Research

A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape

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Graph structures and habitat availability metrics are two recent and complementary approaches for analysing landscape connectivity. They have gained rapid popularity and provided significant conceptual improvements for decision making in conservation planning. We present a further methodological development of the habitat availability concept and metrics by partitioning them into three separate fractions that quantify the different ways in which individual landscape elements can contribute to overall habitat connectivity and availability in the landscape, including stepping stone effects. These fractions are derived from the same concept, are measured in the same units and can be directly compared and combined within a unifying framework. This avoids the problematic and, so far, usual combination of metrics coming from different backgrounds and the arbitrary weighting of connectivity considerations in a broader context of conservation alternatives. We analyse how the relative importance of each fraction varies with species traits. In addition, we show how the critical patches differ for each of the fractions by analysing various forest habitats in the province of Lleida (NE Spain). We discuss the conceptual and conservation implications of this approach, which can be adapted to different degrees of ecological and spatial detail within the graph while still maintaining a coherent framework for the identification of critical elements in the landscape network.

Connectivity is defined as the degree to which the landscape facilitates the movement of species and other ecological flows (Taylor et al. 1993). It is considered a key part of the efforts for biodiversity conservation worldwide and one of the best responses to counteract adverse effects of habitat fragmentation and to facilitate the accommodation of species to the shifts in their natural domains caused by climate change (Crooks and Sanjayan 2006). While some authors conceive connectivity as a feature of an entire landscape (Tischendorf and Fahrig 2000), others, mainly in the field of metapopulation theory, focus on a patch-based description of connectivity (Moilanen and Hanski 2001, Frank and Wissel 2002, Nicholson et al. 2006).

From a methodological point of view, intensive efforts have been made in advancing towards the best way to quantify and incorporate connectivity in landscape planning, from simple structural indices to more complex, biologically detailed, dynamic and spatially explicit metapopulation models (Hanski and Ovaskainen 2000, Calabrese and Fagan 2004, Wiegand et al. 2005). Among the myriad of methods and metrics used for analysing connectivity, graphs (Urban and Keitt 2001) and habitat availability metrics (Pascual-Hortal and Saura 2006) are two recent and complementary approaches that have gained rapid popularity and provided significant conceptual improvements for decision making in conservation planning.

Graph theory offers a wealth of powerful tools and algorithms for analysing network connectivity and vulnerability in many scientific disciplines (Strogatz 2001, Barabási 2002, Lesne 2006, Pascual and Dunne 2006, Grubesic et al. 2008). When dealing with habitat connectivity, graphs can provide a spatially explicit but tractable representation of the complexity of a landscape, and allow investigators to assess the importance of individual landscape elements and to guide conservation or restoration efforts (Chetkiewicz et al. 2006, Bodin and Norberg 2007, Minor and Urban 2007, Schick and Lindley 2007, Estrada and Bodin 2008). Graphs provide a favourable trade-off between how well the model portrays reality and the amount of data it requires to do so (Keitt et al. 1997, Calabrese and Fagan 2004, Bodin and Norberg 2007). For these reasons, and after the seminal paper by Urban and Keitt (2001), the number of studies applying graph-based metrics to the analysis of landscape

connectivity has increased exponentially in recent years (Bodin and Norberg 2007, Fall et al. 2007, Ferrari et al. 2007, Jordán et al. 2007, Minor and Urban 2007, 2008, Neel 2008, Pascual-Hortal and Saura 2008). However, graphs are only a data structure and, in the same way than with the typical vector or raster data structures in geographical information systems, many different outcomes of variable quality can be obtained through them. The key current issue is not why to use graphs, but how to measure connectivity once the landscape has been modelled by a graph. The analysis of landscape connectivity has particular and specific needs that may not be met by some graph metrics developed for other types of complex networks in other scientific disciplines.

Recent analyses (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007) have revealed weaknesses of commonly used graph metrics with respect to the task of prioritising landscape elements for the maintenance of landscape connectivity. They have evaluated the response of those graph metrics to the loss of individual patches and links. Most of the examined metrics did not fully satisfy a set of desirable properties for decision-making considered in those studies. Only two new landscape connectivity metrics, the integral index of connectivity (IIC) and the probability of connectivity (PC), have shown all of the desired properties. Both metrics are based on graph structures and on the concept of measuring habitat availability at the landscape scale (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007). The habitat availability concept consists in considering a patch itself as a space where connectivity exists, measuring the available (reachable) habitat in the landscape through a single metric, which integrates the connected habitat area that exists within the patches (i.e. intrapatch connectivity) with the area made available by the connections among different habitat patches (i.e. interpatch connectivity) (Pascual-Hortal and Saura 2006, Saura 2008). Habitat availability metrics combine purely topological features with ecological characteristics of landscape elements, which meets the need for the development of improved topoecological connectivity metrics (Ricotta et al. 2000). While PC is based on a probabilistic connection model that allows for continuous modulation of the connection strength or dispersal feasibility, IIC is based on a simplified binary connection model in which two habitat patches either are or are not connected. For this reason, hereafter we will focus on the PC metric.

One potential criticism to PC and IIC is that, as is also true for other metrics, they may suffer from a tendency to assign greater importance to larger patches (Ferrari et al. 2007). Conservation planners would indeed prefer to retain the biggest patches (all other factors being equal), but the importance of a patch in relations to its area may be quite straightforward to quantify. Thus, planners may be more interested in evaluating the importance of a patch apart from its area, as a connecting element or stepping stone between other habitat patches. As with fragmentation metrics, the area-based and configuration aspects of conservation need to be distinguished (Fahrig 2003). Even within the configuration aspects, habitat patches may contribute in different ways to the functioning of the landscape network. To assess these contributions, various

sets of metrics have been used from the graph perspective (Bunn et al. 2000, Urban and Keitt 2001, Jordán et al. 2003, 2007, Ferrari et al. 2007, Minor and Urban 2007).

We here present a further theoretical development of the habitat availability concept and metrics to identify critical elements in a patch network. We partition the probability of connectivity metric (PC) into three separate fractions that quantify the different ways in which individual landscape elements (i.e. patches, links) can contribute to the overall habitat connectivity and availability in the landscape, including stepping stone effects. The three fractions are derived from the same concept, are measured in the same units and can be directly compared and summed within a unifying framework. This avoids the common problems of combining and weighting metrics with different backgrounds and characteristics in the decision process. We explore the relative importance of the three fractions for different species traits (here, dispersal distances) and habitat networks in the povince of Lleida (Catalonia, NE Spain). We discuss the conceptual and conservation implications of our approach. Finally, we compare the three fractions of the PC metric with other available approaches for the analysis of landscape network connectivity. We do not pretend to include a detailed case study for a given conservation planning application, but we aim to illustrate our approach and its underlying concepts, which can be adapted to a variety of applications and spatial and biological details within a coherent framework for the identification of critical elements in the landscape network.

Partitioning habitat availability metrics into three different fractions

Graph perspective

We focus on a graph perspective and conceive the landscape as a set of habitat patches (nodes) and connecting elements (links). A link is defined as an element that comprises no habitat area but represents the possibility of dispersal between two habitat patches. A link may correspond to a physical corridor or it may symbolise the potential of an organism to directly disperse between two habitat patches through favourable land cover. A landscape element that contains habitat area is considered a habitat patch, even though its main role may be to serve as a stepping stone or connecting element between other habitat areas.

A habitat patch i is here characterized by an attribute value (a_i), typically habitat area, quality-weighted habitat area (Minor and Urban 2007), habitat suitability, core area, area to the power of a coefficient that typically ranges from 0.1 to 0.5 (Moilanen and Nieminen 2002), probability of occurrence (Pascual-Hortal and Saura 2008), population size (Jordán et al. 2007), or another attribute relevant for the analysis.

The strength of each link is characterised by p_{ij} which is the probability of direct dispersal between patches i and j (without passing through any other intermediate habitat patch) within a given time (e.g. one generation). Values of p_{ij} may be quantified using a variety of input data and methods, depending on the availability of data and the objectives and scale of the analysis. These include simple

Euclidean-distances (Urban and Keitt 2001, Pascual-Hortal and Saura 2008), effective (least-cost) distances (Schadt et al. 2002), spatially-explicit dispersal models (Kramer-Schadt et al. 2004, Revilla et al. 2004), or actual movement data derived from radiotracking or mark-release-recapture experiments (Chetkiewicz et al. 2006).

The probability of connectivity metric

The probability of connectivity (PC) is a graph-based habitat availability metric that quantifies functional connectivity. It is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the links (direct connections) among them (Saura and Pascual-Hortal 2007, Saura 2008). It is given by:

$$PC = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \times a_j \times p_{ij}^*}{A_L^2} = \frac{PCnum}{A_L^2} \qquad (1)$$

where a_i and a_j are the attributes of patches i and j (see previous section). A_L is the maximum landscape attribute; when the patch attribute is habitat area, A_L corresponds to the total landscape area (i.e. area of the study region, comprising both habitat and non-habitat patches). The product probability of a path (where a path is a sequence of patches in which no patch is visited more than once) is the product of all the values of p_{ij} (probability of direct dispersal) for all the links in that path. p_{ij}^* is the maximum product probability of all of the possible paths between patches i and j (including direct dispersal between the two patches). If patches i and j are close enough or have a strong direct connection, the maximum probability path will simply be the direct movement between patches i and j ($p_{ij}^* = p_{ij}$). If patches i and j are more distant or have a weak direct connection, the "best" (maximum probability) path will probably consist of several steps through intermediate stepping stone patches yielding $p_{ij}^* > p_{ij}$. When two patches are completely isolated from each other, then $p_{ij}^* = 0$. When $i = j$ then $p_{ij}^* = 1$ (a patch can always be reached from itself); this relates to the habitat availability concept that applies to PC, in which a patch itself is considered as a space where connectivity exists. The value of $PCnum$ varies with the spatial arrangement and attributes of the habitat patches, and with the dispersal abilities of the species (as quantified through p_{ij}). By dividing $PCnum$ by A_L^2, the PC values are bounded (ranging from 0 to 1) and are defined as a probability of coincidence in a similar way to the degree of coherence of Jaeger (2000). According to Bogaert et al. (2005), the degree of coherence is directly related to the Simpson and Shannon indices. For a given amount of habitat in the landscape, PC is greatest when all the habitat is confined in a single habitat patch (no fragmentation) or when the habitat is dissected into different patches but there is a maximal interpatch connectivity such that $p_{ij}^* = 1$ for each pair of patches.

The prioritisation and ranking of landscape elements (patches and links) by their contribution to overall habitat availability and connectivity can be calculated from the percentage of the variation in PC (dPC_k) caused by the removal of each individual element from the landscape (Keitt et al. 1997, Urban and Keitt 2001, Saura and Pascual-Hortal 2007):

$$dPC_k = 100 \times \frac{PC - PC_{remove,k}}{PC} = 100 \times \frac{\Delta PC_k}{PC} \qquad (2)$$

where dPC_k is the importance of element k for the maintenance of overall habitat availability in the landscape. PC is the metric value in the original intact landscape, when each of the original elements, including k, is present. $PC_{remove,k}$ is the metric value after the removal of k. When k is a habitat patch $PC_{remove,k}$ is computed by setting $a_k = 0$ and $p_{ij} = 0$ when either $i = k$ or $j = k$. When k is a link between two patches, $PC_{remove,k}$ is computed by setting the direct dispersal probability between them to zero ($p_{ij} = 0$). Note that dPC_k and ΔPC_k are affected only by $PCnum$ and not by the denominator in eq. (1), since A_L only depends on the extent of the study area and remains constant after removing any element. On the other hand, although the formula for PC (eq. 1) only depends on the "best" (maximum product probability) path between two patches, the existence of different alternative paths is considered in the importance analysis (dPC_k). When the loss of a certain patch or link k breaks the only path that exists between other patches, this will result in a large dPC_k. On the contrary, when there are many other alternative paths between those patches (paths that are nearly as good as the one that has been broken, as quantified by p_{ij}^*), the removal of k will result in a much lower dPC_k. It should be noted that PC is conceived for its use as a relative metric in order to evaluate the importance of landscape elements or changes (dPC_k). The absolute values of PC are of less interest because they are dependent on the definition of the boundaries of the study area (A_L), and not on the habitat pattern itself, and very low values of PC may be obtained when the habitat patches and total habitat area are very small compared to the entire landscape (Neel 2008).

Hanski and Ovaskainen (2000) presented the metapopulation capacity (λ_M) as a new measure derived from metapopulation theory that can be used to evaluate the persistence of a species as a metapopulation in a given landscape and to compare different landscapes by their capacity to support viable metapopulations. Unlike other metapopulation models, λ_M is independent of the extinction and colonization parameters of the species. Like PC, λ_M can be computed from a set of discrete patches with known areas and spatial locations. λ_M is calculated as the leading eigenvalue of a matrix M with elements m_{ij} given by:

$$m_{ij} = A_i \times A_j \times e^{-\alpha \times d_{ij}} \text{ for } i \neq j, \ m_{ij} = 0 \text{ for } i = j \qquad (3)$$

where A_i and A_j are the areas of patches i and j, d_{ij} is the distance between patches i and j, and α is a constant (Hanski and Ovaskainen 2000). Ovaskainen and Hanski (2001) calculated the value of a patch k (V_k) as the relative decrease in the metapopulation capacity after its removal from the landscape, which is analogous to dPC_k for the case of PC (eq. 2). Given the relevance of this metapopulation metric and that it can be used similarly to PC in order to

prioritize habitat patches by their importance in the landscape network, we will later briefly consider the comparison between PC and λ_M.

Partitioning dPC_k into three different fractions

The dPC_k values can be partitioned into three distinct fractions considering the different ways in which a certain landscape element k (patch or link) can contribute to habitat connectivity and availability in the landscape:

$$dPC_k = dPCintra_k + dPCflux_k + dPCconnector_k \qquad (4)$$

$dPCintra_k$ is the contribution of patch k in terms of intrapatch connectivity, corresponding to $a_i \times a_j$ when $i = j = k$ (a_k^2) in eq. (1), or the available habitat area (or some other relevant patch attribute) provided by the patch k itself, as related to the habitat availability concept. Links do not contribute through this fraction because they contain no habitat area. $dPCintra_k$ is fully independent of how patch k may be connected to other patches, does not depend on the dispersal distance of the focal species, and is the same even if patch k is completely isolated. This fraction is equivalent to the variation in a family of fragmentation indices that take the squared patch area as the basis for their computation, such as the area-weighted mean patch size (Turner et al. 1996, Li and Archer 1997) or the degree of coherence (Jaeger 2000).

$dPCflux_k$ corresponds to the area-weighted dispersal flux through the connections of patch k to or from all of the other patches in the landscape when k is either the starting or ending patch of that connection or flux. $dPCflux_k$ depends both on the attribute (e.g. area) of patch k (a patch with a higher attribute value produces more flux, if the rest of the factors are equal) and on its position within the landscape network. It corresponds to the sum of $a_i \times a_j \times p_{ij}^*$ (eq. 1) for each pair of patches in the landscape for which either $i = k$ or $j = k$ and $i \neq j$. This fraction is similar to the m_{ij} values for the metapopulation capacity by Hanski and Ovaskainen (2000), to the extended IFM indices in Moilanen and Nieminen (2002), or to an area-weighted version of the index by Urban and Keitt (2001), but considering the maximum product probabilities (p_{ij}^*) through connecting elements instead of the probabilities of direct dispersal between patches (p_{ij}). Links do not contribute through this fraction because they do not contain any habitat area and, thus, cannot be the destination or origin of dispersal fluxes. This fraction measures how well patch k is connected to other patches in the landscape (in terms of the amount of flux) but not how important that patch is for maintaining connectivity between the rest of the patches, which is quantified by the next fraction.

$dPCconnector_k$ is the contribution of patch or link k to the connectivity between other habitat patches, as a connecting element or stepping stone between them. This fraction depends only on the topological position of a patch or link in the landscape network. The calculation of $dPCconnector_k$ for a certain habitat patch is independent of its area or any other attribute considered (a_k). A certain patch or link k will contribute to dPC_k through $dPCconnector_k$ only when it is part of the best (maximum product probability) path for dispersal
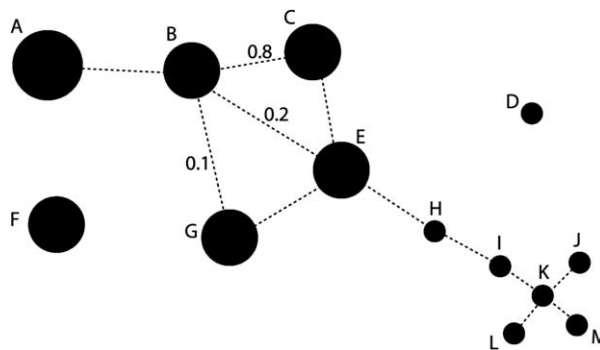

Figure 1. A simple landscape graph to illustrate the dPC_k fractions and the contribution to overall habitat availability and connectivity of different habitat patches (shown in black) and links (dashed lines). Habitat area (circle size) is the patch attribute (a_i), which corresponds to 1 area unit for patches D, H, I, J, K, L and M, 6.8 area units for patches B, C, E, F and G, and 10.5 area units for patch A. All of the links are assumed to have a direct dispersal probability ($p_{ij} = p_{ji}$) of 0.5 except for those where a different value is explicitly shown (links BC, BE and BG). All of the rest are assumed to be unconnected ($p_{ij} = 0$). The resulting values of the dPC_k fractions for each of the patches and links in this landscape graph are shown in Table 1 and 2.

between two other patches i and j (Fig. 1, Table 1, 2). $dPCconnector_k$ corresponds to a part of the sum of $a_i \times a_j \times p_{ij}^*$ (eq. 1) for each pair of patches i and j in which $i \neq k, j \neq k$ and k is part of the maximum probability path between them (p_{ij}^*). A large or small part of this sum may be lost when element k is removed from the landscape, depending on the alternative paths between the remnant patches that are available after losing k (as quantified by the decrease in p_{ij}^* that is produced by the loss of k). This fraction is measured in the same way for both patches and links and their contribution in this respect can be directly compared using $dPCconnector_k$.

$dPCintra_k$ measures intrapatch connectivity, while $dPCflux_k$ and $dPCconnector_k$ measure interpatch connectivity as related to a certain landscape element k. While a link can contribute only through $dPCconnector_k$, a certain habitat patch will be more or less important (dPC_k) due to one or more of these three fractions, depending on its intrinsic characteristics and on its topological position within the landscape network (Fig. 1, Table 1, 2). When

Table 1. Values of dPC_k (%), $dPCintra_k$ (%), $dPCflux_k$ (%) and $dPCconnector_k$ (%) for each patch in Fig. 1.

Patch	dPC_k	$dPCintra_k$	$dPCflux_k$	$dPCconnector_k$
A	35.2	13.6	21.6	0
B	43.9	5.7	25.4	12.8
C	37.9	5.7	25.5	6.7
D	0.1	0.1	0	0
E	33.9	5.7	21.2	7.0
F	5.7	5.7	0	0
G	19.1	5.7	13.4	0
H	5.1	0.1	2.5	2.5
I	3.3	0.1	1.6	1.6
J	0.7	0.1	0.6	0
K	2.5	0.1	1.1	1.3
L	0.7	0.1	0.6	0
M	0.7	0.1	0.6	0

a patch is completely isolated, it will only contribute to dPC_k through $dPCintra_k$ (patches D and F in Fig. 1). When a patch is connected, at least to some degree, to some other patches (and $a_k > 0$), it will surely contribute to dPC_k through $dPCintra_k$ and $dPCflux_k$ and, depending on the cases (topological position in the landscape network), it may also contribute through $dPCconnector_k$. Both patches and links will contribute through $dPCconnector_k$ only when they are part of the maximum product probability path between at least two habitat patches. As reported in Table 1, only six of the ten patches shown in Fig. 1 contribute through $dPCconnector_k$ (B, C, E, H, I and K), while $dPCconnector_k = 0$ for links B-E and B-G (Table 2).

The same partitioning as in eq. (4) can be expressed in terms of the absolute variation in the PC value caused by the removal of a certain landscape element k (by multiplying by $PC/100$ each of the terms in that equation):

$$\Delta PC_k = \Delta PCintra_k + \Delta PCflux_k + \Delta PCconnector_k \qquad (5)$$

Forest habitat data and analysis

To illustrate and provide insights into the behaviour, relationships and conservation implications of each dPC_k fraction, we analysed data from four different forest habitats (Table 3) in the province of Lleida (Catalonia, NE Spain), located between 41°16′N and 42°51′N and 0°19′E and 1°51′E. Lleida is a heterogeneous province with a total area of 12173 km² that covers both mountainous areas like the Pyrenees in the north (with an altitude up to 3143 m) and plains situated in the SW of the province (with altitudes below 150 m) at the eastern limit of the Ebro basin. According to the Papadakis classification, the dominant climate is Mediterranean temperate, with a temperate cold climate in the Pyrenean zones. Forests represent ca 40% of the total area of Lleida, and ca 80% are privately owned.

The four analysed habitats are comprised of patches with a wide range of sizes and have different spatial arrangements and compositional characteristics (Table 3). They are among those defined and mapped for monitoring forest biodiversity within the Third Spanish National Forest Inventory (Ministerio de Medio Ambiente 2005). The data source for the identification of the different habitat patches was the Spanish Forest Map at the scale of 1:50 000. This map, which has a minimum mapping unit of 2.5 ha,

Table 2. Values of $dPCconnector_k$ (%) for each link in Fig. 1.

Link	$dPCconnector_k$
A-B	21.6
B-C	20.8
B-E	0
B-G	0
C-E	13.1
E-G	10.0
E-H	4.8
H-I	2.8
I-K	1.9
K-J	0.6
K-M	0.6
K-L	0.6

Table 3. Main characteristics of the four analysed habitats in the province of Lleida (Catalonia, NE Spain).

Habitat	Composition	Total area (ha) (A_C)	Number of forest habitat patches	Mean patch size (ha)	Largest patch size (ha)	Mean distance to the nearest neighbour patch (m)
1	Pure forest of *Abies alba*	10509	65	163	1114	2253
2	Mixed forest of *Pinus sylvestris* and *Quercus ilex*	8339	87	96	1356	2085
3	Mixed forest of *Quercus ilex*, *Juniperus* spp. and *Buxus sempervirens*	6450	84	77	1221	2010
4	Mixed forest of *Pinus sylvestris* and *Pinus nigra*	16272	98	166	1104	1494

was developed from the interpretation of aerial photographs, combined with the information from pre-existing maps and field inventory data. The distribution and configuration of patches in each of the four habitats is shown in the Supplementary material (Fig. S1). The analyses described below were performed separately for each of the four habitats.

The area of each of the patches was used as the attribute (a_i) for the computation of PC. The direct dispersal probabilities (p_{ij}) that characterise the links were calculated by varying the dispersal abilities of a hypothetical focal species dwelling in the habitat. The median dispersal distance of that species (d, corresponding to $p_{ij} = 0.5$) was varied from 50 to 40 000 m, with 30 different values within that range. The p_{ij} values between each pair of patches were calculated from a negative exponential function of the interpatch edge-to-edge Euclidean distance matching to that median value (Bunn et al. 2000, Hanski and Ovaskainen 2000, Saura and Pascual-Hortal 2007).

The values of dPC_k and ΔPC_k and the values of the three dPC_k and ΔPC_k fractions were calculated for each of the patches and links within each habitat and for each dispersal distance by using a modified version of the Conefor Sensinode software (Saura and Torné 2009, <www.conefor.org>), in addition to the total PC and $PCnum$ values. The total absolute variations in the PC metric and the three fractions that were caused by the individual removal of each element (patches and links) in the landscape ($\Sigma\Delta PC$, $\Sigma\Delta PCintra$, $\Sigma\Delta PCflux$, and $\Sigma\Delta PCconnector$) were calculated as the sum of the ΔPC_k, $\Delta PCintra_k$, $\Delta PCflux_k$, and $\Delta PCconnector_k$ values (respectively) for each of the landscape elements. The parts of $\Sigma\Delta PCconnector$ that were due to habitat patches and to links as connecting elements in the landscape ($\Sigma\Delta PCconnector(patch)$ and $\Sigma\Delta PCconnector(link)$, respectively) were distinguished.

The relative contribution of each dPC_k fraction to the total importance of individual landscape elements (patches and links) for habitat availability and connectivity in the landscape ($\theta PCintra$, $\theta PCflux$, and $\theta PCconnector$) was calculated by dividing the sum of the importance values for all of the individual landscape elements for each fraction ($dPCintra_k$, $dPCflux_k$, and $dPCconnector_k$, respectively) by the sum of the dPC_k values for all of the landscape elements. The parts of $\theta PCconnector$ due to habitat patches ($\theta PCconnector(patch)$) and links ($\theta PCconnector(link)$) were also differentiated.

To evaluate how the prioritisation of habitat patches may differ 1) between the three dPC_k fractions, 2) between the three dPC_k fractions and the total dPC_k and 3) between the habitat patch area (attribute, a_i) and the three dPC_k fractions, we calculated Kendall's tau_b rank correlations (Arndt et al. 1999) between the values of dPC_k, $dPCintra_k$, $dPCflux_k$, $dPCconnector_k$ and patch area for all patches in each habitat.

Finally, to illustrate the conceptual and practical differences between PC and the metapopulation capacity (λ_M), we compared the prioritisation of patches provided by the three dPC_k fractions and V_k by calculating the Kendall's tau_b correlations between them in the set of 65 patches in habitat 1. We calculated PC and λ_M in the most similar way by computing both metrics from the same negative exponential function of interpatch distance and by using area as the attribute of the patches as defined for the metapopulation capacity (Hanski and Ovaskainen 2000).

Results

Absolute variations of habitat availability and dPC_k fractions

The amount of available habitat in the landscape (as measured by $PCnum$) increases with dispersal distance (d), because very mobile species are able to reach and use a larger proportion of the total habitat existing in the landscape (Fig. 2A). However, when d is large enough to connect directly and strongly each pair of habitat patches, further increases in the dispersal distance do not result in large increases in habitat availability (Fig. 2A). Obviously, larger values of $PCnum$ and of the different $\Sigma\Delta PC$ fractions are obtained for those habitats with a larger total area (A_C), such as habitat 4 (Table 3, Fig. 2). $PCnum$ has an asymptote at the value of A_C^2. The pattern of variation of $\Sigma\Delta PC$ is very similar to that described for $PCnum$ (Fig. 2A–B). $\Sigma\Delta PCintra$ is constant and independent of the dispersal distance (Fig. 2C). $\Sigma\Delta PCflux$ increases with d in a similar way to the total $\Sigma\Delta PC$, but with a more steady increase for lower d (Fig. 2D). $\Sigma\Delta PCconnector$ is at its maximum at intermediate and relatively short dispersal distances, both for the links and for the patches that act as stepping stones (Fig. 2E–F).

Relative contributions of the dPC_k fractions to total habitat availability

At short dispersal distances, $dPCintra_k$ is the fraction that makes the largest contribution to overall habitat connectivity and availability, as quantified by $\theta PCintra$ (Fig. 3). In the extreme case, when a species is unable to move any distance outside of the habitat patches ($d = 0$), the only available habitat is the one that exists within the patches where it dwells ($\theta PCintra = 100$). For a large d, the relative contribution of $dPCintra_k$ is minor and $dPCflux_k$ determines nearly all of the habitat connectivity and availability in the landscape (Fig. 3). $dPCconnector_k$, considering the role of both links and patches that function as stepping stones, has the greatest contribution ($\theta PCconnector$) at intermediate dispersal distances, being much lower either for small or large d (Fig. 3). $\theta PCflux$ tends to be greater than $\theta PCconnector$ (Fig. 3) because, for a given dispersal flux, removing the starting or ending patch will completely eliminate that flux, while the loss of an intermediate element may reduce the amount of flux between the starting and ending patches but not necessarily impede it entirely (depending on the alternative paths that are available after losing that element). While this generally occurs when it is related to the sum for all of the individual elements ($\theta PCflux$, $\theta PCconnector$) a particular patch can have a weak role as an origin or destination of dispersal fluxes (low $dPCflux_k$) but still be important as a stepping stone between other big, productive or numerous patches. This would result in $dPCconnector_k$ being larger than $dPCflux_k$ for that patch, as occurs for example for patch
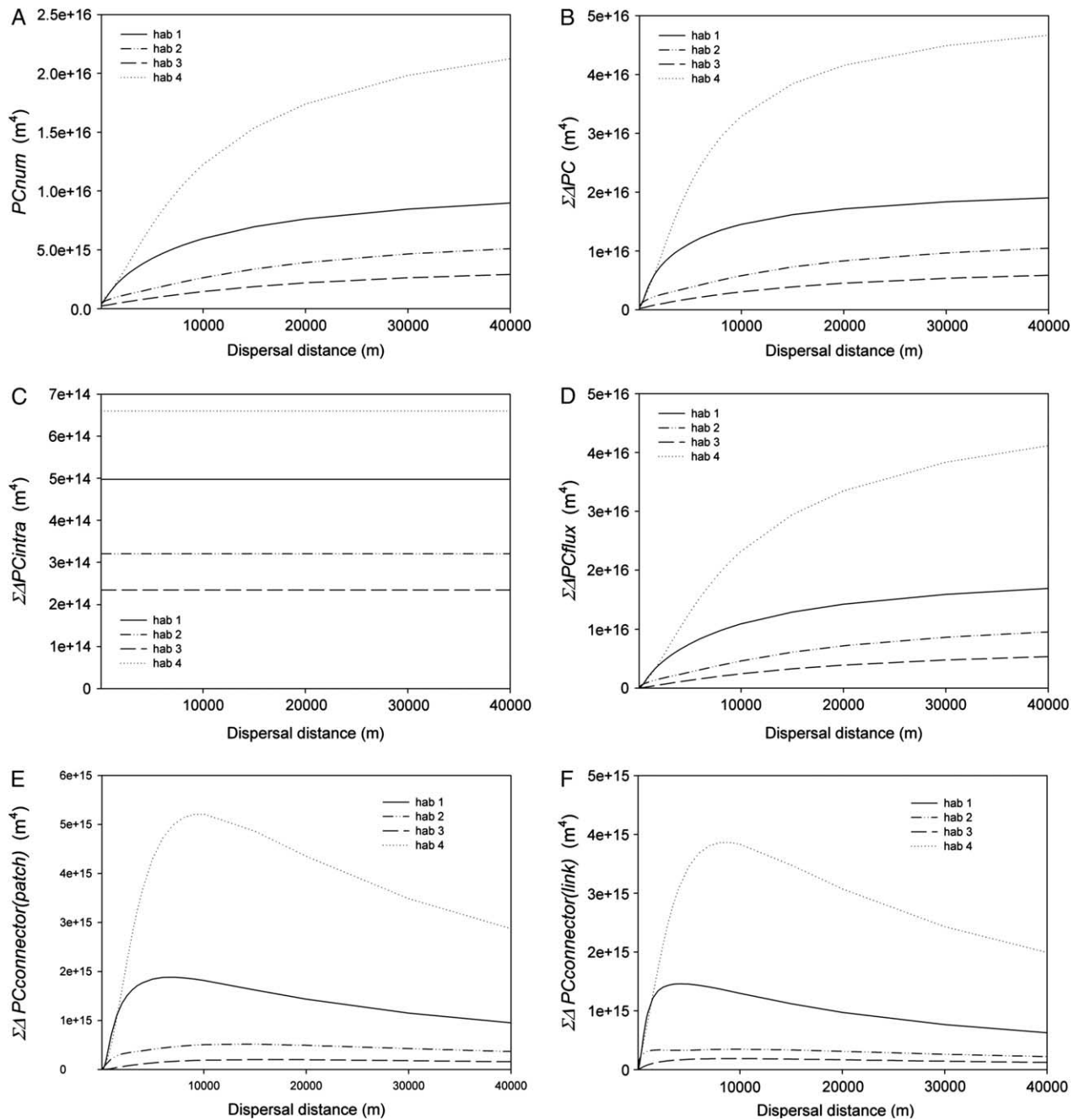
Figure 2. Overall habitat availability (*PCnum,* (A)) and total absolute variation in the *PC* metric ($\Sigma\Delta PC$, (B)) and each of the three fractions ($\Sigma\Delta PCintra$ (C), $\Sigma\Delta PCflux$ (D) and $\Sigma\Delta PCconnector$ (E–F for patches and links respectively)) caused by the individual removal of all of the elements (patches and links) in the landscape, as a function of the median dispersal distance for the four habitats.

K in Fig. 1 (Table 1). $\theta PCconnector(link)$ was higher than $\theta PCconnector(patch)$ at a low d, while the reverse occurred for a larger d (Fig. 3).

Rank correlations between the dPC_k fractions and patch area

The values of $dPCintra_k$ had a perfect rank correlation ($tau_b = 1$) with patch area independent of d (Fig. 4). According to this fraction, the most important patches are simply those with the largest attribute values (e.g. habitat area).

The rank correlation of $dPCflux_k$ with patch area increased steadily with d, being very low for small d and almost equal to 1 for the largest d (Fig. 4). When mobility is greatly restricted, the patches that receive more flux are not the biggest ones, but are those that are near other habitat patches (small tau_b). For large dispersal abilities, the critical patches according to this fraction coincide very much with the largest habitat patches. Because all of the patches can be reached from each other with a high probability (p^*_{ij} near to 1), their attribute (e.g. habitat area) is the only factor that makes a difference in the flux they receive.
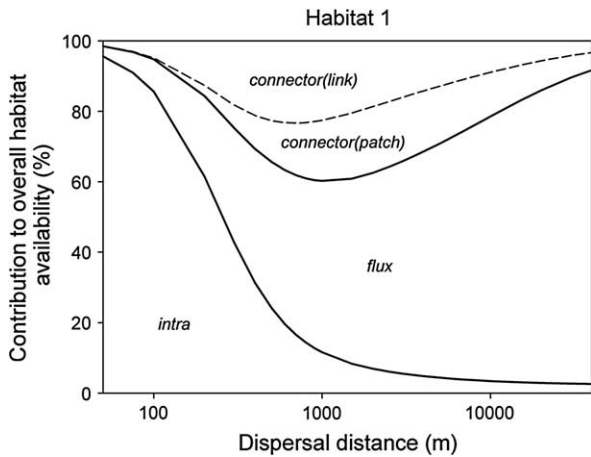
Figure 3. Relative contribution of each dPC_k fraction ($\theta PCintra$, $\theta PCflux$, $\theta PCconnector$) to the total importance of individual landscape elements (patches and links) for habitat availability and connectivity in the landscape, as a function of the median dispersal distance for habitat 1. $\theta PCconnector$ is divided between the contribution of habitat patches ($\theta PCconnector(patch)$) and links ($\theta PCconnector(link)$) in the landscape. Note that the distance values (x axis) are shown in a logarithmic scale. Similar results are found for the other three habitats, as shown in the Supplementary material (Fig. S2).

$dPCconnector_k$ was in all the cases the fraction with the lowest rank correlation with patch area, and tau_b remained low even for large d (Fig. 4). $dPCconnector_k$ measures an aspect of the landscape pattern that is largely independent of the area-based prioritisation. There is some degree of correlation (but not a high one) because when a patch covers a larger area, it is more likely to fall between a larger number of habitat patches and to act as a stepping stone between them. The critical patches that are determined by this fraction may largely differ from those selected based only on their intrinsic habitat attributes.
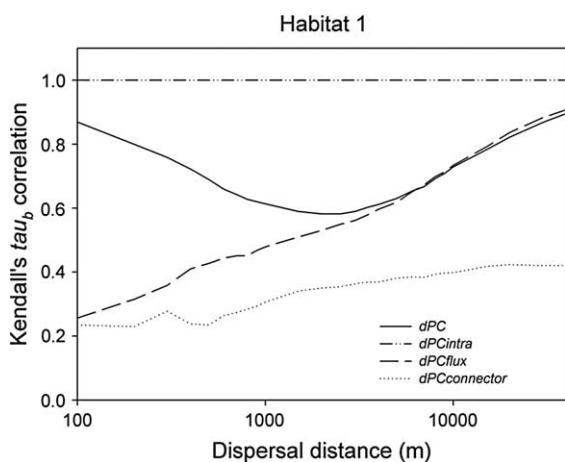
The rank correlation of dPC_k with patch area was high at either very low or large dispersal distances, and low for intermediate d (Fig. 4). This is a result of the combination of the correlation patterns for the different fractions just described.

The correlation between dPC_k and $dPCflux_k$ was low for small dispersal distances but increased for large d (Fig. 5). For highly mobile species, $dPCflux_k$ contributed almost all of the total dPC_k (Fig. 3). Therefore, the prioritisations of the patches provided by dPC_k and $dPCflux_k$ tended to coincide (tau_b close to 1). The rank correlations of $dPCconnector_k$ with either dPC_k or $dPCflux_k$ were low for all d (Fig. 5). This highlights the uniqueness of $dPCconnector_k$ as a fraction that measures an aspect that is largely independent from the other network or habitat characteristics.

Rank correlations between the dPC_k fractions and the metapopulation capacity (V_k)

When the dispersal abilities were moderate, the prioritization of patches by their importance for connectivity was considerably different according to the metapopulation capacity (V_k) and the PC index (dPC_k) (Table 4). For low dispersal distances ($d = 100$ m in Table 4) many patches had an almost negligible value according to V_k, while for PC they still had some importance depending on their intrapatch connectivity. The rank correlations between V_k and dPC_k increased with increasing d (Table 4), yielding similar prioritizations for species with very large dispersal abilities relative to the habitat pattern. For example, $tau_b = 0.861$ when the median dispersal distance was about five times larger than the mean nearest neighbour distance between patches in habitat 1 (Table 3). The value of a patch for the metapopulation capacity (V_k) showed low correlations with $dPCconnector_k$ independently of d, while the correlations of V_k with $dPCintra_k$ and $dPCflux_k$ increased
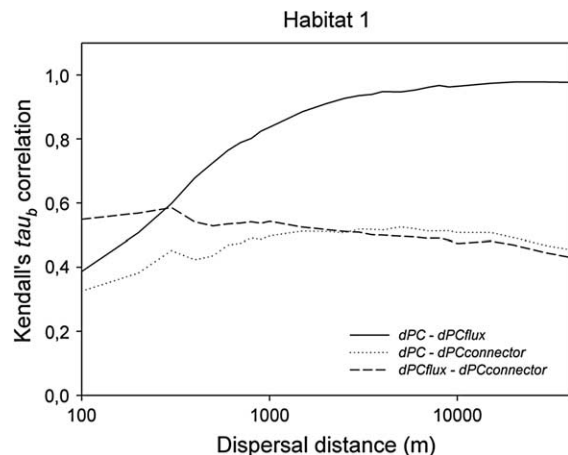

Figure 4. Kendall's rank correlation (tau_b) between patch habitat area (a_i) and the patch importance according to PC (dPC_k) and each of its three fractions ($dPCintra_k$, $dPCflux_k$, $dPCconnector_k$), as a function of the median dispersal distance for habitat 1. Note that the distance values (x axis) are shown in a logarithmic scale. Similar correlation patterns are found for the other three habitats, as shown in the Supplementary material (Fig. S3).

Figure 5. Kendall's rank correlations (tau_b) between dPC_k, $dPCflux_k$ and $dPCconnector_k$, as a function of the median dispersal distance for habitat 1. The rank correlations with $dPCintra_k$ are the same as those with patch area (Fig. 4), and are therefore not shown here. Note that the distance values (x axis) are shown in a logarithmic scale. Similar correlation patterns are found for the other three habitats, as shown in the Supplementary material (Fig. S4).

Table 4. Kendall's rank correlation (tau_b) between patch importance for the metapopulation capacity (V_k) and the importance for PC (dPC_k) and each of its three fractions ($dPCintra_k$, $dPCflux_k$, $dPCconnector_k$) for the 65 patches in habitat 1 and three median dispersal distances representative of the range of distances in which each of the dPC_k fractions is largest, as shown in Fig. 3 (100 m for $dPCintra_k$, 1000 m for $dPCconnector_k$ and 10 000 m for $dPCflux_k$).

Median dispersal distance (m)	dPC_k	$dPCintra_k$	$dPCflux_k$	$dPCconnector_k$
100	0.343	0.246	0.397	0.460
1000	0.621	0.328	0.666	0.347
10 000	0.861	0.616	0.879	0.450

with larger d, especially the latter (Table 4). $dPCflux_k$ was the dPC_k fraction that had the highest correlations with V_k (Table 4).

Discussion

Relative contribution of the three fractions to overall habitat availability for different species traits

Habitat patches have different roles within the landscape network. They not only serve as sites for shelter, foraging and breeding, but also produce (or receive) dispersal fluxes to (or from) other habitat patches, and function as stepping stones that, even when they are not the final destination of the dispersal fluxes, facilitate dispersal between other patches. Within the same landscape and for the same focal species, different patches may play different roles depending on their topological position and intrinsic habitat characteristics, as quantified by the three dPC_k fractions. These roles do not always coincide in the same critical patches, especially when dispersal abilities are not too large (Fig. 4–5). This highlights the need for a separate quantification of these fractions for an adequate understanding of the functions of landscape elements as derived from the habitat availability concept.

The relative contribution of each of these roles (and dPC_k fractions) to the overall habitat availability and connectivity depends on species traits (Fig. 3). For species with low mobility, the habitat area (or other relevant attribute) within the patches where they dwell ($\theta PCintra$) is much more important than the area made available through dispersal to other habitat patches (which may be weakly interconnected and thus difficult to reach). On the contrary, for species with large dispersal abilities the amount of habitat in a particular patch is irrelevant to determine the total available habitat; the species can easily and directly reach many other habitat areas without needing intermediate stepping stones or connecting elements to facilitate this dispersal ($\theta PCflux$ dominates, low $\theta PCintra$ and $\theta PCconnector$) (Fig. 3). Habitat patches are not used as discrete or isolated pieces, but as part of a functionally continuous habitat scattered throughout the landscape.

At intermediate dispersal distances (relative to the landscape pattern) is when the loss of an individual patch or corridor can be more critical and can cause a significant drop in the ability of a species to reach other high-quality or large habitat patches, as indicated by a large $\theta PCconnector$ (Fig. 3). In this case, organisms cannot move directly to every other patch in the landscape but can more easily disperse to a few other nearer habitat patches that

serve as stepping stones and allow further dispersal to a greater amount of available habitat (Keitt et al. 1997).

The relative contribution of each of the dPC_k fractions may also depend on the temporal scale and the different ranges of movements considered, from daily or seasonal foraging movements to natal dispersal and longer-distance movements. Long-distance movements are less frequent but they can contribute significantly to genetic exchange at the landscape and regional scales and to the expansion of ranges across generations (Chetkiewicz et al. 2006). In the short term, the total amount of habitat often may be a more important determinant of the status and persistence of species than the spatial pattern or configuration of habitats within the landscape (Trzcinski et al. 1999, Fahrig 2003, Bennett et al. 2006), while the latter may be the key to allow for the expansion, adaptation and persistence of species at broader temporal and spatial scales.

We did not find any threshold or sharp variation in connectivity as a function of dispersal distance, as quantified through PC and the dPC_k fractions (Fig. 2, 3). There is a range of distances in which, for example, the stepping stone effects ($\theta PCconnector$) are much more important, but we did not find any sudden transition from a connected to an unconnected pattern as in the studies by Keitt et al. (1997) or Neel (2008). These latter studies were, in part, based on metrics such as the correlation length or the graph diameter that present several limitations for the prioritisation of patches for conservation (Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007).

Connectivity and conservation alternatives. Does topology matter? Towards integrated and comparable measures of the various contributions of patches and links

Maintaining connectivity is not the only response to habitat loss and fragmentation, but is a part of a broader toolbox of options to respond to landscape changes (Bennett et al. 2006). In particular, land managers may select sites for conservation according to at least two different criteria. First (criterion A), they can select the best sites individually, according to their intrinsic characteristics (habitat area, quality, etc.), and ignore issues related to interpatch connectivity and the topology of the landscape network. Alternatively (criterion B), they can use some method that selects sites in order to enhance the connectivity and spatial cohesion of the network (McDonnell et al. 2002, Cabeza 2003, Araújo et al. 2004).

Integrating connectivity considerations in the reserve selection process may lead to the exclusion of some of the best individual habitat sites (A) to allow the inclusion of some other sites that are per se poor or suboptimal but

enhance the connectivity between the rest of the sites (Cabeza 2003). Therefore, in any conservation plan there is a trade-off between the relative importance assigned to interpatch connectivity (topology) on the one hand and the intrinsic habitat patch characteristics on the other. One of the major limitations of many of the current approaches related to connectivity is that managers should decide a priori if interpatch connectivity is a relevant issue or a key threat for their conservation problems. If not, they may decide that selecting the best and largest patches (criterion A) is sufficient or even more appropriate (Ferrari et al. 2007). If managers decide to incorporate connectivity considerations, they should further decide how to combine and weight the outcomes of the two different possible plans (A and B). This might be problematic and subjective, potentially leading to some arbitrary decisions on these weights in the final conservation plan (McDonnell et al. 2002, Williams and Araújo 2002, Cabeza 2003, Nicholson et al. 2006).

All of these issues are objectively and naturally solved through the integrated view of the landscape network that the habitat availability metrics provide. Habitat availability metrics (e.g. PC) jointly quantify and consider both alternatives (A and B) within the same background and units of measurement. There is no risk of overweighting connectivity issues in the conservation plan by using PC. If interpatch connectivity is not a real threat for conservation then dPC_k will prioritise the habitat patches simply by their intrinsic habitat characteristics as in criterion A. This occurs both for very small or very large dispersal distances, as reflected in the high rank correlation between dPC_k and patch attribute (Fig. 4). For species with very low mobility and/or very dispersed and fragmented habitat patterns, the connectivity between habitat patches is already lost or is too weak to provide a worthy contribution to habitat availability. In this case, the scarce conservation funding may be better focused on conserving the best and largest existing habitat patches independently of their topological position within the landscape network, assuming that they are still able to maintain a viable population by themselves. For species with very large dispersal abilities and/or continuous habitat patterns, investing funds in maintaining individual connectors or stepping stones may not be efficient because the organisms do not depend on them and can easily and directly reach any other habitat site in the landscape.

If connectivity is important, dPC_k will itself provide the adequate weight to each alternative (A and B) in a single integrated approach resulting from the habitat availability concept. The stepping stones and connecting elements become more critical for species with intermediate mobility (relative to the habitat spatial pattern). In this case, the key sites for habitat availability can be very different from the best sites as considered individually (criterion A). Some rank correlation between patch area and dPC_k may still exist, because if two patches are equally important for interpatch connectivity or have similar topological positions within the landscape network, the biggest one would be preferred for conservation. However, this correlation is not high (Fig. 4). Ignoring topology (interpatch connectivity) in the conservation plan will produce poor results for the maintenance of overall habitat availability and it is not justified in this case. It is at these intermediate dispersal distances when the configuration characteristics, and not just the area-related effects, are more critical for conservation.

Ferrari et al. (2007) stated that when the largest patch comprises most of the total habitat area, a detailed network connectivity analysis that assigns importance to specific patches is generally unnecessary because it would identify the largest patch as the most important regardless of network configuration. Indeed, this is the case with PC and habitat availability metrics in general. However, this is not a problem for the use of these metrics, but rather one of their main advantages and contributions. They do not require connectivity to be treated as a separate part of the conservation problem based on a previous subjective judgement or a threshold value of a particular metric. On the contrary, they jointly integrate the different roles of the habitat patches and links with a common basis that can be treated all together (dPC_k) or separated into their different fractions within the same analysis and conservation plan. As stated by Kareiva (2006) "one valuable extension to our theories and models will occur when connectivity is not treated as a separate issue but instead becomes one of the many alternative conservation investments that can be evaluated with a common currency". We believe that the concepts and quantitative approach presented here are a relevant contribution towards this end from the graph-theoretic perspective.

The PC fractions presented here are not the first attempt to separately quantify the different roles of a habitat patch within the landscape. Apart from the contributions from metapopulation theory (Ovaskainen and Hanski 2003, Nicholson et al. 2006), various authors have proposed different sets of metrics from the graph-theoretic perspective, as summarised in Table 5. These sets contain from two to four different metrics, and include at least one metric intended to capture the relevant topological characteristics in the landscape network (Table 5). Most sets also include a metric related to the area-based aspects of conservation or to other intrinsic habitat characteristics, such as habitat quality or local population size. However, the metrics in these sets come from different backgrounds, such as graph theory, structural spatial metrics from landscape ecology, simplifications or surrogates for metapopulation variables, etc. In addition, some of the metrics are unitless while others correspond to areas, distances, number of neighbours or links, etc., having very different ranges of variation (Table 5). As noted by Cabeza (2003), because different factors are measured in different units there is no uniquely justifiable way of weighting them for compensation against one another. Choosing the desired level of clustering in a spatial reserve design often becomes a subjective step. Indeed, these sets of metrics are very difficult to combine and compare, and they lack of a unifying conceptual framework for their joint analysis. This framework is provided, both for the habitat patches and links, by the habitat availability metrics and their fractions as has been described here.

Table 5. Sets of metrics proposed in previous graph-based landscape analyses to quantify the different roles of habitat patches in the landscape and the different aspects related to connectivity.

	Metric	Description	Units
Bunn et al. (2000), Urban and Keitt (2001)	Recruitment	Habitat area (or quality-weighted habitat area).	Area
	Dispersal flux	Dispersal away from the natal patch, calculated as the product of patch area (or quality-weighted area) by the direct dispersal probability p_{ij}.	Area
	Graph diameter	"Longest shortest path" between the two most distant patches. Total inter-patch distance an organism needs to traverse to span the largest cluster.	Distance
Jordán et al. (2003)	Degree	Number of neighbouring patches directly connected to a patch.	No. neighbours
	Clustering coefficient	Average fraction of the node's neighbours that are also neighbours with each other.	Unitless
	Topographical distance	Number of links between two nodes combined with the permeability values of the links. A higher permeability means smaller topographical distance.	Permeability values
	Maximal connected local population size	Sum of the patch quality (as an estimate of local population size) of all patches connected to the major component of the landscape.	Habitat quality/population size
Ferrari et al. (2007)	Graph diameter	See above.	Distance
	F index	Proportion of habitat in the largest contiguous patch relative to the proportion of habitat found in the largest cluster.	Unitless
Jordán et al. (2007)	Degree	Number of neighbouring patches directly connected to a patch.	No. neighbours
	Topological/topographical distance	The topological distance of two nodes, i and j, is the minimum number of links forming a path through which i is reachable from j in a network. See above for the topographical distance.	No. links/permeability values
	Metapopulation size	Sum of the patch quality (as an estimate of local population size) of all patches connected to the major component of the landscape.	Habitat quality/population size
Minor and Urban (2007)	Quality-weighted area	Patch area multiplied by patch quality.	Area
	Degree	See above.	No. neighbours
	Influx/outflux	Same as dispersal flux described above but differentiating from incoming and outgoing fluxes from a patch.	Area
	Betweenness centrality	Frequency with which a patch falls between other pairs of patches in the network. It is calculated by finding the shortest paths between every pair of patches in the landscape and then counting the number of times those paths cross each node (Bodin and Norberg 2007).	No. paths

Measuring stepping stone effects

The patches and links that are critical as stepping stones or connecting elements between other patches can be adequately identified through $dPCconnector_k$. Other metrics have been previously proposed for these purposes, mainly the change in graph diameter after a patch removal (Bunn et al. 2000, Urban and Keitt 2001, Ferrari et al. 2007), and the betweenness centrality (Bodin and Norberg 2007, Minor and Urban 2007, Estrada and Bodin 2008), described in Table 5.

However, Pascual-Hortal and Saura (2006) showed that the diameter fails to identify and prioritise relevant landscape elements (patches and links) for connectivity and that it presents variable and inconsistent reactions to various spatial changes, which is not the case for PC (Saura and Pascual-Hortal 2007). Bodin and Norberg (2007) also concluded that the diameter lacks the ability to adequately assess the importance of patches unless they are the only connectors between otherwise disconnected components.

There are also some relevant differences between $dPCconnector_k$ and betweenness centrality in terms of prioritizing patches. BC is a purely topological metric that only counts the frequency with which a patch falls within the shortest paths between other patches. It does not take into account the size or habitat quality (or other relevant patch attribute) of the patches that are connected through the shortest paths. BC may identify a patch falling between many small and poor-quality habitat patches (e.g. patch K in Fig. 1) as more important than a patch that is a key stepping stone between a few large or optimal-habitat patches that account for most of the flux and total habitat area in the landscape (e.g. patch B in Fig. 1). Although the computation of $dPCconnector_k$ for a certain patch is independent of the attribute of that patch, it still takes into account the attributes of the patches that are connected to it, according to the habitat availability concept and the good properties and prioritisation abilities that derive from it.

Differences between PC and the metapopulation capacity

There are two fundamental conceptual differences between PC and the metapopulation capacity (λ_M). First, λ_M does

not consider a patch itself as a space where connectivity occurs; it does not measure habitat availability at the landscape scale in the way that PC or IIC do. While for PC the case $i = j$ is computed in the same way as for any other pair of patches, in the metapopulation capacity $m_{ij} = 0$ if $i = j$. This has several key implications for the final results obtained from these metrics. For example, any isolated patch (such as F and D in Fig. 1) contributes to PC (through the $dPCintra_k$ fraction) but not to λ_M. In particular, if patch F (Fig. 1) was large enough, PC would identify this as the most important patch, because F itself may eventually comprise more connected area than the rest of the patches in the landscape together, no matter how well connected they might be. The value of a particular patch for the metapopulation capacity depends on the colonization events that it may receive or generate; if a patch is isolated it will have no value for λ_M, no matter how big it is. For these reasons, a fraction such as $dPCintra_k$ cannot be obtained from λ_M. A species may persist in the landscape as a single viable population in a single large or high-quality patch. However, this is not evaluated by λ_M, which deals only with the possibility of persistence of a species as a metapopulation (various differentiated populations in separated habitat patches throughout the landscape).

The second conceptual difference is that λ_M is computed from the direct dispersal probabilities (p_{ij}), while PC is computed from the maximum product probabilities (p_{ij}^*) that take into account the connecting elements or stepping stones available for movement within the landscape network. This is an important characteristic that provides relevant advantages to PC and requires most of the computational time for its calculation. The metapopulation capacity does not account for any stepping stone effects and does not specifically quantify the role of patches as connecting elements between other habitat areas. A fraction such as $dPCconnector_k$ cannot be obtained from λ_M.

In summary, two of the three fractions that can be partitioned from PC cannot be obtained from and are not considered by λ_M. Only one of the three fractions ($dPCflux_k$) is similar to the metapopulation capacity, but with the difference that $dPCflux_k$ is computed from the maximum product probabilities (p_{ij}^*) and not from the direct dispersal probabilities (p_{ij}).

These conceptual and analytical differences arise when comparing the practical prioritization of patches resulting from λ_M and from the dPC_k fractions, as done for habitat 1 (Table 4). A considerably different prioritization is provided by λ_M and $dPCconnector_k$, especially when the connecting elements have a large impact on total habitat availability. This occurs at a dispersal distance of ca 1000 m for this habitat 1 (Fig. 3). Thus, $dPCconnector_k$ and λ_M measure very different aspects of the landscape mosaic. In the same way, when d is small and the $dPCintra_k$ fraction dominates, the most critical patches identified by λ_M tend to diverge from those identified by $dPCintra_k$ or dPC_k. When the dispersal abilities are very large ($dPCflux_k$ is the dominant fraction), λ_M, $dPCflux_k$ and dPC_k tend to prioritize patches in the same way. However, at these large dispersal distances, dPC_k is itself more strongly correlated with the intrinsic habitat characteristics, such as habitat patch area (Fig. 4). In this case, the results of a connectivity analysis of this kind

will tend to coincide with the simpler decision of conserving the best habitat sites independently of interpatch connectivity (criterion A), as discussed above.

PC and the metapopulation capacity have important conceptual differences and non-overlapping scopes of application. Depending on the needs and objectives of the analysis, PC or λ_M may be used, or they may even be combined to gain from the complementary insights that they can provide. Apart from the differences described above, it should be noted that PC is not suited to evaluate a) whether a species will be able to persist in a certain fragmented landscape and temporal horizon, or b) the spatial and temporal dynamics of the populations (colonization and extinction events, demographic growth, etc.). If these are the objective of a connectivity analysis, λ_M or some other more complex metapopulation models should be used instead of PC and graph-based metrics in general. In addition, we recognise that spatially explicit metapopulation models can also be used to avoid arbitrary weightings between reserve size and configuration in conservation planning (Nicholson et al. 2006), to characterise the different roles of the habitat patches depending on the properties of the landscape and of the species, and to compare and rank networks in terms of their effect on metapopulation survival (Frank and Wissel 2002, Ovaskainen and Hanski 2003). However, some of these metapopulation models are usually more biologically detailed and more difficult to parameterise and to apply to large-scale planning problems than the graph-based habitat availability metrics here described. As stated by Calabrese and Fagan (2004), graph metrics may possess the greatest benefit-to-effort ratio for conservation problems that require the characterisation of connectivity at large scales, due to their ability to provide a detailed picture of connectivity with relatively modest data requirements. Minor and Urban (2007) concluded that graph theory may be a suitable and possibly preferable alternative to spatially explicit population models for species conservation in heterogeneous landscapes. They showed that, in some cases, graph theory can make similar predictions to spatially explicit population models, and may provide additional insights not available from the latter.

Scope of application and further research

We have shown how the habitat availability metrics and their partitioning offer an integrated view of the roles of habitat patches and links in the landscape network and represent a significant advance and a new perspective in the analysis of landscape connectivity. We have illustrated the behaviour and implications of the different fractions through a relatively simple data set and dispersal model to allow for intensive calculations and a broader view of the related concepts. However, the same concepts, metrics and partitioning can be applied to other conservation case studies with more biological and species-specific information. In fact, one of the main strengths of these habitat availability metrics and the landscape graph perspective is their flexibility and adaptability to different degrees of biological and spatial detail. They can accommodate

additional and more detailed data but they do not require them; they are still operational with sparse data. For instance, we could consider patch attributes other than patch area, such as habitat quality, or the area to the power of a coefficient typically ranging from 0.1 to 0.5 for butterflies (see Moilanen and Nieminen (2002) and references therein), which allows considering an appropriate scaling of emigration and immigration as a function of patch size. Similarly, the probabilities of dispersal may be also quantified through effective (least-cost) distances or their modification to account for multiple pathways in the landscape (McRae et al. 2008), or through actual movement data derived from radiotracking or mark-release-recapture experiments (Schadt et al. 2002, Chetkiewicz et al. 2006). As noted by Minor and Urban (2008), although graph theory does not require knowledge of behaviour, fecundity, or mortality parameters, these data can be incorporated and used to create an ecologically rich graph model.

We recognise that the graph-based habitat availability metrics and the relative contribution of the different fractions will require further empirical validation, refinement and calibration for specific species, in order to evaluate their correlation with descriptors of population dynamics such as colonisation or extinction events, population sizes, etc., and this is part of our ongoing research. Indeed, it would be difficult to perform a full validation comprising patch-removal experiments and tracking the distribution and movement of individuals before and after that removal at sufficiently large temporal and spatial scales. However, significant advances in this validation can be made through the analysis of colonisation events and multi-temporal data on species occurrence, as well as by analysing genetic data at the landscape scale to assess the long-term effects of connectivity. Neel (2008) reported a significant recent step in this direction. She analyzed the habitat patches of *Astragalus albens* in the San Bernardino Mountains (USA). The patch prioritization measured by the *IIC* habitat availability metric presented the highest significant rank correlation with three of the various genetic diversity statistics in the habitat patches, among a set of area and connectivity metrics calculated for various dispersal distances.

It should also be noted that *PC* is not the only possible habitat availability metric. The same partitioning that has been presented here can also be applied to *IIC* or to other metrics that may be developed within this conceptual perspective, fitting the specific needs of particular conservation objectives or species traits, as derived from empirical data feeding and calibrating the landscape metrics and graphs. On the other hand, the use of a metric like *PC* or *IIC* and its different fractions, despite their advantages, should not preclude the use of other network metrics that are also valuable and can provide complementary descriptive information on the landscape pattern and the network configuration.

Conservationists have long debated whether a single large reserve or several small reserves having the same total area (SLOSS) is preferable for population persistence. All other factors being equal, *PC* will tend to prioritize a single large reserve, if the small reserves are not too well connected, or consider both solutions as equally adequate if the small reserves are maximally connected. However, this does not account for the effects of extinctions that result from spatially correlated or contagious disturbances. Such effects may reduce the relative value of habitat fragments that are located in tight clusters (which may be at a risk of a mass extinction) in comparison with a higher degree of habitat spreading (Hanski 1989). Kallimanis et al. (2005) concluded that in the face of random or fine-scale disturbance, population viability is highest in large blocks of habitat. The finely subdivided habitat of a several-small reserve strategy may better maintain populations of a focal species when highly aggregated disturbances dominate. These effects are not captured by the *PC* index as here presented but they should be considered in further developments of the habitat availability perspective and in the final conservation plans when appropriate. Our conceptual perspective may also be broadened to incorporate explicitly the habitat and land cover changes that result from climate change scenarios in order to favour the long-term persistence of species in the landscape networks (Araújo et al. 2004). Finally, our approach can be extended easily to the conservation of multiple species and to the analysis of source-sink dynamics. The approach also may be helpful in cases involving asymmetric dispersal (directed graphs), such as topography or wind-driven connectivity (Schooley and Wiens 2003), or fish population dynamics in river networks, for which graph theory and directed network metrics have been recommended as an attractive analytical tool (Schick and Lindley 2007).

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Ecography
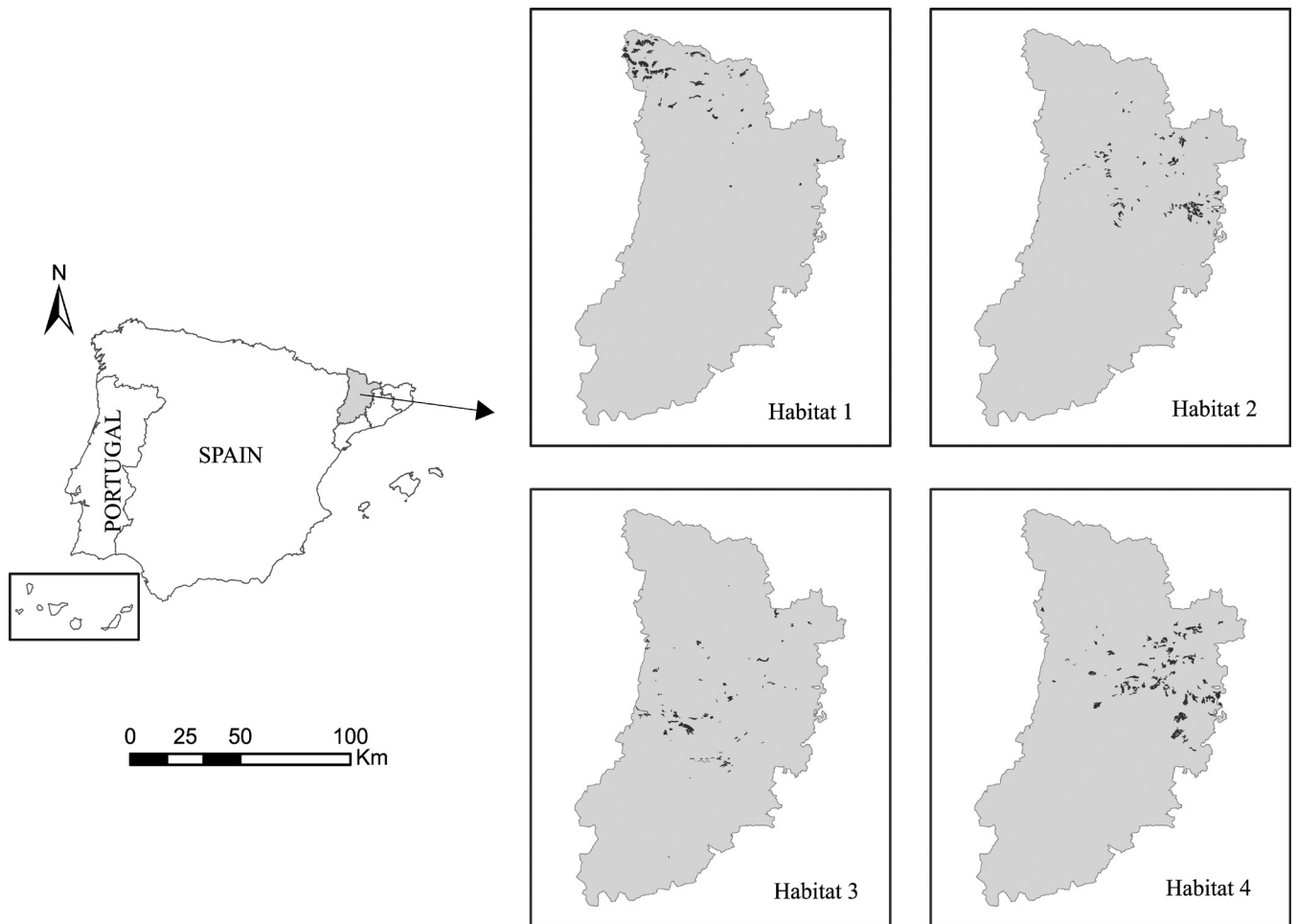
Supplementary material

Figure S1. Distribution and configuration of the four analysed forest habitats in the province of Lleida (Catalonia, NE Spain).
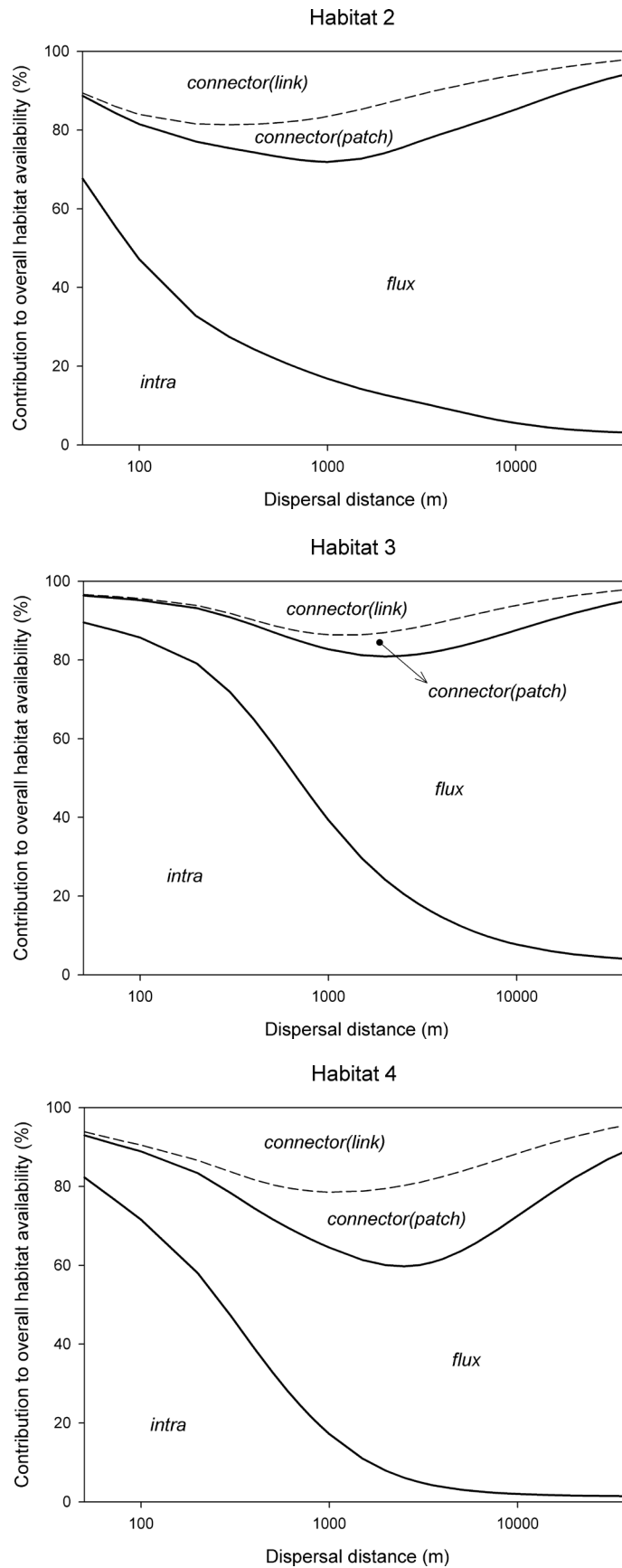
Figure S2. Relative contribution of each dPC_k fraction ($\theta PCintra$, $\theta PCflux$, $\theta PCconnector$) to the total importance of individual land-scape elements (patches and links) for habitat availability and connectivity in the landscape, as a function of the median dispersal distance for habitats 2, 3 and 4. $\theta PCconnector$ is divided between the contribution of habitat patches ($\theta PCconnector(patch)$) and links ($\theta PCconnector(link)$) in the landscape. Note that the distance values (x axis) are shown in a logarithmic scale.
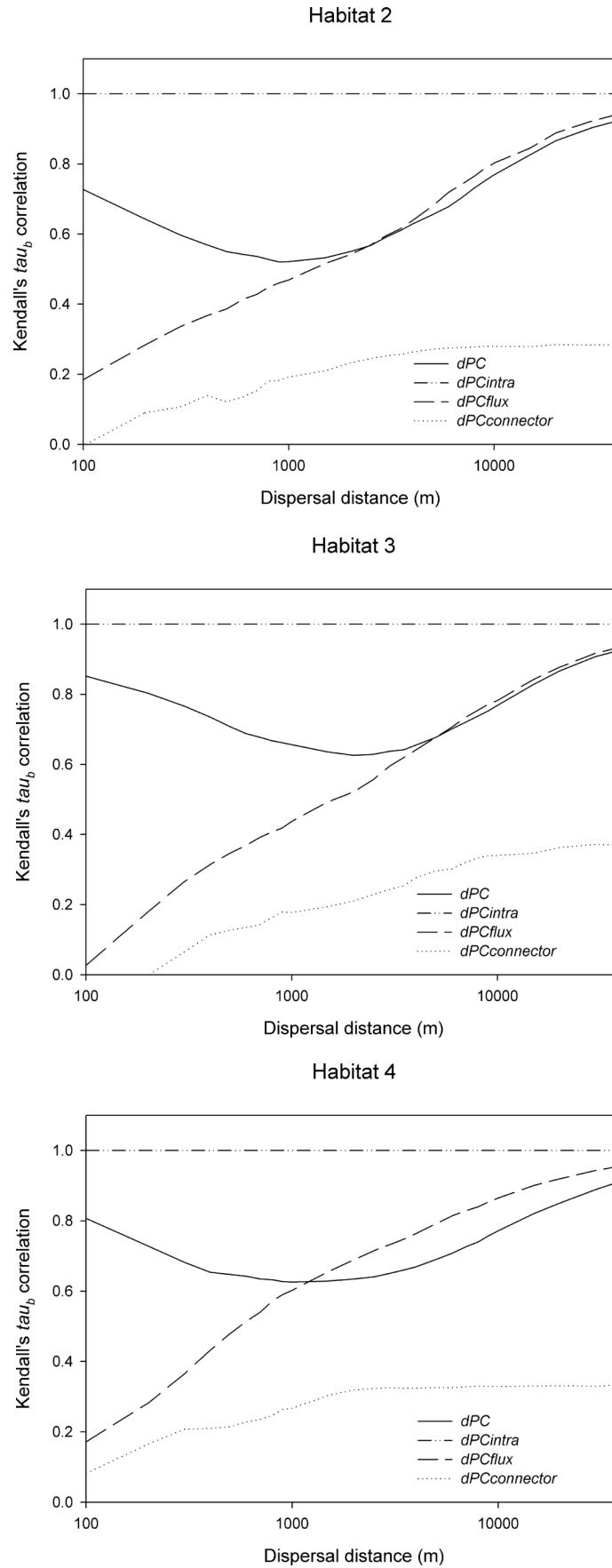
Habitat 2

Habitat 3

Habitat 4

Figure S3. Kendall's rank correlation (tau_b) between patch habitat area (a_i) and the patch importance according to PC (dPC_k) and each of its three fractions ($dPCintra_k$, $dPCflux_k$, $dPCconnector_k$), as a function of the median dispersal distance for habitats 2, 3 and 4. Note that the distance values (x axis) are shown in a logarithmic scale.
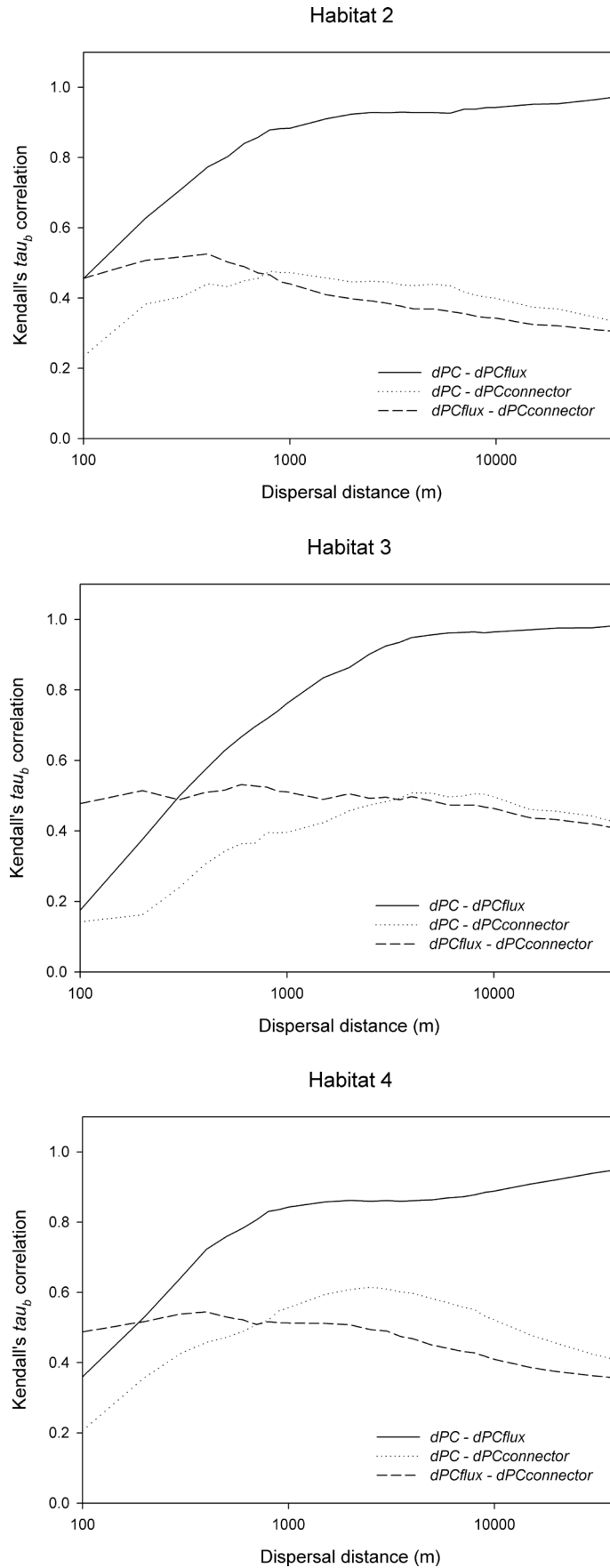
Figure S4. Kendall's rank correlations (tau_b) between dPC_k, $dPCflux_k$ and $dPCconnector_k$, as a function of the median dispersal distance for habitats 2, 3 and 4. The rank correlations with $dPCintra_k$ are the same as those with patch area (Fig. S3), and are therefore not shown here. Note that the distance values (x axis) are shown in a logarithmic scale.