



HAL
open science

Prioritization of habitat patches for landscape connectivity conservation differs between least-cost and resistance distances

C. Avon, Laurent Bergès

► **To cite this version:**

C. Avon, Laurent Bergès. Prioritization of habitat patches for landscape connectivity conservation differs between least-cost and resistance distances. *Landscape Ecology*, 2016, 31 (7), pp.1551-1565. 10.1007/s10980-015-0336-8 . hal-01393253

HAL Id: hal-01393253

<https://hal.science/hal-01393253v1>

Submitted on 7 Nov 2016

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title page

Prioritization of habitat patches for landscape connectivity conservation differs between
least-cost and resistance distances

Catherine Avon^{1*}, Laurent Bergès¹

* Corresponding author e-mail: catherine.avon@hotmail.fr

¹UR EMAX, Irstea, 3275 Route Cézanne, CS 40061, F-13182 Aix-en-Provence, France

Date of manuscript draft: 07/07/15

Word count (ms revised 2°, December 2015): 6579 (without Supporting Material)

1 **Abstract**

2 Context. Methods quantifying habitat patch importance for maintaining habitat network

3 connectivity have been emphasized in helping to prioritize conservation actions. Functional

4 connectivity is accepted as depending on landscape resistance, and several measures of

5 functional inter-patch distance have been designed. However, how the inter-patch distance,

6 i.e. based on least-cost path or multiple paths, influences the identification of key habitat

7 patches has not been explored.

8 Objectives. We compared the prioritization of habitat patches according to least-cost

9 distance (LCD) and resistance distance (RD), using common binary and probabilistic

10 connectivity metrics.

11 Methods. Our comparison was based on a generic functional group of forest mammals with

12 different dispersal distances, and was applied to two landscapes differing in their spatial

13 extent and fragmentation level.

14 Results. We found that habitat patch prioritization did not depend on distance type when

15 considering the role of patch as contributing to dispersal fluxes. However, the role of patch

16 as a connector facilitating dispersal might be overestimated by LCD-based indices compared

17 with RD for short- and medium-distance dispersal. In particular, when prioritization was

18 based on dispersal probability, the consideration of alternatives routes identified the

19 connectors that probably provided functional connectivity for species in the long term.

20 However, the use of LCD might help identify landscape areas that need critical restoration to

21 improve individual dispersal.

22 Conclusions. Our results provide new insights about the way that inter-patch distance is

23 viewed changes the evaluation of functional connectivity. Accordingly, prioritization

24 methods should be carefully selected according to assumptions about population

25 functioning and conservation aims.

26

27 **Keywords.** habitat network connectivity; graph theory; connectivity indices; least-cost path;

28 resistance distance; circuit theory; landscape resistance; species dispersal; landscape

29 fragmentation; habitat patch importance

30 Introduction

31 Landscape connectivity is accepted as being crucial for biodiversity conservation, because
32 land-use changes and habitat fragmentation per se can dramatically damage species'
33 habitats and species' dispersal. The way a landscape allows or impedes movement of species
34 determines the fluxes of individuals or genes that are exchanged between habitat patches,
35 which help to maintain populations and metapopulations (Verbeylen et al. 2003; Stevens et
36 al. 2006; Amos et al. 2014). Recently, applications of graph theory to landscape ecology have
37 shown potential for quantifying the connectivity of landscape for a species or species group
38 by focusing on the role of habitat patches and dispersal linkages between them (Pascual-
39 Hortal and Saura 2006; McRae and Beier 2007; Pinto and Keitt 2009; Rayfield et al. 2011). In
40 particular, researchers have developed methods to identify the most important habitat
41 patches for maintaining the global connectivity of habitat networks (Pascual-Hortal and
42 Saura 2006; Urban et al. 2009; Bodin and Saura 2010; Saura and Rubio 2010; Ernst 2014).
43 These prioritization methods are thought to be particularly useful for conservation biologists
44 and landscape managers: they can guide the location of future finer-scale studies and help
45 to define conservation, restoration or mitigation measures that should favour a better
46 (spatial) allocation of funds and efforts to protect biodiversity (Zetterberg et al. 2010; Foltete
47 et al. 2014; Gurrutxaga and Saura 2014).

48 Habitat patch prioritization based on landscape graphs uses connectivity indices that
49 quantify the importance of each habitat patch for habitat network connectivity, taking into
50 account its position in the habitat network with, for example, centrality indices (e.g. Estrada
51 and Bodin 2008). But, connectivity indices generally consider both the position and the
52 quality (or quantity) of available habitat such as the Integral Index of Connectivity (IIC) and

53 the Probability of Connectivity index (PC) (Pascual-Hortal and Saura 2006; Saura and Pascual-
54 Hortal 2007; Saura and Rubio 2010). These connectivity indices make a compromise
55 between the effects of landscape composition and landscape structure on species presence,
56 a question still debated in the literature (Didham et al. 2012). Different attributes of habitat
57 patches can be used to consider habitat patch quality: this can depend on species
58 requirements, but more often on the information available, often justifying the use of
59 proxies of habitat patch quality calculated from landscape maps such as patch area, patch
60 interior area or level of anthropogenization. How well one habitat patch is linked to the rest
61 of the habitat network depends on the distance between this habitat patch and the other
62 patches, but the way in which the method used to calculate this distance affects the degree
63 of connectivity of habitat patches remains unclear. Traditionally in graph theory, distance
64 between habitat patches was just the topological distance, i.e. Euclidean distance, but in this
65 last decade many studies on animal dispersal movement have shown that Euclidean distance
66 is not realistic because it does not integrate the difficulty or mortality encountered by a
67 species moving through a landscape mosaic (Adriaensen et al. 2003; Belisle 2005). Many
68 efforts have been made to integrate landscape resistance more fully with species
69 movement, and two methods are now widely used to quantify the distance a species has to
70 travel to disperse between habitat patches.

71 The classical least-cost path is based on friction maps reflecting the difficulty for a
72 species to move between two source patches (Adriaensen et al. 2003). A species
73 accumulates a cost with increasing distance from source patches, depending on its dispersal
74 capacities and specific habitat encountered. The least-cost distance (LCD) is the accumulated
75 cost distance of the most likely route an individual would take to move between the two
76 habitat patches considered, i.e. the least-cost path (LCP). However, LCP implies that species

77 know the optimal path to get to a new habitat patch, and a major criticism is that it does not
78 take into account the existence of other optimal paths, whereas species generally use
79 random or alternative dispersal routes depending on individual behaviour (Belisle 2005).
80 Nevertheless, LCD itself indicates the minimum distance separating the individual habitat
81 patches and so the reachability of habitat for species. LCD is therefore now preferred to
82 Euclidean distance for parameterizing connectivity indices prioritizing habitat patch
83 importance (Zetterberg et al. 2010; Gurrutxaga et al. 2011; Clauzel et al. 2013). A recent
84 significant advance in quantifying resistance distance separating habitat patches was
85 provided by circuit theory, which takes into account random movement paths and path
86 redundancy (McRae and Beier 2007; McRae et al. 2008). An electric current flowing through
87 landscape resistance maps represents species dispersal flux at each point of the landscape:
88 all the alternative paths between two habitat patches are used to calculate resistance
89 distance (RD), which represents the effective distance separating the two habitat patches for
90 a species. The more alternative paths there are, the shorter RD is compared to LCD. RD has
91 been particularly widely used in genetic studies to evaluate functional landscape
92 connectivity by correlating RD to genetic distance between population patches (Amos et al.
93 2014; Marrotte et al. 2014), and current maps are considered to identify dispersal corridors
94 well (Roever et al. 2013). Some studies have used both LCD and RD (or resulting maps) to
95 find out which is the better predictor of species movement corridors (Poor et al. 2012;
96 LaPoint et al. 2013) or how they change with cost map parameterization (Koen et al. 2012).
97 One recent study (Ayram et al. 2014) used both LCD and circuit theory to identify important
98 landscape elements: IIC index was based on LCD to determine key habitat patches, and
99 current maps were used to locate corridors for two mammal species. However, to our
100 knowledge, how LCD and RD influence patch importance and the identification of key

101 elements maintaining habitat network connectivity has never been studied. It remains
102 unclear whether the modelling of alternative paths, which is very time-consuming, is really
103 required to identify key elements for habitat connectivity, or whether the modelling of the
104 one best path, which is faster, is sufficient to approximate habitat patch importance
105 adequately.

106 In this article, we compare the prioritization of habitat patches from graph models
107 based on LCP and from graph models based on RD. We used binary and probabilistic
108 connectivity indices, i.e. Betweenness Centrality (BC), patch importance based on Integral
109 Index of Connectivity (dIIC) and based on Probability of Connectivity (dPC), in order to
110 provide support in the use of the most commonly employed connectivity indices in
111 conservation studies. We hypothesized that the identification of key habitat patches would
112 tend to agree with increasing dispersal distance, but that identification could remain
113 different in certain cases, particularly when the probability of dispersal was considered, since
114 RD integrates multiple paths unlike LCD. We go on to discuss ecological hypotheses that
115 might explain these differences. Our comparison is based on two real landscapes (e.g. Koen
116 et al. 2010; Koen et al. 2012) ranging in habitat cover, fragmentation level, and spatial extent
117 to verify consistency of relationship with landscape structure. Habitat patch prioritization
118 focused on forest mammal species with different dispersal distances using a generic
119 approach and following a conservation perspective, not a restoration or mitigation
120 perspective. In this case, habitat patch prioritization aims to evaluate the importance of each
121 habitat patch for maintaining the global connectivity of the habitat network for the species.

122

123 **Material and Methods**

124 **Study area and land cover map**

125 Two study cases were selected in the South of France (43°01' – 45°07' N and 4°13' – 7°43' E).
126 The first study case, hereafter named "Region", followed the administrative boundaries of
127 Region PACA, excluding isolated parts (e.g. Mediterranean islands) and encompassed about
128 31700 km². Region was mainly covered by forests (38%), other semi-natural and natural
129 areas (35%), agricultural areas (17%) and artificial areas (7%); other areas were wetlands and
130 water bodies (3%). A second landscape hereafter named "Sub-region" was a sub-area of
131 about 7090 km², and contained strong human-created barriers. Sub-region was affected by a
132 higher level of anthropogenization than Region, with a lower cover of forests and other
133 semi-natural and natural areas (27% and 26% respectively), and a higher cover of agricultural
134 areas and artificial areas (31% and 11% respectively). Other areas were wetlands and water
135 bodies (3%). The study area was bordered by the Alps at the East, anthropogenized areas at
136 the West and the Mediterranean Sea at the South. Landscape habitats came from the map
137 ocsol2006 of Crige PACA (www.crige-paca.org), an adaptation of the CORINE land cover
138 nomenclature of the European Environmental Agency ([http://www.eea.europa.eu/data-](http://www.eea.europa.eu/data-and-maps)
139 [and-maps](http://www.eea.europa.eu/data-and-maps)) for French Mediterranean landscapes with a smaller spatial resolution. The land
140 cover map identified 42 types of landscape features, including natural and human-
141 dominated lands, highways and major railways, with a minimal mapping unit varying from
142 0.5 to 2.5 ha.

143

144 **Functional group approach**

145 We focused on generalist forest mammal species using a generic approach for our
146 connectivity models, because these species depend on a well-defined habitat and are known
147 to be sensitive to landscape features of interest for land managers, such as transportation
148 infrastructures, and urban and other anthropogenized areas. We collected scientific
149 literature on forest mammal species and consulted studies using a generic forest species
150 approach (Verbeylen et al. 2003; Watts et al. 2010; Garcia-Feced et al. 2011; Gurrutxaga et
151 al. 2011; Gimona et al. 2012) to determine the resistance of landscape features to animal
152 movement. The attribution of cost values to landscape features is still under debate (Zeller
153 et al. 2012; Mateo-Sanchez et al. 2015) and would be based on ad hoc data, i.e. showing
154 species dispersal movement (pathways data), in the ideal but very uncommon case.
155 Consequently, we focused on studies that conducted sensitivity analyses to model
156 connectivity between forest habitat patches, such as that of Verbeylen et al. (2003), who
157 tested a range of cost values and cost classes to find the best combination explaining the
158 presence of forest species in forest habitat patches. Our review caused the original land
159 cover map to turn into a landscape resistance map with five cost classes: 1 for forest areas
160 (species habitat), 10 for less open areas with trees (or potential feeding-seed trees), 300 for
161 more open areas including shrubs or gardens, 800 for areas with low vegetation such as
162 agricultural lands, and 1000 for landscape features that most impeded animal movement
163 such as highways, buildings and permanent snow. We then rasterized the cost map at a 100
164 m pixel size to reduce calculation time for analysis (McRae et al. 2008). Habitat patches were
165 defined as entirely covered by forest, up to the upper tree-line at 2100 m a.s.l. and with a
166 surface area of at least 10 ha. We kept 621 forest habitat patches for Sub-region and 2482
167 forest habitat patches for Region. GIS calculations were performed with ArcGis 10 (ESRI®).

168

169 **Least-cost distance and resistance distance**

170 Linkages were modelled between habitat patches using a maximum distance according to
171 species dispersal capacities and the extent of the study area. For connectivity analyses (see
172 below), we used a range of distances rather than only one, enabling us to take into account
173 information disparity in the literature and variation in species dispersal distance (e.g.
174 juvenile dispersal, adult dispersal, long-distance dispersal events). Most importantly, this
175 enabled us to analyse how our connectivity models changed with dispersal distance and so
176 to what extent LCP-based prioritization is correlated to RD-based prioritization. Our review
177 prompted us to use the following dispersal distances (edge-to-edge of habitat patches): 200
178 m, 700 m, 1000 m, 4000 m, 6000 m, 10 km, 15 km, 20 km and 25 km. Our connectivity
179 models thus considered a range of dispersal distances ranging from 200 m to 25 km,
180 enabling us to consider short-, medium- and long-distance dispersal of forest mammal
181 species. The maximum dispersal distance of 25 km yielded 898 linkages for Sub-region and
182 3399 for Region. In this article, dispersal distance was in kilometres but it was actually a cost
183 distance: in the analyses, dispersal distance was multiplied by the median value of the cost
184 raster to reflect the cost of the path travelled by the species (e.g. Gurrutxaga et al. 2011). A
185 species moves a larger geographical distance through permeable landscape features than
186 through landscape features with high resistance. Dispersal distances stated in the literature
187 often result from straight-line distance calculations between pre- and post-dispersal habitat
188 patches (e.g. Wauters et al. 2010), whereas species had actually moved through different
189 landscape features along a much longer non-linear path (Rowcliffe et al. 2012).

190 We used Linkage Mapper 1.0.3 (McRae and Kavanagh 2011), a free tool box
191 implemented in ArcGis, to calculate LCD between each pair of habitat patches: LCD is the
192 accumulated cost distance of the most likely route an individual would take to move
193 between the two habitat patches considered. Only direct linkages between habitat patches
194 were considered to construct the habitat network model (see below). Using circuit theory
195 with Circuitscape (McRae et al. 2008; Shah and McRae 2008), we then calculated RD
196 between each pair of habitat patches (pairwise mode and connection option with eight
197 neighbours). Calculating RD was particularly time-consuming with a large numbers of
198 patches and linkages, because all the paths between two habitat patches have to be
199 considered. The resistance to current flow was therefore computed on the entire landscape
200 area, and for each pair of habitat patches. We were not interested in the precise location of
201 dispersal corridors, but in a measure of distance between habitat patches that took into
202 account alternative paths. Hence to calculate RD, we restricted the current flow analysis to a
203 corridor surrounding the least-cost path determined previously by applying a cut-off of
204 700 m (cost width of corridor) and using an extension of Linkage Mapper that applied
205 Circuitscape in this specific way (McRae 2012). Consequently, all alternative paths not
206 exceeding 700 m from the least-cost path were kept to compute RD between a pair of
207 patches. When landscape impedes species movement, least-cost corridors are narrow and
208 there are few alternative paths between patches for species, so RD approximates to or
209 equals LCD, but when landscape is favourable to species movement, least-cost corridors are
210 wide and there are many alternative paths, making RD strongly shorter than LCD. In this
211 case, individuals have more chance of reaching the other habitat patch. We also calculated
212 RD for a corridor cut-off of 4000 m in order to verify how corridor cut-off could change the
213 estimation of habitat patch importance. Habitat patch importance for the two cut-offs was

214 closely correlated: Spearman's rho was at least 0.92, but generally above 0.94 for both
215 Region and Sub-region. We therefore kept RD based on a corridor cut-off of 700 m in what
216 follows. The calculation of LCD and RD for Sub-region was applied to the spatial extent of
217 Region (acting as a buffer, see Koen et al. 2010), to make the estimation of distance
218 independent of artificial boundary (only present at the North of Sub-region, see Material and
219 Methods).

220

221 **Connectivity indices for evaluating habitat patch importance**

222 The habitat network model was composed of nodes representing habitat patches
223 characterized by their surface area, and of direct links representing linkages between habitat
224 patches characterized by their travel cost (LCD or RD). A set of connectivity indices was
225 calculated from the habitat network model with the free software Conefor 2.6 (Saura and
226 Torne 2009) in order to quantify the relative importance of habitat patches for global
227 network connectivity. Here we present the different indices used only briefly, all being
228 detailed and their use justified in an abundant literature. Moreover, our aim was not to
229 investigate the differences between connectivity indices (see Bodin and Saura 2010; Baranyi
230 et al. 2011), but to compare habitat patch ranking according to LCD-based linkages and RD-
231 based linkages for different connectivity indices currently used in the conservation biology
232 literature. A path or linkage is always the direct dispersal between two habitat patches (i.e.
233 with no other intermediate habitat patch), whereas the term pathway is used with a general
234 meaning, i.e. dispersal ways in habitat network (direct or indirect). All connectivity indices
235 used in this study are given in Table 1. Betweenness Centrality (BC) considers the number of
236 shortest pathways between all pair of nodes that go through a particular node, and so does

237 not consider the node attribute (surface area). $dIIC_{flux}$ ($dIICf$), $dIIC_{connector}$ ($dIICc$), dPC_{flux} ($dPCf$)
238 and $dPC_{connector}$ ($dPCc$) are fractions resulting from the decomposition of the node
239 importance value ($dIIC$, dPC) based on Integral Index of Connectivity (IIC) and on Probability
240 of Connectivity (PC) respectively (Table 1). Flux fraction of a particular node ($dIICf$, $dPCf$)
241 quantifies the amount of dispersal flux that occurs between the node and the rest of the
242 network, and depends on the node attribute and the shortest pathways that link the node to
243 the network (topological position). Connector fraction of a particular node ($dIICc$, $dPCc$)
244 exists only if the shortest pathways between other nodes pass through the node, and so
245 depends only on topological position; it quantifies the importance of the node as a stepping-
246 stone for dispersal, i.e. facilitating dispersal between excessively far nodes. We also
247 computed the last fraction of node importance, the intra fraction ($dIICi$, $dPCi$) of a particular
248 node, which depends only on the node attribute, and so has the same value whether the
249 node is connected or not (see Saura and Rubio 2010). Investigating how the fractions
250 connector and flux change with linkage type helped us to make a better evaluation of how
251 connectivity models impact the importance of patch, and so support more precise
252 recommendations for the use of prioritization methods. All indices were calculated for the
253 nine dispersal distances and for the two landscapes. Dispersal distance acted as a threshold
254 determining the presence of a link between two nodes in the case of binary indices (BC,
255 $dIICf$, $dIICc$). In the case of probabilistic indices ($dPCf$, $dPCc$), dispersal distance determined
256 the median probability associated with a link, defining the distance-decay constant α in the
257 relation $p_{ij} = e^{-\alpha d_{ij}}$ (Urban and Keitt 2001; Saura and Pascual-Hortal 2007) where p_{ij} is the
258 probability of dispersal between nodes i and j , and d_{ij} their distance (LCD or RD). BC, $dIICf$,
259 $dIICc$, $dPCf$ and $dPCc$ have been shown to be non-redundant indicators of patch contribution
260 in the maintaining of habitat network connectivity (Baranyi et al. 2011). Finally, we summed

261 node importance values for each fraction flux, connector and intra over all the nodes, and
262 then calculated the percentage of each sum relative to the total node importance values
263 (Saura and Rubio 2010). This percentage was calculated for each dispersal distance in order
264 to examine how habitat network connectivity (flux fraction and connector fraction of habitat
265 network) changes according to LCD-based or RD-based indices. Connector fraction peaks
266 when key stepping-stones become connected to habitat network, and flux fraction increases
267 with connection of large habitat patches (high quality patches) and with the number of
268 alternative pathways in the habitat network (Saura and Rubio 2010). We also calculated
269 BC(IIC) and BC(PC), which are modifications of BC integrating properties of IIC and PC and are
270 argued to be further useful indices (Bodin and Saura 2010), but we do not present the
271 results for these indices since they were very closely correlated to dIICc and dPCc for both
272 LCD and RD linkages (Spearman's rho was at least 0.91) and showed the same correlation
273 pattern as dIICc and dPCc (see below).

274

275 **Comparison of LCD- and RD-based connectivity indices**

276 The higher the value of connectivity index, the greater the importance of the node for global
277 habitat network connectivity. For each connectivity index and each dispersal distance, we
278 compared node importance given by the LCD-based index to node importance given by the
279 RD-based index by ranking importance values and applying rank correlation with Spearman's
280 coefficient rho, which allowed control for extreme values and non-linear relationships. Only
281 a limited number of habitat patches have a significant importance for the persistence of
282 overall connectivity, and financial resources for nature conservation are generally restricted
283 (e.g. Bodin and Saura 2010; Zetterberg et al. 2010; Gurrutxaga et al. 2011). Thus, after

284 examining quantile distributions of index values, we kept only the 25 top-ranked habitat
285 patches according to the LCD-based index and the RD-based index in further analyses,
286 focusing on Sub-region, since results were closely similar at Region (see Supporting
287 Material). We identified in which cases habitat patches were top-ranked only by the LCD-
288 based index, only by the RD-based index and by both indices, and projected them on the
289 habitat network map.

290

291 **Results**

292 **Habitat patch prioritization according to LCD-based and RD-based**

293 **indices**

294 Correlations between LCD-based indices and RD-based indices increased with dispersal
295 distance for the two landscapes Sub-region and Region (Fig. 1 and Fig. S1). Correlations
296 strongly increased from 200 m to 1000 m, then increased more slowly up to 4000 m, where
297 Spearman's rho generally exceeded 0.9, and were stable further away. For the smallest
298 dispersal distances, a large part of LCD-based linkages was not established between habitat
299 patches since linkage length exceeded the dispersal distance considered: 37.1%, 17.4%,
300 13.5% and 2.9% of LCD-based linkages exceeded dispersal distance at 200 m, 700 m, 1000 m
301 and 4000 m for Sub-region respectively (27.1%, 12.3%, 8.8%, 1.7% for Region respectively).
302 As expected, there were only a few cases where RD-based linkages exceeded the dispersal
303 distance (2.6% and 1.6% at 200 m for Sub-region and Region respectively). Hence habitat
304 network models based on LCD and on RD strongly differed for small dispersal distances,

305 while they became more similar with increasing dispersal distances. The sum of node
306 importances reflected this convergence with increasing dispersal distances (Fig. 2 and Fig.
307 S2). Differences persisted at slightly longer dispersal distances for probabilistic indices than
308 for binary indices, particularly for connector fraction (Figs 1 and 2). The sum of node
309 importances for Sub-region showed that dPCc peaked at 200 m and was rather stable from
310 1000 m when based on RD, but strongly decreased after 4000 m when based on LCD. By
311 contrast, values of dIICc were similar at least from 4000 m for both distance types (same
312 results for Region, Fig. S2). This difference occurred because for probabilistic indices,
313 dispersal probability associated with the linkages increased much more rapidly when
314 considering RD and alternative paths than when considering LCP and only one optimal path.

315 **Figure 1. Correlation between habitat patch importance according to LCD-based and RD-based index for binary (a) and**
316 **probabilistic indices (b) for Sub-region.** Intra fraction (i), flux fraction (f) and connector fraction (f) are the partition of node
317 importance dIIC and dPC. Tick marks without labels are 700, 1000 and 6000 m respectively.

318 **Figure 2. Relative contribution of each fraction intra (i), flux (f), connector (c) to habitat network connectivity according**
319 **to LCD-based and RD-based indices for Sub-region.** Each fraction represents the contribution of all individual habitat
320 patches relative to their total importance for maintaining connectivity. Tick marks without labels are 700, 1000 and 6000 m
321 respectively.

322 The comparison of habitat patch ranking according to importance values given by
323 LCD-based indices and by RD-based indices showed strong similarities (Fig. 3 and Fig. S3) that
324 could be explained by strong correlations between connectivity indices for a type of linkages.
325 First, the comparison of habitat patch ranking followed the same pattern for dIICf and dPCf,
326 and their correlations were above 0.92 both for LCD-based and RD-based indices for Sub-
327 region (>0.9 for Region). Second, comparison showed the same pattern for dIICc and BC, and
328 their correlation was above 0.91 for both LCD-based and RD-based indices for Sub-region
329 (>0.92 for LCD-based indices and >0.87 for RD-based indices for Region). The pattern was

330 slightly different for dPCc and its correlation with other indices was lower (<0.8 in all cases).
331 Indeed, three different cases occurred concerning habitat patch prioritization. Firstly, LCD-
332 based indices gave a much higher importance to habitat patches than RD-based indices. The
333 most illustrative case occurred when habitat patches had a moderate importance with LCD-
334 based indices and had null importance (rank 1) with RD-based indices (see Fig. 3). Secondly,
335 RD-based indices gave a much higher importance to habitat patches than LCD-based indices.
336 The most illustrative case occurred when habitat patches had a moderate-to-high
337 importance with RD-based indices and null importance with LCD-based indices. Thirdly, LCD-
338 based and RD-based indices attributed closely similar importance value to habitat patches.

339 **Figure 3. Habitat patch importance rank according to LCD-based versus RD-based indices for Sub-region.** Minimal rank is
340 attributed when several importance values are the same. Other dispersal distances are not shown. Circles illustrate some
341 cases where prioritization strongly differed.

342

343 **Identification of top-ranked habitat patches**

344 We focused on the 25 habitat patches with the greatest contribution for maintaining global
345 habitat network connectivity at Sub-region level and projected the three different cases on
346 the habitat network map. From the 700-m dispersal distance, almost the same habitat
347 patches were identified by IICf and PCf based on LCD or RD linkages, whereas they strongly
348 differed until the 1000-m dispersal distance for BC and IICc (Figs 4 and 5). The prioritization
349 of habitat patches by dPCc remained divergent even when considering large dispersal
350 distances, and only about 50% of top-ranked habitat patches were identified by both index
351 types whatever the distance (Fig. 4). This means that when connectivity indices were
352 weighted by patch attributes (IICf and PCf), linkage type had very little importance for patch

353 prioritization in our study, but it had high importance when connectivity indices were based
354 only on dispersal distance for short- and medium-distance dispersers (BC and IICc) or when
355 they were based on dispersal probability (dPCc). In certain cases for binary indices, habitat
356 patches were top-ranked by the RD-based index, whereas the LCD-based index gave them a
357 null importance as habitat patches were at one end or totally isolated in the LCD-based
358 habitat network (see arrow 1 on Fig. 5). However, in other cases, habitat patches were top-
359 ranked only by the RD-based index, although they might have been expected to be top-
360 ranked also by the LCD-based index (arrows 2, Fig. 5): the loss of these habitat patches
361 seriously affected dispersal between group of patches and the rest of the LCD-based habitat
362 network for short-distance and medium-distance dispersers, because there was no
363 alternative pathway, or only much longer pathways with many intermediate steps. LCD-
364 based indices evaluated other habitat patches as being more important for network
365 connectivity (e.g. arrows 3 on Fig. 5), their loss causing the total isolation of a large part of
366 the habitat network. However, RD linkages showed several alternative pathways with an
367 equivalent or smaller number of steps, thus providing other connections with the rest of the
368 habitat network. Consequently, LCD-based indices tended to overestimate the role of certain
369 habitat patches compared with RD-based indices, because they seemed to act as key
370 connectors for maintaining habitat network connectivity whereas alternative pathways
371 existed (see Figs 5 and 6). This resulted in a decrease in the importance of the other habitat
372 patches identified as key-elements by RD-based indices.

373 **Figure 4. Among the 25 top-ranked habitat patches, number of patches identified commonly by LCD-based and RD-based**
374 **indices.**

375 **Figure 5. Map showing the 25 top-ranked habitat patches according to dIICc for a maximum dispersal distance of 1000 m.**
376 Top-ranked patches only by RD-based (green), only by LCD-based (orange) and by both indices (lilac), other habitat patches

377 in grey. Difference between LCD-based rank and RD-based rank in bold. Linkages are established when $RD \leq 1000$ m (red
378 and green); and in fewer cases when $LCD \leq 1000$ m (red).

379 LCD linkages were up to 74 times longer than RD linkages, so habitat network based
380 on LCD strongly differed from habitat network based on RD for small and medium dispersal
381 distances, dispersal probability associated with LCD being very small compared with RD (Fig.
382 6). As dispersal capacity increased, dispersal probability increased strongly for LCD linkages,
383 and the habitat patches identified only by RD-based dPCc tended to be identified also by
384 LCD-based dPCc, i.e. the disparity of patch ranking for these patches decreased (compare
385 top-ranked patches by RD-based dPCc between Figs 6 and 7). However, the disparity of
386 patch ranking increased for the patches identified only by LCD-based dPCc (compare Figs 6
387 and 7): they occurred in landscape areas that remained poorly connected by LCD linkages at
388 a large distance (Fig. 7a), whereas these areas became well connected by RD linkages (Fig.
389 7b). There were alternative pathways with high dispersal probabilities since large corridors
390 and different paths between patches could be used by individuals to disperse (Fig. S4).

391 **Figure 6. Maps showing the 25 top-ranked habitat patches according to dPCc for the 6000-m median dispersal distance.**

392 LCD-based (a) and RD-based linkages (b) are represented according to their dispersal probability. See Fig. 5 for other details.

393 **Figure 7. Maps showing the 25 top-ranked habitat patches according to dPCc for the 25-km median dispersal distance.**

394 LCD-based (a) and RD-based linkages (b) are represented according to their dispersal probability. See Fig. 5 for other details.

395

396 Discussion

397 We report evidence that there was strong divergence between habitat patch prioritization
398 based on linkage reflecting the least-cost path and that based on linkage reflecting multiple
399 paths, depending on the type of connectivity indices and species dispersal distance. The

400 same patterns of prioritization occurred for both landscapes Region and Sub-region, which
401 strongly differed in terms of spatial extent, landscape composition and fragmentation. This
402 suggests that the correlation patterns we found in this study may not depend on landscape
403 extent and landscape structure. However, further investigations are needed to measure to
404 what extent the correlation between LCP-based prioritization and RD-based prioritization
405 will follow the same pattern when landscape structure changes. Prioritization indices are
406 presented as tools helping practitioners to orientate field conservation measures by the use
407 of available knowledge about dispersal capacities and species requirements (Galpern et al.
408 2011), since it is not (or only rarely) possible to obtain robust data on real species fluxes
409 between habitat patches at large scales. Hence, the use of prioritization indices and least-
410 cost corridors or current maps identifying potential key landscape areas is an important
411 advance for landscape and species conservation management (Beier et al. 2011; Lawler et al.
412 2013; Ayram et al. 2014). LCD and RD are methods with marked conceptual differences, and
413 we showed that the way they influence prioritization of landscape features is not trivial.

414 LCD-based and RD-based indices identified almost the same habitat patches even for
415 short dispersal (from 700 m) when considering the role of patches as providers (or receivers)
416 of individual fluxes. Habitat patch attribute weighted the influence of distance type, and
417 when large habitat patches were well connected to the habitat network (mean patch area
418 was 178 ha for Sub-region but 3140 ha for the 25 top-ranked habitat patches by dIICf or
419 dPCf), it was sufficient to calculate LCD to properly quantify the importance of habitat
420 patches for dispersal fluxes into the habitat network. Accordingly, we recommend that
421 conservation managers calculate only LCD in a first line approach, and then verify the degree
422 of connection between large (high quality) habitat patches and the rest of the habitat

423 network before deciding whether the calculation of RD is required for quantifying the
424 contribution of patches to dispersal fluxes at the scale of the landscape.

425 Concerning the role of habitat patches as stepping-stones, i.e. facilitating species
426 dispersal between far habitat patches, the choice of RD or LCD could depend on the
427 assumptions about how the species population functions. Considering the presence or
428 absence of the linkage, i.e. the use of binary indices (BC, dIICc), almost all linkages were
429 established for LCP above a certain dispersal distance of the species. In one study on a plant
430 species (Neel 2008), IIC tended to explain genetic differences between populations better
431 than PC, but for a Euclidean distance less than 2500 m, so actually a much shorter distance
432 than in our study. If we hypothesize that one individual would be sufficient to change the
433 genetic structure of population (see Wang 2004), the convergence of patch prioritization
434 based on LCD and on RD should be expected. LCD indicated the minimum distance a
435 particular individual had to move between habitat patches, and when the individual
436 dispersal capacity was at least LCD, the individual was able to move to any population patch.
437 Accordingly, our results show that the calculation of RD did not provide any further
438 information about key stepping stones in the landscape.

439 When considering the linkage probability between habitat patches (dPCc), strong
440 differences remained whatever the dispersal distance. RD considered the probability of
441 dispersal between habitat patches taking into account path redundancy, i.e. it indicated the
442 resistance distance one species moved between population patches (Fletcher et al. 2014).
443 RD can be more closely correlated with genetic distance compared with LCP, which implies
444 that taking into account the flux of dispersers better reflects genetic differences between
445 populations than considering one (best) disperser (McRae and Beier 2007). Consequently,

446 we can hypothesize that RD-based dPCc predicts functional connectivity between
447 populations better than LCD-based dPCc, since the establishment of linkages between
448 patches is proportional to the number of dispersers, and not only to the inter-patch distance
449 (Fletcher et al. 2014). The current map (Fig. S4) illustrates the differentiation of narrow
450 corridors for forest species dispersal (pinchpoints), versus large corridors or alternative paths
451 between habitat patches that increase the probability of dispersal for the species (compare
452 dispersal probability in Figs 7a and 7b).

453 Future studies will use genetic data to corroborate that RD best identifies key
454 landscape elements that contribute to the long-term persistence of species. Our results also
455 show that LCD-based dPCc allowed the identification of landscape parts that remain difficult
456 to reach for one individual because of a strong impedance of the surrounding landscape:
457 restoration actions to facilitate individual dispersal will ameliorate the connectivity with
458 other landscape parts, and probably also the long-term persistence of the species. Habitat
459 patch importance was evaluated similarly according to RD based on 700-m corridor cut-off
460 and 4000-m corridor cut-off, but if RD was calculated considering the entire surrounding
461 landscape as space for dispersal movements, the prioritization differences between LCD and
462 RD might be accentuated. Our results suggest that resistance-based connectivity is
463 substantially affected by different conceptual approaches and not only by the way resistance
464 values are parameterized (Mateo-Sanchez et al. 2015). Importantly, these approaches do
465 not replace species monitoring or genetic studies nor finer-scaled investigations before
466 protection or restoration actions are attempted.

467

468 **Acknowledgments**

469 C.A. was supported by Region PACA (APRF 2011 projet Alterbio PACA) and Irstea.

470

471 **Table 1**

472 Table 1. Binary and probabilistic connectivity indices used for prioritization of habitat
 473 patches in our study

	INDEX	TYPE	MEANING	REFERENCES
BC	Betweenness Centrality	Binary	Considers the role of patch <i>i</i> as connecting other patches (stepping-stone) with shortest pathways	Estrada and Bodin 2008; Bodin and Saura 2010
dIIC	delta IIC	Binary	Importance of patch <i>i</i> according to Integral Index of Connectivity. IIC considers both habitat amount and habitat reachability in habitat network, and linkages as dispersal events between patches. dIIC quantifies the loss of connectivity if patch <i>i</i> is removed from habitat network and can be decomposed into dIICf, dIICc, dIICi	Urban and Keitt 2001; Pascual-Hortal and Saura 2006; Saura and Rubio 2010
dPC	delta PC	Probabilistic	Importance of patch <i>i</i> according to Probability of Connectivity. Like IIC, PC considers both habitat amount and habitat reachability in habitat network, but the probability of dispersal between patches. dPC can also be decomposed into dPCf, dPCc, dPCi	Saura and Pascual-Hortal 2007; Saura and Rubio 2010
dIICf	Flux fraction of dIIC	Binary	Quantifies the role of patch <i>i</i> as receiving (emitting) flux from (to) other patches. It considers the attributes of <i>i</i> and of other patches, and the shortest pathways between them	Saura and Rubio 2010
dPCf	of dPC	Probabilistic		
dIICc	Connector fraction of dIIC	Binary	Quantifies the role of patch <i>i</i> as connecting other patches (stepping-stone). It considers shortest pathways passing through <i>i</i> and the attribute of other patches	Saura and Rubio 2010; Gurrutxaga et al. 2011; Saura et al. 2014
dPCc	of dPC	Probabilistic		
dIICi	Intra fraction of dIIC	Binary	Quantifies the role of patch <i>i</i> as providing intra-connectivity so considering only the attribute of <i>i</i> .	Saura and Rubio 2010
dPCi	of dPC	Probabilistic		

474

475

476 **Figure Captions**

477 **Figure 1.** Correlation between habitat patch importance according to LCD-based and RD-
478 based index for binary (a) and probabilistic indices (b) for Sub-region. Intra fraction (i), flux
479 fraction (f) and connector fraction (f) are the partition of node importance dIIC and dPC. Tick
480 marks without labels are 700, 1000 and 6000 m respectively.

481 **Figure 2.** Relative contribution of each fraction intra (i), flux (f), connector (c) to habitat
482 network connectivity according to LCD-based and RD-based indices for Sub-region. Each
483 fraction represents the contribution of all individual habitat patches relative to their total
484 importance for maintaining connectivity. Tick marks without labels are 700, 1000 and 6000
485 m respectively.

486 **Figure 3.** Habitat patch importance rank according to LCD-based versus RD-based indices for
487 Sub-region. The higher the patch importance, the higher the rank. Minimal rank is attributed
488 when several importance values are the same. Other dispersal distances are not shown.
489 Circles illustrate some cases where prioritization strongly differed.

490 **Figure 4.** Among the 25 top-ranked habitat patches, number of patches identified by both
491 LCD-based and RD-based indices.

492 **Figure 5.** Map showing the 25 top-ranked habitat patches according to dIICc for a maximum
493 dispersal distance of 1000 m. Top-ranked patches only by RD-based (green), only by LCD-
494 based (orange) and by both indices (lilac), other habitat patches in grey. Difference between
495 LCD-based rank and RD-based rank in bold. Linkages are established when $RD \leq 1000$ m (red
496 and green); and in fewer cases when $LCD \leq 1000$ m (red). Numbered arrows indicate three
497 typical cases resulting from the difference in patch prioritization (see Results).

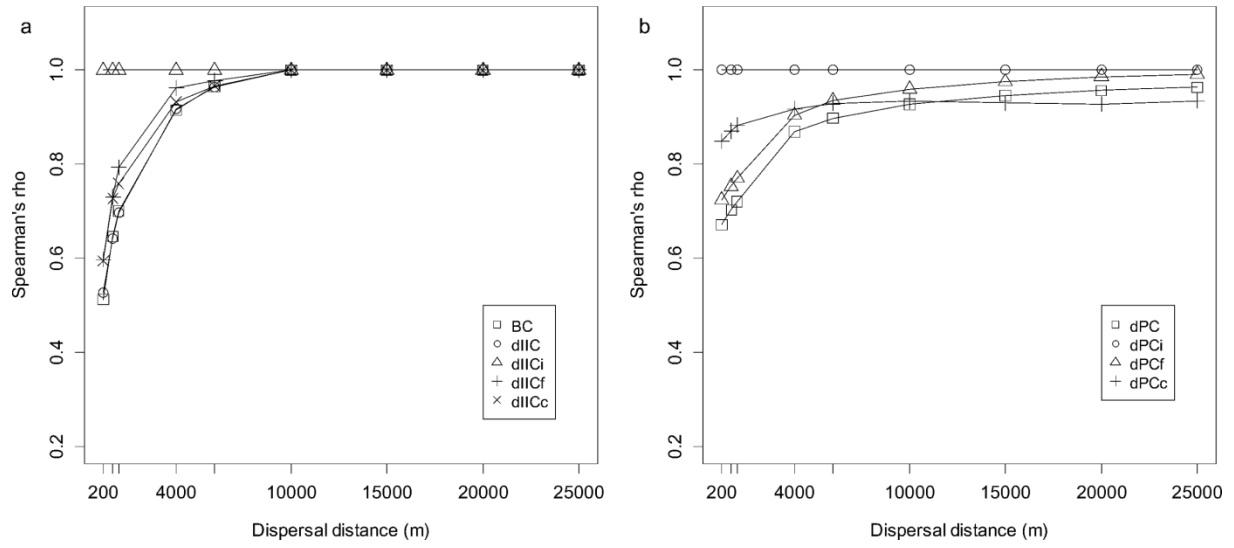
498 **Figure 6.** Maps showing the 25 top-ranked habitat patches according to dPCc for the 6000-m
499 median dispersal distance. LCD-based (a) and RD-based linkages (b) are represented
500 according to their dispersal probability. See Fig. 5 for other details.

501 **Figure 7.** Maps showing the 25 top-ranked habitat patches according to dPCc for the 25-km
502 median dispersal distance. LCD-based (a) and RD-based linkages (b) are represented
503 according to their dispersal probability. See Fig. 5 for other details.

504

505 **Figures**

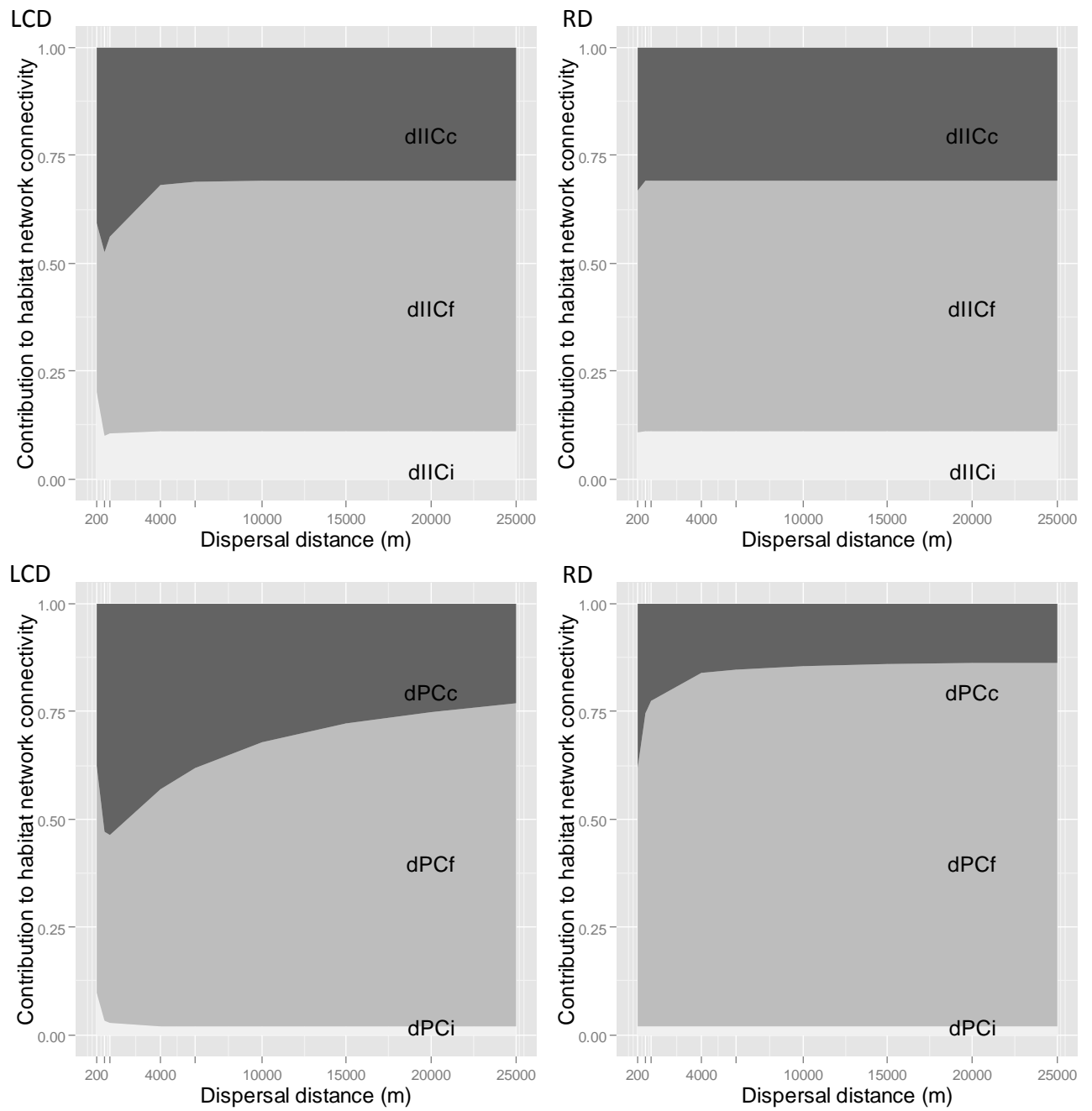
506 **Figure 1**



507

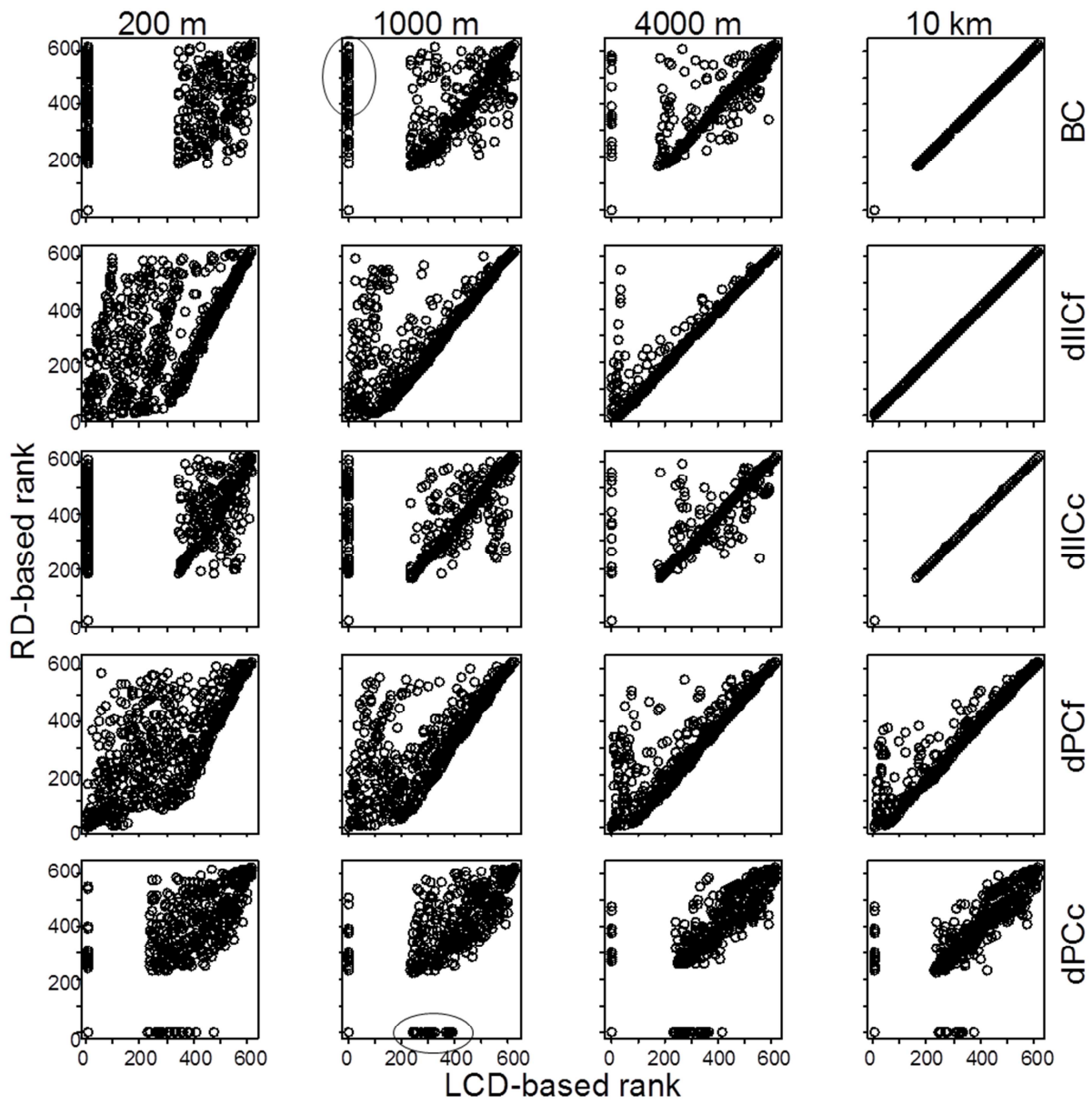
508

Figure 2



510

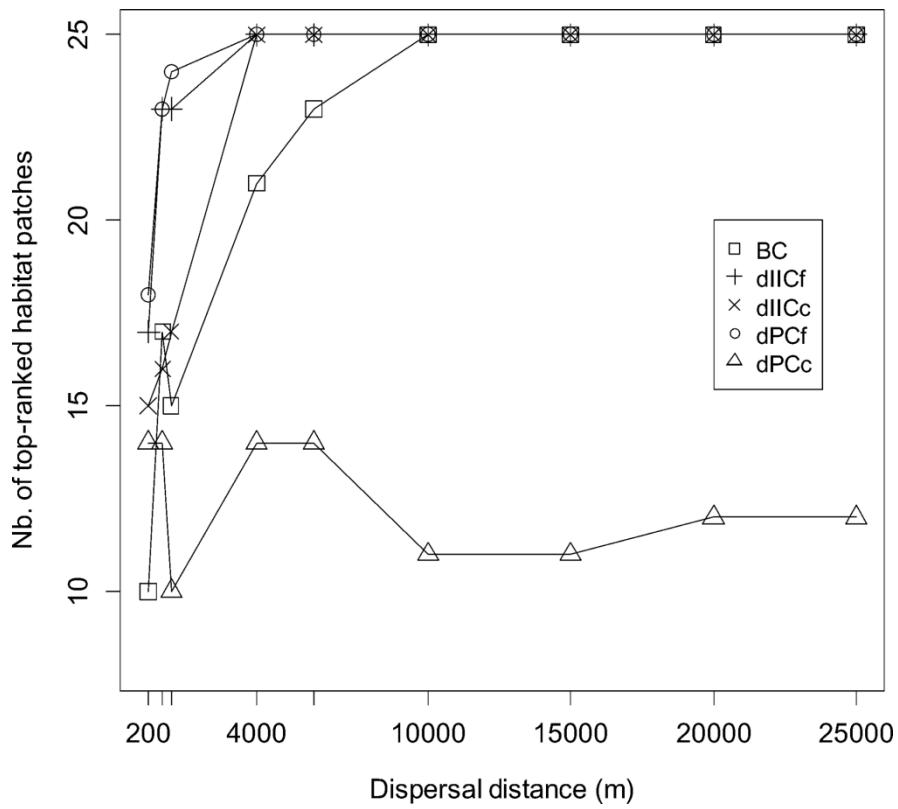
511 **Figure 3**



512

513

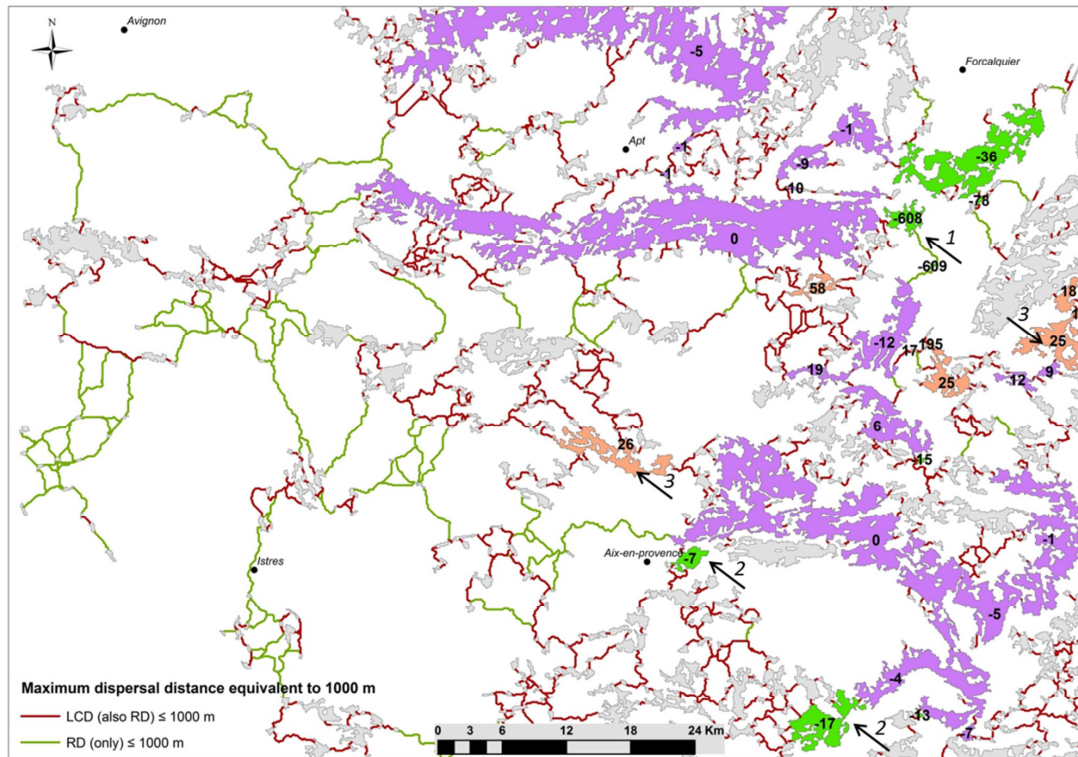
514 **Figure 4**



515

516

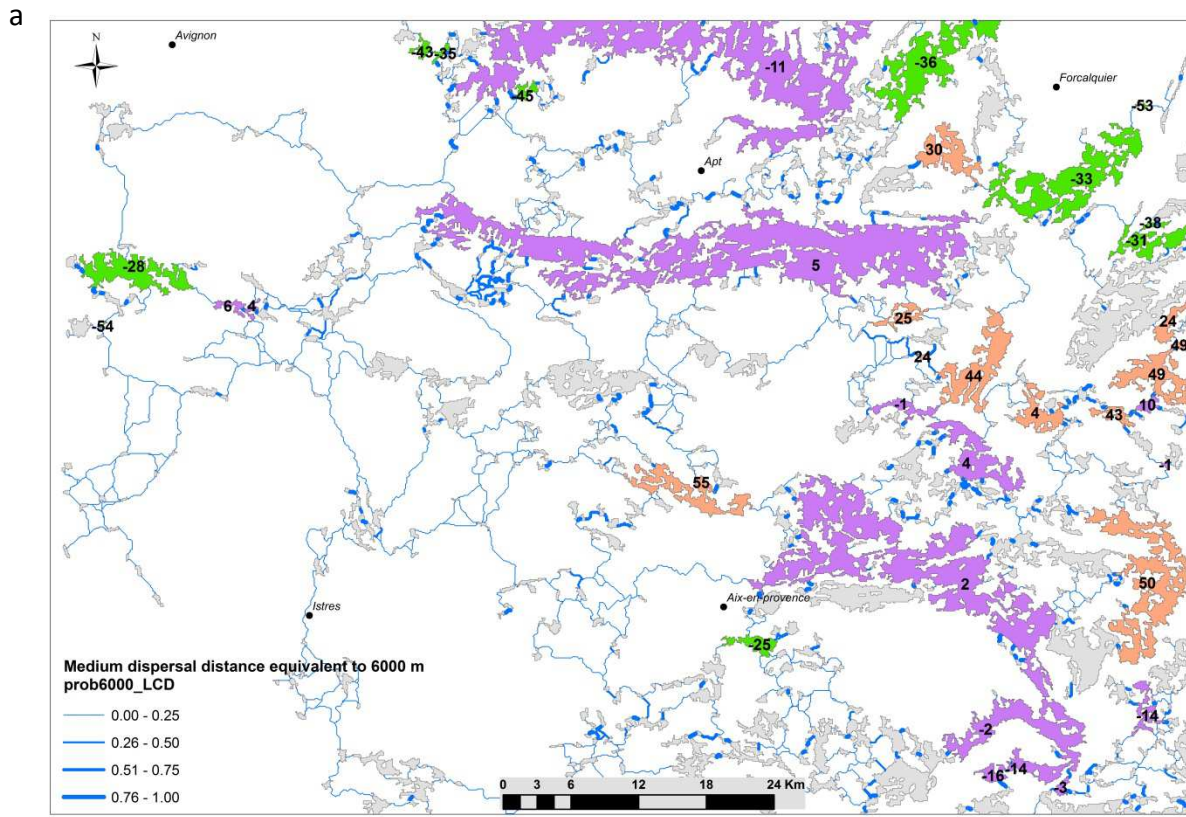
517 **Figure 5**



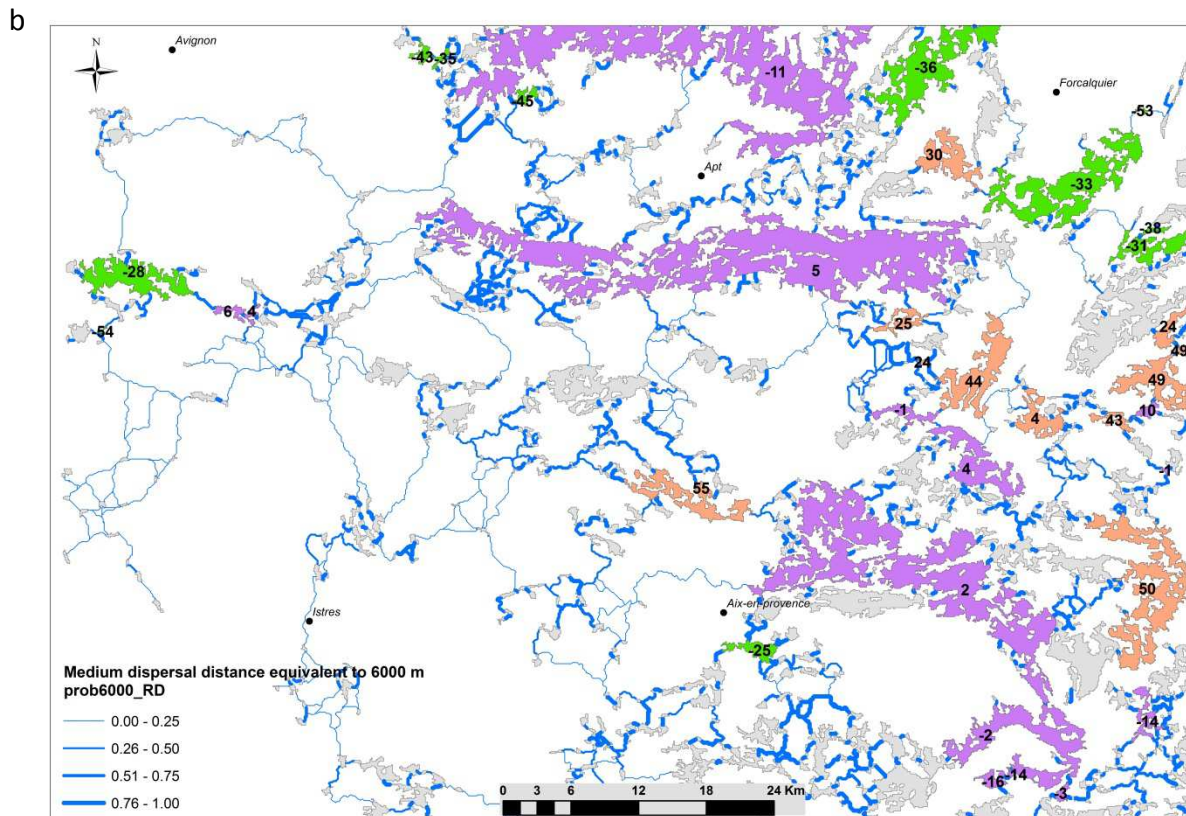
518

519

520 **Figure 6**

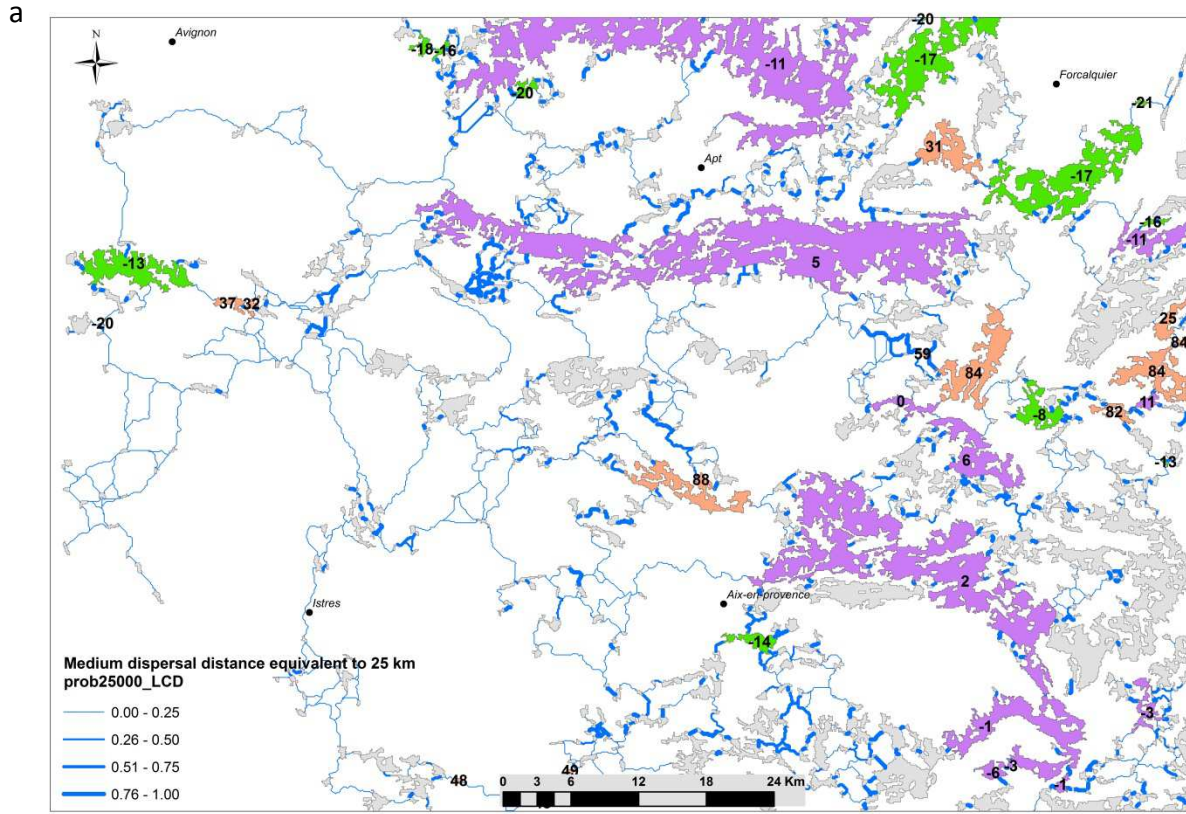


521

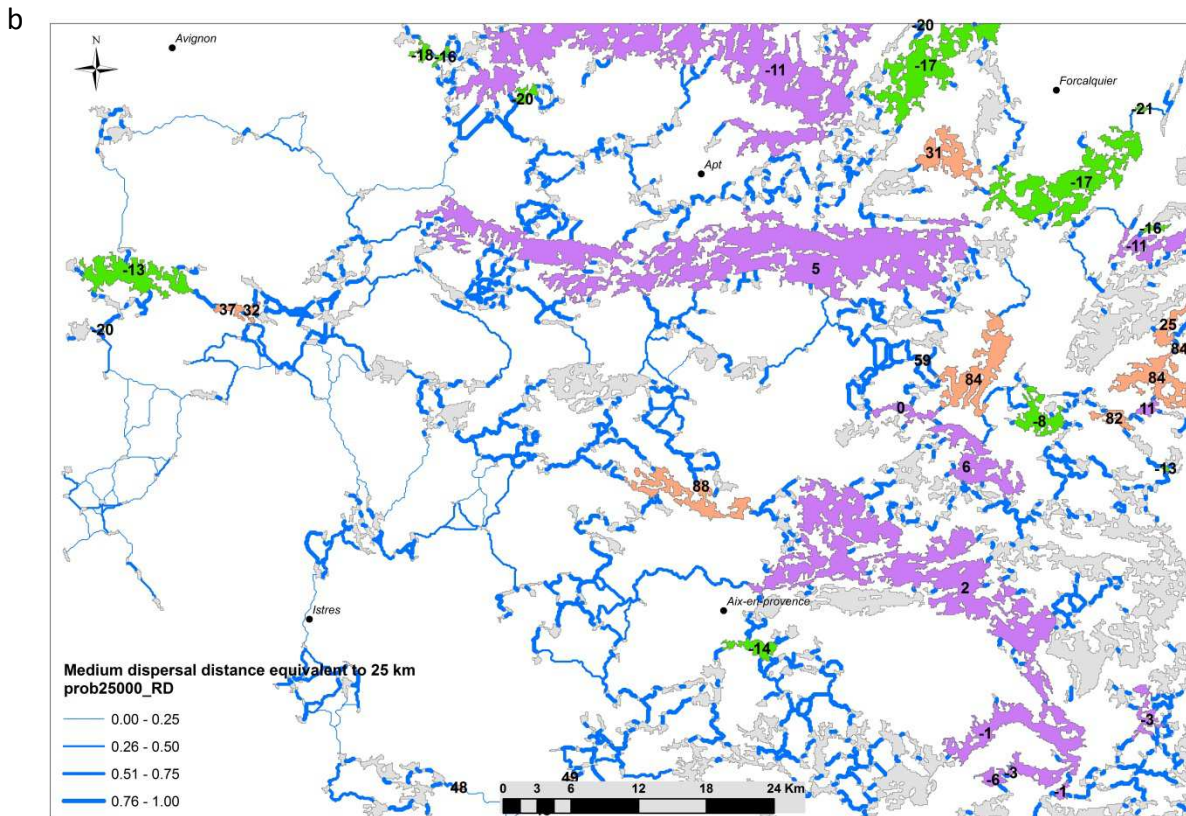


522

523 **Figure 7**



524



525

526 **Supporting Material Captions**

527

528 **Figure S1.** Correlation between habitat patch importance according to LCD-based and RD-
529 based index for binary and probabilistic indices for Region.

530 **Figure S2.** Relative contribution of each fraction intra, flux and connector to habitat network
531 connectivity according to LCD-based and RD-based indices for Region.

532 **Figure S3.** Habitat patch importance rank according to LCD-based versus RD-based indices
533 for Region.

534 **Figure S4.** Current intensity map represented areas with high density of dispersal flux, taking
535 into account alternative paths for Sub-region.

536

537 **References**

538

- 539 Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003)
540 The application of 'least-cost' modelling as a functional landscape model. *Landscape Urban*
541 *Plan* 64(4):233-247
- 542 Amos JN, Harrison KA, Radford JQ, White M, Newell G, Mac Nally R, Sunnucks P, Pavlova A
543 (2014) Species- and sex-specific connectivity effects of habitat fragmentation in a suite of
544 woodland birds. *Ecology* 95(6):1556-1568
- 545 Ayram CAC, Mendoza ME, Salicrup DRP, Granados EL (2014) Identifying potential
546 conservation areas in the Cuitzeo Lake basin, Mexico by multitemporal analysis of landscape
547 connectivity. *J. Nat. Conserv.* 22(5):424-435
- 548 Baranyi G, Saura S, Podani J, Jordan F (2011) Contribution of habitat patches to network
549 connectivity: Redundancy and uniqueness of topological indices. *Ecol Indic* 11(5):1301-1310
- 550 Beier P, Spencer W, Baldwin RF, McRae BH (2011) Toward Best Practices for Developing
551 Regional Connectivity Maps. *Conserv Biol* 25(5):879-892
- 552 Belisle M (2005) Measuring landscape connectivity: The challenge of behavioral landscape
553 ecology. *Ecology* 86(8):1988-1995
- 554 Bodin O, Saura S (2010) Ranking individual habitat patches as connectivity providers:
555 Integrating network analysis and patch removal experiments. *Ecol Model* 221(19):2393-2405
- 556 Clauzel C, Girardet X, Foltete JC (2013) Impact assessment of a high-speed railway line on
557 species distribution: Application to the European tree frog (*Hyla arborea*) in Franche-Comte.
558 *J Environ Manage* 127:125-134

- 559 Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat
560 fragmentation research. *Oikos* 121(2):161-170
- 561 Ernst BW (2014) Quantifying landscape connectivity through the use of connectivity
562 response curves. *Landscape Ecol* 29(6):963-978
- 563 Estrada E, Bodin O (2008) Using network centrality measures to manage landscape
564 connectivity. *Ecol Appl* 18(7):1810-1825
- 565 Fletcher RJ, Acevedo MA, Robertson EP (2014) The matrix alters the role of path redundancy
566 on patch colonization rates. *Ecology* 95(6):1444-1450
- 567 Foltete JC, Girardet X, Clauzel C (2014) A methodological framework for the use of landscape
568 graphs in land-use planning. *Landscape Urban Plan* 124:140-150
- 569 Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: A guide
570 to construction, analysis and application for conservation. *Biol Conserv* 144(1):44-55
- 571 Garcia-Feced C, Saura S, Elena-Rossello R (2011) Improving landscape connectivity in forest
572 districts: A two-stage process for prioritizing agricultural patches for reforestation. *Forest*
573 *Ecol Manag* 261(1):154-161
- 574 Gimona A, Poggio L, Brown I, Castellazzi M (2012) Woodland networks in a changing climate:
575 Threats from land use change. *Biol Conserv* 149(1):93-102
- 576 Gurrutxaga M, Rubio L, Saura S (2011) Key connectors in protected forest area networks and
577 the impact of highways: A transnational case study from the Cantabrian Range to the
578 Western Alps (SW Europe). *Landscape Urban Plan* 101(4):310-320
- 579 Gurrutxaga M, Saura S (2014) Prioritizing highway defragmentation locations for restoring
580 landscape connectivity. *Environ Conserv* 41(2):157-164
- 581 Koen EL, Bowman J, Walpole AA (2012) The effect of cost surface parameterization on
582 landscape resistance estimates. *Molecular Ecology Resources* 12(4):686-696

- 583 Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The Effect of Map Boundary on Estimates
584 of Landscape Resistance to Animal Movement. *Plos One* 5(7)
- 585 LaPoint S, Gallery P, Wikelski M, Kays R (2013) Animal behavior, cost-based corridor models,
586 and real corridors. *Landscape Ecol* 28(8):1615-1630
- 587 Lawler JJ, Ruesch AS, Olden JD, McRae BH (2013) Projected climate-driven faunal movement
588 routes. *Ecol Lett* 16(8):1014-1022
- 589 Marrotte RR, Gonzalez A, Millien V (2014) Landscape resistance and habitat combine to
590 provide an optimal model of genetic structure and connectivity at the range margin of a
591 small mammal. *Mol Ecol* 23(16):3983-3998
- 592 Mateo-Sanchez MC, Balkenhol N, Cushman S, Perez T, Dominguez A, Saura S (2015)
593 Estimating effective landscape distances and movement corridors: comparison of habitat
594 and genetic data. *Ecosphere* 6(4)
- 595 McRae BH (2012) Pinchpoint Mapper Connectivity Analysis Software. The Nature
596 Conservancy, Seattle WA
- 597 McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations.
598 *P Natl Acad Sci USA* 104(50):19885-19890
- 599 McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using Circuit Theory to Model Connectivity
600 in Ecology, Evolution, and Conservation. *Ecology* 89(10):2712-2724
- 601 McRae BH, Kavanagh DM (2011) Linkage Mapper Connectivity Analysis Software. The Nature
602 Conservancy, Seattle WA
- 603 Neel MC (2008) Patch connectivity and genetic diversity conservation in the federally
604 endangered and narrowly endemnic plant species *Astragalms albens* (Fabaceae). *Biol*
605 *Conserv* 141(4):938-955

- 606 Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based
607 landscape connectivity indices: towards the prioritization of habitat patches and corridors for
608 conservation. *Landscape Ecol* 21(7):959-967
- 609 Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a
610 graph-theoretic approach. *Landscape Ecol* 24(2):253-266
- 611 Poor EE, Loucks C, Jakes A, Urban DL (2012) Comparing Habitat Suitability and Connectivity
612 Modeling Methods for Conserving Pronghorn Migrations. *Plos One* 7(11)
- 613 Rayfield B, Fortin MJ, Fall A (2011) Connectivity for conservation: a framework to classify
614 network measures. *Ecology* 92(4):847-858
- 615 Roever CL, van Aarde RJ, Leggett K (2013) Functional connectivity within conservation
616 networks: Delineating corridors for African elephants. *Biol Conserv* 157:128-135
- 617 Rowcliffe JM, Carbone C, Kays R, Kranstauber B, Jansen PA (2012) Bias in estimating animal
618 travel distance: the effect of sampling frequency. *Methods Ecol Evol* 3(4):653-662
- 619 Saura S, Bodin O, Fortin MJ (2014) Stepping stones are crucial for species' long-distance
620 dispersal and range expansion through habitat networks. *J Appl Ecol* 51(1):171-182
- 621 Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in
622 landscape conservation planning: Comparison with existing indices and application to a case
623 study. *Landscape Urban Plan* 83(2-3):91-103
- 624 Saura S, Rubio L (2010) A common currency for the different ways in which patches and links
625 can contribute to habitat availability and connectivity in the landscape. *Ecography* 33(3):523-
626 537
- 627 Saura S, Torne J (2009) Conefor Sensinode 2.2: A software package for quantifying the
628 importance of habitat patches for landscape connectivity. *Environ Modell & Softw* 24(1):135-
629 139

- 630 Shah VB, McRae BH Circuitscape: a tool for landscape ecology. In: Varoquaux G., Vaught, T.,
631 Millman, J. (ed) Proceedings of the 7th Python in Science Conference (SciPy 2008), 2008. pp.
632 62-66
- 633 Stevens VM, Verkenne C, Vandewoestijne S, Wesselingh RA, Baguette M (2006) Gene flow
634 and functional connectivity in the natterjack toad. *Mol Ecol* 15(9):2333-2344
- 635 Urban D, Keitt T (2001) Landscape connectivity: A graph-theoretic perspective. *Ecology*
636 82(5):1205-1218
- 637 Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. *Ecol Lett*
638 12(3):260-273
- 639 Verbeylen G, De Bruyn L, Adriaensen F, Matthysen E (2003) Does matrix resistance influence
640 Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? *Landscape Ecol*
641 18(8):791-805
- 642 Wang JL (2004) Application of the one-migrant-per-generation rule to conservation and
643 management. *Conserv Biol* 18(2):332-343
- 644 Watts K, Eycott AE, Handley P, Ray D, Humphrey JW, Quine CP (2010) Targeting and
645 evaluating biodiversity conservation action within fragmented landscapes: an approach
646 based on generic focal species and least-cost networks. *Landscape Ecol* 25(9):1305-1318
- 647 Wauters LA, Verbeylen G, Preatoni D, Martinoli A, Matthysen E (2010) Dispersal and habitat
648 cuing of Eurasian red squirrels in fragmented habitats. *Popul Ecol* 52(4):527-536
- 649 Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a
650 review. *Landscape Ecol* 27(6):777-797
- 651 Zetterberg A, Mortberg UM, Balfors B (2010) Making graph theory operational for landscape
652 ecological assessments, planning, and design. *Landscape Urban Plan* 95(4):181-191
- 653

