

# Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling

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## 1 Environmental mitigation hierarchy and biodiversity offsets revisited

## 2 through habitat connectivity modelling

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## 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
- 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 **1. Introduction**

2 Biodiversity loss has accelerated in recent decades (IPBES, 2019) and has become a major 3 environmental concern. Two of the main drivers of biodiversity erosion are anthropogenic activities 4 and land cover change that result in natural habitat loss and fragmentation (Fahrig, 2017; Newbold et 5 al., 2016). Following the Convention on Biological Diversity in Rio (1992), a large number of 6 countries adopted the mitigation hierarchy to slow down biodiversity erosion (Bull et al., 2016; 7 Business and Biodiversity Offsets Programme, 2012). The mitigation hierarchy includes three steps 8 designed to regulate development project impacts on biodiversity: (i) avoiding impacts by looking for 9 alternative locations for development where impacts will be less severe, (ii) reducing the impacts at 10 the chosen development site, and (iii) offsetting residual unavoidable damage on biodiversity (Bull et 11 al., 2016). The whole process should lead to No Net Loss (NNL) of biodiversity, where all the impacts 12 of a development project on biodiversity have been minimized and fully compensated for (Bull et al., 13 2016). Biodiversity offset policies that require NNL of biodiversity are in place in over 80 countries 14 (Maron et al., 2018), where they target different components of biodiversity (Bezombes et al., 2018; 15 Carreras Gamarra et al., 2018). For example, the mitigation hierarchy in France should apply to 16 biodiversity as a whole but, in practise, only applies to protected species and habitats (i.e. Natura 17 2000) including wetlands and woodlands ("Law for the Recovery of Biodiversity, Nature and 18 Landscapes", law n°2016-1087 of 8 August 2016). In Australia, the offset policy targets endemic 19 vegetation (Gibbons and Lindenmayer, 2007) and in the USA, wetland functions and endangered 20 species habitats must be offset under the Clean Water and Endangered Species Acts. 21 However, mitigation planning often underestimated the impacts of development projects on 22 landscape connectivity (Bruggeman et al., 2005). Moreover, even when it is considered, landscape 23 connectivity is not assessed sufficiently in advance to be included in a mitigation hierarchy process 24 (Clauzel et al., 2015; Kujala et al., 2015; Li et al., 2017; Underwood, 2011). In theory, the Law for the 25 Recovery of Biodiversity, Nature and Landscapes in France obliges developers to assess the impact of 26 their project at the landscape level, in particular for the offset aspect (article 69): "Compensation 27 measures are implemented as a priority on the damaged site or, in any case, in its vicinity, in order to 28 guarantee its sustainable functions". The methodological framework for environmental assessments 29 clearly changed with this law, but the legislation does not clearly specify how to proceed in order to 30 meet the objective of preserving connectivity. 31 Conversely, when connectivity studies focus on conservation and restoration measures expected to 32 compensate for the negative effects of habitat loss and fragmentation, they usually do not explicitly 33 refer to the NNL objective [but see Bruggeman et al. (2005), Kiesecker et al. (2009), Underwood 34 (2011), Dalang et Hersperger (2012), Kujala et al. (2015) and Tarabon et al. (2019a, b)] and none of

35 the studies to date concern the full spectrum of the mitigation hierarchy (i.e. including impact

avoidance, reduction and offset). Therefore, the main challenges today are to combine the mitigation
 hierarchy with conservation planning, and to switch from the current vision where the environmental
 impacts of development projects are assessed at a local scale to a vision where impacts and solutions
 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;

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

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

#### 82 **2. Landscape connectivity analysis**

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

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

110 where  $\alpha$  is a distance-decay coefficient.  $\alpha$  is usually set so that  $p_{ij}=0.5$  for the median or mean dispersal distance of the focal species, or so that  $p_{ij}=0.05$  equals the maximal dispersal distance (Saura 111 112 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 
$$EC = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^*} \quad (2)$$

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

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

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

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

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

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).



**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  $p_{ii}$  (line thickness proportional to  $p_{ii}$ ).

169

### 170 Impact avoidance

171 We simulated the impact of a linear transport infrastructure (LTI) that would cross the landscape 172 from north to south and removed the dispersal links intersected by the LTI (Figure 2a). This reduced 173 the probability of connection between links 1-2, 2-5 and 3-4 to zero because we assumed that the LTI 174 was an ecological barrier for the focal species in the NNL objective. In order to identify the 175 infrastructure location (s) that would avoid major impact on the habitat network for the focal species, 176 we tested then ranked 12 potential routes by degree of variation in EC (Figure 2b, Table 1). We 177 assumed that eleven of the routes did not go through any habitat patches, only the landscape matrix; 178 however, route F passes through patch 6, entirely removing it. In our study case, route A was the least 179 impacting while the highest impact routes, H and I, did up to 7.5 times more damage. Interestingly, 180 route F, which removed 3 ha of habitat (patch 6), had a lower impact than routes H or I, which only 181 affected links.

182





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
- 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

	EC	$\varDelta EC_{base}$	$\Delta EC_{init}$
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			
Baseline: 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			
Baseline: 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 ( $\Delta EC_{init}$ ). For impact reduction, we also calculated the difference in *EC* 195 between the reduction scenario and the avoidance scenario ( $\Delta EC_{base}$ ). For impact offset, we calculated
- 196 the difference in *EC* between the offset scenario and the reduction scenario ( $\Delta EC_{base}$ ).

#### 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 reduction scenarios with each other and with the initial state. We assumed that impact would be 202 203 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 example, we limited the number of wildlife crossings to four, parallel to the number of dispersal links 213 214 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 the first best location by screening each of the p links that intersect the infrastructure and seeking the 216 217 second most beneficial location among the remaining p-1 links once the first link is restored, and so on 218 (Tarabon et al., 2019b).





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.

#### **Impact offset**

225 Once the LTI route chosen, technical or cost reasons could prevent from construct as many 226 crossings as the number of disrupted links. We assumed that the reduction scenario involved only one 227 wildlife crossing reconnecting patches 6 and 8. However, wildlife crossings are not the only way to 228 reverse negative LTI effects and reach NNL of connectivity. Different types of offsets can be 229 proposed: (1) increasing the area of existing patches, (2) creating/improving links between patches and 230 (3) creating new patches and their associated links. We therefore proposed five scenarios with 231 additional offsets for *route H* to illustrate this approach (Figure 4). In order to quantify the gain in 232 connectivity from the offset measures, EC was computed for each offset scenario and compared with 233 two EC values: (a) the value obtained after impact avoidance and reduction and (b) the initial EC 234 value (Table 1). For the first scenario, we created a new corridor between patches 1 and 14 to 235 reconnect patch 14 with the western part of the network after the patch had become isolated. For the 236 second scenario, we added a new patch with its associated links between patches 1 and 14. This 237 scenario was the most interesting because connectivity increased by 12.8 ha (Table 1); however, a net 238 loss of 9.8 ha remained. The three other scenarios were less interesting than the first two, but we did 239 find that EC gain depended on where the 10 ha of new habitat were located (we compared an increase

- in size for patches 5 and 7). To fully offset the impact of *route H*, we had to combine three scenarios:
- creating link 1-14, improving link 6-8 and increasing patch 5 by10 ha.
- 242



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

#### 250 **Patch importance**

The ratio between the contribution of each patch k to overall habitat reachability ( $dEC_k$ ) and patch size ( $dA_k$ ) varied considerably (Table 2): some patches had a ratio above 1 (6, 13 and 10), meaning that 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,

other patches displayed a ratio below 1 (*e.g.* 3, 4 11, 12).

2	5	6
4	J	υ

Patch k	$VarA_k$	$VarEC_k$	VarEC <sub>k</sub> /VarA <sub>k</sub>
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

**Table 2.** Contribution of each patch to overall habitat area and to overall habitat reachability (patch removal analysis).  $VarA_k$  is patch area,  $VarEC_k$  is the contribution of the patch in terms of *EC* resulting 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**?

Populations, communities and ecological processes are more likely to be maintained in landscapes that encompass an interconnected system of habitats than they are in landscapes where natural habitats occur as dispersed isolated fragments (Crooks and Sanjayan, 2006). Because previous work has not explicitly addressed the NNL of biodiversity objective, we advocate for using landscape graphs and

- 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
- 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

significant indirect impact on the habitat network even though no habitat patches are destroyed. 273 274 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 assumptions and the rationale are clearly documented. In addition, applying EC is a time-efficient, 302 303 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 or estimate it from species traits; (2) collect maps of environmental data (topography, climate, land use 314 315 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	Mitigation	Explicit
				indices used	steps	ref. to
					addressed	NNL
Vasas et al. (2009)	Hungary,	LTI	carabid beetle	core index,	А	No
	Ukraine			reachability index		
Girardet (2014)	France	LTI	Virtual species (range of home range size and dispersal distance	PC	A, R	No
Gurrutxaga et al.	Spain	LTI	Forest species (range of dispersal distance)	PC	R	No
(2014)						
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	PC	R	No
Tarabon et al. (2019b)	France	Stadium	Three mammals (Red squirrel, Eurasian badger and European	EC	A, R	Yes
			hedgehog)			
Ascensão et al. (2019)	Spain	LTI	13 carnivorous mammals	IIC, AWM	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 indicated, while isolated or redundant patches contributed less. Thus, the ratio between the 365 366 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).

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

- 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
- radius at least equal to the maximal dispersal distance of the focal species. To assess the cumulative
- 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**

Building on previous attempts (Bruggeman et al., 2005; Dalang and Hersperger, 2012; Kujala et al., 2015; Tambosi et al., 2014; Underwood, 2011), we have presented how connectivity conservation can be included in the "no net loss" of biodiversity objective. Our starting assumption was that 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.

We fully support the idea that a change in environmental policy is required to move beyond the ineffective project-by-project approach currently proposed by national and international environmental organizations if we wish to successfully offset human impact on biodiversity (Quétier et al., 2014). A more effective conservation planning policy should rely on a cumulative environmental impact 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

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

- Albert, C.H., Rayfield, B., Dumitru, M., Gonzalez, A., 2017. Applying network theory to prioritize
  multispecies habitat networks that are robust to climate and land-use change. Conserv Biol 31,
  1383-1396.
- Ascensão, F., Mestre, F., Barbosa, A.M., 2019. Prioritizing road defragmentation using graph-based
  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.
- Belisle, M., 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology.
  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.
- Bergsten, A., Zetterberg, A., 2013. To model the landscape as a network: A practitioner's perspective.
  Landscape Urban Plan 119, 35-43.
- Bezombes, L., Gaucherand, S., Spiegelberger, T., Gouraud, V., Kerbiriou, C., 2018. A set of organized
  indicators to conciliate scientific knowledge, offset policies requirements and operational
  constraints in the context of biodiversity offsets. Ecol Indic 93, 1244-1252.
- Bigard, C., Pioch, S., Thompson, J.D., 2017. The inclusion of biodiversity in environmental impact
  assessment: Policy-related progress limited by gaps and semantic confusion. J Environ Manage
  200, 35-45.
- Bishop-Taylor, R., Tulbure, M.G., Broich, M., 2015. Surface water network structure, landscape
  resistance to movement and flooding vital for maintaining ecological connectivity across
  Australia's largest river basin. Landscape Ecol 30, 2045-2065.
- Boitani, L., Falcucci, A., Maiorano, L., Rondinini, C., 2007. Ecological networks as conceptual
  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

- Briggs, S., Hudson, M.D., 2013. Determination of significance in Ecological Impact Assessment: Past
  change, current practice and future improvements. Environmental Impact Assessment Review 38,
  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.

<sup>474</sup> Biological Conservation. Springer New York, New York, NY, pp. 405-427.

- Business and Biodiversity Offsets Programme, B., 2012. Guidance notes to the standard on
  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
- developments on connectivity across multiple scales: Application to Yunnan snub-nosed monkey
  conservation. Biol Conserv 192, 207-217.
- Conrad, J.M., Gomes, C.P., van Hoeve, W.J., Sabharwal, A., Suter, J.F., 2012. Wildlife corridors as a
  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.,
- Baguette, M., Travis, J.M.J., 2015. A stochastic movement simulator improves estimates of
  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.
- Cushman, S.A., Landguth, E.L., Flather, C.H., 2013. Evaluating population connectivity for species of
   conservation concern in the American Great Plains. Biodivers Conserv 22, 2583-2605.
- Dalang, T., Hersperger, A.M., 2012. Trading connectivity improvement for area loss in patch-based
   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 Duflot, R., Avon, C., Roche, P., Bergès, L., 2018. Combining habitat suitability models and spatial
- graphs for more effective landscape conservation planning: an applied methodological frameworkand a species case study. Journal for Nature Conservation 46, 38-47.
- Fahrig, L., 2017. Ecological responses to habitat fragmentation per se. Annual Review of Ecology,
  Evolution, and Systematics 48, 1-23.
- Fletcher, R.J., Reichert, B.E., Holmes, K., 2018. The negative effects of habitat fragmentation operate
  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.
- Foltête, J.C., Clauzel, C., Vuidel, G., 2012. A software tool dedicated to the modelling of landscape
  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.

- Forman, R.T.T., 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University
   Press, Cambridge.
- Garcia-Feced, C., Saura, S., Elena-Rossello, R., 2011. Improving landscape connectivity in forest
   districts: A two-stage process for prioritizing agricultural patches for reforestation. Forest Ecol
   Manag 261, 154-161.
- 523 Gardner, T.A., Von Hase, A., Brownlie, S., Ekstrom, J.M.M., Pilgrim, J.D., Savy, C.E., Stephens,
- R.T.T., Treweek, J., Ussher, G.T., Ward, G., Ten Kate, K., 2013. Biodiversity offsets and the
  challenge of achieving no net loss. Conserv Biol 27, 1254-1264.
- Gibbons, P., Lindenmayer, D.B., 2007. Offsets for land clearing: No net loss or the tail wagging the
   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 "Languages, 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.
- Gonzalez, A., Thompson, P., Loreau, M., 2017. Spatial ecological networks: planning for
  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
- ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and
   Ecosystem Services. IPBES secretariat, Bonn, Germany.
- Jongman, R.H.G., Külvik, M., Kristiansen, I., 2004. European ecological networks and greenways.
  Landscape Urban Plan 68, 305-319.
- Kiesecker, J.M., Copeland, H., Pocewicz, A., McKenney, B., 2010. Development by design: blending
  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
- biodiversity loss using spatial prioritization concepts and tools: A case study on mining impacts inAustralia. Biol Conserv 192, 513-521.
- Laitila, J., Moilanen, A., Pouzols, F.M., 2014. A method for calculating minimum biodiversity offset
   multipliers accounting for time discounting, additionality and permanence. Methods Ecol Evol 5,
- 553 1247-1254.

- LaPoint, S., Gallery, P., Wikelski, M., Kays, R., 2013. Animal behavior, cost-based corridor models,
  and real corridors. Landscape Ecol 28, 1615-1630.
- Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity for
   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.
- Loro, M., Ortega, E., Arce, R.M., Geneletti, D., 2015. Ecological connectivity analysis to reduce the
   barrier effect of roads. An innovative graph-theory approach to define wildlife corridors with
   multiple paths and without bottlenecks. Landscape Urban Plan 139, 149-162.
- Maron, M., Brownlie, S., Bull, J.W., Evans, M.C., von Hase, A., Quetier, F., Watson, J.E.M., Gordon,
  A., 2018. The many meanings of no net loss in environmental policy. Nature Sustainability 1, 19-
- 566 27.
- Mcrae, B.H., Dickson, B.G., Keitt, T.H., Shah, V.B., 2008. Using circuit theory to model connectivity
  in ecology, evolution, and conservation. Ecology 89, 2712-2724.
- Mimet, A., Clauzel, C., Foltête, J.C., 2016. Locating wildlife crossings for multispecies connectivity
   across linear infrastructures. Landscape Ecol 31, 1955-1973.
- Moilanen, A., van Teeffelen, A.J.A., Ben-Haim, Y., Ferrier, S., 2009. How much compensation is
  enough? A framework for incorporating uncertainty and time discounting when calculating offset
- 573 ratios for impacted habitat. Restor Ecol 17, 470-478.
- Murdoch, W., Polasky, S., Wilson, K.A., Possingham, H.P., Kareiva, P., Shaw, R., 2007. Maximizing
  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.,
- Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the
  planetary boundary? A global assessment. Science 353, 288-291.
- Quétier, F., Lavorel, S., 2011. Assessing ecological equivalence in biodiversity offset schemes: Key
  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
- review of the French no net loss policy. Environ Sci Policy 38, 120-131.
- Rayfield, B., Fortin, M.J., Fall, A., 2010. The sensitivity of least-cost habitat graphs to relative cost
  surface values. Landscape Ecol 25, 519-532.
- Rayfield, B., Fortin, M.J., Fall, A., 2011. Connectivity for conservation: a framework to classify
  network measures. Ecology 92, 847-858.

- 589 Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J.A., Gonzalez, A., 2016. Multipurpose habitat
- networks for short-range and long-range connectivity: a new method combining graph and circuitconnectivity. Methods Ecol Evol 7, 222-231.
- 592 Rincón, G., Solana-Gutiérrez, J., Alonso, C., Saura, S., García de Jalón, D., 2017. Longitudinal
- connectivity loss in a riverine network: accounting for the likelihood of upstream and downstream
   movement across dams. Aquatic Sciences, 1-13.
- 595 Rödder, D., Nekum, S., Cord, A.F., Engler, J.O., 2016. Coupling satellite data with species
- distribution and connectivity models as a tool for environmental management and planning in
   matrix-sensitive species. Environ Manage, 1-14.
- Saenz, S., Walschburger, T., Gonzalez, J.C., Leon, J., McKenney, B., Kiesecker, J., 2013. A
  framework for implementing and valuing biodiversity offsets in Colombia: a landscape scale
  perspective. Sustainability 5, 4961-4987.
- Sahraoui, Y., Foltête, J.C., Clauzel, C., 2017. A multi-species approach for assessing the impact of
  land-cover changes on landscape connectivity. Landscape Ecol 32, 1819-1835.
- Santini, L., Saura, S., Rondinini, C., 2016. A composite network approach for assessing multi-species
   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,
- M.T., Burfeind, D.D., 2016. Human impacts on connectivity in marine and freshwater ecosystems
   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.
- Saura, S., Estreguil, C., Mouton, C., Rodriguez-Freire, M., 2011. Network analysis to assess landscape
  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.
- Saura, S., Rubio, L., 2010. A common currency for the different ways in which patches and links can
  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
- biodiversity restoration efforts based on habitat amount and landscape connectivity. Restor Ecol 22,
- 623 169-177.

- Tarabon, S., Bergès, L., Dutoit, T., Isselin-Nondedeu, F., 2019a. Environmental impact assessment of
  development projects improved by merging species distribution and habitat connectivity modelling.
  J Environ Manage 241, 439-449.
- 627 Tarabon, S., Bergès, L., Dutoit, T., Isselin-Nondedeu, F., 2019b. Maximizing habitat connectivity in
- the mitigation hierarchy. A case study on three terrestrial mammals in an urban environment. JEnviron Manage 243, 340-349.
- Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape
  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, 1205637 1218.
- Urban, D.L., Minor, E.S., Treml, E.A., Schick, R.S., 2009. Graph models of habitat mosaics. Ecol Lett
  12, 260-273.
- Vasas, V., Magura, T., Jordan, F., Tothmeresz, B., 2009. Graph theory in action: evaluating planned
  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
- net loss but uncertainty of the net gain. Biol Conserv 237, 200-208.