Dispersal also determines the scale of metapopulation connectivity with implications for population persistence (e.g., Hanski 1999), and dispersal plays an important role in genetic differentiation and evolution of local adaptations (Kawecki and Ebert 2004).

Connectivity among subpopulations is also of practical importance for management and conservation, e.g., in the design of protected areas and nature reserves (Carr et al. 2003, Gaines et al. 2003, Van Teeffelen et al. 2006). Critical questions include the effects of habitat fragmentation, and if protected networks are sufficiently self-recruiting or connected through dispersal to allow metapopulation persistence (Ovaskainen and Hanski 2001, Jones et al. 2007). Conservation of genetic diversity further depends on identification of dispersal barriers that may affect loss of genetic variation and evolution of local adaptations with implications for conservation of isolated and genetically distinct populations (Holt et al. 2004, Trakhtenbrot et al. 2005).

There is a general call for including connectivity in the site selection of protected areas (Gaines et al. 2003, Ovaskainen and Hanski 2003, Jones et al. 2007). Current site selection algorithms are usually habitat based (e.g., Possingham et al. 2000) and rarely include information on dispersal and connectivity (Kaplan et al. 2009).

Connectivity is difficult to estimate directly, in particular for species that disperse by producing numerous and small propagules, and/or show long-distance dispersal. Direct empirical methods include active tags recording time-dependent spatial positions (Bonfil et al. 2005) and mark–recapture techniques (Jones et al. 1999). In addition, several indirect empirical methods have been used based on genetic markers (Bacles and Ennos 2008) and micro-chemical fingerprinting of inorganic body parts (Swearer et al. 1999). Empirical methods are often costly and suffer from limited spatial and temporal coverage. Instead connectivity is increasingly estimated from models, e.g., network models of habitat patches (Urban and Keitt 2001), and in marine environments connectivity has been estimated from models of ocean circulation (Roberts 1997, Cowen and Sponaugle 2009). Regardless of the actual technique of estimating population connectivity, a theoretical challenge is how to interpret connectivities in terms of population dynamic effects and barriers to gene flow, and how this may guide selection of optimal networks of reserves and protected areas. Networks with many subpopulations may result in a large number of direct dispersal routes...
and if connectivity is considered across multiple dispersal events the number of indirect routes will increase rapidly with nonintuitive results. In a series of papers, Otso Ovaskainen and Ilkka Hanski demonstrated the use of eigenvalue perturbation analysis of patch-occupancy models to evaluate how individual patches contribute to metapopulation size and persistence (Ovaskainen and Hanski 2001, 2003). Other studies have analyzed connectivity in combination with population growth in metapopulation models with internal patch dynamics to identify sources and sinks (Bode et al. 2006, Cowen et al. 2006, Figueira 2009), to explore conditions for population regulation (Armstrong 2002) and for metapopulation persistence (Hastings and Botsford 2006). Some recent studies employ graph theory to analyze the topology of dispersal networks, e.g., for identification of clusters of well-connected populations, and hubs controlling the gene flow within a metapopulation (Esstrada and Bodin 2008, Rozenfeld et al. 2008, Treml et al. 2008).

In this paper, we aim to improve site-selection of nature reserves and protected areas based on connectivity among sites. Similar to Ovaskainen and Hanski (2003) we base our analysis on the observation that the growth rate in subpopulations or patches are linked to the corresponding eigenvalues of the connectivity matrix. We use perturbation theory, frequently applied in, e.g., classical and quantum mechanics (Sakurai 1993, Goldstein et al. 2001) and for sensitivity analysis of population matrices (Caswell 1978), to predict how protection of different sites will impact the dominating eigenvalues, which in turn affect the growth in the different subpopulations. Our analysis is focused on the fecundity or survival probability in subpopulations at low abundance. This is particularly relevant for conservation scenarios of rare or declining populations. Based on this framework we present a novel procedure for how to select optimal networks of protected areas. We apply this theory to a logistic population model with stochastic migration or survival and/or fecundity. Technically this can be achieved by multiplying the connectivity matrix by a diagonal matrix $E$ either from the left or from the right (representing survival before or after dispersal), where the diagonal elements $E_{ii}$ measure the increase in survival probability at site $i$, i.e., increased growth rate, compared to the background survival probability. Later we briefly discuss a generalization to select protected dispersal routes that can be described with a non-diagonal matrix. The overall efficiency in the dispersal process is measured by the dominant eigenvalue of the connectivity matrix, $\lambda_{\text{max}}$, which measures the fraction of the individuals that survive during dispersal if the population is in its stationary state. Under the assumption that the local population dynamics are linear, and that the dispersal process is the dominating factor limiting the growth in the population, the following assumption is motivated: To maximize efficiency in the choice of protected areas we want to select sites with maximal effect on the dominant eigenvalue of the connectivity matrix.

A similar idea was used in (Hanski and Ovaskainen 2000), where they define the largest eigenvalue of a connectivity matrix as the population capacity. The assumption about approximate linear population dynamics is less restrictive than it appears if we are primarily interested in protecting the population when it is close to extinction, see, e.g., Hastings and Botsford (2006). This implies that the dominant eigenvalue of the matrix $CE$ or $EC$ should be as large as possible, where

$$\begin{align*}
E_{ii} = \begin{cases} 
1 + \delta_i & \text{if } i \text{ is a protected area} \\
1 & \text{if } i \text{ is not a protected area} 
\end{cases}
\end{align*}$$

i.e., $\delta_i$ defines the, possibly site-specific, effect of protecting site $i$. In general, choosing which sites to protect to maximize the increase of the eigenvalue is a nonlinear optimization problem that can be hard to solve. However, if we assume that protection has a small impact on the probability of survival, i.e., that $\delta_i$ are relatively small and that the dominant eigenvalue is well separated from the rest of the spectrum, then we can treat the protection as a perturbation and analyze the optimization using eigenvalue perturbation theory (EPT), which we summarize in the following, see also Caswell (2001) and Ovaskainen (2003).

Consider a matrix $C$ with an eigenvalue $\lambda_n$ and its corresponding left respective right eigenvectors $v_n$ and $u_n$. If $\delta$ is small, perturbation theory can be used to estimate the eigenvalues of the matrix $CE$ or $EC$, constructed as in Eq. 3. Under the assumption that an eigenvalue $\lambda_n$ is well separated from the rest of the spectrum, it can be assumed that the eigenvalue of the perturbed matrix can be expressed as the old eigenvalues with an added perturbation proportional to $\delta$, i.e., $\lambda_n^{\text{new}} =
\( \lambda_n + \delta \hat{k} \) and \( u_{n}^{\text{new}} = u_n + \delta \hat{u}_n \). This leads to the relation \( EC (u_n + \delta \hat{u}_n) = (\lambda_n + \hat{\lambda}) (u_n + \delta \hat{u}_n) \), or the equivalent expression for \( CE \) using the left eigenvectors. We recall that the matrix \( E \) was constructed so that \( E = I + \delta D \), where \( I \) is the identity matrix and \( D \) is a diagonal matrix with zeros and ones on the diagonal (indicating protected sites). Multiplying with the left eigenvector \( v_n \) and recalling the orthogonality relation \( v_n^T u_m = 0 \) if \( n \neq m \), gives the following (to first order in \( \delta \)):

\[
\lambda_n = \frac{v_n^T Du_n}{v_n^T u_n}.
\]

Note that both \( EC \) and \( CE \) has the same perturbation expansion to first order, which is not surprising since the matrices commute to first order.

As will be demonstrated in the Baltic Sea example, the assumption that the effect of protection is small is not very important for the result of our analysis. For small values of \( \delta \), the perturbed dominant eigenvalue can be determined from the left \( (v_k) \) and right \( (u_k) \) eigenvectors of \( C \):

\[
\lambda_{n}^{\text{new}} = \max_k \left( 1 + \sum_{i \in P} \delta_i v_k^T u_i \right)
\]

where \( P \) are the protected areas and the index \( k \) enumerates the eigenvalue associated with a specific subpopulation. From this expression follows that the maximal effect of protection is achieved by choosing sites with large values of \( \lambda_k (1 + \delta_i v_k^T u_i) \) for some \( k \).

Following a similar argument as Ronald Fisher used to define the reproductive index (Fisher 1930, Caswell 2001), the elements in the dominant left and right eigenvectors can be viewed as a measure of the corresponding site’s capacity to contribute or receive recruits, respectively. The capacity of a patch to act as a net contributor or a net receiver of recruits is linked to the concept of source and sink dynamics (e.g., Pulliam 1988). However, classic source and sink dynamics also includes local mortality and to avoid confusion we here view a patch as a donor and/or a recipient of recruits. Note that a patch may be both a donor and a recipient. It should also be noted that our definition of donor and recipient is different from that used in some other studies of dispersal (see Discussion). For example, in Figueira and Crowder (2006) and Figueira (2009) the donor value for a patch is effectively defined by the corresponding column sum in the connectivity matrix. This can be viewed as an approximation of the dominating left eigenvectors and is thereby correlated with our defini-
tion of donor value. However, in Figueira and Crowder (2006) and Figueira (2009) there is no independent definition of a recipient, which is rather defined as not being a donor. In our framework, both the donor and recipient values for each patch carry information and both values are important for the selection of effective protection networks. The term $\delta_i v_k \mu_{ki}$ can be interpreted as the product between the donor and the recipient strength of site $i$. We summarize this finding in the following conclusion: the sites that act as both donor and recipient simultaneously are most important for the persistence of the population.

For a well-connected population, i.e., a population with no significant dispersal barriers, the choice of protected areas can be made by maximizing the increase of the single dominant eigenvalue, according to Eq. 3. However, a population extending over large coastal areas is typically not well connected (Bode et al. 2006). In this case, focusing on only the dominant eigenvalue leads to a protection scheme that only benefits a single subpopulation with minimal overall dispersal leakage. In the example from the Baltic Sea, discussed in the next section, the stationary distribution of the spreading process only contains a significant population at three sites (see Fig. 1). This is obviously an artifact of over-interpreting the assumption of linear population dynamics. To account for a spatially fragmented population, eigenvectors representing a larger number of subpopulations should be included in the analysis. In practice, this means that protected areas should be selected to maximize the shift of a set of dominant eigenvalues that each represent the growth in one subpopulation. Based on this argument, and Eq. 3, we suggest the following scheme for selecting protected areas that have maximal effect on the sustainability:

1) Assume that the effect of protection at a site $i$, $\delta_i$, is known. Set the parameters $M$ and $\theta$ that control how many sites to select in each subpopulation (a set of well-connected sites). The parameter $\theta$ is the threshold of donor times recipient value that a site must have to be selected and $M$ is the maximal number of sites selected from each subpopulation even if there are more sites above the threshold $\theta$ (see point 3 below for details).

2) Calculate the $K$ dominating eigenvalues, $\lambda_k$, $k = 1,\ldots,K$, and the respective left and right eigenvectors, $v_k$ and $u_k$ of the connectivity matrix. If $u_k$ has significant negative or imaginary components, remove it from the list. Normalize the eigenvectors so that $v_k^T u_k = 1$.

3) For each $k$: select at most $M$ sites with maximal donor times recipient values above the threshold $\theta$, $\delta_i v_k \mu_{ki} > \theta$, where the index $i$ refers to the site. Predict the impact on the corresponding eigenvalue based on Eq. 3, $\lambda_k^{new} = \lambda_k (1 + \sum_{i\in P_k} \delta_i v_k \mu_{ki})$, where $P_k$ is the set of selected sites.

4) Sort the groups of sites $P_k$ according to their expected eigenvalues $\lambda_k^{new}$. The resulting list is a priority list for choosing protected areas. A site might occur in more than one group $P_k$, in this case the occurrences further down the priority list can be ignored.

The intuitive interpretation of the algorithm is that each eigenvalue, with its corresponding pair of left and right eigenvectors, typically represents one subpopulation. The $M$ sites selected at stage 3 in the algorithm are all part of the same subpopulation (this assumes that the corresponding eigenvalue is non-degenerate), i.e., they constitute a small network of protected areas that mutually support each other. The parameters $\theta$ and $M$ determine how many sites are selected from each subpopulation, whereas $K$ defines the total number of subpopulations to be considered. The number of selected sites is determined by the overall management goal, often dictated by criteria such as biological representativity, replication and socioeconomics.

As an alternative to selecting sites, one could focus on identifying the most important connections, so called corridors. This only requires a small change in the algorithm above. The expected importance of protecting an edge from site $i$ to $j$ in the subpopulation associated with eigenvalue $\lambda_k$ is measured by $v_k^T u_{ij}$, which can be used as a criterion for selecting the most important connections.

Generating the connectivity matrix

To derive the connectivity matrix, the dispersal of the blue mussel *Mytilus edulis* (see Plate 1) in the Baltic Sea was modeled using the three-dimensional ocean circulation model RCO (described in Döscher et al. 2002) hindcast mode for 25 years (1981–2005) with a horizontal resolution of 3.704 km (2 nautical miles), a vertical resolution of 3–12 m, and a temporal resolution of 6 h. Dispersal of bivalve larvae in surface waters was simulated with particle trajectories lasting for 21 days calculated with the Lagrangian trajectory model TRACMASS, which is based on Döös (1995). Trajectories were simulated using the velocity fields generated by the RCO model. We considered only dispersal of larvae in shallow, coastal waters and trajectories were started in 5168 grid cells (2 × 2 nautical miles [3.704 × 3.704 km]) with a mean depth $\leq 12$ m. For each year, 140 trajectories per grid cell were started between 0 and 6 m depth. This was repeated every 6 h for 6 days resulting in a total of 452 200 000 trajectories over 25 years. Dispersal probabilities were calculated as the proportion of trajectories starting in grid cell $j$ and ending in grid cell $i$, and then summarized in a $5168 \times 5168$ connectivity matrix, shown as an inset in Fig. 1. The distribution of dispersal distances, estimated from the trajectories, showed a positive skew with the 50th percentile at 10 km and the 90th percentile at 46 km.
We assume that the population dynamics is governed by a modified discrete-time logistic growth model:

\[ x_{t+1} = \chi(t) \sum_j E_{ij} C_{ij} [x_i + a_j x_{t+1}(1 - x_{t+1}/\kappa)] \]  

where \( x_i \) is the population at site \( i \), \( C_{ij} \) is the \( ij \)th element of the connectivity matrix, \( a_j \) is the reproduction rate at site \( j \), and \( \kappa \) is the carrying capacity (which we assume to be equal for all sites), and \( E_{ii} \) is the \( ii \)th element of the diagonal matrix defining which areas are protected (see Eq. 1). The reproduction rate \( a_j \) reflects the habitat quality at site \( j \) and is in general not known, we will return to this in Conclusions. The time-dependent coefficient \( \chi(t) \) is a stochastic variable defined as

\[ \chi(t) = \begin{cases} \varepsilon < 1 & \text{with probability } 1/\tau \text{ at each time step} \\ 1 & \text{otherwise.} \end{cases} \]  

The rationale behind Eq. 4 is that we assume the population typically has a logistic growth but reductions of the overall population with a factor \( \varepsilon \) occur at random times with an intensity \( 1/\tau \). An example of a realization of the population dynamics is shown in Fig. 2.

**RESULTS**

Applying the criterion of joint donor and recipient strengths for site selection we generated an optimal network based on modeled connectivity for shallow areas in the Baltic Sea (Fig. 3). This optimal network...
consists of 220 grid cells aggregated into 48 clusters of sites with a size of 9 ± 7.4 km (mean ± SD) and a nearest neighbor distance of 49 ± 31 km. The mean size of the clusters of sites is similar to the mean (10 km, 50th percentile) dispersal distance estimated from the trajectory simulation, and the nearest neighbor distance is on a scale that allows for significant connectivity between many sites. The mean size of cluster of sites and the nearest neighbor distance are also rather close to proposed rule-of-thumb dimensions of marine protected areas based on mean dispersal distance (e.g., in Shanks et al. 2003 and Almany et al. 2009). The size of the network is chosen arbitrary since different network sizes where shown to produce similar results. In reality the number of protected sites will be determined, e.g., by socioeconomic factors. The efficiency of the select protected areas is investigated using the population dynamics Eq. 4 over 500 years. We test the algorithm for different levels of efficiency of protecting a site: 10%, 50%, and 500% increase in survival or fecundity. As a reference, we select the five years with lowest overall population size and compare the result to the population size when some of the protected sites are changed to random locations, always keeping the total number of protected sites constant. The results are shown in Fig. 4. All the changes to the network of protected sites resulted in decreased population sizes during the years with low abundance. Note that the perturbation theory used in the construction of our algorithm assumes the effect of protection to be small. We therefore expect the selected marine protected area to be a good choice when the efficiency is as low as for example 10%. However, the results show that the selected areas remain optimal also when the efficiency goes up to 50% and even to 500%.

To compare our protection schemes we compare its performance to some other alternatives. A simple approach to protection would be to select sites with low leakage, i.e., high values on the diagonal in the connectivity matrix. Panel A in Fig. 5 shows that this approach typically performs worse than our scheme. Another idea would be to use the sink value alone, as defined in Figueira (2009). Panel C in Fig. 5 shows that this approach also results in less effective networks than our algorithm. Finally we also test the sink value when defined as the row sum in the connectivity matrix and the product of the summation based donor and the recipient values, the results are shown in panels B and D, respectively.

**Discussion**

The increasing rate of biodiversity loss and over-exploitation of biological resources call for management and conservation policies often including questions how to best design networks of protected areas. One key aspect is the effect of dispersal. This requires an analysis of connectivity within the area of distribution for target species in order to identify dispersal links between subpopulations or sites that may be critical to population size and persistence of protected areas. In this study, we propose a general theoretical framework for selection of networks of protected areas based on connectivities among sites. This theoretical framework is based on perturbation theory for the eigenvalues (EPT) of the connectivity matrix, also introduced by Ovaskainen and Hanski (2001) to measure the significance of individual patches for metapopulation persistence. Ovaskainen and Hanski (2001) considered patch-occupancy metapopulation models with no internal
patch dynamics. Many open marine populations are characterized by patches interconnected through dispersal but without regular local extinctions (Kritzer and Sale 2004), and we here expand the EPT approach also to population networks with internal dynamics depending on both local and external supply of recruits. The effect of a perturbation, i.e., the expected impact from protecting a specific site, is directly linked to each site's characteristics as a dispersal donor or recipient of propagules. Based on the connectivity matrix we select optimal protected networks maximizing expected metapopulation growth rate, which could significantly improve designs of networks of protected areas.

The optimal network in Fig. 3 includes sites that are ranked according to their strengths as both donor and recipient of propagules using the EPT approach. A comparison with other selection criteria shows that EPT is superior in finding the optimal network that maximizes metapopulation growth rate, which could significantly improve designs of networks of protected areas.

The histograms show the distribution of the minimal total population size for different networks normalized against the total population size from our suggested network, i.e., a value below 1 means that our network performs better. Each histogram is based on 1000 realizations of the population dynamics with different stochastic decimation occurrences. In panel A, the protected areas are selected based on minimal leakage, i.e., sites with largest diagonal component in the connectivity matrix are protected. In panel C we use a selection criterion inspired by the donor value defined in Figueira (2009) as the column sum for each site. In panel D we instead prioritize according to an equivalent definition of recipient value as the row sum in the connectivity matrix. Finally, panel B uses the product of the donor and the recipient value defined as in panel C and D.

Patches acting as net donors or net recipients of recruits are related to classic source-sink dynamics (Pulliam 1988) and there is some confusion in the use of these concepts. In Pulliam's classic paper a patch of high quality (e.g., abundant resources or low mortality risk) acts as a source of surplus individuals that disperse into sink patches, i.e., low-quality patches that without immigration would go extinct. In this scenario with strong local recruitment, there is a clear dichotomy between subpopulations that act as either sources or sinks. The use of sources and sinks has been extended in marine environments with many open populations of
invertebrates that are connected through high rates of larval dispersal (Roberts 1997, Cowen et al. 2006). In networks of open populations the distinction between source and sink populations is less clear and the effect of a subpopulation on the metapopulation size is a function of both how many larvae it delivers and receives. In the extreme case of open populations without local recruitment, no single population is a classic source. We acknowledge this complexity by using the terms donor and recipient of recruits instead of sources and sinks. Our definition of connectivity also differs from, e.g., Figueira (2009) where intra- and inter-patch dispersal are separated. Using our definition of connectivity the EPT approach correctly ranks the patches according to their effect on the metapopulation size through their strength as donors and recipient of recruits without classifying patches as either sources and sinks. Crowder et al. (2000) used a spatially explicit model of reef-fish populations to explore the effect of reducing fishery mortality in selected protected areas. It was found that, in most cases, the protection of sites acting as sources yielded the best effect on the overall population. However, in their study, each site was considered a closed population up to some carrying capacity and only above this density did offspring disperse to other sites. Their model may be realistic where self-recruitment into high-quality patches is large (e.g., Jones et al. 1999) but for highly open populations, characteristic of many invertebrates, the successful dispersal (leading to recruitment) may be less correlated to the local density. For many marine species, local population density depends on the supply of recruits from elsewhere, i.e., being a recipient, while the success of released larvae to reach favorable areas depends on patches acting as strong donors (Caley et al. 1996). In such open populations, our theoretical analysis using EPT shows that it is best to protect areas that act both as donors and recipients. Further analysis will allow us to explore how the EPT framework performs when the populations are more closed.

Strictly, predictions from EPT are valid only to systems with linear dynamics. Linear dynamics may, however, be particularly relevant for assessment of conservation strategies ensuring protection of species that have declined to low abundances. Even so, the evaluation of selected networks with the metapopulation model defined in Eq. 4 showed that the optimal solution was surprisingly robust across cycles of density-dependent population growth and decimations. The selection of the optimal network was also quite insensitive to changes in the effect size of protection (Fig. 4). Applying the criterion of joint donor and recipient strengths for site selection we generated an optimal network based on modeled connectivity for shallow areas in the Baltic Sea (Fig. 3). This optimal network consists of 220 grid cells aggregated into 48 clusters of sites with a size of $9 \pm 7.4$ km (mean $\pm$ SD) and a nearest neighbor distance of $49 \pm 31$ km. The mean size of the clusters of sites is similar to the mean (10 km, 50th percentile) dispersal distance estimated from the trajectory simulation, and the nearest neighbor distance is on a scale that allows for significant connectivity between many sites. The mean size of cluster of sites and the nearest neighbor distance are also rather close to proposed rule-of-thumb dimensions of marine protected areas based on mean dispersal distance (e.g., in Shanks et al. 2003 and Almany et al. 2009).

In most of the relatively few published theoretical analyses of connectivities, graph theory has been applied in order to identify subpopulations or areas within a landscape that are critical for sustainable protection. Cantwell and Forman (1993) demonstrated the use of graph theory to describe and classify the connectivity of different landscape features, while Urban and Keitt (2001) introduced graph theory as a tool to aid conservation of metapopulations. Recently, graph theory has been applied to identify key populations for conservation of metapopulations of seagrass (Rozenfeld et al. 2008), corals (Treml et al. 2008), and birds (Minor and Urban 2007). Several standard techniques used for network analysis are based on spectral analysis of the adjacency matrix. Particularly, clustering in the second eigenvector of the (modified) Laplacian graph is often used to identify modularity in networks (Fiedler 1973, Newman 2006), and the authority/hub score based on the dominating eigenvector is used in many web-based search engines (Kleinberg 1999, Newman 2003). The latter method has recently been suggested as a tool for predicting extinction patterns in ecosystems (Allesina and Pascual 2009). Other methods that analyze effects of population connectivity include permutations of the connectivity matrix to find isolated regions (Bode et al. 2006), and combining connectivities with a population dynamic model to explore the effect of connectivity structure on metapopulation growth (Figueira 2009) or persistence (Hastings and Botsford 2006, Van Teeffelen et al. 2006, Kaplan et al. 2009).

These models generally support the significance of connectivity although the relative importance of local dynamics and immigration partly depends on how intra- and inter-site connectivity is represented in the models. However, none of these methods offer a clear framework for how to select optimal networks of protected areas. The EPT presented in this paper more directly links connectivity to the growth rate in different subpopulations, as also previously shown in Ovaskainen and Hanski (2001 and 2003). By design, this method can therefore be used to select optimal protected networks with respect to population growth and persistence. To our knowledge, this is a novel possibility not offered by other methods.

Ideally, spatial management of endangered populations or overexploited stocks should be based on metapopulation models with information on site-specific reproduction and mortality as well as among-site dispersal and colonization probabilities. Rarely are data available on reproduction and mortality, although it is
sometimes possible to find proxies in terms of habitat quality (e.g., Van Teeffelen et al. 2006, Minor and Urban 2007) and risk (Game et al. 2008). Often, however, it can be possible to estimate connectivities among geographically mapped subpopulations or sub-areas through tags, genetic markers, landscape analysis of corridors, or models of dispersal based on distance or physical transport. For open populations, e.g., in the ocean, EPT applied to simple estimates of connectivities can play an important role in initial spatial management when more detailed data on vital population parameters are lacking. An initial analysis assuming homogeneous habitat quality may suggest key populations where more detailed information should be sought. As more data on habitat quality or local population dynamics become available these can be used to improve estimates of dispersal with connectivities weighted according to reproduction which can be seamlessly added to the EPT. Even when data are sufficient to model the dynamics of the metapopulation EPT offers an efficient way to rank subpopulations according to donor and recipient strength. The EPT procedure also allows the ranking of new sites to be added to an existing protected network, or the assessment of the least valuable sites in an existing network. Although the selection of protected area is the focus in this paper the EPT approach can easily be applied to find dynamically important connections, so called “blue corridors,” between sites.

We have so far only considered the protection of one species or at least a single combination of life-history traits. In some cases the objective is indeed the protection of a single species, e.g., for exploited fish and shell-fish. However, often the intention is to protect general biodiversity with whole assemblages of species (e.g., Nicholson et al. 2006). From the perspective of connectivity, the challenge is then to find a consensus network that will offer sufficient protection for all target species (e.g., Van Teeffelen et al. 2006). The framework presented in this paper is based on a priority list constructed by ranking sites according to their donor times recipient strength. In a situation with multiple species each connectivity matrix will similarly produce a quality measure for each site. By optimizing the collective information in the resulting quality vectors we believe that the theoretical framework based on EPT can be extended to also include several connectivity matrices.

Our proposed theoretical framework offers an innovative contribution to the design of networks of protected areas. Recent reviews (e.g., Jones et al. 2007, Botsford et al. 2009) stress the importance of connectivity when designing sustainable networks of protected areas. However, at present connectivity is rarely considered in practice, partly because of difficulties in how to implement information of connectivity (e.g., Jones et al. 2009). We believe that the EPT framework presented here that finds optimal protected networks with respect to their internal connectivity can be readily combined with more holistic conservation planning tools, e.g., habitat-based optimal sitting algorithms (Possingham et al. 2000).

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