

**This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.**

**Author(s):** Bergès, Laurent; Avon, Catherine; Bezombes, Lucie; Clauzel, Céline; Duflot, Rémi; Foltête, Jean-Christophe; Gaucherand, Stéphanie; Girardet, Xavier; Spiegelberger, Thoma

**Title:** Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling

**Year:** 2020

**Version:** Accepted version (Final draft)

**Copyright:** © 2020 Elsevier

**Rights:** CC BY-NC-ND 4.0

**Rights url:** <https://creativecommons.org/licenses/by-nc-nd/4.0/>

**Please cite the original version:**

Bergès, L., Avon, C., Bezombes, L., Clauzel, C., Duflot, R., Foltête, J.-C., Gaucherand, S., Girardet, X., & Spiegelberger, T. (2020). Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling. *Journal of Environmental Management*, 256, Article 109950. <https://doi.org/10.1016/j.jenvman.2019.109950>

1 **Environmental mitigation hierarchy and biodiversity offsets revisited**  
2 **through habitat connectivity modelling**

3

4 Laurent Bergès<sup>a</sup>, Catherine Avon<sup>b</sup>, Lucie Bezombes<sup>a</sup>, Céline Clauzel<sup>c</sup>, Rémi Duflot<sup>d,e</sup>, Jean-Christophe  
5 Foltête<sup>f</sup>, Stéphanie Gaucherand<sup>a</sup>, Xavier Girardet<sup>f</sup>, Thomas Spiegelberger<sup>a</sup>

6

7 <sup>a</sup> Univ. Grenoble Alpes, Irstea, UR LESSEM, 2, rue de la papeterie, BP 76, F-38402 Saint-Martin-  
8 d'Hères Cedex, France

9 <sup>b</sup> Semperfloris, 10 rue du Petit Jean, 38610 Gières, France

10 <sup>c</sup> University Paris-Diderot, Sorbonne Paris Cité, LADYSS, UMR 7533 CNRS, 5 rue Thomas Mann,  
11 75013 Paris, France

12 <sup>d</sup> Department of Biological and Environmental Sciences, University of Jyväskylä, P.O. Box 35, FI-  
13 40014 Jyväskylä, Finland

14 <sup>e</sup> School of Resource Wisdom, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland

15 <sup>f</sup> ThéMA, UMR 6049 CNRS / University Bourgogne Franche-Comté, 32, rue Mégevand, 25030  
16 Besançon, France

17

18 \* Corresponding author; e-mail: [laurent.berges@irstea.fr](mailto:laurent.berges@irstea.fr); phone: +33 (0)4 76 76 27 72

19

20 **Key-words**

21 Spatial conservation planning, environmental impact assessment, green veining, habitat reachability  
22 metric, landscape graph, No Net Loss.

23

## 24 **Abstract**

25 Biodiversity loss is accelerating because of unceasing human activity and land clearing for  
26 development projects (urbanisation, transport infrastructure, mining and quarrying...). Environmental  
27 policy-makers and managers in different countries worldwide have proposed the mitigation hierarchy  
28 to ensure the goal of "no net loss (NNL) of biodiversity" and have included this principle in  
29 environmental impact assessment processes. However, spatial configuration is hardly ever taken into  
30 account in the mitigation hierarchy even though it would greatly benefit from recent developments in  
31 habitat connectivity modelling incorporating landscape graphs. Meanwhile, national, European and  
32 international commitments have been made to maintain and restore the connectivity of natural habitats  
33 to face habitat loss and fragmentation.

34 Our objective is to revisit the mitigation hierarchy and to suggest a methodological framework for  
35 evaluating the environmental impact of development projects, which includes a landscape connectivity  
36 perspective. We advocate the use of the landscape connectivity metric *equivalent connectivity (EC)*,  
37 which is based on the original concept of "amount of reachable habitat". We also refine the three main  
38 levels of the mitigation hierarchy (impact avoidance, reduction and offset) by integrating a landscape  
39 connectivity aspect.

40 We applied this landscape connectivity framework to a simple, virtual habitat network composed of 14  
41 patches of varying sizes. The mitigation hierarchy was addressed through graph theory and *EC* and  
42 several scenarios of impact avoidance, reduction and compensation were tested.

43 We present the benefits of a habitat connectivity framework for the mitigation hierarchy, provide  
44 practical recommendations to implement this framework and show its use in real case studies that had  
45 previously been restricted to one or two steps of the mitigation hierarchy. We insist on the benefits of  
46 a habitat connectivity framework for the mitigation hierarchy and for ecological equivalence  
47 assessment. In particular, we demonstrate why it is risky to use a standard offset ratio (the ratio  
48 between the amount of area negatively impacted and the compensation area) without performing a  
49 connectivity analysis that includes the landscape surrounding the zone impacted by the project. We  
50 also discuss the limitations of the framework and suggest potential improvements. Lastly, we raise  
51 concerns about the need to rethink the strategy for biodiversity protection. Given that wild areas and  
52 semi-natural habitats are becoming scarcer, in particular in industrialised countries, we are convinced  
53 that the real challenge is to quickly reconsider the current vision of "developing first, then assessing  
54 the ecological damage", and instead urgently adopt an upstream protection strategy that would identify  
55 and protect the land that must not be lost if we wish to maintain viable species populations and  
56 ecological corridors allowing them the mobility necessary to their survival.

57

## 58 **1. Introduction**

59 Biodiversity loss has accelerated in recent decades (IPBES, 2019) and has become a major  
60 environmental concern. Two of the main drivers of biodiversity erosion are anthropogenic activities  
61 and land cover change that result in natural habitat loss and fragmentation (Fahrig, 2017; Newbold et  
62 al., 2016). Following the Convention on Biological Diversity in Rio (1992), a large number of  
63 countries adopted the mitigation hierarchy to slow down biodiversity erosion (Bull et al., 2016;  
64 Business and Biodiversity Offsets Programme, 2012). The mitigation hierarchy includes three steps  
65 designed to regulate development project impacts on biodiversity: (i) avoiding impacts by looking for  
66 alternative locations for development where impacts will be less severe, (ii) reducing the impacts at  
67 the chosen development site, and (iii) offsetting residual unavoidable damage on biodiversity (Bull et  
68 al., 2016). The whole process should lead to No Net Loss (NNL) of biodiversity, where all the impacts  
69 of a development project on biodiversity have been minimized and fully compensated for (Bull et al.,  
70 2016). Biodiversity offset policies that require NNL of biodiversity are in place in over 80 countries  
71 (Maron et al., 2018), where they target different components of biodiversity (Bezombes et al., 2018;  
72 Carreras Gamarra et al., 2018). For example, the mitigation hierarchy in France should apply to  
73 biodiversity as a whole but, in practise, only applies to protected species and habitats (*i.e.* Natura  
74 2000) including wetlands and woodlands ("*Law for the Recovery of Biodiversity, Nature and*  
75 *Landscapes*", law n°2016-1087 of 8 August 2016). In Australia, the offset policy targets endemic  
76 vegetation (Gibbons and Lindenmayer, 2007) and in the USA, wetland functions and endangered  
77 species habitats must be offset under the *Clean Water and Endangered Species Acts*.

78 However, mitigation planning often underestimated the impacts of development projects on  
79 landscape connectivity (Bruggeman et al., 2005). Moreover, even when it is considered, landscape  
80 connectivity is not assessed sufficiently in advance to be included in a mitigation hierarchy process  
81 (Clauzel et al., 2015; Kujala et al., 2015; Li et al., 2017; Underwood, 2011). In theory, the Law for the  
82 Recovery of Biodiversity, Nature and Landscapes in France obliges developers to assess the impact of  
83 their project at the landscape level, in particular for the offset aspect (article 69): "*Compensation*  
84 *measures are implemented as a priority on the damaged site or, in any case, in its vicinity, in order to*  
85 *guarantee its sustainable functions*". The methodological framework for environmental assessments  
86 clearly changed with this law, but the legislation does not clearly specify how to proceed in order to  
87 meet the objective of preserving connectivity.

88 Conversely, when connectivity studies focus on conservation and restoration measures expected to  
89 compensate for the negative effects of habitat loss and fragmentation, they usually do not explicitly  
90 refer to the NNL objective [but see Bruggeman et al. (2005), Kiesecker et al. (2009), Underwood  
91 (2011), Dalang et Hersperger (2012), Kujala et al. (2015) and Tarabon et al. (2019a, b)] and none of  
92 the studies to date concern the full spectrum of the mitigation hierarchy (*i.e.* including impact  
93 avoidance, reduction and offset). Therefore, the main challenges today are to combine the mitigation

94 hierarchy with conservation planning, and to switch from the current vision where the environmental  
95 impacts of development projects are assessed at a local scale to a vision where impacts and solutions  
96 are addressed at a larger geographical scale and include landscape connectivity issues (Kiesecker et  
97 al., 2009; Kujala et al., 2015).

98 The current application of the NNL objective suffers from several practical limitations (Gardner et  
99 al., 2013). First, any type of development project in any location is likely to have an impact on  
100 biodiversity in the wider landscape, because any project could cause the disruption or degradation of  
101 species fluxes between habitat patches. This aspect is currently disregarded in the local-scale  
102 application of NNL. Second, offset areas near the impacted site and of similar habitat types are usually  
103 preferred, but little effort is made to ensure that the locations chosen as offset sites provide the greatest  
104 conservation benefit (Saenz et al., 2013). Further, the calculation of offset ratios, *i.e.* the ratio between  
105 damaged and compensation areas, even if scaled to include success uncertainty and the delayed  
106 emergence of offsetting gains for biodiversity (Kujala et al., 2015), assumes that the location of the  
107 impacted or offset sites within the habitat network does not matter. Third, even if linear transportation  
108 infrastructure projects, which cross many ecosystems over wide areas, naturally incorporate the  
109 landscape context (Clauzel et al., 2015; Loro et al., 2015), the assessment of other local development  
110 projects such as storage sheds, power stations and quarries simply follows a "project-by-project"  
111 procedure. This application of the mitigation hierarchy ignores the cumulative landscape-scale impacts  
112 of several development projects within the same geographic region (Bigard et al., 2017; Kiesecker et  
113 al., 2010; Tarabon et al., 2019b). We believe that these challenges could be better addressed through a  
114 landscape connectivity approach.

115 Meanwhile, connectivity conservation has become a central objective in conservation planning in  
116 the last decades (Boitani et al., 2007; Crooks and Sanjayan, 2006; Gonzalez et al., 2017; Jongman et  
117 al., 2004). Political commitments have been made at national, continental and global scales: the green-  
118 blue veining from the "Grenelle Environnement" in France ([www.trameverteetbleue.fr](http://www.trameverteetbleue.fr)), the Green  
119 Infrastructure Strategy in Europe ([http://ec.europa.eu/environment/nature/ecosystems/index\\_en.htm](http://ec.europa.eu/environment/nature/ecosystems/index_en.htm)),  
120 Aichi Biodiversity Target 11 of the Strategic Plan for Biodiversity 2011-2020 of the Convention on  
121 Biological diversity at the global scale (<https://www.cbd.int/sp/>). Compared to previous biodiversity  
122 conservation schemes, these strategies emphasise the role of biological corridors connecting protected  
123 areas together and linking them to the wider landscape (Bennett and Mulongoy, 2006; Boitani et al.,  
124 2007). Landscape connectivity is defined as the degree to which the landscape facilitates the  
125 movement of species, individuals and genes between habitat resources (Taylor et al., 1993). Recent  
126 developments in landscape ecology have proposed new approaches of landscape functional  
127 connectivity that provide meaningful guidance for conservation decisions (Bergsten and Zetterberg,  
128 2013; Correa Ayram et al., 2016; Saura and de la Fuente, 2017). Habitat network analysis based on  
129 landscape graphs and associated connectivity metrics (Rayfield et al., 2011; Saura and Rubio, 2010;

130 Urban and Keitt, 2001) allow environmental managers to identify the natural areas that should be  
131 priorities for conservation at the landscape scale (Saura and de la Fuente, 2017).

132 Our aim therefore is to enhance the NNL objective by proposing a methodological framework for  
133 assessing the environmental impact of development projects that would consider habitat connectivity  
134 issues. First, we present the methodological framework based on landscape graphs and related  
135 connectivity metrics and explain how it would improve the implementation of the mitigation  
136 hierarchy. Second, we illustrate our proposed approach through a virtual example. Finally, we discuss  
137 the benefit of our habitat connectivity framework, provide practical recommendations and real case  
138 applications, discuss the framework's limitations and suggest potential improvements.

## 139 **2. Landscape connectivity analysis**

140 A convenient, and popular, model for conceptualizing habitat networks is the 'patch-corridor-  
141 matrix model' (Forman, 1995), which considers three landscape elements: (1) habitat patches – any  
142 discrete area that is used by a species for reproduction, food and shelter; (2) corridors – a functional  
143 zone connecting wildlife populations otherwise separated by human activities or structures, which  
144 allows the exchange of individuals between populations; and (3) the matrix – defined as the non-  
145 habitat portion of the landscape in which habitat patches and corridors are embedded.

146 Landscape graphs are simplified representations of habitat networks where habitat patches appear  
147 as nodes and the potential movements of individuals or gene fluxes between patches appear as links  
148 connecting pairs of nodes (Urban et al., 2009). Among the different connectivity metrics used for a  
149 graph and that include species dispersal capacity (Rayfield et al., 2011), the equivalent connectivity  
150 metric *EC* addresses the wider concept of 'amount of reachable habitat' for a focal species or group of  
151 species at the landscape scale (Saura et al., 2011; Saura and Rubio, 2010). Habitat reachability  
152 assumes connectivity exists within the habitat patch itself and integrates the amount of habitat and the  
153 degree of connectivity between habitat patches within a common metric (Saura and Rubio, 2010). *EC*  
154 corresponds to "*the size of a single patch (maximally connected) that would provide the same*  
155 *probability of connectivity as the actual habitat pattern in the landscape*" (Saura et al., 2011). *EC*  
156 fulfils all the desired properties that a connectivity metric should have for landscape conservation  
157 planning purposes and to adequately integrate connectivity in landscape planning applications; *i.e.*  
158 effective detection of relevant changes that occur in the landscape and the ability to identify the most  
159 critical landscape elements; see Table 1 in Saura and Pascual-Hortal (2007). Using *EC* is of particular  
160 interest in terms of interpretation because changes in *EC* can be compared to changes in total habitat  
161 area *S*. *EC* is the amount of reachable/connected habitat and the difference *S-EC* is the amount of  
162 unreachable/unconnected habitat. *EC* is based on node attribute (patch area, habitat quality, quality-  
163 weighted habitat area, population size...) and link attribute transformed into a probability of dispersal

164  $p_{ij}$  between nodes  $i$  and  $j$ .  $p_{ij}$  values are usually calculated with a decreasing exponential function of the  
 165 distance  $d_{ij}$  between patch  $i$  and  $j$ , taking into account the dispersal capacity of the focal species:

$$166 \quad p_{ij} = e^{-\alpha d_{ij}} \quad (1)$$

167 where  $\alpha$  is a distance-decay coefficient.  $\alpha$  is usually set so that  $p_{ij}=0.5$  for the median or mean  
 168 dispersal distance of the focal species, or so that  $p_{ij}=0.05$  equals the maximal dispersal distance (Saura  
 169 and Pascual-Hortal, 2007). These distances are generally obtained from least-cost pathways or least-  
 170 cost corridors through species-specific resistance surfaces (Avon and Bergès, 2016; Rayfield et al.,  
 171 2011); this accounts for the species' capacity to move through the different elements of the landscape  
 172 matrix. Species-specific dispersal distances for animals can be obtained by merging literature reviews,  
 173 then estimating distances from body size and life-history traits (Albert et al., 2017; Sahraoui et al.,  
 174 2017).

175 The metric  $EC$  for a whole network is calculated as follows (Saura et al., 2011):

$$176 \quad EC = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*} \quad (2)$$

177 where  $n$  is the number of nodes,  $a_i$  is the attribute of node  $i$ ,  $a_j$  is the attribute of node  $j$  and  $p_{ij}^*$  is  
 178 the maximum product probability between node  $i$  and  $j$ , *i.e.* the maximum value of the product of the  
 179 link weights ( $p_{ij}$ ) of all the possible paths connecting patches  $i$  and  $j$ . One or several intermediate links  
 180 can be included when computing  $p_{ij}^*$ , thus representing all the intermediate steps that an individual  
 181 would have to cross when following the 'optimal' path (in terms of probability) from  $i$  to  $j$ . If  $i=j$ , then  
 182  $p_{ij}^* = 1$  (a patch can always be reached from itself).

183 Land use change caused either by development projects or landscape restoration will modify the  
 184 habitat network, and therefore the graph structure. Overall change in the habitat network is measured  
 185 by the absolute or relative change in  $EC$ , computed as follows:

$$186 \quad varEC = EC_{after} - EC_{before} \quad (3)$$

$$187 \quad dEC = \frac{EC_{after} - EC_{before}}{EC_{before}} \quad (4)$$

188 where  $EC_{before}$  and  $EC_{after}$  are the values of  $EC$  before and after land use change, respectively.

189 In addition, patches can be ranked according to their contribution to overall habitat reachability by  
 190 the percentage of variation in  $EC$  ( $dEC_k$ ) following the removal of each element  $k$  from the graph  
 191 (Saura and Pascual-Hortal, 2007). To investigate whether using the standard offset ratio in ecological  
 192 equivalence assessment is relevant regarding landscape connectivity, we calculated the ratio between  
 193 the size of patch  $k$  ( $dA_k$ ) and its contribution to overall habitat reachability ( $dEC_k$ ).

### 194 **3. Integrating habitat reachability in the mitigation hierarchy**

195 To better integrate connectivity in the NNL objective, we adapted the connectivity conservation  
196 strategy proposed by Foltête *et al.* (2014) and refined the three time steps of the mitigation hierarchy:

197 (1) Impact avoidance (planning phase): Where can we locate a development project in the  
198 landscape to have minimal impacts on habitat reachability?

199 (2) Impact reduction (implementation phase): Once the geographical location of the development  
200 project has been chosen, where and how can we reduce the impact on habitat reachability?

201 (3) Impact offset (post-implementation phase): Once reduction measures have been implemented,  
202 where and how can we improve the habitat network to maximise gain in habitat reachability and  
203 reach a value equal or higher than the habitat reachability of the initial habitat network?

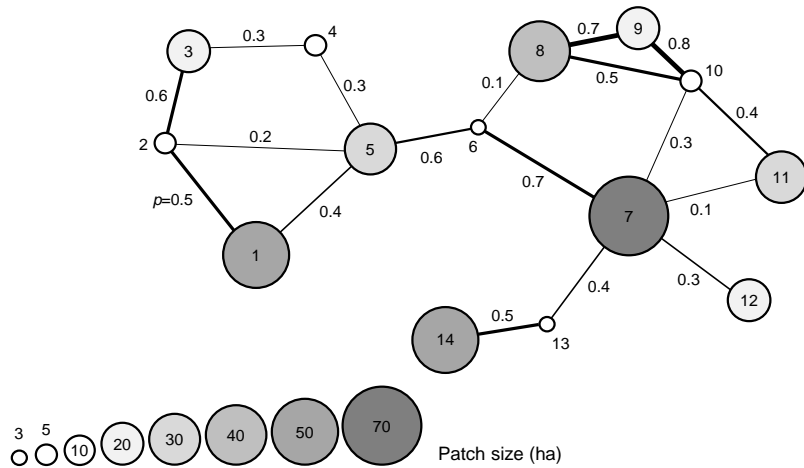
204 Decisions can be made with the help of successive landscape graph transformations corresponding  
205 to alternative scenarios. First, alternative avoidance scenarios can be compared for different locations  
206 proposed for the project and the scenarios can be ranked in terms of habitat reachability loss. Second,  
207 alternative reduction scenarios can be compared to detect and prioritize the best solutions to reduce  
208 habitat reachability loss, by maximising gain through one or several cumulated reduction actions.  
209 Finally, alternative offset scenarios can be proposed to prioritize the most effective solutions – *i.e.*  
210 create new habitats or improve permeability of the landscape mosaic to compensate for habitat  
211 reachability loss resulting from the project and reach the objective of "no net loss of connectivity".

### 212 **4. Application to a virtual graph**

213 Our study focuses on changes in landscape graphs, not on graph construction: abundant literature  
214 explains how to construct landscape graphs so we insist on only on a few key points related to  
215 construction in our Discussion.

216 We created a virtual graph composed of 14 patches of different sizes (from 3 to 70 ha) linked by 18  
217 connections with various connection probability values (from  $p=0.1$  to 0.8, Figure 1). We generate a  
218 graph with a specific layout to be as instructive as possible. The total patch surface area ( $S$ ) was 350 ha  
219 and the amount of reachable habitat according to *EC* was 174.9 ha (Table 1), because the probability  
220 of connection between all the patches were below 1. All network connectivity analyses were  
221 performed with the *Conefor* software (Saura and Torné, 2009).





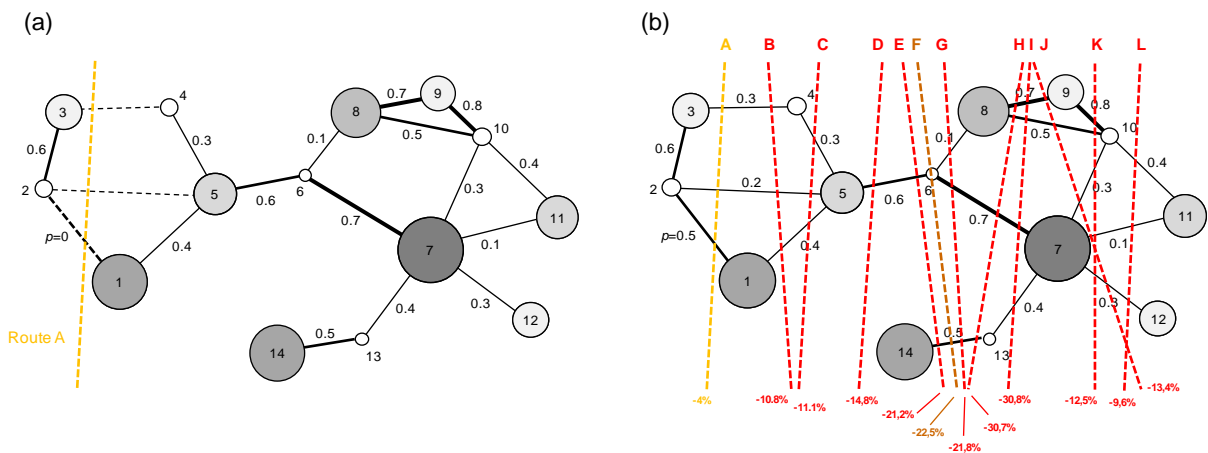
222

223 **Figure 1.** Virtual habitat network composed of 14 nodes and 18 links. Graph nodes are represented by  
 224 numbered circles (circle size proportional to patch area) and links by straight lines connecting the  
 225 nodes with a probability of connection  $p_{ij}$  (line thickness proportional to  $p_{ij}$ ).  
 226

227 **Impact avoidance**

228 We simulated the impact of a linear transport infrastructure (LTI) that would cross the landscape  
 229 from north to south and removed the dispersal links intersected by the LTI (Figure 2a). This reduced  
 230 the probability of connection between links 1-2, 2-5 and 3-4 to zero because we assumed that the LTI  
 231 was an ecological barrier for the focal species in the NNL objective. In order to identify the  
 232 infrastructure location (s) that would avoid major impact on the habitat network for the focal species,  
 233 we tested then ranked 12 potential routes by degree of variation in  $EC$  (Figure 2b, Table 1). We  
 234 assumed that eleven of the routes did not go through any habitat patches, only the landscape matrix;  
 235 however, *route F* passes through patch 6, entirely removing it. In our study case, *route A* was the least  
 236 impacting while the highest impact routes, *H* and *I*, did up to 7.5 times more damage. Interestingly,  
 237 *route F*, which removed 3 ha of habitat (patch 6), had a lower impact than *routes H* or *I*, which only  
 238 affected links.  
 239

239



240

241 **Figure 2.** Impact avoidance: (a) changes in habitat network structure after implementation of the  
 242 linear transportation infrastructure (LTI) (*route A* in yellow), which disrupted three links: 1-2, 2-5 and  
 243 3-4 (black dotted lines); (b) the twelve potential routes tested to identify the route with the least impact  
 244 and the corresponding percentages of *EC* loss. *Route A* displayed the lowest impact on *EC* (-4.1%)  
 245 whereas routes *H* and *I* had the highest impact (-30.7% and -30.8% resp.).  
 246

|   | <i>EC</i> | $\Delta EC_{base}$ | $\Delta EC_{init}$ |
|---|-----------|--------------------|--------------------|
| <b>Impact avoidance</b>   |           |                    |                    |
| initial network   | 174.9     | -                  | 0.0                |
| route A   | 170.8     | -                  | -4.1               |
| route B   | 164.2     | -                  | -10.8              |
| route C   | 163.8     | -                  | -11.1              |
| route D   | 160.1     | -                  | -14.8              |
| route E   | 153.7     | -                  | -21.2              |
| route F   | 152.4     | -                  | -22.5              |
| route G   | 153.1     | -                  | -21.8              |
| route H   | 144.3     | -                  | -30.7              |
| route I   | 144.1     | -                  | -30.8              |
| route J   | 161.5     | -                  | -13.4              |
| route K   | 162.4     | -                  | -12.5              |
| route L   | 165.3     | -                  | -9.6               |
| <b>Impact reduction</b>   |           |                    |                    |
| <u>Baseline</u> : route H   | 144.3     | 0.0                | -30.7              |
| restoration of link 8-9   | 154.7     | 10.5               | -20.2              |
| restoration of link 8-10  | 152.3     | 8.1                | -22.6              |
| restoration of link 6-7   | 159.9     | 15.7               | -15.0              |
| restoration of link 13-14   | 150.4     | 6.2                | -24.5              |
| restoration of links 6-7 & 8-9  | 167.5     | 23.2               | -7.4               |
| restoration of links 6-7 & 8-10   | 165.4     | 21.1               | -9.5               |
| restoration of links 6-7 & 13-14  | 167.4     | 23.1               | -7.5               |
| restoration of links 6-7, 8-9 & 8-10  | 167.5     | 23.2               | -7.4               |
| restoration of links 6-7, 8-9 & 13-14   | 174.9     | 30.7               | 0.0                |
| <b>Impact offset</b>  |           |                    |                    |
| <u>Baseline</u> : route H + restoration of link 8-10                                | 152.3     | 0.0                | -22.6              |
| creation of link 1-14 ( $p=0.4$ )   | 161.8     | 9.5                | -13.1              |
| creation of a patch 15 (10 ha), link 5-15 ( $p=0.8$ ) and link<br>14-15 ( $p=0.5$ ) | 165.1     | 12.8               | -9.8               |
| patch 5 increased by 10 ha  | 156.7     | 4.4                | -18.2              |
| patch 7 increased by 10 ha  | 158.8     | 6.5                | -16.1              |
| link 6-8 improved (from $p=0.1$ to $p=0.7$ )  | 161.8     | 9.5                | -13.1              |
| creation of link 1-14 + link 6-8 improved   | 171.8     | 19.5               | -3.1               |
| creation of link 1-14 + link 6-8 improved + patch 5<br>increased by 10 ha           | 177.4     | 25.1               | 2.5                |

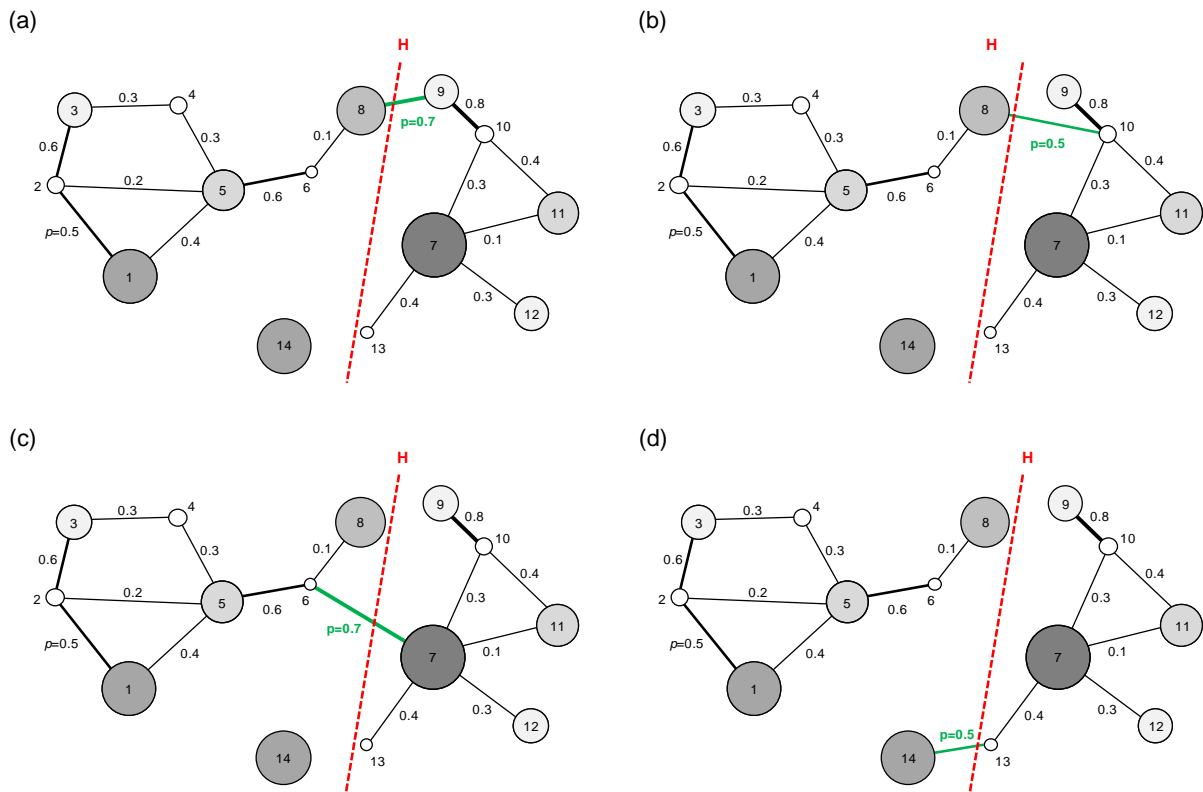
247 **Table 1.** Summary of the steps in the NNL mitigation hierarchy for habitat connectivity applied to the  
 248 virtual graph (see Figures 1-4): impact avoidance (twelve location scenarios of a linear transport  
 249 infrastructure - LTI), reduction (four wildlife crossings along the LTI and their cumulated benefits)  
 250 and offset (five scenarios and their cumulated benefits). For each scenario, we calculated *EC* and its

251 variation from the initial graph ( $\Delta EC_{init}$ ). For impact reduction, we also calculated the difference in  $EC$   
252 between the reduction scenario and the avoidance scenario ( $\Delta EC_{base}$ ). For impact offset, we calculated  
253 the difference in  $EC$  between the offset scenario and the reduction scenario ( $\Delta EC_{base}$ ).

254

### 255 **Impact reduction**

256 We chose *route H* to demonstrate impact reduction, but it should be noted that, in real conditions,  
257 we probably would have selected a route that offered a trade-off between impact avoidance and  
258 technical, funding or political aspects. Once *route H* was chosen, we compared different impact  
259 reduction scenarios with each other and with the initial state. We assumed that impact would be  
260 reduced by setting up wildlife crossings along the LTI. We hypothesised that the probability of  
261 connection  $p_{ij}$  between node  $i$  and node  $j$  would be fully restored by the wildlife crossings, an  
262 optimistic though achievable hypothesis. For *route H*, wildlife crossings would restore four broken  
263 connections (Figure 3). The four scenarios were ranked according to their ability to restore habitat  
264 reachability (Table 1). The wildlife crossing that restored link 6-7 was revealed to be the most efficient  
265 way to reduce the LTI's impact (Figure 3c), while the three other choices had a lower positive impact.  
266 Repairing two links (6-7 and 8-9) had the highest cumulated increase in  $EC$  (Table 1). It is important  
267 to note, however, that none of these options was able to offset the total impact of *route H*, as  $EC$   
268 remained below its reference value in all cases: restoring link 6-7 alone displayed a net deficit of 15.0  
269 ha while restoring links 6-7 and 8-9 (the best mitigation) resulted in a net loss of 7.4 ha. In our  
270 example, we limited the number of wildlife crossings to four, parallel to the number of dispersal links  
271 disrupted by the LTI, but more potential graph change are expected in much larger graphs. To solve  
272 this problem, *Graphab 2.0* software (Foltête et al., 2012) has a stepwise algorithm that iteratively finds  
273 the first best location by screening each of the  $p$  links that intersect the infrastructure and seeking the  
274 second most beneficial location among the remaining  $p-1$  links once the first link is restored, and so on  
275 (Tarabon et al., 2019b).



276

277

278

279

280

**Figure 3.** Impact reduction after building *route H*. Impact reduction was calculated for four possible wildlife crossing locations: restoring link 8-9 (a), link 8-10 (b), link 6-7 (c) or link 13-14 (d). Restored links are in green. The stepwise restoration of several wildlife crossings is presented in Table 1.

### 281 Impact offset

282

283

284

285

286

287

288

289

290

291

292

293

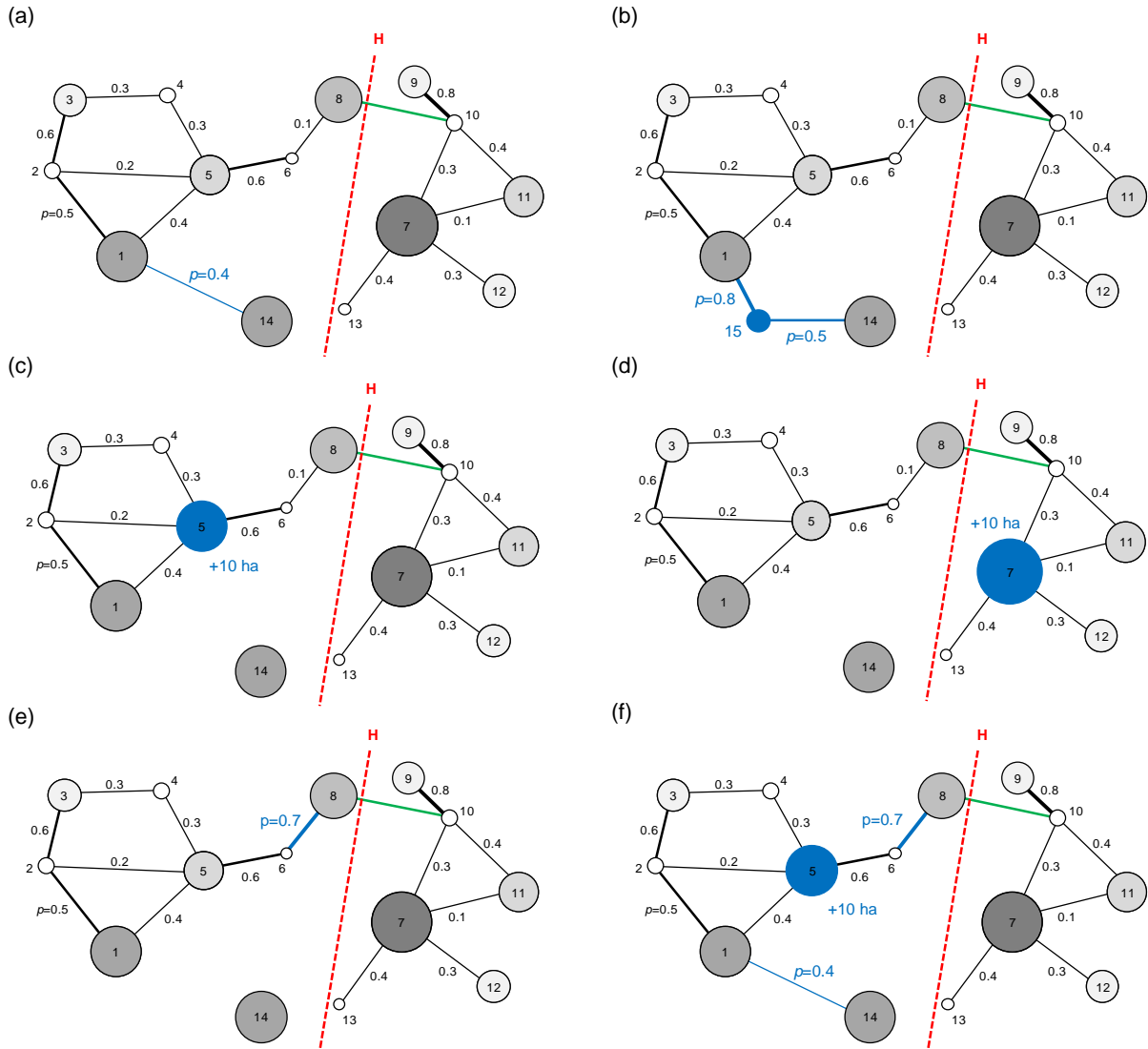
294

295

296

Once the LTI route chosen, technical or cost reasons could prevent from construct as many crossings as the number of disrupted links. We assumed that the reduction scenario involved only one wildlife crossing reconnecting patches 6 and 8. However, wildlife crossings are not the only way to reverse negative LTI effects and reach NNL of connectivity. Different types of offsets can be proposed: (1) increasing the area of existing patches, (2) creating/improving links between patches and (3) creating new patches and their associated links. We therefore proposed five scenarios with additional offsets for *route H* to illustrate this approach (Figure 4). In order to quantify the gain in connectivity from the offset measures, *EC* was computed for each offset scenario and compared with two *EC* values: (a) the value obtained after impact avoidance and reduction and (b) the initial *EC* value (Table 1). For the first scenario, we created a new corridor between patches 1 and 14 to reconnect patch 14 with the western part of the network after the patch had become isolated. For the second scenario, we added a new patch with its associated links between patches 1 and 14. This scenario was the most interesting because connectivity increased by 12.8 ha (Table 1); however, a net loss of 9.8 ha remained. The three other scenarios were less interesting than the first two, but we did find that *EC* gain depended on where the 10 ha of new habitat were located (we compared an increase

297 in size for patches 5 and 7). To fully offset the impact of *route H*, we had to combine three scenarios:  
 298 creating link 1-14, improving link 6-8 and increasing patch 5 by 10 ha.  
 299



300  
 301 **Figure 4.** Impact offset: scenarios to offset the impacts of *route H*. Six options were compared: (a)  
 302 establishment of a corridor between patches 1 and 14; (b) creation of a new patch 15 and its related  
 303 links between patches 1 and 14; (c) patch 5 increased by 10 ha; (d) patch 7 increased by 10 ha; (e) link  
 304 6-8 improved; (f) three measures combined (creation of link 1-14 + link 6-8 improved + patch 5  
 305 increased by 10 ha). Graph changes related to offset in blue and reduction in green.

306

307 **Patch importance**

308 The ratio between the contribution of each patch  $k$  to overall habitat reachability ( $dEC_k$ ) and patch  
 309 size ( $dA_k$ ) varied considerably (Table 2): some patches had a ratio above 1 (6, 13 and 10), meaning that  
 310 the contribution of these patches to overall reachability were higher than their size: for example, for

311 patch 6, its contribution to overall connectivity is 5-fold higher than its size (Table 2). Conversely,  
 312 other patches displayed a ratio below 1 (e.g. 3, 4 11, 12).  
 313

| <i>Patch k</i> | <i>VarA<sub>k</sub></i> | <i>VarEC<sub>k</sub></i> | <i>VarEC<sub>k</sub>/VarA<sub>k</sub></i> |
|----------------|-------------------------|--------------------------|---|
| 1              | 50                      | 19.4                     | 0.39                                      |
| 2              | 5                       | 3.4                      | 0.68                                      |
| 3              | 20                      | 4.5                      | 0.22                                      |
| 4              | 5                       | 1.1                      | 0.22                                      |
| 5              | 30                      | 22.5                     | 0.75                                      |
| 6              | 3                       | 16.2                     | 5.41                                      |
| 7              | 70                      | 50.1                     | 0.72                                      |
| 8              | 40                      | 14.9                     | 0.37                                      |
| 9              | 20                      | 9.9                      | 0.50                                      |
| 10             | 5                       | 10.1                     | 2.02                                      |
| 11             | 30                      | 8.0                      | 0.27                                      |
| 12             | 20                      | 5.4                      | 0.27                                      |
| 13             | 2                       | 7.7                      | 3.87                                      |
| 14             | 50                      | 14.8                     | 0.30                                      |

314  
 315 **Table 2.** Contribution of each patch to overall habitat area and to overall habitat reachability (patch  
 316 removal analysis). *VarA<sub>k</sub>* is patch area, *VarEC<sub>k</sub>* is the contribution of the patch in terms of *EC* resulting  
 317 from patch removal, and *VarEC<sub>k</sub>/VarA<sub>k</sub>* is the ratio between *VarEC<sub>k</sub>* and *VarA<sub>k</sub>*.

## 318 5. Discussion

### 319 How does habitat connectivity modelling enhance the application of the NNL 320 objective?

321 Populations, communities and ecological processes are more likely to be maintained in landscapes  
 322 that encompass an interconnected system of habitats than they are in landscapes where natural habitats  
 323 occur as dispersed isolated fragments (Crooks and Sanjayan, 2006). Because previous work has not  
 324 explicitly addressed the NNL of biodiversity objective, we advocate for using landscape graphs and  
 325 the connectivity metric *EC* in the mitigation hierarchy to address landscape connectivity issues  
 326 (Clauzel et al., 2015; Girardet et al., 2013; Sahraoui et al., 2017; Santini et al., 2016).

327 Modelling habitat connectivity implies a vision where impact and solutions are spatially addressed  
 328 at the landscape scale (Gardner et al., 2013; Kujala et al., 2015). Accounting for landscape  
 329 composition and configuration when addressing the NNL objective can reveal projects with a

330 significant indirect impact on the habitat network even though no habitat patches are destroyed.  
331 Indeed, changing or disrupting the connections between patches can strongly modify the flux of  
332 individuals or genes between patches and thereby reduce the probability of maintaining species  
333 populations over the long-term. In our example, even the routes that did not destroy habitat patches  
334 caused habitat reachability to decrease according to *EC* (Table 1). Currently, landscape-level impacts  
335 are not evaluated when applying the NNL objective, because impacts are only considered when habitat  
336 patches are cleared or species are removed from the patches by the project (Briggs and Hudson, 2013).  
337 Even when corridor aspects are taken into account, only local effects are considered; the global impact  
338 on landscape connectivity is not quantified.

339 Habitat connectivity modelling is designed to quantify and spatialise the expected impacts of one or  
340 several development projects in terms of habitat reachability (Girardet et al., 2013) and to optimize  
341 and prioritize areas for restoration and compensation (Li et al., 2017). This spatially-explicit approach  
342 opens up a wide range of possibilities in terms of reduction and offset scenarios, based on an objective  
343 quantification of their potential positive impact on habitat reachability (Foltête, 2019). The framework  
344 makes it possible to compare different options according to a common currency: increasing the  
345 quality/size of existing habitat patches, improving the permeability of the matrix or creating/restoring  
346 habitat patches or links (Saura and Rubio, 2010). Inversely, without calculating *EC*, it is difficult to  
347 prioritise avoidance, reduction or offsetting options. For example, it was not easy to predict whether  
348 restoring 10 ha of habitat adjacent to patch 5 or 7 would be an equivalent or a better option than  
349 improving the corridor between patches 6 and 8 (Figure 4). We also underlined that improving  
350 connections among patches was a suitable alternative to creating new patches. Using the *EC* metric  
351 makes it possible to evaluate whether gains on the offset site will compensate for losses caused by  
352 land clearing (Gibbons and Lindenmayer, 2007). Including *EC* provides a response to spatial  
353 conservation planning objectives concerned with the respective effect of habitat loss and  
354 fragmentation on biodiversity, *i.e.* how to balance mitigation efforts between restoring habitat amount  
355 and reducing patch isolation (Fahrig, 2017).

356 The *EC* metric meets the different criteria for suitability according to the standards recommended  
357 by the Business and Biodiversity Offsets Programme (2012): *EC* is quantitative and can evaluate  
358 change before and after project implementation. Using this metric is ecologically relevant because  
359 assumptions and the rationale are clearly documented. In addition, applying *EC* is a time-efficient,  
360 cost-effective and scientifically rigorous method, making it appealing for stakeholders (Bergsten and  
361 Zetterberg, 2013; Carreras Gamarra et al., 2018).

## 362 **Practical recommendations and implementation on real-world landscapes**

363 Landscape graphs and connectivity metrics combine to make a flexible holistic, approach that can  
364 be applied to terrestrial as well as aquatic ecosystems (Bishop-Taylor et al., 2015; Rincón et al., 2017;  
365 Saunders et al., 2016) at varying levels of knowledge on species ecology and biology (Saura and

366 Pascual-Hortal, 2007). We advise that practitioners follow five different steps to calculate the amount  
367 of reachable habitat for a given focal species (Avon and Bergès, 2016; Duflot et al., 2018; Tarabon et  
368 al., 2019a): (1) define the focal species, collect data (literature, expert opinions, species distribution  
369 models, radio-tracking information...) to specify the species habitat preferences and its capacity to  
370 move through the landscape, then to determine mean/maximal dispersal distances from the literature  
371 or estimate it from species traits; (2) collect maps of environmental data (topography, climate, land use  
372 maps, resource data maps, human impact index maps, distance to roads...); (3) using previous maps,  
373 model suitable habitat patches based on home-range size, individual territory, surface area for a  
374 permanent population, protected areas...; (4) parameterize resistance to species movement and model  
375 the cost of moving between habitat patches (energy cost, mortality risk, reproduction cost, physical  
376 resistance, thermal stress, habitat suitability) by applying one of the methods available (Avon and  
377 Bergès, 2016; Belisle, 2005; Coulon et al., 2015; LaPoint et al., 2013; Mcrae et al., 2008); and finally,  
378 (5) once habitat patches and cost distances have been defined, build the landscape graph and compute  
379 *EC*. Sensitivity analysis can be performed to evaluate model uncertainty, notably resistance map  
380 parameterization (Rayfield et al., 2010). Species distribution models (combining species occurrence  
381 and environmental data) can be valuable in obtaining habitat-matrix and matrix resistance maps before  
382 creating the final landscape graph and running the connectivity analysis (Duflot et al., 2018; Rödder et  
383 al., 2016; Tarabon et al., 2019b).

384 Table 3 gives an overview of the connectivity studies that have addressed one or two steps of the  
385 mitigation hierarchy, though rarely with an explicit reference to the NNL objective (Tarabon et al.,  
386 2019b). Girardet (2014) addressed impact avoidance in the case of highway construction and Vasa et  
387 al. (Vasas et al., 2009) a high-speed railway line project; they compared the connectivity impacts of  
388 several possible tracks. In each case, the analysis emphasised that a one-route scenario minimized the  
389 loss of connectivity at the regional scale. Several authors have addressed reduction impact to optimize  
390 the location of wildlife crossings along highway networks and reduce the barrier effect of transport  
391 infrastructure for different species (Ascensão et al., 2019; Gurrutxaga and Saura, 2014; Mimet et al.,  
392 2016). Lastly, Tarabon et al. (2019b) addressed avoidance and reduction scenarios to evaluate the  
393 impact on connectivity of a project completed in 2012: the new stadium in Lyon, France. They applied  
394 species distribution models, landscape graphs and *EC* to three mammals (the red squirrel, the Eurasian  
395 badger and the European hedgehog) to identify and locate avoidance and reduction measures that  
396 would best reduce project impact in accordance with the technical possibilities of the site (creation of  
397 meadows, hedges and groves and implementation of wildlife passages).

398



| Publication              | Country          | Project type | Species involved  | Connectivity indices used      | Mitigation steps addressed | Explicit ref. to NNL |
|--------------------------|------------------|--------------|---|--------------------------------|----------------------------|----------------------|
| Vasas et al. (2009)      | Hungary, Ukraine | LTI          | carabid beetle  | core index, reachability index | A                          | No                   |
| Girardet (2014)          | France           | LTI          | Virtual species (range of home range size and dispersal distance)   | <i>PC</i>                      | A, R                       | No                   |
| Gurrutxaga et al. (2014) | Spain            | LTI          | Forest species (range of dispersal distance)  | <i>PC</i>                      | R                          | No                   |
| Mimet et al. (2016)      | France           | LTI          | 8 virtual species based on 14 real species habitat preferences, daily and dispersal distances, and minimum area of habitat to support a viable population | <i>PC</i>                      | R                          | No                   |
| Tarabon et al. (2019b)   | France           | Stadium      | Three mammals (Red squirrel, Eurasian badger and European hedgehog)   | <i>EC</i>                      | A, R                       | Yes                  |
| Ascensão et al. (2019)   | Spain            | LTI          | 13 carnivorous mammals  | <i>IIC, AWM</i>                | R                          | No                   |

400

401 Table 3. Overview of the literature where landscape graphs and/or connectivity indices were used to perform environmental impact assessments of  
402 development projects. The table indicates which steps of the mitigation hierarchy were addressed: avoidance (A) or reduction (R). Please refer to the  
403 publications cited for the definition of the connectivity indices.

## 404 **Improving ecological equivalence assessment**

405 Adopting a landscape perspective within the NNL objective has implications for ecological  
406 equivalence assessment (Quétier and Lavorel, 2011). How to define offset multipliers, *i.e.* the suitable  
407 ratio between damaged and compensated amounts (areas) of biodiversity, has been extensively  
408 discussed (Laitila et al., 2014; Moilanen et al., 2009). Biodiversity offsetting is being criticized  
409 because, with this approach, certain immediate losses are exchanged for uncertain future gains  
410 (Gibbons and Lindenmayer, 2007). We agree that using *EC* does not solve this problem: indeed, while  
411 patch or link removals are immediate, the creation or restoration of good quality patches or corridors  
412 may only become effective after decades or even centuries (depending on habitat type), and with  
413 considerable uncertainty (Moilanen et al., 2009; Weissgerber et al., 2019). For example, using a  
414 simplified model to estimate the absolute minimum offset multipliers that arise from time discounting  
415 and delayed emergence of offsetting gains for biodiversity, Laitila *et al.* (2014) concluded that  
416 absolute minimum multipliers may be quite large, in the order of dozens of times larger than the loss.

417 However, so far the connectivity component of the problem has been poorly taken into account,  
418 and this may have exacerbated the ecological shortcomings of the method (Kujala et al., 2015). When  
419 we applied patch prioritization to our virtual network (Table 2), it became clear that one patch cannot  
420 simply be substituted for another one anywhere in the landscape. Instead, it is all about location. Well-  
421 connected patches (high  $varEC_k$ ) contributed more to overall reachability than their actual size  
422 indicated, while isolated or redundant patches contributed less. Thus, the ratio between the  
423 contribution of a patch to overall habitat reachability and its size mostly depends on the location of the  
424 patch within the network. In large networks composed of hundreds of patches of various sizes, the  
425 connectivity analysis is able to detect small patches with a higher contribution to overall reachability  
426 compared to their actual size. In terms of conservation, identifying these small stepping-stone habitat  
427 patches is critical: indeed, because they are small and generally are embedded in a human-modified  
428 matrix, they are more likely to be affected by development projects. They are also easier for planners  
429 to overlook.

## 430 **Methodological limitations and suggestions for improvement**

431 Among the methods available for functional connectivity modelling, graph connectivity metrics are  
432 the most operational due to a good compromise between information yielded and data requirements  
433 (Saura and de la Fuente, 2017). Connectivity models based on spatially-explicit metapopulation  
434 models can also be an alternative because they provide detailed results in terms of population  
435 dynamics (Dalang and Hersperger, 2012); however, they are more difficult for practitioners to  
436 implement (Breininger et al., 2002).

437 Another consideration is the definition of the spatial extent at which the habitat network should be  
438 investigated (Correa Ayram et al., 2016). The size of the study area depends on the extent of the

439 development project, the focal species' dispersal capacity, and the availability of land-use and  
440 environmental geo-data. We recommend adapting the extent of the study area to species dispersal  
441 capacity (Fletcher et al., 2018) and applying a buffer zone around the development project, with a  
442 radius at least equal to the maximal dispersal distance of the focal species. To assess the cumulative  
443 impact of several projects, we recommend first defining the minimum bounding polygon that includes  
444 all the projects, then creating a buffer zone with a radius at least equal to the maximal dispersal  
445 distance of the focal species around this polygon.

446 Connectivity conservation and mitigation measures are multi-species issues (Rayfield et al., 2016;  
447 Santini et al., 2016). Environmental impact assessments should always concern many species, or  
448 habitat types, as possible (Rayfield et al., 2016; Santini et al., 2016). Two generic approaches have  
449 been proposed to address multi-species conservation goals. The first approach considers a virtual  
450 "model species" living in one habitat type (forest, wetland, open-habitat...) as a proxy for the species  
451 guild living in this habitat and the range of dispersal distances to be tested and compared (Garcia-  
452 Feced et al., 2011; Lechner et al., 2017). In a second approach, landscape connectivity may be  
453 modelled for a list of real species or 'ecoprofiles'. The species can be selected with different methods,  
454 but one of the most advanced procedures selects species from a multivariate analysis of species traits  
455 known to characterise the species vulnerability to habitat fragmentation: the traits include habitat  
456 requirements, population dynamics and dispersal ability (Albert et al., 2017). The overall impact of the  
457 project can be assessed and the different scenarios of mitigation hierarchy compared by calculating the  
458 sum of the  $dEC_k$  for each species  $k$ , or a sum weighted by the importance given to each species  $k$ . In  
459 addition, the species graphs obtained for each species can be overlaid to spatialize multi-species  
460 connectivity (Albert et al., 2017; Cushman et al., 2013; Sahraoui et al., 2017; Santini et al., 2016).

461 Including cost estimates in the NNL objective would account for trade-offs between ecological  
462 benefits and operating costs and help prioritize lands to be conserved/restored/mitigated (Conrad et al.,  
463 2012; Murdoch et al., 2007; Torrubia et al., 2014). For example, Torrubia et al. (2014) identified  
464 where the removal of barriers to movement could improve connectivity the most, with and without  
465 considering the financial costs of land purchase and restoration. They found that accounting for land-  
466 purchasing costs could reduce overall restoration costs by 55% while increasing the area of land  
467 restored by 30%.

## 468 **6. Conclusion**

469 Building on previous attempts (Bruggeman et al., 2005; Dalang and Hersperger, 2012; Kujala et  
470 al., 2015; Tambosi et al., 2014; Underwood, 2011), we have presented how connectivity conservation  
471 can be included in the "no net loss" of biodiversity objective. Our starting assumption was that  
472 whatever the methodology followed, the impact of a project cannot be fully assessed at the local scale

473 but rather must be evaluated at the landscape scale, *i.e.* by considering the landscape mosaic  
474 surrounding the area concerned by the project.

475 We fully support the idea that a change in environmental policy is required to move beyond the  
476 ineffective project-by-project approach currently proposed by national and international environmental  
477 organizations if we wish to successfully offset human impact on biodiversity (Quétier et al., 2014). A  
478 more effective conservation planning policy should rely on a cumulative environmental impact  
479 assessment strategy at a large geographical scale (Bigard et al., 2017; Kiesecker et al., 2010).

480 Unfortunately, we believe that even this more ambitious objective will not be sufficient to slow  
481 down biodiversity erosion. Indeed, a detailed analysis of the offsetting measures for 24 infrastructure  
482 projects implemented in France during the period 2012-2017 highlighted the discrepancy between the  
483 principles of NNL and the implementation of the offset policy (Weissgerber et al., 2019). Because our  
484 planet is finite and the human population keeps increasing, competition for land is growing between  
485 natural ecosystems and the agricultural, urban and industrial sectors. In this context, "sustainable  
486 human development" appears to be a mirage. We must reverse our approach: instead of trying to heal  
487 the wounds of land degradation caused by human activities, we must put stronger emphasis on  
488 avoidance. To maintain the biological flow within our increasingly human-modified landscapes, we  
489 strongly advocate adopting a spatial planning policy that would identify land areas that should  
490 absolutely not be cleared for human economic needs and would set those areas aside for permanent  
491 conservation. To finally halt biodiversity erosion, there is an urgent need to identify the biological  
492 corridors that functionally connect all existing protected areas and reserve networks, to ensure those  
493 corridors are protected and to concentrate our restoration efforts on precious connecting zones (de la  
494 Fuente et al., 2018).

## 495 **Acknowledgments**

496 This work was funded by the French Ministry of the Environment through the Irstea Convention  
497 DEB 2017-2018 (project CONNECT-ERC). RD was supported by a postdoctoral fellowship from the  
498 Kone Foundation.

## 499 **Authors' contribution**

500 LB conceived the ideas and led the writing. All authors contributed substantially to the drafts and  
501 gave final approval for publication. We thank the three anonymous referees who significantly  
502 contributed to improving the quality of the manuscript.

503 **References**

- 504 Albert, C.H., Rayfield, B., Dumitru, M., Gonzalez, A., 2017. Applying network theory to prioritize  
505 multispecies habitat networks that are robust to climate and land-use change. *Conserv Biol* 31,  
506 1383-1396.
- 507 Ascensão, F., Mestre, F., Barbosa, A.M., 2019. Prioritizing road defragmentation using graph-based  
508 tools. *Landscape Urban Plan* 192, 103653.
- 509 Avon, C., Bergès, L., 2016. Prioritization of habitat patches for landscape connectivity conservation  
510 differs between least-cost and resistance distances. *Landscape Ecol* 31, 1551-1565.
- 511 Belisle, M., 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology.  
512 *Ecology* 86, 1988-1995.
- 513 Bennett, G., Mulongoy, K.J., 2006. Review of experience with ecological networks, corridors and  
514 buffer zones, Technical Series No. 23. Secretariat of the Convention on Biological Diversity,  
515 Montreal, p. 100.
- 516 Bergsten, A., Zetterberg, A., 2013. To model the landscape as a network: A practitioner's perspective.  
517 *Landscape Urban Plan* 119, 35-43.
- 518 Bezombes, L., Gaucherand, S., Spiegelberger, T., Gouraud, V., Kerbiriou, C., 2018. A set of organized  
519 indicators to conciliate scientific knowledge, offset policies requirements and operational  
520 constraints in the context of biodiversity offsets. *Ecol Indic* 93, 1244-1252.
- 521 Bigard, C., Pioch, S., Thompson, J.D., 2017. The inclusion of biodiversity in environmental impact  
522 assessment: Policy-related progress limited by gaps and semantic confusion. *J Environ Manage*  
523 200, 35-45.
- 524 Bishop-Taylor, R., Tulbure, M.G., Broich, M., 2015. Surface water network structure, landscape  
525 resistance to movement and flooding vital for maintaining ecological connectivity across  
526 Australia's largest river basin. *Landscape Ecol* 30, 2045-2065.
- 527 Boitani, L., Falcucci, A., Maiorano, L., Rondinini, C., 2007. Ecological networks as conceptual  
528 frameworks or operational tools in conservation. *Conserv Biol* 21, 1414-1422.
- 529 Breininger, D.R., Burgman, M.A., Akçakaya, H.R., O'Connell, M.A., 2002. Use of metapopulation  
530 models in conservation planning, in: Gutzwiller, K.J. (Ed.), *Applying Landscape Ecology in*  
531 *Biological Conservation*. Springer New York, New York, NY, pp. 405-427.
- 532 Briggs, S., Hudson, M.D., 2013. Determination of significance in Ecological Impact Assessment: Past  
533 change, current practice and future improvements. *Environmental Impact Assessment Review* 38,  
534 16-25.
- 535 Bruggeman, D.J., Jones, M.L., Lupi, F., Scribner, K.T., 2005. Landscape equivalency analysis:  
536 methodology for estimating spatially explicit biodiversity credits. *Environ Manage* 36, 518-534.
- 537 Bull, J.W., Gordon, A., Watson, J.E.M., Maron, M., 2016. Seeking convergence on the key concepts  
538 in 'no net loss' policy. *J Appl Ecol* 53, 1686-1693.

539 Business and Biodiversity Offsets Programme, B., 2012. Guidance notes to the standard on  
540 biodiversity offsets. BBOP, Washington, D.C.

541 Carreras Gamarra, M.J., Lassoie, J.P., Milder, J., 2018. Accounting for no net loss: A critical  
542 assessment of biodiversity offsetting metrics and methods. *J Environ Manage* 220, 36-43.

543 Clauzel, C., Xiqing, D., Gongsheng, W., Giraudoux, P., Li, L., 2015. Assessing the impact of road  
544 developments on connectivity across multiple scales: Application to Yunnan snub-nosed monkey  
545 conservation. *Biol Conserv* 192, 207-217.

546 Conrad, J.M., Gomes, C.P., van Hove, W.J., Sabharwal, A., Suter, J.F., 2012. Wildlife corridors as a  
547 connected subgraph problem. *Journal of Environmental Economics and Management* 63, 1-18.

548 Correa Ayram, C.A.C., Mendoza, M.E., Etter, A., Salicrup, D.R.P., 2016. Habitat connectivity in  
549 biodiversity conservation: A review of recent studies and applications. *Prog Phys Geog* 40, 7-37.

550 Coulon, A., Aben, J., Palmer, S.C.F., Stevens, V.M., Callens, T., Strubbe, D., Lens, L., Matthysen, E.,  
551 Baguette, M., Travis, J.M.J., 2015. A stochastic movement simulator improves estimates of  
552 landscape connectivity. *Ecology* 96, 2203-2213.

553 Crooks, K.R., Sanjayan, M., 2006. Connectivity conservation, *Conserv Biol*. Cambridge University  
554 Press, New York, p. 712.

555 Cushman, S.A., Landguth, E.L., Flather, C.H., 2013. Evaluating population connectivity for species of  
556 conservation concern in the American Great Plains. *Biodivers Conserv* 22, 2583-2605.

557 Dalang, T., Hersperger, A.M., 2012. Trading connectivity improvement for area loss in patch-based  
558 biodiversity reserve networks. *Biol Conserv* 148, 116-125.

559 de la Fuente, B., Mateo-Sánchez, M.C., Rodríguez, G., Gastón, A., Pérez de Ayala, R., Colomina-  
560 Pérez, D., Melero, M., Saura, S., 2018. Natura 2000 sites, public forests and riparian corridors: The  
561 connectivity backbone of forest green infrastructure. *Land Use Policy* 75, 429-441.

562 Dufлот, R., Avon, C., Roche, P., Bergès, L., 2018. Combining habitat suitability models and spatial  
563 graphs for more effective landscape conservation planning: an applied methodological framework  
564 and a species case study. *Journal for Nature Conservation* 46, 38-47.

565 Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. *Annual Review of Ecology,*  
566 *Evolution, and Systematics* 48, 1-23.

567 Fletcher, R.J., Reichert, B.E., Holmes, K., 2018. The negative effects of habitat fragmentation operate  
568 at the scale of dispersal. *Ecology* 99, 2176-2186.

569 Foltête, J.-C., 2019. How ecological networks could benefit from landscape graphs: A response to the  
570 paper by Spartaco Gippoliti and Corrado Battisti. *Land Use Policy* 80, 391-394.

571 Foltête, J.C., Clauzel, C., Vuidel, G., 2012. A software tool dedicated to the modelling of landscape  
572 networks. *Environ Modell Softw* 38, 316-327.

573 Foltête, J.C., Girardet, X., Clauzel, C., 2014. A methodological framework for the use of landscape  
574 graphs in land-use planning. *Landscape Urban Plan* 124, 140-150.

575 Forman, R.T.T., 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University  
576 Press, Cambridge.

577 Garcia-Feced, C., Saura, S., Elena-Rossello, R., 2011. Improving landscape connectivity in forest  
578 districts: A two-stage process for prioritizing agricultural patches for reforestation. *Forest Ecol*  
579 *Manag* 261, 154-161.

580 Gardner, T.A., Von Hase, A., Brownlie, S., Ekstrom, J.M.M., Pilgrim, J.D., Savy, C.E., Stephens,  
581 R.T.T., Treweek, J., Ussher, G.T., Ward, G., Ten Kate, K., 2013. Biodiversity offsets and the  
582 challenge of achieving no net loss. *Conserv Biol* 27, 1254-1264.

583 Gibbons, P., Lindenmayer, D.B., 2007. Offsets for land clearing: No net loss or the tail wagging the  
584 dog? *Ecological Management & Restoration* 8, 26-31.

585 Girardet, X., 2014. Paysage & infrastructures de transport - modélisation des impacts des  
586 infrastructures sur les réseaux écologiques, Ecole Doctorale "Langues, Espaces, Temps,  
587 Sociétés". Université de Franche-Comté, Besançon, p. 261.

588 Girardet, X., Foltête, J.C., Clauzel, C., 2013. Designing a graph-based approach to landscape  
589 ecological assessment of linear infrastructures. *Environmental Impact Assessment Review* 42, 10-  
590 17.

591 Gonzalez, A., Thompson, P., Loreau, M., 2017. Spatial ecological networks: planning for  
592 sustainability in the long-term. *Curr Opin Env Sust* 29, 187-197.

593 Gurrutxaga, M., Saura, S., 2014. Prioritizing highway defragmentation locations for restoring  
594 landscape connectivity. *Environ Conserv* 41, 157-164.

595 IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and  
596 ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and  
597 Ecosystem Services. IPBES secretariat, Bonn, Germany.

598 Jongman, R.H.G., Külvik, M., Kristiansen, I., 2004. European ecological networks and greenways.  
599 *Landscape Urban Plan* 68, 305-319.

600 Kiesecker, J.M., Copeland, H., Pocerwicz, A., McKenney, B., 2010. Development by design: blending  
601 landscape-level planning with the mitigation hierarchy. *Front Ecol Environ* 8, 261-266.

602 Kiesecker, J.M., Copeland, H., Pocerwicz, A., Nibbelink, N., Mckenney, B., Dahlke, J., Holloran, M.,  
603 Stroud, D., 2009. A framework for implementing biodiversity offsets: selecting sites and  
604 determining scale. *Bioscience* 59, 77-84.

605 Kujala, H., Whitehead, A.L., Morris, W.K., Wintle, B.A., 2015. Towards strategic offsetting of  
606 biodiversity loss using spatial prioritization concepts and tools: A case study on mining impacts in  
607 Australia. *Biol Conserv* 192, 513-521.

608 Laitila, J., Moilanen, A., Pouzols, F.M., 2014. A method for calculating minimum biodiversity offset  
609 multipliers accounting for time discounting, additionality and permanence. *Methods Ecol Evol* 5,  
610 1247-1254.

611 LaPoint, S., Gallery, P., Wikelski, M., Kays, R., 2013. Animal behavior, cost-based corridor models,  
612 and real corridors. *Landscape Ecol* 28, 1615-1630.

613 Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity for  
614 conservation planning using a dispersal guild approach. *Landscape Ecol* 32, 99-113.

615 Li, W., Clauzel, C., Dai, Y., Wu, G., Giraudoux, P., Li, L., 2017. Improving landscape connectivity  
616 for the Yunnan snub-nosed monkey through cropland reforestation using graph theory. *Journal for*  
617 *Nature Conservation* 38, 46-55.

618 Loro, M., Ortega, E., Arce, R.M., Geneletti, D., 2015. Ecological connectivity analysis to reduce the  
619 barrier effect of roads. An innovative graph-theory approach to define wildlife corridors with  
620 multiple paths and without bottlenecks. *Landscape Urban Plan* 139, 149-162.

621 Maron, M., Brownlie, S., Bull, J.W., Evans, M.C., von Hase, A., Quétier, F., Watson, J.E.M., Gordon,  
622 A., 2018. The many meanings of no net loss in environmental policy. *Nature Sustainability* 1, 19-  
623 27.

624 Mcrae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity  
625 in ecology, evolution, and conservation. *Ecology* 89, 2712-2724.

626 Mimet, A., Clauzel, C., Foltête, J.C., 2016. Locating wildlife crossings for multispecies connectivity  
627 across linear infrastructures. *Landscape Ecol* 31, 1955-1973.

628 Moilanen, A., van Teeffelen, A.J.A., Ben-Haim, Y., Ferrier, S., 2009. How much compensation is  
629 enough? A framework for incorporating uncertainty and time discounting when calculating offset  
630 ratios for impacted habitat. *Restor Ecol* 17, 470-478.

631 Murdoch, W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P., Shaw, R., 2007. Maximizing  
632 return on investment in conservation. *Biol Conserv* 139, 375-388.

633 Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins,  
634 A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale,  
635 G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H.B.,  
636 Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the  
637 planetary boundary? A global assessment. *Science* 353, 288-291.

638 Quétier, F., Lavorel, S., 2011. Assessing ecological equivalence in biodiversity offset schemes: Key  
639 issues and solutions. *Biol Conserv* 144, 2991-2999.

640 Quétier, F., Regnery, B., Levrel, H., 2014. No net loss of biodiversity or paper offsets? A critical  
641 review of the French no net loss policy. *Environ Sci Policy* 38, 120-131.

642 Rayfield, B., Fortin, M.J., Fall, A., 2010. The sensitivity of least-cost habitat graphs to relative cost  
643 surface values. *Landscape Ecol* 25, 519-532.

644 Rayfield, B., Fortin, M.J., Fall, A., 2011. Connectivity for conservation: a framework to classify  
645 network measures. *Ecology* 92, 847-858.



646 Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J.A., Gonzalez, A., 2016. Multipurpose habitat  
647 networks for short-range and long-range connectivity: a new method combining graph and circuit  
648 connectivity. *Methods Ecol Evol* 7, 222-231.

649 Rincón, G., Solana-Gutiérrez, J., Alonso, C., Saura, S., García de Jalón, D., 2017. Longitudinal  
650 connectivity loss in a riverine network: accounting for the likelihood of upstream and downstream  
651 movement across dams. *Aquatic Sciences*, 1-13.

652 Rödder, D., Nekum, S., Cord, A.F., Engler, J.O., 2016. Coupling satellite data with species  
653 distribution and connectivity models as a tool for environmental management and planning in  
654 matrix-sensitive species. *Environ Manage*, 1-14.

655 Saenz, S., Walschburger, T., Gonzalez, J.C., Leon, J., McKenney, B., Kiesecker, J., 2013. A  
656 framework for implementing and valuing biodiversity offsets in Colombia: a landscape scale  
657 perspective. *Sustainability* 5, 4961-4987.

658 Sahraoui, Y., Foltête, J.C., Clauzel, C., 2017. A multi-species approach for assessing the impact of  
659 land-cover changes on landscape connectivity. *Landscape Ecol* 32, 1819-1835.

660 Santini, L., Saura, S., Rondinini, C., 2016. A composite network approach for assessing multi-species  
661 connectivity: an application to road defragmentation prioritisation. *Plos One* 11.

662 Saunders, M.I., Brown, C.J., Foley, M.M., Febria, C.M., Albright, R., Mehling, M.G., Kavanaugh,  
663 M.T., Burfeind, D.D., 2016. Human impacts on connectivity in marine and freshwater ecosystems  
664 assessed using graph theory: a review. *Marine and Freshwater Research* 67, 277-290.

665 Saura, S., de la Fuente, B., 2017. Connectivity as the amount of reachable habitat: conservation  
666 priorities and the roles of habitat patches in landscape networks, in: Gergel, S.E., Turner, M.G.  
667 (Eds.), *Learning Landscape Ecology: A Practical Guide to Concepts and Techniques*. Springer,  
668 New York, pp. 229-254.

669 Saura, S., Estreguil, C., Mouton, C., Rodriguez-Freire, M., 2011. Network analysis to assess landscape  
670 connectivity trends: Application to European forests (1990-2000). *Ecol Indic* 11, 407-416.

671 Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in  
672 landscape conservation planning: Comparison with existing indices and application to a case study.  
673 *Landscape Urban Plan* 83, 91-103.

674 Saura, S., Rubio, L., 2010. A common currency for the different ways in which patches and links can  
675 contribute to habitat availability and connectivity in the landscape. *Ecography* 33, 523-537.

676 Saura, S., Torné, J., 2009. Conefor Sensinode 2.2: A software package for quantifying the importance  
677 of habitat patches for landscape connectivity. *Environ Modell Softw* 24, 135-139.

678 Tambosi, L.R., Martensen, A.C., Ribeiro, M.C., Metzger, J.P., 2014. A framework to optimize  
679 biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restor Ecol* 22,  
680 169-177.

681 Tarabon, S., Bergès, L., Dutoit, T., Isselin-Nondedeu, F., 2019a. Environmental impact assessment of  
682 development projects improved by merging species distribution and habitat connectivity modelling.  
683 *J Environ Manage* 241, 439-449.

684 Tarabon, S., Bergès, L., Dutoit, T., Isselin-Nondedeu, F., 2019b. Maximizing habitat connectivity in  
685 the mitigation hierarchy. A case study on three terrestrial mammals in an urban environment. *J*  
686 *Environ Manage* 243, 340-349.

687 Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape  
688 structure. *Oikos* 68, 571-573.

689 Torrubia, S., McRae, B.H., Lawler, J.J., Hall, S.A., Halabisky, M., Langdon, J., Case, M., 2014.  
690 Getting the most connectivity per conservation dollar. *Front Ecol Environ* 12, 491-497.

691 Underwood, J.G., 2011. Combining landscape-level conservation planning and biodiversity offset  
692 programs: a case study. *Environ Manage* 47, 121-129.

693 Urban, D., Keitt, T., 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology* 82, 1205-  
694 1218.

695 Urban, D.L., Minor, E.S., Treml, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. *Ecol Lett*  
696 12, 260-273.

697 Vasas, V., Magura, T., Jordan, F., Tothmeresz, B., 2009. Graph theory in action: evaluating planned  
698 highway tracks based on connectivity measures. *Landscape Ecol* 24, 581-586.

699 Weissgerber, M., Roturier, S., Julliard, R., Guillet, F., 2019. Biodiversity offsetting: Certainty of the  
700 net loss but uncertainty of the net gain. *Biol Conserv* 237, 200-208.

701