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

3

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19

20 **Abstract**

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

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

36 We applied this landscape connectivity framework to a simple, virtual habitat network composed of 14
37 patches of varying sizes. The mitigation hierarchy was addressed through graph theory and *EC* and
38 several scenarios of impact avoidance, reduction and compensation were tested.
39 We present the benefits of a habitat connectivity framework for the mitigation hierarchy, provide
40 practical recommendations to implement this framework and show its use in real case studies that had
41 previously been restricted to one or two steps of the mitigation hierarchy. We insist on the benefits of
42 a habitat connectivity framework for the mitigation hierarchy and for ecological equivalence
43 assessment. In particular, we demonstrate why it is risky to use a standard offset ratio (the ratio
44 between the amount of area negatively impacted and the compensation area) without performing a
45 connectivity analysis that includes the landscape surrounding the zone impacted by the project. We
46 also discuss the limitations of the framework and suggest potential improvements. Lastly, we raise
47 concerns about the need to rethink the strategy for biodiversity protection. Given that wild areas and
48 semi-natural habitats are becoming scarcer, in particular in industrialised countries, we are convinced
49 that the real challenge is to quickly reconsider the current vision of "developing first, then assessing
50 the ecological damage", and instead urgently adopt an upstream protection strategy that would identify
51 and protect the land that must not be lost if we wish to maintain viable species populations and
52 ecological corridors allowing them the mobility necessary to their survival.

53 **Key-words**

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

1. Introduction

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

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

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

36 avoidance, reduction and offset). Therefore, the main challenges today are to combine the mitigation
37 hierarchy with conservation planning, and to switch from the current vision where the environmental
38 impacts of development projects are assessed at a local scale to a vision where impacts and solutions
39 are addressed at a larger geographical scale and include landscape connectivity issues (Kiesecker et
40 al., 2009; Kujala et al., 2015).

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

58 Meanwhile, connectivity conservation has become a central objective in conservation planning in
59 the last decades (Boitani et al., 2007; Crooks and Sanjayan, 2006; Gonzalez et al., 2017; Jongman et
60 al., 2004). Political commitments have been made at national, continental and global scales: the green-
61 blue veining from the "Grenelle Environnement" in France (www.trameverteetbleue.fr), the Green
62 Infrastructure Strategy in Europe (http://ec.europa.eu/environment/nature/ecosystems/index_en.htm),
63 Aichi Biodiversity Target 11 of the Strategic Plan for Biodiversity 2011-2020 of the Convention on
64 Biological diversity at the global scale (<https://www.cbd.int/sp/>). Compared to previous biodiversity
65 conservation schemes, these strategies emphasise the role of biological corridors connecting protected
66 areas together and linking them to the wider landscape (Bennett and Mulongoy, 2006; Boitani et al.,
67 2007). Landscape connectivity is defined as the degree to which the landscape facilitates the
68 movement of species, individuals and genes between habitat resources (Taylor et al., 1993). Recent
69 developments in landscape ecology have proposed new approaches of landscape functional
70 connectivity that provide meaningful guidance for conservation decisions (Bergsten and Zetterberg,
71 2013; Correa Ayram et al., 2016; Saura and de la Fuente, 2017). Habitat network analysis based on
72 landscape graphs and associated connectivity metrics (Rayfield et al., 2011; Saura and Rubio, 2010;

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

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

82 **2. Landscape connectivity analysis**

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

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

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

$$109 \quad p_{ij} = e^{-\alpha d_{ij}} \quad (1)$$

110 where α is a distance-decay coefficient. α is usually set so that $p_{ij}=0.5$ for the median or mean
 111 dispersal distance of the focal species, or so that $p_{ij}=0.05$ equals the maximal dispersal distance (Saura
 112 and Pascual-Hortal, 2007). These distances are generally obtained from least-cost pathways or least-
 113 cost corridors through species-specific resistance surfaces (Avon and Bergès, 2016; Rayfield et al.,
 114 2011); this accounts for the species' capacity to move through the different elements of the landscape
 115 matrix. Species-specific dispersal distances for animals can be obtained by merging literature reviews,
 116 then estimating distances from body size and life-history traits (Albert et al., 2017; Sahraoui et al.,
 117 2017).

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

$$119 \quad EC = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*} \quad (2)$$

120 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
 121 the maximum product probability between node i and j , *i.e.* the maximum value of the product of the
 122 link weights (p_{ij}) of all the possible paths connecting patches i and j . One or several intermediate links
 123 can be included when computing p_{ij}^* , thus representing all the intermediate steps that an individual
 124 would have to cross when following the 'optimal' path (in terms of probability) from i to j . If $i=j$, then
 125 $p_{ij}^* = 1$ (a patch can always be reached from itself).

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

$$129 \quad varEC = EC_{after} - EC_{before} \quad (3)$$

$$130 \quad dEC = \frac{EC_{after} - EC_{before}}{EC_{before}} \quad (4)$$

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

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

137 **3. Integrating habitat reachability in the mitigation hierarchy**

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

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

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

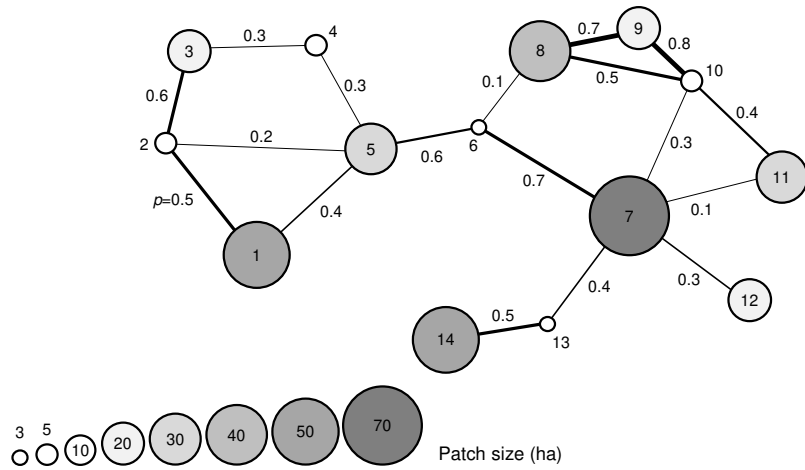
144 (3) Impact offset (post-implementation phase): Once reduction measures have been implemented,
145 where and how can we improve the habitat network to maximise gain in habitat reachability and
146 reach a value equal or higher than the habitat reachability of the initial habitat network?

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

155 **4. Application to a virtual graph**

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

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



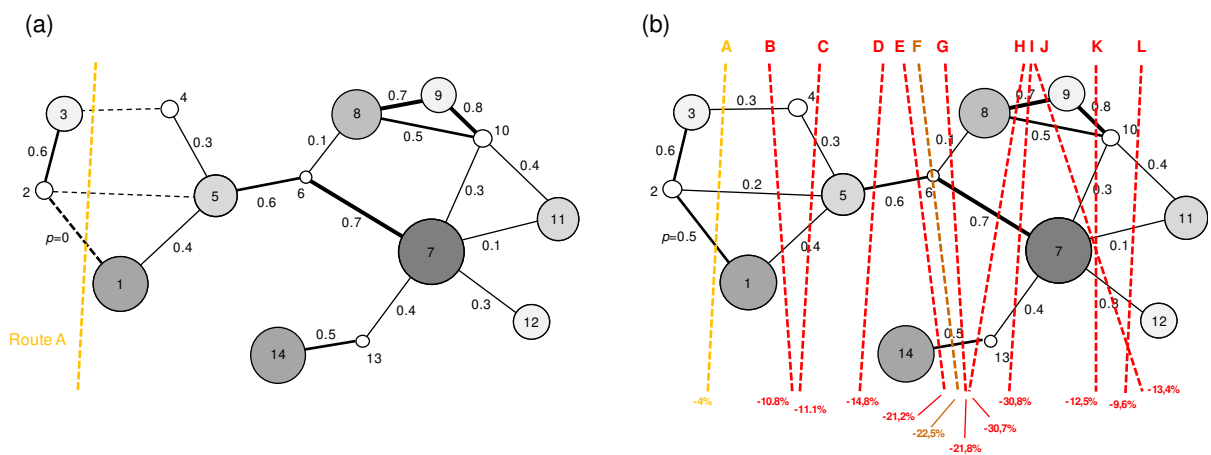
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Figure 1. Virtual habitat network composed of 14 nodes and 18 links. Graph nodes are represented by numbered circles (circle size proportional to patch area) and links by straight lines connecting the nodes with a probability of connection p_{ij} (line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

Impact avoidance

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



183

184 **Figure 2.** Impact avoidance: (a) changes in habitat network structure after implementation of the
 185 linear transportation infrastructure (LTI) (*route A* in yellow), which disrupted three links: 1-2, 2-5 and
 186 3-4 (black dotted lines); (b) the twelve potential routes tested to identify the route with the least impact
 187 and the corresponding percentages of *EC* loss. *Route A* displayed the lowest impact on *EC* (-4.1%)
 188 whereas routes *H* and *I* had the highest impact (-30.7% and -30.8% resp.).
 189

	<i>EC</i>	ΔEC_{base}	ΔEC_{init}
Impact avoidance			
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
Impact reduction			
<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
Impact offset			
<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 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 increased by 10 ha	177.4	25.1	2.5

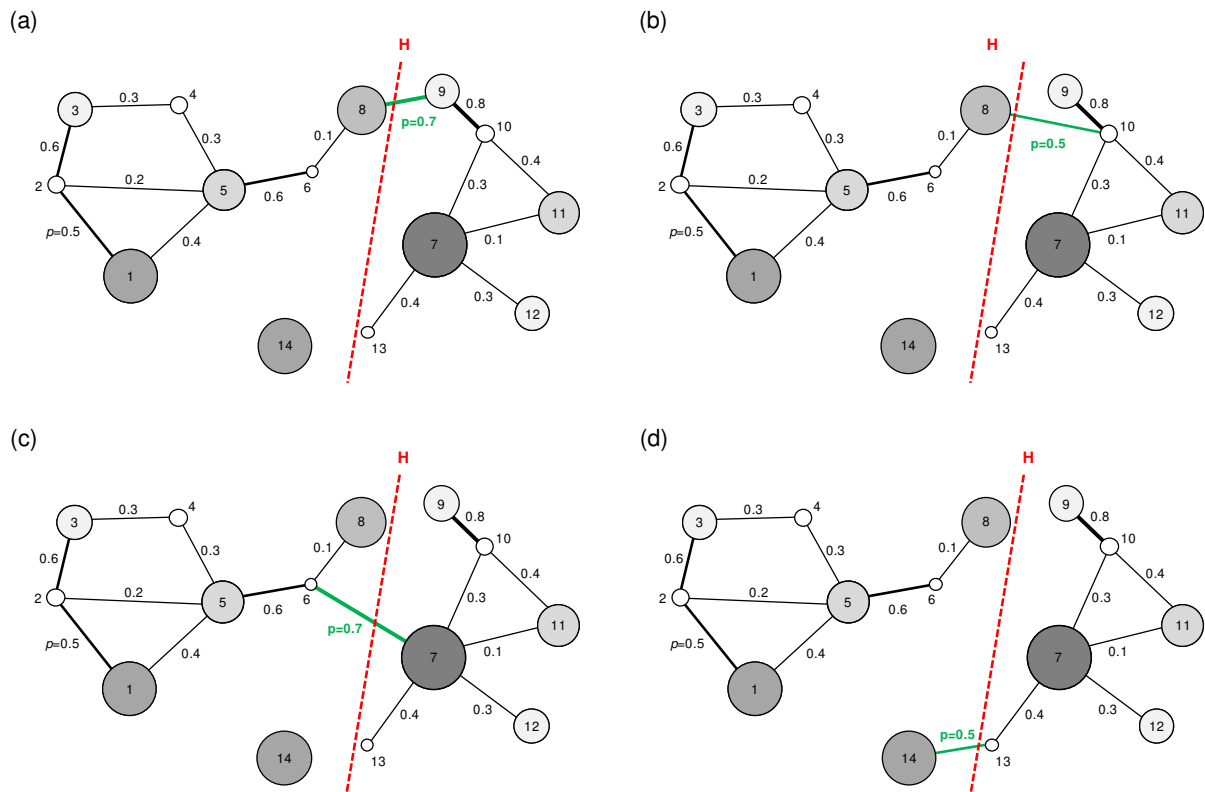
190 **Table 1.** Summary of the steps in the NNL mitigation hierarchy for habitat connectivity applied to the
 191 virtual graph (see Figures 1-4): impact avoidance (twelve location scenarios of a linear transport
 192 infrastructure - LTI), reduction (four wildlife crossings along the LTI and their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

194 variation from the initial graph (ΔEC_{init}). For impact reduction, we also calculated the difference in EC
195 between the reduction scenario and the avoidance scenario (ΔEC_{base}). For impact offset, we calculated
196 the difference in EC between the offset scenario and the reduction scenario (ΔEC_{base}).

197

198 **Impact reduction**

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



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Impact offset

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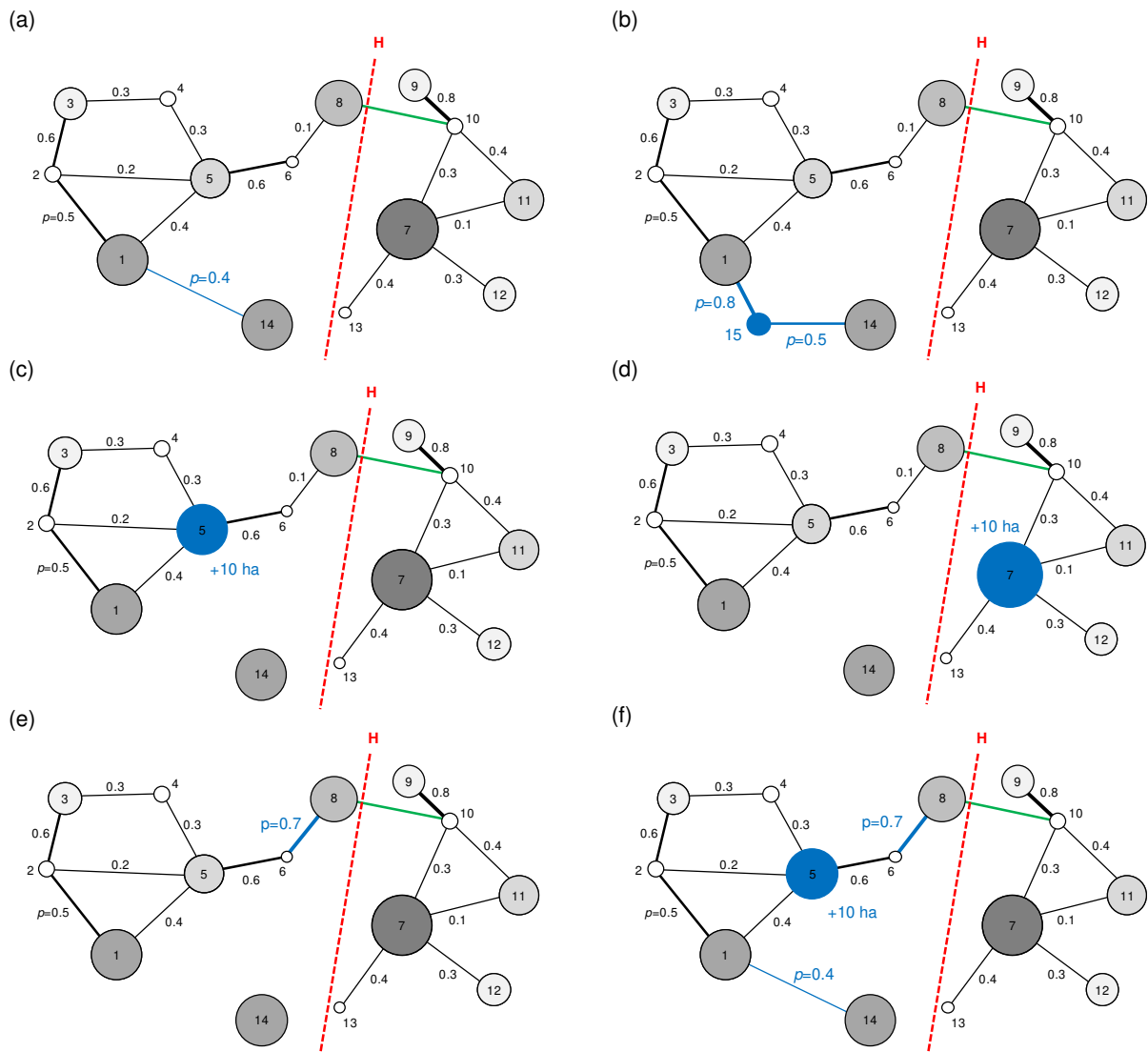
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Figure 3. Impact reduction after building *route H*. Impact reduction was calculated for four possible wildlife crossing locations: restoring link 8-9 (a), link 8-10 (b), link 6-7 (c) or link 13-14 (d). Restored links are in green. The stepwise restoration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

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

240 in size for patches 5 and 7). To fully offset the impact of *route H*, we had to combine three scenarios:
 241 creating link 1-14, improving link 6-8 and increasing patch 5 by 10 ha.
 242



243
 244 **Figure 4.** Impact offset: scenarios to offset the impacts of *route H*. Six options were compared: (a)
 245 establishment of a corridor between patches 1 and 14; (b) creation of a new patch 15 and its related
 246 links between patches 1 and 14; (c) patch 5 increased by 10 ha; (d) patch 7 increased by 10 ha; (e) link
 247 6-8 improved; (f) three measures combined (creation of link 1-14 + link 6-8 improved + patch 5
 248 increased by 10 ha). Graph changes related to offset in blue and reduction in green.

249

250 Patch importance

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

254 patch 6, its contribution to overall connectivity is 5-fold higher than its size (Table 2). Conversely,
 255 other patches displayed a ratio below 1 (e.g. 3, 4 11, 12).
 256

<i>Patch k</i>	<i>VarA_k</i>	<i>VarEC_k</i>	<i>VarEC_k/VarA_k</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

257
 258 **Table 2.** Contribution of each patch to overall habitat area and to overall habitat reachability (patch
 259 removal analysis). *VarA_k* is patch area, *VarEC_k* is the contribution of the patch in terms of *EC* resulting
 260 from patch removal, and *VarEC_k/VarA_k* is the ratio between *VarEC_k* and *VarA_k*.

261 5. Discussion

262 How does habitat connectivity modelling enhance the application of the NNL 263 objective?

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

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

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

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

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

305 **Practical recommendations and implementation on real-world landscapes**

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

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

327 Table 3 gives an overview of the connectivity studies that have addressed one or two steps of the
328 mitigation hierarchy, though rarely with an explicit reference to the NNL objective (Tarabon et al.,
329 2019b). Girardet (2014) addressed impact avoidance in the case of highway construction and Vasa et
330 al. (Vasas et al., 2009) a high-speed railway line project; they compared the connectivity impacts of
331 several possible tracks. In each case, the analysis emphasised that a one-route scenario minimized the
332 loss of connectivity at the regional scale. Several authors have addressed reduction impact to optimize
333 the location of wildlife crossings along highway networks and reduce the barrier effect of transport
334 infrastructure for different species (Ascensão et al., 2019; Gurrutxaga and Saura, 2014; Mimet et al.,
335 2016). Lastly, Tarabon et al. (2019b) addressed avoidance and reduction scenarios to evaluate the
336 impact on connectivity of a project completed in 2012: the new stadium in Lyon, France. They applied
337 species distribution models, landscape graphs and *EC* to three mammals (the red squirrel, the Eurasian
338 badger and the European hedgehog) to identify and locate avoidance and reduction measures that
339 would best reduce project impact in accordance with the technical possibilities of the site (creation of
340 meadows, hedges and groves and implementation of wildlife passages).

341

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

343

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

347 **Improving ecological equivalence assessment**

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

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

373 **Methodological limitations and suggestions for improvement**

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

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

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

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

404 Including cost estimates in the NNL objective would account for trade-offs between ecological
405 benefits and operating costs and help prioritize lands to be conserved/restored/mitigated (Conrad et al.,
406 2012; Murdoch et al., 2007; Torrubia et al., 2014). For example, Torrubia et al. (2014) identified
407 where the removal of barriers to movement could improve connectivity the most, with and without
408 considering the financial costs of land purchase and restoration. They found that accounting for land-
409 purchasing costs could reduce overall restoration costs by 55% while increasing the area of land
410 restored by 30%.

411 **6. Conclusion**

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

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

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

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

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442 **Authors' contribution**

443 LB conceived the ideas and led the writing. All authors contributed substantially to the drafts and
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446 **References**

- 447 Albert, C.H., Rayfield, B., Dumitru, M., Gonzalez, A., 2017. Applying network theory to prioritize
448 multispecies habitat networks that are robust to climate and land-use change. *Conserv Biol* 31,
449 1383-1396.
- 450 Ascensão, F., Mestre, F., Barbosa, A.M., 2019. Prioritizing road defragmentation using graph-based
451 tools. *Landscape Urban Plan* 192, 103653.
- 452 Avon, C., Bergès, L., 2016. Prioritization of habitat patches for landscape connectivity conservation
453 differs between least-cost and resistance distances. *Landscape Ecol* 31, 1551-1565.
- 454 Belisle, M., 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology.
455 *Ecology* 86, 1988-1995.
- 456 Bennett, G., Mulongoy, K.J., 2006. Review of experience with ecological networks, corridors and
457 buffer zones, Technical Series No. 23. Secretariat of the Convention on Biological Diversity,
458 Montreal, p. 100.
- 459 Bergsten, A., Zetterberg, A., 2013. To model the landscape as a network: A practitioner's perspective.
460 *Landscape Urban Plan* 119, 35-43.
- 461 Bezombes, L., Gaucherand, S., Spiegelberger, T., Gouraud, V., Kerbiriou, C., 2018. A set of organized
462 indicators to conciliate scientific knowledge, offset policies requirements and operational
463 constraints in the context of biodiversity offsets. *Ecol Indic* 93, 1244-1252.
- 464 Bigard, C., Pioch, S., Thompson, J.D., 2017. The inclusion of biodiversity in environmental impact
465 assessment: Policy-related progress limited by gaps and semantic confusion. *J Environ Manage*
466 200, 35-45.
- 467 Bishop-Taylor, R., Tulbure, M.G., Broich, M., 2015. Surface water network structure, landscape
468 resistance to movement and flooding vital for maintaining ecological connectivity across
469 Australia's largest river basin. *Landscape Ecol* 30, 2045-2065.
- 470 Boitani, L., Falcucci, A., Maiorano, L., Rondinini, C., 2007. Ecological networks as conceptual
471 frameworks or operational tools in conservation. *Conserv Biol* 21, 1414-1422.
- 472 Breininger, D.R., Burgman, M.A., Akçakaya, H.R., O'Connell, M.A., 2002. Use of metapopulation
473 models in conservation planning, in: Gutzwiller, K.J. (Ed.), *Applying Landscape Ecology in*
474 *Biological Conservation*. Springer New York, New York, NY, pp. 405-427.
- 475 Briggs, S., Hudson, M.D., 2013. Determination of significance in Ecological Impact Assessment: Past
476 change, current practice and future improvements. *Environmental Impact Assessment Review* 38,
477 16-25.
- 478 Bruggeman, D.J., Jones, M.L., Lupi, F., Scribner, K.T., 2005. Landscape equivalency analysis:
479 methodology for estimating spatially explicit biodiversity credits. *Environ Manage* 36, 518-534.
- 480 Bull, J.W., Gordon, A., Watson, J.E.M., Maron, M., 2016. Seeking convergence on the key concepts
481 in 'no net loss' policy. *J Appl Ecol* 53, 1686-1693.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

528 Girardet, X., 2014. Paysage & infrastructures de transport - modélisation des impacts des
529 infrastructures sur les réseaux écologiques, Ecole Doctorale "Langages, Espaces, Temps,
530 Sociétés". Université de Franche-Comté, Besançon, p. 261.

531 Girardet, X., Foltête, J.C., Clauzel, C., 2013. Designing a graph-based approach to landscape
532 ecological assessment of linear infrastructures. *Environmental Impact Assessment Review* 42, 10-
533 17.

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

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

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

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

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

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

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

551 Laitila, J., Moilanen, A., Pouzols, F.M., 2014. A method for calculating minimum biodiversity offset
552 multipliers accounting for time discounting, additionality and permanence. *Methods Ecol Evol* 5,
553 1247-1254.

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

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

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

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

564 Maron, M., Brownlie, S., Bull, J.W., Evans, M.C., von Hase, A., Quétier, F., Watson, J.E.M., Gordon,
565 A., 2018. The many meanings of no net loss in environmental policy. *Nature Sustainability* 1, 19-
566 27.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

621 Tambosi, L.R., Martensen, A.C., Ribeiro, M.C., Metzger, J.P., 2014. A framework to optimize
622 biodiversity restoration efforts based on habitat amount and landscape connectivity. *Restor Ecol* 22,
623 169-177.

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

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

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

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

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

636 Urban, D., Keitt, T., 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology* 82, 1205-
637 1218.

638 Urban, D.L., Minor, E.S., Treml, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. *Ecol Lett*
639 12, 260-273.

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

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

644