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Environmental mitigation hierarchy and biodiversity offsets revisited through habitat connectivity modelling

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Key-words

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Abstract

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

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

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

We present the benefits of a habitat connectivity framework for the mitigation hierarchy, provide practical recommendations to implement this framework and show its use in real case studies that had previously been restricted to one or two steps of the mitigation hierarchy. We insist on the benefits of a habitat connectivity framework for the mitigation hierarchy and for ecological equivalence assessment. In particular, we demonstrate why it is risky to use a standard offset ratio (the ratio between the amount of area negatively impacted and the compensation area) without performing a connectivity analysis that includes the landscape surrounding the zone impacted by the project. We also discuss the limitations of the framework and suggest potential improvements. Lastly, we raise concerns about the need to rethink the strategy for biodiversity protection. Given that wild areas and semi-natural habitats are becoming scarcer, in particular in industrialised countries, we are convinced that the real challenge is to quickly reconsider the current vision of "developing first, then assessing 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 ecological corridors allowing them the mobility necessary to their survival.

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 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 al., 2009; Kujala et al., 2015).

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

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

2. Landscape connectivity analysis

A convenient, and popular, model for conceptualizing habitat networks is the 'patch-corridor-matrix 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 non-habitat portion of the landscape in which habitat patches and corridors are embedded.

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

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

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

where α is a distance-decay coefficient. α 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 and Pascual-Hortal, 2007). These distances are generally obtained from least-cost pathways or least-cost corridors through species-specific resistance surfaces (Avon and Bergès, 2016; Rayfield et al., 2011); this accounts for the species' capacity to move through the different elements of the landscape matrix. Species-specific dispersal distances for animals can be obtained by merging literature reviews, then estimating distances from body size and life-history traits (Albert et al., 2017; Sahraoui et al., 2017).

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

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

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:

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

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

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

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

3. Integrating habitat reachability in the mitigation hierarchy

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

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

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

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

Decisions can be made with the help of successive landscape graph transformations corresponding to alternative scenarios. First, alternative avoidance scenarios can be compared for different locations proposed for the project and the scenarios can be ranked in terms of habitat reachability loss. Second, alternative reduction scenarios can be compared to detect and prioritize the best solutions to reduce habitat reachability loss, by maximising gain through one or several cumulated reduction actions. Finally, alternative offset scenarios can be proposed to prioritize the most effective solutions – *i.e.* 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".

4. Application to a virtual graph

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

We created a virtual graph composed of 14 patches of different sizes (from 3 to 70 ha) linked by 18 connections with various connection probability values (from $p=0.1$ to 0.8, Figure 1). We generate a 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 of connection between all the patches were below 1. All network connectivity analyses were 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_{ij} (line thickness proportional to p_{ij}).

Impact avoidance

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.

Figure 2. Impact avoidance: (a) changes in habitat network structure after implementation of the linear transportation infrastructure (LTI) (*route A* in yellow), which disrupted three links: 1-2, 2-5 and 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%) whereas routes *H* and *I* had the highest impact (-30.7% and -30.8% resp.).

	<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

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

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

Impact reduction

We chose *route H* to demonstrate impact reduction, but it should be noted that, in real conditions, we probably would have selected a route that offered a trade-off between impact avoidance and 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 reduced by setting up wildlife crossings along the LTI. We hypothesised that the probability of connection p_{ij} between node i and node j would be fully restored by the wildlife crossings, an optimistic though achievable hypothesis. For *route H*, wildlife crossings would restore four broken connections (Figure 3). The four scenarios were ranked according to their ability to restore habitat reachability (Table 1). The wildlife crossing that restored link 6-7 was revealed to be the most efficient way to reduce the LTI's impact (Figure 3c), while the three other choices had a lower positive impact. Repairing two links (6-7 and 8-9) had the highest cumulated increase in EC (Table 1). It is important to note, however, that none of these options was able to offset the total impact of *route H*, as EC remained below its reference value in all cases: restoring link 6-7 alone displayed a net deficit of 15.0 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 disrupted by the LTI, but more potential graph change are expected in much larger graphs. To solve 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 second most beneficial location among the remaining $p-1$ links once the first link is restored, and so on (Tarabon et al., 2019b).

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 by 10 ha.

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.

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

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).

<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

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*.

5. Discussion

How does habitat connectivity modelling enhance the application of the NNL 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 (Clauzel et al., 2015; Girardet et al., 2013; Sahraoui et al., 2017; Santini et al., 2016).

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 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. Indeed, changing or disrupting the connections between patches can strongly modify the flux of individuals or genes between patches and thereby reduce the probability of maintaining species populations over the long-term. In our example, even the routes that did not destroy habitat patches caused habitat reachability to decrease according to *EC* (Table 1). Currently, landscape-level impacts are not evaluated when applying the NNL objective, because impacts are only considered when habitat patches are cleared or species are removed from the patches by the project (Briggs and Hudson, 2013). Even when corridor aspects are taken into account, only local effects are considered; the global impact on landscape connectivity is not quantified.

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

The *EC* metric meets the different criteria for suitability according to the standards recommended by the Business and Biodiversity Offsets Programme (2012): *EC* is quantitative and can evaluate 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, cost-effective and scientifically rigorous method, making it appealing for stakeholders (Bergsten and Zetterberg, 2013; Carreras Gamarra et al., 2018).

Practical recommendations and implementation on real-world landscapes

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

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

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

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

400

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

Improving ecological equivalence assessment

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

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

Methodological limitations and suggestions for improvement

Among the methods available for functional connectivity modelling, graph connectivity metrics are the most operational due to a good compromise between information yielded and data requirements (Saura and de la Fuente, 2017). Connectivity models based on spatially-explicit metapopulation models can also be an alternative because they provide detailed results in terms of population dynamics (Dalang and Hersperger, 2012); however, they are more difficult for practitioners to 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 environmental geo-data. We recommend adapting the extent of the study area to species dispersal 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 all the projects, then creating a buffer zone with a radius at least equal to the maximal dispersal distance of the focal species around this polygon.

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

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

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

but rather must be evaluated at the landscape scale, *i.e.* by considering the landscape mosaic 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).

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

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Authors' contribution

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

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.
- Avon, C., Bergès, L., 2016. Prioritization of habitat patches for landscape connectivity conservation 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.
- Bennett, G., Mulongoy, K.J., 2006. Review of experience with ecological networks, corridors and buffer zones, Technical Series No. 23. Secretariat of the Convention on Biological Diversity, 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.
- Breining, D.R., Burgman, M.A., Akçakaya, H.R., O'Connell, M.A., 2002. Use of metapopulation models in conservation planning, in: Gutzwiller, K.J. (Ed.), *Applying Landscape Ecology in Biological Conservation*. Springer New York, New York, NY, pp. 405-427.
- 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.
- Bruggeman, D.J., Jones, M.L., Lupi, F., Scribner, K.T., 2005. Landscape equivalency analysis: methodology for estimating spatially explicit biodiversity credits. *Environ Manage* 36, 518-534.
- Bull, J.W., Gordon, A., Watson, J.E.M., Maron, M., 2016. Seeking convergence on the key concepts in 'no net loss' policy. *J Appl Ecol* 53, 1686-1693.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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 circuit connectivity. *Methods Ecol Evol* 7, 222-231.

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.

Rödger, 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.

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.

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

Saura, S., Pascual-Hortal, L., 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: Comparison with existing indices and application to a case study. *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.

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

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, 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.
- 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. *J Environ 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.
- Torrubia, S., McRae, B.H., Lawler, J.J., Hall, S.A., Halabisky, M., Langdon, J., Case, M., 2014. Getting the most connectivity per conservation dollar. *Front Ecol Environ* 12, 491-497.
- Underwood, J.G., 2011. Combining landscape-level conservation planning and biodiversity offset programs: a case study. *Environ Manage* 47, 121-129.
- Urban, D., Keitt, T., 2001. Landscape connectivity: A graph-theoretic perspective. *Ecology* 82, 1205-1218.
- 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.
- 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.