RESEARCH ARTICLE

Linking like with like: optimising connectivity between environmentally-similar habitats

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Abstract Habitat fragmentation is one of the greatest threats to biodiversity. To minimise the effect of fragmentation on biodiversity, connectivity between otherwise isolated habitats should be promoted. However, the identification of linkages favouring connectivity is not trivial. Firstly, they compete with other land uses, so they need to be cost-efficient. Secondly, linkages for one species might be barriers for others, so they should effectively account for distinct mobility requirements. Thirdly, detailed information on the auto-ecology of most of the species is lacking, so linkages need being defined based on surrogates. In order to address these challenges we develop a framework that (a) identifies environmentally-similar habitats; (b) identifies environmental barriers (i.e., regions with a very distinct environment from the areas to be linked), and; (c) determines cost-efficient linkages between environmentally-similar habitats, free from environmental barriers. The assumption is that species with similar ecological requirements occupy

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the same environments, so environmental similarity provides a rationale for the identification of the areas that need to be linked. A variant of the classical minimum Steiner tree problem in graphs is used to address c). We present a heuristic for this problem that is capable of handling large datasets. To illustrate the framework we identify linkages between environmentally-similar protected areas in the Iberian Peninsula. The Natura 2000 network is used as a positive 'attractor' of links while the human footprint is used as 'repellent' of links. We compare the outcomes of our approach with cost-efficient networks linking protected areas that disregard the effect of environmental barriers. As expected, the latter achieved a smaller area covered with linkages, but with barriers that can significantly reduce the permeability of the landscape for the dispersal of some species.

Introduction

Habitat fragmentation ranks among the highest threats to global biodiversity (Butchart et al. 2010; IUCN 2010) and this threat is likely to be exacerbated with climate change (Hannah et al. 2007; Araújo et al. 2011a). To minimise this threat, landscape connectivity should be enhanced with the identification and protection of linkages between areas of high conservation value (Fahrig and Merriam 1994; Hanski 1999). The underlying idea is that connectivity facilitates species dispersal, thus the rescue of small populations from local extinction (due to demographic or environmental stochasticity), while favouring the recolonization of suitable habitats (Bull et al. 2007). A major challenge in conservation and landscape ecology is to develop automated procedures that effectively identify linkages for multitude of species of conservation concern (Beier et al. 2011).

Several approaches have been developed to identify linkages between natural areas. These approaches are usually derived from two different bodies of literature: reserve design and corridor design. Reserve design typically involves strategies to achieve maximum representation of species in reserves given sets of constraints. Such constraints are often derived from the Island Biogeography and Metapopulation theories and seek to achieve a spatial reserve configuration that maximises species persistence (for a review see, Araújo 2009). Mathematical programming techniques have been proposed to address species persistence in reserve design. The techniques included rules to achieve contiguous reserve systems (e.g., Williams 2002; Cerdeira et al. 2005; Önal and Briers 2005; Önal and Wang 2008; Wu et al. 2011), contiguous areas of distribution for the focal species (e.g., Cerdeira et al. 2010), or approaches where spatial criteria are incorporated in the objective function to be optimised (for a review see, Williams et al. 2005). Criteria include compactness (e.g., Williams and ReVelle 1998; Rothley 1999; McDonnell et al. 2002; Fischer and Church 2003; Önal and Briers 2003), diameter (e.g., Önal and Briers 2002) and proximity between pairs of reserves (e.g., Önal and Briers 2002; Alagador and Cerdeira 2007).

Corridor design seeks to optimally link habitats where species of conservation interest occur. The primary input for corridor design is a permeability surface representing the cost of moving across landscape units (Taylor et al. 1993). Ideally, movement costs should be tuned for individual species, but since information is usually lacking for large numbers of species, multi-species corridor design focuses on general measures of landscape permeability (Chetkiewicz and Boyce 2009).

Graph theory provides an appropriate framework for corridor design (Urban and Keitt 2001; Calabrese and Fagan 2004). If one assumes that each landscape unit is a node in a graph (with an associated permeability measure) and edges between pairs of nodes represent the ability of a species to directly move between the corresponding landscape units, then the most efficient way to link a set of particular nodes (called terminals) is readily-expressed by a classical optimisation problem, called minimum Steiner tree (MST) problem in graphs (Du and Hu 2008). MST was introduced in the context of spatial conservation planning by Sessions (1992), who discussed the limitations of algorithms to find optimal MST solutions for real conservation problems, which are characterized by vast amount of data. Subsequently, Williams (1998) and Conrad et al. (2010) worked on extensions of the MST problem to obtain solutions

where linkage costs are balanced with suitability of the selected linkages. Recently, an open-access software package (LQGraph) was released to implement MST for corridor design (Fuller et al. 2006; Fuller and Sarkar 2006).

The identification of efficient linkages when several types of terminal nodes (i.e. habitat units) exist, and nodes for linking these different types may not coincide, is a new variant of the MST problem. In this work, we address this problem as a major step of a framework to effectively promote connectivity for multiple species. The framework consists of: (a) identification of environmentally-similar habitats (expected to accommodate groups of species with similar environmental requirements); (b) identification of environmental barriers (i.e., regions with a very distinct environment from the environmentally-similar areas to be linked), and; (c) selection of cost-efficient linkages between environmentally-similar habitats, free from environmental barriers (i.e., not including regions environmentally distinct from the habitats to be linked). We handle (a) and (b) using cluster analysis and we tackle c) using a heuristic that treats the problem as a sequence of MST problems.

We illustrate the framework using the Iberian Peninsula protected areas as the habitat units to be linked. We use climatic variables to assign protected areas into classes (under the assumption that climatically-similar areas hold similar pools of species) and to characterise landscape permeability for each species pool. Linkages between environmentally similar protected areas were favourably established across Natura 2000 areas (European Community Directive 92/43/EEC) because these are already under some form of protection. In contrast, areas highly modified by human activities, i.e., with high human footprint (Sanderson et al. 2002), were excluded from candidate linkages as they are unlikely suitable for species dispersal. The outcomes of our approach for selecting linkages between protected areas are compared with networks selected using an identical approach but ignoring climatic information.

Methods

The framework is exemplified using Iberian Peninsula protected areas as the habitat units (i.e., terminals) to be connected. The Iberian Peninsula map was divided into 580,696 cells following the UTM 1 km × 1 km grid. The map resolution was chosen to ensure consistency with the resolution of the climatic dataset (see below) and to generate a sufficiently high number of cells to challenge the practicability of the linkage algorithm proposed herein (see below).

Protected areas data were obtained from the Portuguese and Spanish Environmental Ministries and included 681 areas encompassing a wide range of national and international conservation conventions and cells with some amount of protected areas were treated as terminal nodes for analysis (80,871 cells, approx. 14% of the cells in the Iberian Peninsula) (Fig. S1.1 in the Supplementary material). Natura 2000 areas not overlapping with protected areas were not considered as terminal nodes.

The Natura 2000 network (European Community Directive 92/43/EEC) is a European-scale conservation scheme designed to complement nationally-defined protected areas. It is widely present across the European landscape and therefore has potential to be used for connectivity purposes (Saura and Pascual-Hortal 2007). We used Natura 2000 point/polygon data (downloaded from http://www.eea.europa.eu/data-and-maps/data/natura-1) (Fig. S1.1 in the Supplementary material) to calculate the proportion of each cell not covered by Natura 2000 areas. These values were used as linkage-costs $c(s)$, for each cell s. We settled $c(s) = 0$ for each terminal cell.

We used the human footprint index (Sanderson et al. 2002; downloaded from: http://www.ciesin.columbia.edu/wild_areas/register1.html), at 1 km × 1 km cell size (Fig. S1.1 in the Supplementary material), as a measure of human modification, $hf(s)$ (Baldwin et al. 2010; Theobald 2010). The human footprint index ranges from 1 (low human impact) to 100 (high human impact). Since a negative relationship between human footprint and permeability of the cells for species' dispersal was assumed, cells with $hf(s)$ over a specified threshold (see below) were not considered as candidates for linkages. We settled $hf(s) = 0$ for terminal cells.

Monthly data of four climatic variables (maximum temperature, minimum temperature, total precipitation and standard deviation of the minimum temperature), from 1961 to 1990, were averaged to characterize current climatic conditions in the Iberian Peninsula (Fig. S1.1 in the Supplementary material). These variables were selected because they are considered

important drivers of species' distributions at large spatial scales (Hawkins et al. 2003; Whittaker et al. 2007). Climatic data, at 1 km × 1 km, were provided by the Instituto de Meteorologia (Portugal) and the Agencia Estatal de Meteorologia (España) (for a full description of data see, Araújo et al. 2011b).

Environmental classification of protected areas

We carried out a principal components analysis (PCA) to reduce the dimensionality and the correlative effects of the climatic data. We retained the two PCA components that explained the greatest proportion of the data variability (Fig. S2.1, Tables S2.1 and S2.2 in the Supplementary material). These components were then used to group Iberian protected areas into climatically similar clusters. Specifically, we computed the arithmetic mean of the two PCA components in the centroids of all individual protected areas. These centroids were chosen as units for the cluster analysis. We developed a k-means algorithm (Fielding 2007) for grouping protected areas into homogeneous climatic units (i.e., minimizing the summed Euclidean distances of each class-member to its respective class-centroid). The algorithm is a simulated annealing approach (Aarts et al. 1997), which, at each iteration, randomly selects a protected-area centroid and considers the possibility of its allocation in a different class. We used 10,000 iterations for each 50 uniformly selected initial classification-seeds, and saved the best solution. The number of climatic types ($k = 4$) was selected a priori to limit the number of climatic clusters in Iberian Peninsula (i.e., alpine, continental, Mediterranean, and oceanic), in line with the Koppen-Geiger climatic classification for the region (Peel et al. 2007) (Table S2.3 in the Supplementary material).

Identification of barriers

We considered two types of barriers: one defined by the human footprint index and the other defined by climate data. Areas with high human footprint $hf(s)$ values were assumed to be poorly permeable to species' movement. We defined a threshold, H, and excluded as candidate areas for linkages between protected areas the cells s, for which $hf(s) > H$. We used $H \in \{50, 60\}$, as low values of H would retrieve an excessively fragmented landscape (i.e., many landscape barriers)

and high values of H resulted in highly disturbed cells being included (Fig. S3.1 and Table S3.1 in the Supplementary material).

In addition to the human footprint barriers we also considered climatic barriers. Here, the centroid of each climatic class in the final cluster was used as an archetype of the climate of that class, and the Euclidean distances, in the climatic space, of each (unprotected and protected) cell to the centroid of each class were computed. This retrieves k values, $d_i(s)$, for each cell, expressing the dissimilarity of cell s to every climatic class-i.

Since the goal is to link climatically similar protected areas across cells that do not differ significantly from the mean climatic conditions of protected areas, we defined a threshold value B_i assuming that cells with $d_i(s) > B_i$ are climatic barriers, thus not adequate for linking protected areas of class-i. We defined B_i according to two scenarios. In the first scenario, B_i was defined as the largest dissimilarity $d_i(s)$, among the protected cells s in every protected area of class-i [$max\ d_i(s)$]. In the second and more restrictive scenario, the barriers for class-i were established as the top 25% $d_i(s)$ values for cells s not belonging to i, i.e., [$Q_3\ d_i(s)$] (Table S4.1 in the Supplementary material).

The linkage algorithm

Linking protected areas within each class-i, with minimum cost and with no environmental barriers for class-i, is a generalization of the (node weighted) MST problem in graphs, where protected areas act as terminal nodes. The MST is the special case when only one class exists. The MST is a difficult problem, and heuristics are the only option to handle even moderate size instances (say a few hundred of nodes and a few dozens of terminals). A simple heuristic for the MST problem is what is called the minimum spanning tree approach (see Du and Hu 2008). First, minimum cost paths (*min cost paths*: Dijkstra 1959) are computed between every pair of terminals. Next, these *min* cost paths are used to weight the edges of a complete graph whose nodes are terminals, and the minimum spanning tree for this graph (Kruskal 1956; Prim 1957) is obtained. Finally, the union of paths, corresponding to the edges of the minimum spanning tree, is pruned from redundant nodes (i.e., nodes that are not necessary to link all terminals of each class). The pruning

process ends when the solution is minimal, i.e., every node is needed for linkage.

We extended this approach when there are $k > 1$ classes. For each of the $k!$ permutations of the k climatic classes, we applied the above MST procedure to link protected areas of the class appearing first on the permutation. We then assigned "cost zero" to every cell of that linkage, and proceed as above to link the protected areas belonging to the second class of the permutation. This was repeated for the third, fourth,…and k classes. At the end, the solution consisting of the union the k linkages was turned minimal. The final climate network was the minimum cost network among the $k!$ networks considered (see a schematic diagram of the algorithm in Fig. 1).

In our implementation, special concern was given to data structures to allow the heuristic to run large instances, such as the Iberian Peninsula example.

It should be noted that, depending on the specific parameterization of climatic barriers (B_i) and the human footprint threshold (H), pairs of protected areas of the same class might not be linked in the final solution. This can happen when all paths connecting two protected areas belonging to some class-i include some cell, s, with $d_i(s) > B_i$ or $hf(s) > H$. In other words, for some climatic classes, the resulting climate network can have more than one connected component (Fig. 2a). A connected component of class-i is a maximal (with respect to inclusion) subset of (protected and unprotected) cells connecting protected areas of class-i that are not barriers for that class. This generalizes the notion of a connected component in a graph (e.g., Rayfield et al. 2011).

Our algorithm generates a climate network with the minimum number of connected components for each class. We used the number of components (which strictly depends on the values used for B_i and H) as an indicator of linkage effectiveness. A large number of components for a given class reflect a highly fragmented network. This may indicate an ineffective linkage for that class.

We also considered balancing the cost of the final solution with the number of selected cells using an area-penalty. For every cell, s, we added a positive fixed term ε to the cost, $c(s)$, obtaining the modified cost $\bar{c}(s) = c(s) + \varepsilon$. Larger ε values determine fewer cells in the solution (Fig. 2b). We tested three different values ($\varepsilon = 0$; $\varepsilon = 0.1$ and $\varepsilon = 0.5$).
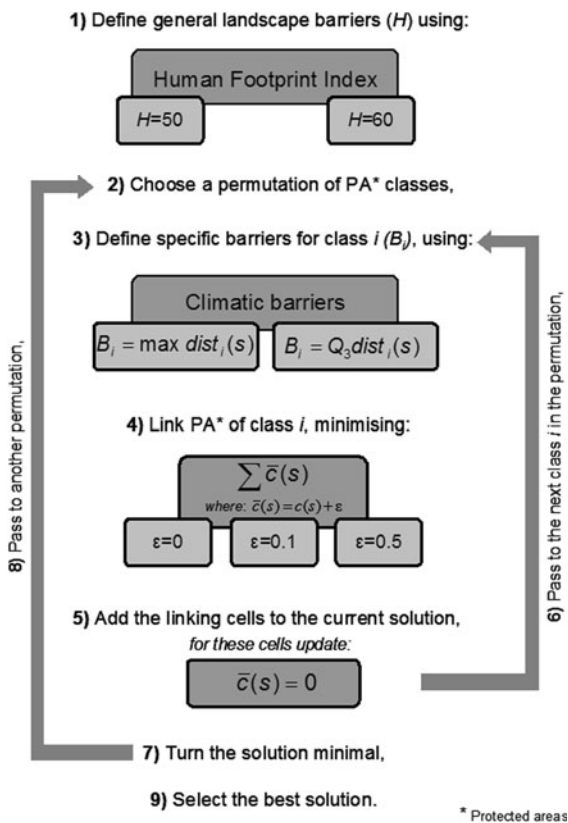

Fig. 1 Simplified overview of the procedures implemented in the connectivity algorithm

Comparing network effectiveness

We compared the climate networks with linkages obtained without use of climatic information, i.e., using the procedure described above, but assuming that all protected areas belong to the same climatic class and that no climatic barriers exists. We denote these networks as simple networks.

We obtained climate networks and simple networks for each of the 12 parameterizations above described (2 human footprint thresholds $\times 2$ climatic barriers assumptions $\times 3$ area-penalty values). We compared solutions in terms of efficiency (i.e., total surface area and total cost) and effectiveness. To assess effectiveness of simple networks we recovered the protected areas climatic classification and for each climatic class-i we removed the barriers for that class. Then, we counted the number of connected components of class-i, which we compared with the number of
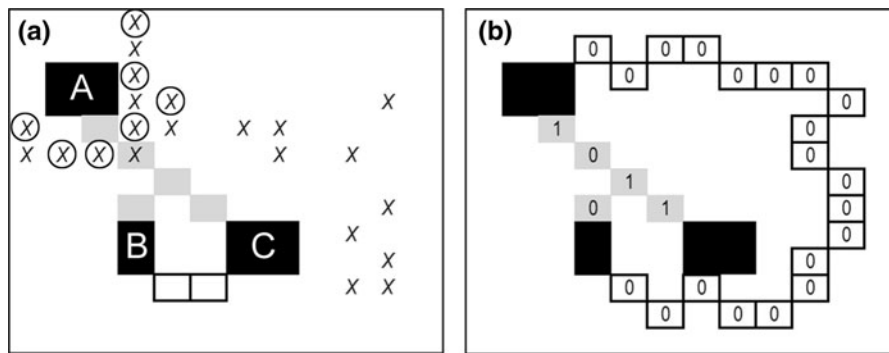
Fig. 2 The effect of changing parameters over the linkage solutions, using a synthetic example where three habitat units (*A*, *B* and *C*) are to be linked. **a** The barrier effect (landscape and environmental barriers). When barriers (*circles*) do not isolate sets of habitats the *grey cells* are a likely solution to connect *A*, *B* and *C*. Otherwise, when barriers (*crossed-cells*) isolate sets of habitats, a linkage is only required to connect *B* and *C* (*thick-*

bordered white cells), while *A* stays isolated; **b** The effect of the area-penalty value, epsilon (ε). When $\varepsilon < 0.2$, the "cheapest" connection is the one passing through the 20 *thick-bordered zero-cost white cells* (total cost $= 20 \times \varepsilon$). When $\varepsilon > 0.2$, the cheapest connection is the one passing through the *grey cells with zero and one-costs* (solution cost $= 3 \times (1 + \varepsilon) + 2 \times \varepsilon$)

Results

Outputs from the two types of networks (climate and simple networks) obtained under different parameterizations ($\varepsilon \times H \times B_i$) showed marked variability on the extent (Table 1), effectiveness (Fig. 3) and spatial location (Fig. 4, and Table S5.1 in the Supplementary material) of linkages connecting the Iberian protected areas. While climate networks ranged from 5,328 to 6,666 km^2, simple networks varied from 4,873 to 6,373 km^2. This means that climate networks required 3.2–14.4% more area than simple networks, and also identified more linkages outside the Natura 2000 network (3.8–19.2% more area). Models penalizing the number of cells and the total area in the solution ($\varepsilon = 0.5$) retrieved more distinct solutions between the approaches; a trend that is true for both $H = 50$ and $H = 60$ scenarios (Table 1).

As expected, climate networks performed better in terms of avoiding climatic barriers than equivalent simple networks. In fact, by identifying and bypassing climatic barriers, climate networks included 6.0–35.2% less protected area components than simple networks, a fact that is contingent on the spatial pattern of unsuitable areas provided by H and B_i. Differences in the number of components vary with the climatic classes, because linkages between

connected components in the corresponding climate network.

protected areas in particular classes are more challenged by barriers.

When barriers included the 25% more dissimilar cells outside protected areas of each type [$B_i > Q_3$ $d_i(s)$], greater differences between the climate and simple networks were obtained for the alpine protected area network (Table 1). With climate networks, linkages for these protected areas retrieved few components (2–3) being 72.7–86.7% more effective at guaranteeing connectivity than linkages in the simple networks. Turning $H = 50$ to $H = 60$ greatly affected comparisons of both approaches for the continental protected areas, as effectiveness gains with climate networks varied approximately from 30 to 60%. This means that the general (landscape) barriers are the major determinant of fragmentation for these protected areas. Differences between approaches were less marked when connecting Mediterranean and oceanic protected areas, with gains in effectiveness being approximately 15% for climate networks. Using $H = 50$, effectiveness gains in oceanic protected areas were narrower (3.0–5.9%).

Comparing efficiency and effectiveness of climate and simple networks enables the assessment of the extent to which a fixed budget produces solutions performing differently in terms of realized linkage achievements. Climate networks are inevitably more costly than simple networks when the same parameterization is used. Therefore, we manipulated area-penalty to obtain climate and simple networks with similar costs. For example, analysing the more

Table 1 Summary of networks of Iberian protected areas, obtained with climate data (climate networks; CN) and without climate data (simple networks; SN) using different parameterizations of the human footprint threshold H, the area-penalty parameter ε, and climatic barriers B_i

B_i	H	ε	Total selected area (km²)			Selected area outside Natura (km²)			Number of components in protected area networks																
									Alpine			Continental			Mediterranean			Oceanic			Total		
			CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)	CN	SN	Δ (%)
$max\ d_i$	50	0.0	6,361	6,140	3.6	2,083	1,988	4.8	1	1	0.0	19	25	−24.0	59	63	−6.3	31	31	0.0	110	120	−8.3
		0.1	5,934	5,639	5.2	2,163	2,026	6.8	1	1	0.0	19	23	−17.3	59	62	−4.8	31	31	0.0	110	117	−6.0
		0.5	5,331	4,901	8.8	2,473	2,244	10.2	1	1	0.0	19	25	−24.0	59	63	−6.3	31	31	0.0	110	120	−8.3
	60	0.0	6,577	6,373	3.2	2,034	1,959	3.8	1	1	0.0	8	15	−46.7	43	45	−4.4	17	17	0.0	69	78	−11.5
		0.1	5,890	5,622	4.7	2,138	2,010	6.4	1	1	0.0	8	14	−42.9	43	46	−6.5	17	17	0.0	69	78	−11.5
		0.5	5,328	4,873	9.3	2,562	2,229	14.9	1	1	0.0	8	13	−38.5	43	45	−4.4	17	17	0.0	69	76	−9.2
$Q_3\ d_i$	50	0.0	6,383	6,140	4.0	2,126	1,988	6.9	3	15	−80.0	20	31	−35.5	59	70	−15.7	32	34	−5.9	114	150	−24.0
		0.1	5,985	5,640	6.1	2,193	2,026	8.2	3	14	−78.6	20	30	−33.3	59	69	−14.5	32	34	−5.9	114	147	−22.4
		0.5	5,506	4,901	12.3	2,531	2,244	12.8	3	11	−72.7	20	27	−25.9	59	69	−14.5	32	33	−3.0	114	140	−18.6
	60	0.0	6,666	6,362	4.8	2,143	1,956	9.6	2	15	−86.7	8	22	−63.6	43	51	−15.7	17	20	−15.0	70	108	−35.2
		0.1	6,029	5,622	7.2	2,223	2,010	10.6	2	14	−85.7	8	20	−60.0	43	53	−18.9	17	20	−15.0	70	107	−34.6
		0.5	5,576	4,875	14.4	2,657	2,229	19.2	2	11	−81.1	8	17	−52.9	43	54	−20.4	17	19	−10.5	70	101	−30.7

Percentage-differences [Δ (%)] between CN and SN are presented for the total selected area, the selected area outside Natura 2000 network, the total number of protected area components and for the number of components within each of the climatic classes (alpine, continental, Mediterranean and oceanic)
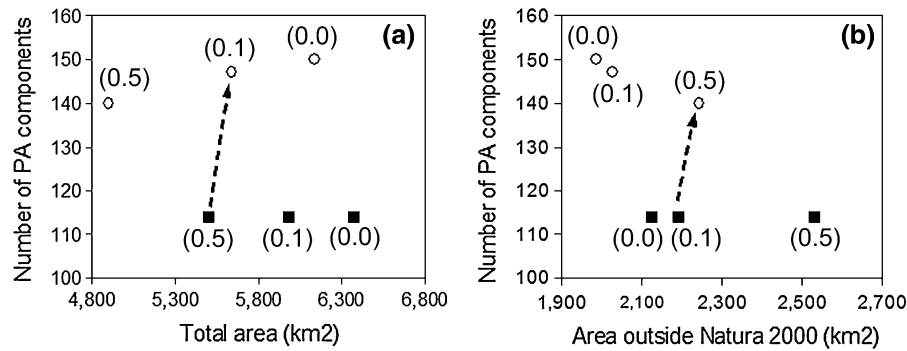
Fig. 3 Comparison of networks delineated with climate data (climate networks *CN*) (*filled squares*) with simple networks without climatic data (simple networks *SN*) (*open circles*) in terms of efficiency: **a** Total area selected, **b** Total area selected not listed in Natura 2000; and effectiveness (number

components in protected area networks), for the most conservative scenario under consideration [$H = 50$, $B_i > Q_3$ $d_i(s)$], using distinct area-penalty parameterizations (ε values in *parenthesis*). *Arrows* represent comparisons of pairs of networks sharing similar costs
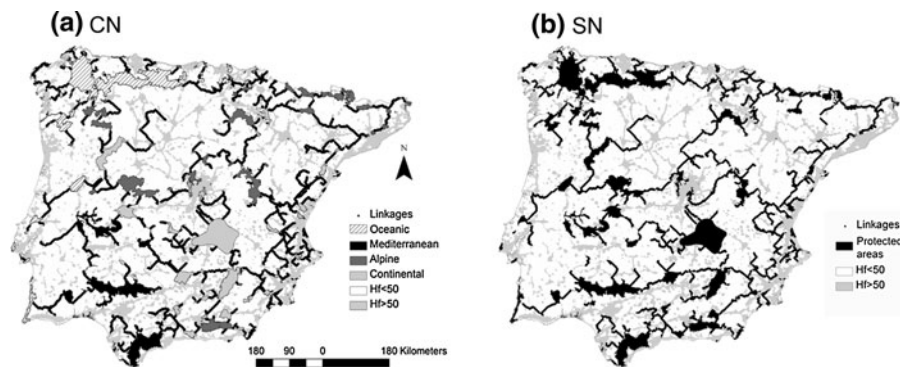

Fig. 4 Maps of linkages for the Iberian Peninsula protected areas obtained with climate data (climate networks *CN*), using an area-penalty $\varepsilon = 0.1$ and climatic barriers $B_i > Q_3$ $d_i(s)$, and without climate data (simple networks *SN*) using an area-penalty $\varepsilon = 0.5$. Both networks are delineated over a similar amount of

land not listed within Natura 2000 (see Table 1). Landscape barriers (*light grey areas*) are defined after applying a threshold value ($H = 50$) to filter out the areas with the highest human footprint values

conservative scenario (i.e., with more barriers) [$H = 50$, $B_i > Q_3$ $d_i(s)$], the climate networks requiring less surface area targeted 5,506 km², encompassing 114 protected area components, while a similar-size simple networks (5,640 km²) contained 147 protected area components (Fig. 3a). An equivalent loss of linkage effectiveness for the simple networks occurred when the selected area outside Natura 2000 was used as a measure of efficiency (Fig. 3b). In this case the most-costly simple network (2,244 km²) presented more 22.8% protected areas components than the climate network using a similar amount of area outside Natura 2000 (2,193 km²). These differences are directly translated to the spatial patterns obtained for both network types (Fig. 4).

Discussion

We have shown that extending the MST to account for different types of terminal habitats provides a useful framework for identifying linkages between natural areas using environmental data. The framework is based on the assumption that the environment drives, at least partially, species' distributions, so that habitats with similar environments are likely to share similar assemblages of species or act as potential 'sources' and 'sinks' for species' dispersal. It follows from this assumption that linkages between protected areas should preferentially be established between environmentally-similar areas. Although this assumption is problematic for the selection of complementary sets of

areas in reserve selection (see, Araújo et al. 2001; Araújo et al. 2004; Hortal et al. 2009), it is reasonable to expect that when species occupying a given environment are, for whatever reason, forced to move elsewhere, they preferentially move to similar environments (Chetkiewicz et al. 2006; Sawyer et al. 2011). The choice of the relevant environmental attributes to be used should be concerted with the autoecology of focal species and the scale of analysis (i.e., extent and resolution of the study area). For example, we used climate to obtain a broad characterization of species' permeability in Iberian Peninsula as it is seen highly correlated with plant and animal species' distributions at such spatial extent and grain size (Hawkins et al. 2003; Whittaker et al. 2007). Several other environmental variables could be used instead (e.g., vegetation types, topography, geology, biogeography, phylogeny and disturbance data, or different combinations of them).

Two problems may arise when using climatic variables in our framework in a context of climate change. First, sets of climatically-similar habitats are likely to be shuffled with climate change and therefore an habitat unit A initially targeted to be linked with a similar unit B, may no longer need such linking, but requires a linkage with a new similar unit C. Second, areas identified as linkages for a given habitat class may lose climatic suitability for that class. In an extreme scenario, they may even turn into barriers to species' movements. To develop conservation maps robust to climate change (without relying on projected emissions of greenhouse gases, air-ocean circulation models, and climate-envelope models), several studies support the use of more steady factors driving biodiversity patterns and processes, like topographic and geomorphologic variation (Anderson and Ferree 2010; Beier and Brost 2010; Game et al. 2011).

Our framework is flexible enough to accommodate simple conservation purposes. For example, natural habitats may be so heavily fragmented that no continuous swaths of land are left to be conserved. Furthermore, there are species able to cross some amount of inhospitable land. In cases such as these, linking habitats with stepping-stones may open opportunities for effective and less-conflicting conservation measures, because stepping stones require lesser area than continuous linkages. Our framework may be easily adapted to delineate stepping-stones optimally. This can be accomplished by using adjacency rules

between cells that integrate a "functional distance" defined by the distance that the least mobile focal species are able to move across unsuitable habitat. Once a given cell is chosen for linkage at least one other cell, distancing no more than the "functional distance", needs also to be selected.

The cost-optimised networks obtained with our framework only require a unique path between each pair of habitat units of the same class. This may not be the most precautionary option to take (Pinto and Keitt 2009). One can increase network robustness by identifying multiple paths to link habitats of the same class. Our framework is able to reach this by replacing the execution of the last step of the linkage algorithm (i.e., turning the solution minimal), with the removal of only the non-terminal cells that are connected to no more than one other cell. Then, if non-overlapping linkages are desired, the heuristic can be repeatedly run removing all the selected non-terminal cells from the previous solutions. Clearly, this can be executed only for those habitat classes with greater numbers of threatened species or for the classes requiring longer linkages, as these are less likely to be implemented or are more exposed to threats (Beier and Noss 1998). Furthermore, in circumstances where lengthy linkages are not critical to maintain long distance dispersal events, it may be wiser to avoid linking distant habitat units. For example, the analysed region may be subdivided in order to obtain sub-areas with higher densities of habitat units for each habitat class. Independent solutions for each of these sub-areas may be obtained thereafter.

Finally, it is critical to realize that if the main interest of conservation is the persistence of species in fragmented landscapes, the sole integration of species' movement patterns is insufficient. Species' dispersal data should be combined with other factors that determine species' persistence at various spatial and temporal scales. The framework here presented should be considered as part of a broader analysis towards the promotion of such complex and integrative objective as it is allowing species to persist.

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