Author(s): Kosma, Maari; Laita, Anne; Duflot, Rémi

Title: No net loss of connectivity : Conserving habitat networks in the context of urban expansion

Year: 2023

Version: Published version

Please cite the original version:

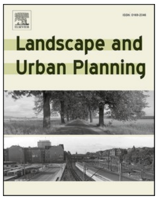
Kosma, M., Laita, A., & Duflot, R. (2023). No net loss of connectivity : Conserving habitat networks in the context of urban expansion. Landscape and Urban Planning, 239, Article 104847. https://doi.org/10.1016/j.landurbplan.2023.104847

Landscape and Urban Planning 239 (2023) 104847

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan



Research Paper

No net loss of connectivity: Conserving habitat networks in the context of urban expansion

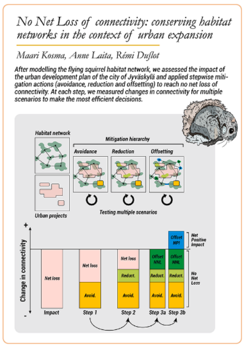
Maari Kosma [a,b], Anne Laita [c], Rémi Duflot [a,b,*]

[a] Department of Biological and Environmental Sciences, University of Jyvaskyla, P.O. Box 35, FI-40014 Jyvaskyla, Finland
[b] School of Resource Wisdom, University of Jyvaskyla, P.O. Box 35, FI-40014 Jyvaskyla, Finland
[c] City of Jyvaskyla, P.O. Box 193, 40101 Jyvaskyla, Finland

HIGHLIGHTS

- We illustrate how spatial graph modelling can be used to implement a landscape approach to mitigation hierarchy.
- Urban development plan in a Finnish city negatively impacts the connectivity of the Siberian flying squirrel habitat network.
- The most efficient scenarios to mitigate negative impacts were avoidance actions, followed by offsetting.
- The most efficient reduction scenarios were actions in which both habitat patches and connections were saved from development.
- Uncertain dispersal distance of the focal species can lead to insufficient mitigation.

GRAPHICAL ABSTRACT



No Net Loss of connectivity: conserving habitat networks in the context of urban expansion

Maari Kosma, Anne Laita, Rémi Duflot

After modelling the flying squirrel habitat network, we assessed the impact of the urban development plan of the city of Jyväskylä and applied stepwise mitigation actions (avoidance, reduction and offsetting) to reach no net loss of connectivity. At each step, we measured changes in connectivity for multiple scenarios to make the most efficient decisions.

ARTICLE INFO

Keywords:
Biodiversity offsetting
Spatial graph
Mitigation hierarchy
Land use planning
Landscape planning
Pteromys volans
Siberian flying squirrel
Urban green infrastructure

ABSTRACT

Increasing urbanisation calls for careful landscape conservation planning to maintain biodiversity in urban areas. Urbanisation not only decreases the amount and quality of habitats, but it also affects habitat connectivity, which is crucial for species' long-term persistence. The mitigation hierarchy approach of avoiding, reducing and offsetting the negative impacts of development projects is a powerful tool to prevent biodiversity loss. However, this process is typically used at the local scale and on a project-by-project basis, ignoring the cumulated effects of several projects on habitat connectivity. We applied a landscape-level approach to the mitigation hierarchy to achieve no net loss of connectivity during urban planning. Using spatial graphs, we assessed avoidance, reduction and offsetting scenarios for mitigating the impact of ten urban development projects in the city of Jyväskylä, Finland, here focusing on the habitat network of the endangered Siberian flying squirrel (*Pteromys volans*). We found a negative impact of urban development on network connectivity and prioritised habitat patches and corridors, which should be maintained to avoid and reduce the impacts. The no net loss of connectivity was achieved by adding new habitat patches in locations that maximise connectivity. We also found that the results were highly sensitive to variations in the dispersal distance of the focal species used in the connectivity model. An inadequate reference value for this parameter may lead to underestimation of the impacts of development projects and, therefore, insufficient mitigation actions. With a case study, we showed that spatial graph analysis

---

* Corresponding author at: Department of Biological and Environmental Sciences, University of Jyvaskyla, P.O. Box 35, FI-40014 Jyvaskyla, Finland.
E-mail addresses: maari.h.kosma@jyu.fi (M. Kosma), anne.laita@jyvaskyla.fi (A. Laita), remi.r.duflot@jyu.fi (R. Duflot).

https://doi.org/10.1016/j.landurbplan.2023.104847
Received 9 September 2022; Received in revised form 17 July 2023; Accepted 18 July 2023

can support decision-making by identifying and prioritising the actions needed to maintain habitat connectivity in urban landscapes.

1. Introduction

Land use change is the primary factor of the current biodiversity crisis in terrestrial ecosystems (IPBES, 2019). Urbanisation plays a critical role because more than half of the world's human population live in urban landscapes, with further increase projected (United Nations, 2019). Moreover, urban land use increases twice as fast as urban population and is forecasted to quadruple by 2050 when compared with 2000 (Angel et al., 2011). During the urbanisation process, vegetated lands are turned into impervious surfaces (artificialisation), within existing urban areas (increased density) or at their edges (spatial expansion). Meanwhile, the area and quality of remaining native habitats and of various forms of managed green areas have decreased, leading to habitat loss and fragmentation and a negative impact on biodiversity (Aronson et al., 2014; Piano et al., 2020).

Urban landscape planning often considers green areas as habitat networks (i.e., spatial ecological network or green infrastructures; Lepczyk et al., 2017). These networks consist of multiple habitat patches connected by corridors to allow organisms to move across landscapes (Boitani et al., 2007; Jongman et al., 2004). By decreasing the amount and quality of habitat patches, as well as the permeability of the matrix between them, urbanisation reduces habitat network connectivity, which can have major effects on species survival and the long-term persistence of biodiversity (Crooks & Sanjayan, 2006; Fletcher et al., 2018).

To achieve biodiversity conservation objectives, many international and national policies have been formalised to integrate human activities and biodiversity conservation (e.g., Global Aichi Targets, the post-2020 global biodiversity framework, and the EU biodiversity strategy). Among the suggested strategies, the principle of No Net Loss (NNL) of biodiversity is now in use in many countries and is discussed worldwide. The concept of NNL is based on a harm mitigation hierarchy, where the impacts of development should first be avoided, then minimised and/or restored and, finally, the remaining impacts offset (Bull et al., 2016). The mitigation steps should fully compensate for the total impact of development projects, leading to the achievement of NNL. A net positive impact (i.e., a gain in biodiversity value) can even be achieved by offsetting more than the total impacts. Currently, over 100 countries have policies in place that either mandate offsetting or make its voluntary use possible (GIBOP, 2023). In many countries, mitigation hierarchy and offsetting are operationalised through the environmental impact assessment process (Madsen et al., 2010) and go hand in hand with the planning of development projects. In Finland, waivers to the Nature Conservation Act that allow disturbing or destroying protected habitat (e.g., of the Siberian flying squirrel, *Pteromys Volans*) can mandate biodiversity offsetting.

Most mitigation regulations and procedures operate at a local scale, on a project-by-project basis, and often only consider the amounts of altered habitats; thus, they ignore the global impacts of development projects on habitat networks and connectivity (Bergès et al., 2020; Kiesecker et al., 2010). Because connectivity is crucial for species persistence and has become a key feature in biodiversity conservation, a mitigation hierarchy should include an assessment of the impacts at the landscape scale as well. So far, habitat connectivity has mostly been considered a precondition for restoration or offsetting success. Indeed, the connectivity of offsetting sites to existing similar habitats should facilitate their colonisation by associated species while contributing to better connected habitat networks (Kujala et al., 2015; Moilanen & Kotiaho, 2018).

Recently, Bergès et al. (2020) formalised the use of graph-based connectivity analyses in the mitigation hierarchy, introducing the concept of the 'no net loss of connectivity'. Spatial graphs are representations of habitat networks where habitat patches are depicted as spatially explicit nodes and potential movements as links between the nodes (Galpern et al., 2011; Urban & Keitt, 2001). Graph-based connectivity metrics are highly efficient in defining priority actions in landscape conservation planning and assessing the impacts of development projects on habitat networks (Foltête et al., 2014; Rubio & Saura, 2012). Several studies have incorporated graph-based connectivity analyses into the mitigation hierarchy steps, particularly to avoid and reduce the impact of linear transportation infrastructure, such as highways or railways (see Bergès et al., 2020). Examples of mitigating urban development are, however, limited and focused either on a single project (Tarabon et al., 2019b, 2019a), impact assessment (Tannier et al., 2016) or partial mitigation hierarchy (see, e.g., Tarabon et al. 2020 for avoidance and offsetting steps). To the best of our knowledge, to date, there have been no applications of NNL of connectivity using actual city development plans (and not urban growth simulations) and that have gone through all of the mitigation steps (though the categorisation of reduction vs. offsetting actions is not always clear, see Tarabon et al., 2019b).

We applied the framework of Bergès et al. (2020) to mitigate the impact of an urban development plan in Finland on the habitat network of the Siberian flying squirrel (hereafter flying squirrel). The flying squirrel is a flagship and umbrella species in Finland whose population is still declining, despite strict protection (Hurme et al., 2008; Hyvärinen et al., 2019). Flying squirrels are, however, commonly found in urban landscapes compared with forest-dominated landscapes that experience intensive forestry, creating many conflicts between urban planning and species conservation (Selonen & Mäkeläinen, 2017).

We implemented a stepwise procedure using habitat network modelling and scenario comparison (Fig. 1). The flying squirrel habitat network was modelled as a spatial graph using an expert-based habitat suitability index (Mönkkönen et al., 2014) to identify habitat patches and least-cost path analysis to characterise potential movements between patches. Then, we evaluated the impact of ten urban development projects, which delineates areas where urban development is planned in the future. Next, we developed alternative scenarios of avoidance, reduction and offsetting actions and evaluated them using graph-based connectivity metrics. Finally, the NNL of connectivity was achieved by making successive decisions based on the most efficient mitigation actions. In addition, to evaluate the risk of insufficient mitigation action, we calculated the sensitivity of potential impact and benefit measurements with respect to variations in the dispersal capacity of flying squirrels.

2. Methods

All datasets used in the present study are summarised in Supplementary Table S1. ArcGIS (v10.6.1, ESRI) was used to process all georeferenced data and generate map outputs. The coordinate system was EUREF FIN TM35FIN, as used by all official datasets. Graphab v2.4 (Foltête et al., 2012) was used to generate spatial graphs and calculate connectivity metrics.

2.1. Study area and urban development projects

The study area is the medium-sized city of Jyväskylä, Finland (144,500 inhabitants in 2021; Fig. 2). To study the effects of urbanisation on the flying squirrel habitat network, we used ten development projects provided by the city of Jyväskylä, delineating areas where urban development is planned in the future (P1–P10, Fig. 2). The total area of these development projects was 1800 ha, and the individual project sizes ranged from 25 ha to 631 ha (see short description of the projects in Supplementary Table S2). Following the recommendation from Bergès et al. (2020), the study area was defined based on the spatial locations of the development projects and by applying a buffer to these projects equal to the maximum dispersal distance of the flying squirrel (9 km, Hanski & Selonen, 2009; Selonen & Mäkeläinen, 2017). This resulted in a total area of 693.97 km^2 with the main land cover types being forests (55.8%), waters (20.1%), urban areas (12.4%) and agricultural areas (5.8%).

2.2. Study species

The Siberian flying squirrel is registered in the EU's habitats directive and its habitat (or resting and feeding sites) is strictly protected by the Finnish Nature Conservation Act. The flying squirrel is a well-studied species in Finland (Selonen & Mäkeläinen, 2017). Its preferred habitat is an old spruce–dominated forest, mixed with deciduous trees (Hanski, 1998; Selonen et al., 2001). Female flying squirrels occupy, on average, 8 ha territories (defended area), while males can have overlapping home ranges (non-defended living area) of up to 60 ha (Selonen et al., 2001). However, these areas are usually not fully covered by optimal habitats because flying squirrels can also use young or pine forests for movement and foraging and are known to use smaller habitat patches in urban areas (Mäkeläinen et al., 2016). Flying squirrels move mainly in tree canopy by gliding between trees (30–40 m on average) and are, thus, unable to cross wide open areas (Selonen & Hanski, 2003). The mean natal dispersal distance of flying squirrels is 2 km on average; however, dispersal distance varies greatly between sexes (mean of 2.4 km for females and 1.1 km for males), across individuals (short vs. long dispersers) and between studies (Hanski & Selonen, 2009; Selonen et al., 2012; Selonen & Hanski, 2004). To account for the variability in the dispersal distance of flying squirrel found in the literature and study its impact on the connectivity assessment, different dispersal distances were used based on the mean natal dispersal distance of 2 km. This sensitivity analysis was performed using positive and negative deviations of 5%, 10%, 20% and 40% from the mean dispersal distance, that is, ranging from 1.2 and 2.8 km. Such a range of dispersal values encompasses the variability observed between males and females.

2.3. Modelling the habitat network

2.3.1. Habitat mapping

Flying squirrel habitats were mapped using an expert-based habitat suitability index (HSI) previously formulated by Mönkkönen et al. (2014). The HSI was based on the volume of spruce (m^3/ha), the proportion of spruce relative to the total tree volume (%) and the volume of deciduous trees (m^3/ha); formulas are provided in Supplementary Section S3. The HSI provides values ranging from 0 (unsuitable) to 1 (highly suitable). We used two complementary forest datasets to calculate the HSI: forest stand data from the Finnish Forest Centre (update of 2019) and the Multisource National Forest Inventory of Finland (year 2017, Supplementary Table S1 for more details). Forest areas where HSI was over 0.5 were considered habitats, and habitat patches larger than 0.5 ha from the two forest data sources were combined to the final habitat map (4 m pixel resolution). In addition, the flying squirrel's 'core areas', that is, protection sites defined by the city of Jyväskylä based on field inventories, were added to the habitat map (130 'core areas', total area = 173.36 ha, mean area = 1.3 ha). The resulting habitat map was evaluated using observation records of flying squirrels gathered by expert field observers and citizens in the municipality of Jyväskylä between 2008 and 2019 (N = 4,272). We calculated the proportion of these observations that were located within suitable habitats.

2.3.2. Spatial graph construction

We built spatial graphs of the habitat network using the habitat map and a least-cost path (LCP) analysis with Graphab (Foltête et al., 2012). The LCP analysis calculates the path between two habitat patches with the lowest cumulative resistance to species movement (Adriaensen et al., 2003). In the spatial graph, these paths became links connecting nodes that model the potential movements of species individuals across the habitat networks. We created a resistance map by assigning a resistance value to each land cover type in the landscape based on the movement ability of the species within that land cover type. Low values indicate good movement ability and high values indicate low movement ability or obstacles. The land cover map was produced at the same resolution as the habitat map (i.e., 4 m pixel size) by combining several sources, as illustrated in Supplementary Fig. S4.

Resistance values (Table 1) were selected based on the literature and expert opinions about flying squirrels' movement ecology (Mäkeläinen et al., 2016; Selonen & Hanski, 2003) and on previous general literature about connectivity modelling (Sawyer et al., 2011; Zeller et al., 2012). For all graphs, we calculated the LCPs only between topologically neighbouring patches (i.e., minimum planar graph), except for offsetting scenarios where we used a complete graph (i.e., calculates LCPs between all pairs of patches; Clauzel et al., 2019). We used an eight-connexity neighbour of the pixel for delineating patches and calculated the LCPs without any maximum threshold. We ignored links crossing patches but included intra-patch distances to the metrics.

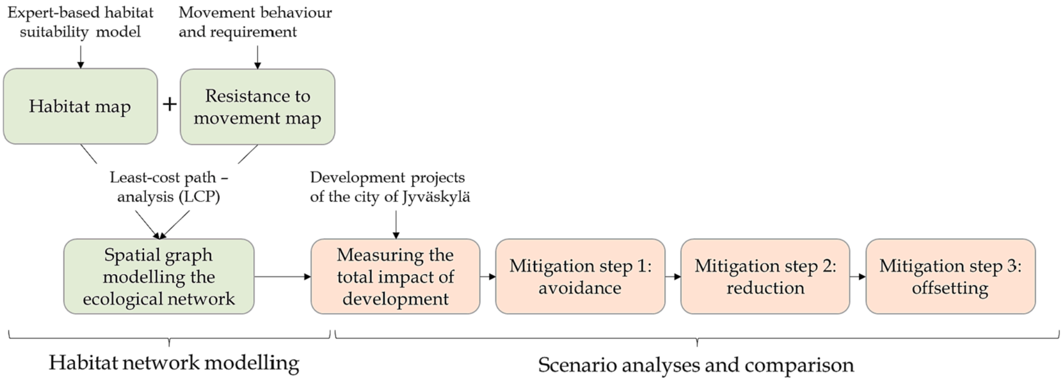


Fig. 1. Stepwise implementation of habitat network modelling and scenario analyses and comparison to reach no net loss of connectivity. The habitat network modelling phase (green boxes) uses a combination of spatial data, least-cost path, and spatial graph modelling methods. The scenario analyses and comparison phase (orange boxes) use iteratively for each mitigation hierarchy step: (i) modifications of spatial graph according to relevant actions, (ii) a connectivity assessment and comparison of action benefits, (iii) and adoption of best mitigation actions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3.3. Connectivity analyses

We used Equivalent Connectivity (EC) as a global-network connectivity metric in all calculations. EC expresses connectivity as the 'amount of reachable habitat' (Saura & Pascual-Hortal, 2007) for a focal species and is calculated as follows (in this study in hectares):

$$EC = \sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j p_{ij}^{*}} \tag{1}$$

where n is the total number of nodes, a_i and a_j are the area of nodes i and j, and p_{ij}* is the maximum product probability of dispersal between nodes i and j (Saura et al., 2011). p_{ij}* is determined by considering all possible paths along the graph between patch i and j. One or several intermediate links can be included when computing *pij**, which represents all the intermediate steps that an individual would have to move through. *pij** is then calculated as the product of the probability of dispersal of all links along the shortest path. The probability of dispersal of each link is calculated from link attributes (cumulative resistance/cost), and it takes the dispersal capacity of the focal species into account:

$$p_{ij} = e^{-\alpha d_{ij}} \tag{2}$$

where α is a distance-decay coefficient and d_{ij} is the cost distance between patch i and j. In the current study, α was set so that $p_{ij} = 0.5$ for the mean dispersal distance of flying squirrels (Saura & Pascual-Hortal, 2007). The metric mean dispersal distance of the flying squirrel was transformed to cumulative cost distance using a log–log regression between the metric distance and cost distance of all links in the graph (Clauzel et al., 2019; Tournant et al., 2013). Connectivity analyses were performed using the mean dispersal distance of 2 km and the +/- 5, 10, 20 and 40% deviations from that value (see section 2.2. Study species).

2.4. Mitigating the impacts of development

To study the impacts of the ten development projects on the habitat network and possible mitigation actions, we generated different scenarios of urban development or mitigation actions and compared their connectivity values. (i) The total impact of the development plan (including all ten projects) is assessed to set a reference for mitigation; (ii) at the avoidance step, the impact of each individual development project is assessed to identify the one that provides the largest benefits if avoided; (iii) at the reduction step, patches and links within the project areas whose conservation (i.e., excluded from constructions) leads to the largest positive impact on connectivity are identified; (iv) at the offsetting step, forest patches located outside the development project areas are identified for potential restoration measures and added to the network until the remaining negative impacts are fully offset. For each scenario, we constructed a new spatial graph by modifying the resistance-to-movement layer and habitat map based on the develop-

Table 1
Resistance values used to model flying squirrel's movement ability in each land cover type. Low and high values indicate good and low movement ability respectively.

Land cover	Resistance value	Movement ability
Suitable habitat	1	good
Forest, height > 10 m	2	good
Conservation areas	2	good
Forest, height unknown	15	medium
Forest, 1 m < height < 10 m	30	medium
High vegetation (bushes)	80	medium
Urban area with many trees	100	medium
Forest, height < 1 m	400	low
Low vegetation	400	low
Powerline	400	low
Urban area with few trees	500	low
No vegetation	1000	no movement
Road	1000	no movement
Building or pool	1000	no movement
Water	1000	no movement
Mask	10,000	defines the study area

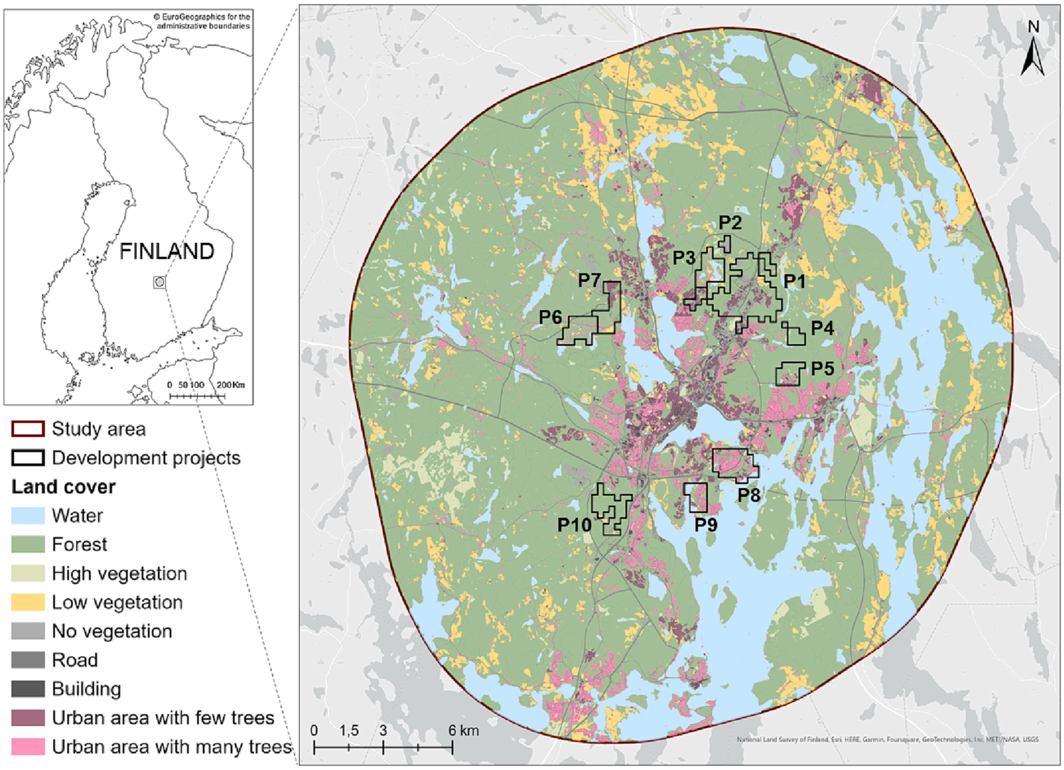


Fig. 2. Geographical location of the study area (Jyväskylä, Finland) with simplified land cover map and spatial locations of studied urban development projects (P1–P10).

ment projects or suggested mitigation actions. The difference in connectivity (ΔEC) between the scenarios and the reference scenario (i.e., the initial network or the network originating from the previous mitigation step) represents the connectivity loss or gain of the scenarios and was calculated as follows:

$$\Delta EC = EC_{before} - EC_{after} \tag{3}$$

where EC_{before} is the EC of the reference network (i.e., the initial network or the network originated from the previous mitigation step) and EC_{after} is the EC of the scenario (i.e., after land use change or mitigation action; Bergès et al., 2020).

2.4.1. Total impact assessment and avoidance scenarios

To assess the overall impact of the ten development projects and, thus, the total connectivity loss that should be mitigated, we created one scenario where all development projects are built and compared it to the initial network. In that scenario (and in all avoidance scenarios), we assumed that, in the development areas, there would be no habitats or movement possibilities for flying squirrels (a resistance value of 10,000 was used) because of comprehensive land use change.

In avoidance, we studied the individual impacts of each development project by generating a scenario in which all other projects except the project in question are built. This allowed us to calculate the gain in EC obtained by avoiding the development of each project relative to the scenario where all projects are built. To facilitate comparisons between projects, the gain in EC was also expressed as EC per avoided hectare, that is, divided by total project area. Based on the results, the projects that should be avoided were decided, and a new reference network based on selected actions was defined. This new reference network showed the remaining total impacts after avoidance and, thus, was used as a baseline for the next mitigation step (i.e., reduction).

2.4.2. Reduction scenarios

The reduction scenarios were done with the perspective that, in the project areas, some important network components (patches or links), would be saved from land use changes and excluded from construction. Several scenarios illustrating different options of mitigation actions were generated for the development projects with the highest impacts and not selected for avoidance action. To facilitate the creation of reduction scenarios, individual nodes and links were ranked according to their contribution to the overall connectivity of the initial network using the *dPC connector* connectivity metric (Supplementary Fig. S5; Duflot et al., 2018; Rubio & Saura, 2012).

Reduction actions were selected based on node and link importance to connectivity, flying squirrel observations, and green connections proposed by the city of Jyväskylä in the existing loosely defined green infrastructure map. These various criteria were accounted for by overlying spatial data in GIS and manually delineating the reduction areas accordingly, that is, saving these nodes and patches from construction. The tested reduction actions are illustrated in Fig. 3 and described in Table 2. Different combinations of reduction actions were then tested (see Supplementary Table and Fig. S6). The flying squirrel's 'core areas' are protected from future development and, therefore, were always included in these reduction combinations. The best combination of actions was selected, and this defined a new reference network for offsetting.

2.4.3. Offsetting scenarios

To offset the remaining impacts of development, we identified the best locations for implementing new habitat patches for flying squirrels

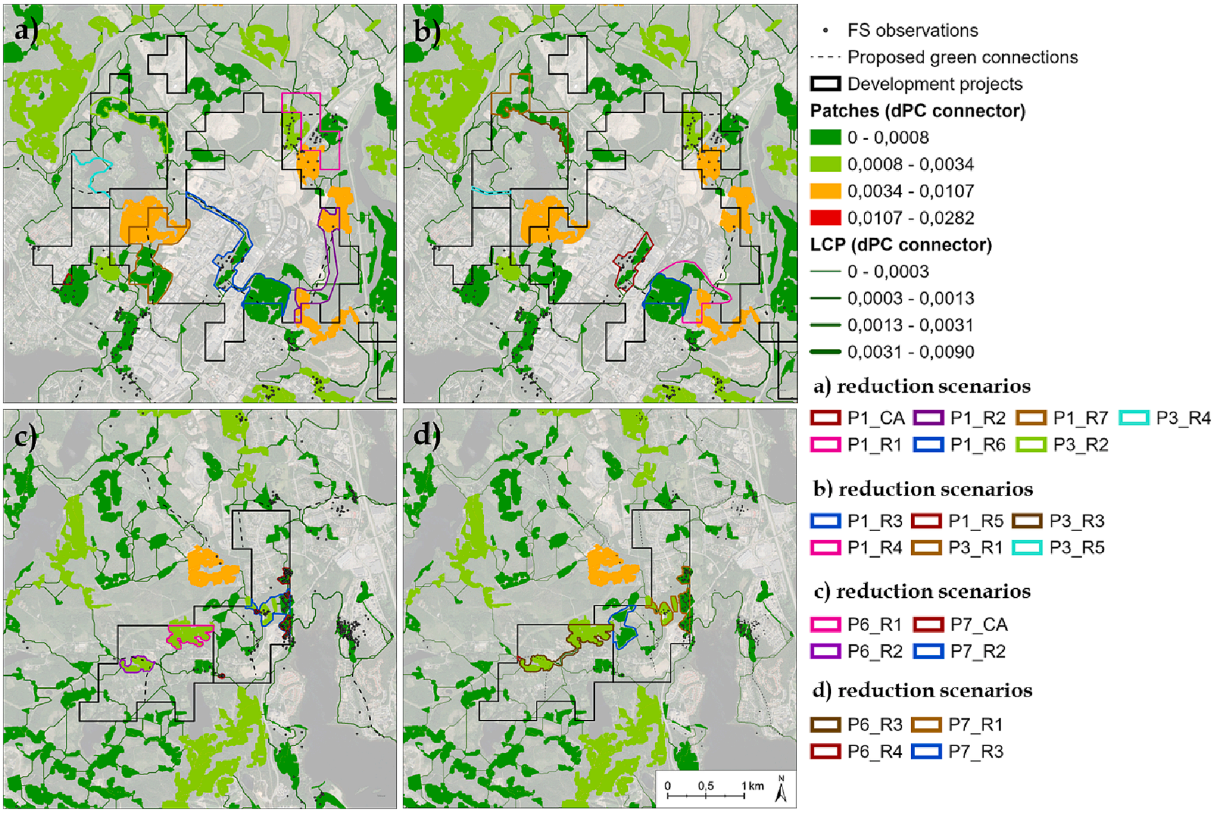


Fig. 3. Maps illustrating the reduction scenarios delineated by coloured lines for development projects 1 and 3 (a-b), and projects 6 and 7 (c-d). Suitable habitat patches and least-cost paths (LCP) of the flying squirrel habitat networks are presented regarding their importance to overall connectivity (*dPC connector*). Flying squirrel observations (black points) and possible future green connections proposed by the city of Jyväskylä (dashed lines) were also used in determining reduction actions. For a detailed descriptions of the tested reduction actions see Table 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Descriptions of the actions tested in each reduction scenario. A graphical representation of the scenarios is available in Fig. 3.

Project	Scenario	Reduction action(s)
All	CA	All core areas for flying squirrel defined by city saved (seven)
Project 1	P1_CA	All core areas in Project 1 saved (two)
Project 1	P1_R1	Upper right corner saved (many patches and observations)
Project 1	P1_R2	Lower right corner saved (important habitats, one green connection)
Project 1	P1_R3	Bottom mid patch saved (large patch)
Project 1	P1_R4	Bottom mid area saved (many patches, one important for connectivity)
Project 1	P1_R5	Middle patch saved (many observations and one little core area)
Project 1	P1_R6	Bottom mid and middle patch and two connections saved
Project 1	P1_R7	Left area saved (important patches and green connection)
Project 3	P3_R1	Upper corner saved (three nearby patches and their connections)
Project 3	P3_R2	Upper patches saved (three nearby patches and their connections)
Project 3	P3_R3	Whole upper area saved (many nearby patches and their connections)
Project 3	P3_R4	One important link saved following LCP
Project 3	P3_R5	One important link saved following city proposed green connection
Project 6	P6_R1	Upper right patch saved (important for connectivity)
Project 6	P6_R2	Left patch saved (important for connectivity)
Project 6	P6_R3	Upper right and left patch and their connection saved
Project 6	P6_R4	Upper right and left patch and two connections saved
Project 7	P7_CA	All core areas in Project 7 saved (five)
Project 7	P7_R1	Middle patches saved (six patches)
Project 7	P7_R2	Middle area saved (six patches and their connections)
Project 7	P7_R3	Left corner saved (three patches and their connections)

using a cumulative patch addition process in Graphab (Foltête et al., 2014). Because of the high computational requirement in this process, the study area was reduced by buffering the minimum bounding polygon of the development projects by the mean dispersal distance of flying squirrel (2 km), thus concentrating the offsetting actions near the urban centre. Then, possible offsetting areas, which could be transformed into suitable habitats for flying squirrels by active management, were defined. Only forests owned by the city of Jyväskylä that were not in the project areas or already suitable habitats for flying squirrels, were considered possible offsetting sites. City-owned forests were divided using a regular grid of 4 ha squared cells, creating patches of various sizes because these cells were usually not fully covered by forests. From the resulting forest patches, only those greater than 0.5 ha were included. This resulted in 1,833 possible offsetting sites with a mean size of 1.64 ha (SD 1.02 ha). Non-forest land uses were excluded from the potential offsetting site because these cannot be turned into flying squirrel habitats (old spruce-deciduous mixed forest) in a reasonable time frame.

The cumulative patch addition process first calculates the EC of the reference network before adding a new potential patch, creates links between this new patch and the existing patches, and calculates the EC again (Foltête et al., 2014). This metric was computed for all potential new patches, and the one leading to the highest EC gain was selected. Then, the process starts again, and the second-best patch is selected. This process was repeated until a given number of new patches is reached. In the current study, we targeted the addition of 20 new patches to ensure that the NNL of connectivity is achieved.

3. Results

3.1. Modelling the habitat network and connectivity

The potential suitable habitat of the flying squirrel covered 9,406.0 ha (i.e., 13.6% of the study area; Supplementary Fig. S5). The mean size of habitat patches was 4.7 ha (SD 11.2), and the size distribution was highly positively skewed, meaning that most of the patches (79.6%) were smaller than the mean size. From all the observations of flying squirrel occurrence (N = 4272), 57.8% fell within suitable habitats and 70.9% within suitable areas buffered with the mean gliding distance of flying squirrel (40 m). If only observations were carried out within forest areas (i.e., excluding observations outside forest land covers), 61.9% of observations fell within suitable habitats and 75.2% with the same buffer distance (N = 3608).

The spatial graph of the initial habitat network of the flying squirrel consisted of 1,935 nodes representing suitable habitat patches and 3,678 links representing the LCPs connecting these patches (Supplementary Fig. S5). The overall connectivity EC was 3,039 ha, which was based on the mean dispersal distance of the flying squirrel. When removing the links with a cost distance superior to the mean dispersal distance of the flying squirrel, the habitat network was split into 80 disconnected components.

3.2. Impacts of development projects and avoidance scenarios

Urban development had a negative impact on the connectivity of the flying squirrel habitat network. Together, the development projects (total area = 1800 ha) theoretically removed 264.8 ha (2.8%) of suitable habitats for flying squirrels and decreased the overall connectivity by 3.2% (97.9 ha; Fig. 4a). The individual effects of the development projects varied greatly (Fig. 4a). The avoidance of Project 10 and Project 1 (i.e., not implementing the projects) had the most positive impact on connectivity, while the avoidance of projects 2, 9 and 8 had almost no effect on connectivity. Avoiding projects 3–7 increased connectivity. When considering the effects of project avoidance per hectare of avoided development (see Supplementary Fig. S7a), Project 10 had by far the highest impact, indicating that a large part of the development area was important for the habitat network. The avoidance of Project 10 was the best action for this step to increase the connectivity for flying squirrels (EC gain = 42.8 ha), mitigating 43.8% of the total impact.

3.3. Reduction

After avoidance, the theoretical remaining EC loss was 54.9 ha (56.2% of the total impact). Because projects 1, 3, 6 and 7 had the highest negative impact on connectivity after Project 10, they were selected for reduction actions (Fig. 3 and Table 2). The EC gain associated with the reduction actions varied greatly, thus revealing the best actions (Fig. 4b). Some of the actions, such as those related to maintaining the city ‘core areas’ or individual patches, had very limited benefits for connectivity. When considering the effect per area lost for development, two reduction scenarios of Project 3, both related to saving important links from development (P3_R4 and P3_R5), had a very high positive impact (Supplementary Fig. S7b). Among the different combinations of reduction actions tested, the combination of the five

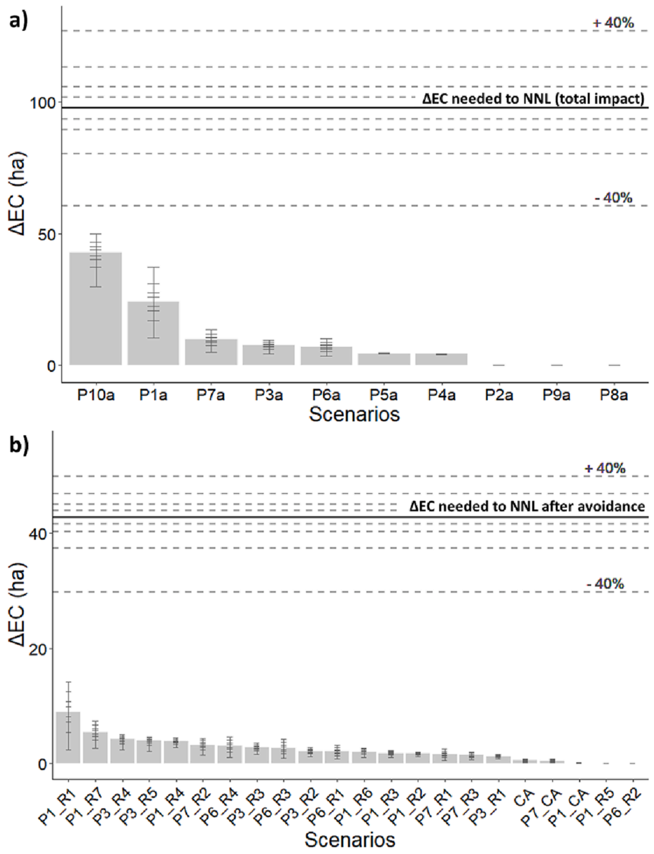


Fig. 4. a) Connectivity gains (ΔEC) obtained by avoiding each individual development project (scenarios P1a – P10a), as compared to the flying squirrel habitat network where all projects are developed. Horizontal lines represent the ΔEC needed to achieve no net loss of connectivity, i.e., the total impact of development projects as compared to the initial intact network. b) Connectivity gains (ΔEC) obtained from the different reduction actions (scenarios, see Table 2 and Fig. 3), as compared to the flying squirrel habitat network after avoidance actions. Horizontal lines represent the ΔEC needed to achieve no net loss of connectivity after avoidance actions, i.e., the remaining impacts compared to the initial intact network. Upper and lower error bars and dashed lines represent respectively the ΔEC values for the positive and negative deviations from the mean dispersal distance of flying squirrel (+/- 5, 10, 20 and, 40 %).

individual reduction actions with the highest EC gain per area lost for development was the most efficient (EC gain of 20.9 ha, 21.4% of the total impact, see Supplementary Fig. S6).

3.4. Offsetting

After avoidance and reduction, the theoretical remaining EC loss was 34.0 ha (34.8% of the total impact). The patch addition process identified 20 new habitat patches that would maximise connectivity for flying squirrels (Fig. 5, see Supplementary Fig. S8 for a map of these 20 sites). The gain in EC with all 20 new patches was 43.0 ha, which exceeded the total impact of development projects by 9.0 ha (Fig. 5). The NNL of connectivity was reached by offsetting 14 new patches, following the ranking priority.

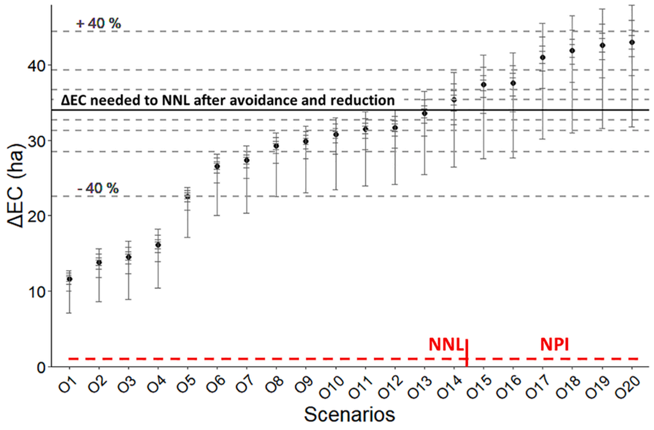


Fig. 5. Connectivity gains (ΔEC) obtained from patch addition (offsetting actions), as compared to the habitat network after avoidance and reduction actions. The numbering of offsetting scenarios (O1 – O20) relates to the number of new patches added. Horizontal lines represent the ΔEC needed to achieve no net loss of connectivity after avoidance and reduction actions, i.e., the remaining impacts compared to the initial intact network. When using the mean dispersal distance of flying squirrel, no net loss (NNL) of connectivity is achieved by offsetting 14 new habitat patches, net positive impact is obtained when more habitat patches are added (red dashed line). Upper and lower error bars and dashed lines represent respectively the ΔEC values for the positive and negative deviation from the mean dispersal distance of flying squirrel (+/- 5, 10, 20 and, 40 %). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.5. Sensitivity of results to dispersal distance

Variation in the dispersal distance of flying squirrels caused large variability in the connectivity measurements, even though this effect was uneven across the mitigation scenarios, independently from their level of impact (Figs. 4 and 5). For example, the effect on EC gain in the avoidance step was greater in Project 1 than in Project 10 and was minimal for Project 5 and Project 4 (Fig. 4a). In the offsetting step, the sensitivity increased when the number of new patches increased, that is, as the habitat network became better connected. Variability in the dispersal distance affected the number of offsetting patches needed to reach the NNL of connectivity: deviation of −40% and −20% of the mean dispersal distance led to only 8 or 11 new patches needed, while deviations of + 40% and + 20% resulted in 17 or 15 new patches needed to reach NNL of connectivity.

3.6. Summary of mitigation actions

The NNL of connectivity was possible to achieve by avoiding, reducing and finally offsetting the impacts of development projects (see graphical abstract). The effectiveness of the different mitigation actions selected in the mitigation steps varied. When comparing the effects of mitigation steps with each other, avoidance led to the highest increase in connectivity, while reduction increased connectivity least. In addition to the NNL of connectivity, a net positive impact of 1.4 ha on EC was achieved when offsetting 14 new patches and 29.95 ha when offsetting all 20 new patches. The spatial locations of all mitigation actions needed to reach the NNL of connectivity are shown in the Supplementary Fig. S9.

4. Discussion

We have illustrated how spatial graphs can be used together with a before–after scenario analysis to identify and quantify the best strategy to achieve no net loss of connectivity. We further developed the application of all steps of the mitigation hierarchy at the landscape level with a real-world multi-project urban development plan, as highlighted in separate previous studies (e.g., Clauzel & Godet, 2020; Tarabon et al., 2019, 2020). We showed that the urban development plan of the city of Jyväskylä would have a negative impact on the connectivity of the flying squirrel habitat network, with a cumulated loss of 3.2% (98 ha) of Equivalent Connectivity (EC). Although this impact seems limited, it is important to keep in mind that the current development plan does not account for previous loss and is valid for a couple of decades; in addition, the cumulated impact beyond that horizon could further increase.

We found that the initial network of the flying squirrel, before the implementation of development projects, was highly fragmented in the study area. Only 12.4% of habitat patches were larger than the mean home range size reported for female flying squirrels (8 ha; Selonen et al., 2001). However, flying squirrels can use habitats other than those preferred for foraging and movement (especially males) and accommodate smaller territories in urban landscapes (Mäkeläinen et al., 2016). The network consisted of 80 subnetworks connected by links with higher cost distance than the mean dispersal distance, indicating a reduced probability of dispersal. Most of the suitable habitats were in larger forest areas or in semi-urban areas of the city. Fewer habitats were detected in the urban area, which reflects both past habitat fragmentation caused by the development of the city over time and lack of comprehensive forest data for urban areas in Finland. Similar results have been found in the larger and nearby city of Tampere, where the habitat network of flying squirrels was found to be badly connected as well (Hirvonen, 2018).

The impact of the ten individual projects varied greatly because they differed in size and contained different amounts of suitable habitats and important connections. For instance, Project 10 had a very high potential impact. Thus, by avoiding its development, the total impact of all development projects could almost be halved (43.8%). Avoidance of Project 10 was a very effective action compared with the size of the project, as shown by its very high EC gain per hectare of development. In comparison, Project 1 had a large impact but a much smaller impact per ha of development; thus, reduction actions were preferred for this project. Indeed, targeting the important habitat patches and connections within that project can mitigate a high proportion of the impacts while affecting only a small percentage of the whole project area. The decision to avoid the development of a whole project (here, Project 10) clearly has a huge impact on the general development plan of a city. These decisions should necessarily come very early in the planning process, that is, during the preliminary delineation of development areas at the municipality level and before the detailed project planning (i.e., exact locations of building and infrastructures). To maintain municipality objectives (e.g., in number of new housing), the cancellation of a project could be balanced by denser urbanisation in another planned project area (i.e., geographic avoidance).

The best reduction scenarios were actions in which both patches and connections were saved from development. The potential gain in connectivity was lower for actions in which only a single large patch or groups of neighbouring patches were saved. The highest increase in connectivity was obtained with actions that saved patches and/or connections with high importance for connectivity, here identified using the *dPC connector* of individual elements calculated from the initial network, hence highlighting the value of that metric in prioritising conservation actions (see, e.g., Duflot et al., 2018). Connections were the most effective from the perspective of connectivity gain per area spared for development. The reduction step was also an opportunity to evaluate the green connections and ‘core areas’ for flying squirrels identified by the city of Jyväskylä, that is, to evaluate the existing conservation plan. We found that some of the connections in the green infrastructure map would be effective for flying squirrels. However, ‘core areas’ had a minor effect in increasing connectivity, especially those in Project 1, which were isolated. These results are in line with previous findings that the present regulations for conservation actions of flying squirrels are insufficient (Santangeli et al., 2013; Wistbacka et al., 2018). Although many reduction scenarios were evaluated, the reduction actions were not tested systematically. However, this would be possible in cases where there is a reasonable number of options (see e.g., Tarabon et al., 2019b).

By offsetting 14 new habitat patches, the NNL of connectivity was theoretically achieved. The new patches were strategically located within the network of existing suitable patches, sometimes very close to the development projects (see Supplementary Fig. S8). For most of the new patches, the gain in connectivity was higher than the size of the patch, indicating very good effectiveness (e.g., the EC gain per ha of the offsetting site was up to 11.6 ha). This highlights the understanding of habitat networks that ‘location matters’. Expressing together habitat area and connectivity loss in a common ‘currency’ (Saura & Rubio, 2010) allows for comparing the contribution of patches, corridors or a combination of the two, as we did in the reduction scenarios (Bergès et al., 2020). Although not tested here for offsetting, the NNL of connectivity can also be achieved by the creation of new corridors or lowering the resistance to movement within the landscape (Foltête et al., 2014; Tarabon et al., 2019a). This option should be considered if suitable sites for new habitats are lacking within the urban landscape and can lead to great benefits for highly fragmented networks. However, this should not be seen as an easy alternative to habitat creation or restoration, which remains the main principle of the mitigation hierarchy.

Potential offsetting habitat sites or connections can be restricted and prioritised to account for ecological, economic or social criteria (Foltête et al., 2014). For example, in our case, the offsetting areas were restricted to city-owned forests where restoration actions, such as limited tree cutting and selection of deciduous and spruce tree species, could easily be implemented. Sites could have been further restricted to forests that already contain mature deciduous trees and spruce, facilitating habitat restoration into old, mixed forests. Potential offsetting sites could have also been preselected based on a high HSI. Current ecological state, land availability and price, or human frequentation (which is a disturbance to many species) are relevant criteria for narrowing down the set of potential offsetting sites to be tested in the graph-based patch addition process. Careful preselection of offsetting sites is particularly critical because they will be protected in the long term to ensure they can no longer be lost (avoided loss).

The impacts of the development and benefits of mitigation actions were highly sensitive to the used dispersal distance, which is the key parameter of the connectivity metric. However, the magnitude of this effect was highly variable across the scenarios. Therefore, there is a risk of underestimating the impacts of development or overestimating the effectiveness of mitigation actions if the dispersal capacity is not accurately measured. Depending on the dispersal distance considered, more or fewer offsetting sites were needed to reach the NNL of connectivity. If there is uncertainty in the dispersal distance of the focal species because of an insufficient number of dispersal observations or the use of observations from a different region, this should be considered when modelling connectivity. Choosing the less optimistic scenario should ensure the achievement of the NNL of connectivity. However, accounting for such variability increases the complexity of the already complex process of the mitigation hierarchy.

It is important to keep in mind that the application of the NNL of connectivity suffers from the same limitations as offsetting based on local impacts. For instance, Gelot and Bigard (2021) found that, in France, most reported offsetting actions were planned to occur during the project construction phase (not beforehand) and did not always offer true additionality to other environmental policies. In addition, avoidance actions were far less often used than reduction and offsetting ones, suggesting a low inclination from decision-makers to seriously consider avoidance scenarios (which should come first) and to question the socio-economic benefits of development projects as compared with negative impacts on biodiversity.

5. Conclusion

With a case study and actual city development plan, we showed how the mitigation hierarchy can improve landscape conservation planning in urban areas with respect to the connectivity of habitat networks. The method is flexible and allows decision-makers to test several scenarios to mitigate the negative effects of development projects and reach NNL or net positive impact of connectivity. The results highlight a direct application for the city of Jyväskylä while also illustrating a general framework applicable to any kind of multi-project development elsewhere. Although the flying squirrel is an umbrella species whose habitat is useful to many other forest species, future research should develop ways to account for multiple species or species groups (e.g., see Clauzel & Godet, 2020). This would help account for different biodiversity facets in the urban landscape.

The authors warmly thank the City of Jyväskylä and the ELY Centre of Central Finland for collaboration and data sharing. M. Kosma received financial support from the Finnish Foundation for Nature Conservation, the Vanamo Foundation, and from the Flying Squirrel LIFE program (LIFE17/NAT/FI/000469) funded by the European Commission. The material reflects the views of the authors, and the Agency is not responsible for any use that may be made of the information it contains. R. Duflot was supported by a postdoctoral fellowship from the Kone Foundation. The authors are extremely grateful to Jérémy Cours for the artwork he made for the graphical abstract.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The geographic data used in this study are available (upon request) at https://doi.org/10.17011/jyx/dataset/87522

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2023.104847.

References

Adriaensen, F., Chardon, J. P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H., & Matthysen, E. (2003). The application of "least-cost" modelling as a functional landscape model. *Landscape and Urban Planning, 64*(4), 233–247.

Angel, S., Parent, J., Civco, D. L., Blei, A., & Potere, D. (2011). The dimensions of global urban expansion: Estimates and projections for all countries, 2000–2050. *Progress in Planning, 75*(2), 53–107. https://doi.org/10.1016/j.progress.2011.04.001

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences, 281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330

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

Boitani, L., Falcucci, A., Maiorano, L., & Rondinini, C. (2007). Ecological networks as conceptual frameworks or operational tools in conservation. *Conservation Biology, 21* (6), 1414–1422. https://doi.org/10.1111/j.1523-1739.2007.00828.x

Bull, J. W., Gordon, A., Watson, J. E. M., & Maron, M. (2016). Seeking convergence on the key concepts in 'no net loss' policy. *Journal of Applied Ecology, 53*(6), 1686–1693. https://doi.org/10.1111/1365-2664.12726

Clauzel, C., Foltête, J.-C., Girardet, X., & Vuidel, G. (2019). *Graphab 2.4 User Manual.* https://sourcesup.renater.fr/graphab.

Clauzel, C., & Godet, C. (2020). Combining spatial modeling tools and biological data for improved multispecies assessment in restoration areas. *Biological Conservation, 250* (July), Article 108713. https://doi.org/10.1016/j.biocon.2020.108713

Crooks, K. R., & Sanjayan, M. (2006). *Connectivity Conservation.* Cambridge University Press.

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 framework and a species case study. *Journal for Nature Conservation, 46*, 38–47. https://doi.org/10.1016/j.jnc.2018.08.005

Fletcher, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., Holt, R. D., Gonzalez, A., Pardini, R., Damschen, E. I., Melo, F. P. L., Ries, L., Prevedello, J. A., Tscharntke, T., Laurance, W. F., Lovejoy, T., & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity? *Biological Conservation, 226*, 9–15. https://doi.org/10.1016/j.biocon.2018.07.022

Foltête, J. C., Clauzel, C., & Vuidel, G. (2012). A software tool dedicated to the modelling of landscape networks. *Environmental Modelling & Software, 38*, 316–327. https://doi.org/10.1016/j.envsoft.2012.07.002

Foltête, J. C., Girardet, X., & Clauzel, C. (2014). A methodological framework for the use of landscape graphs in land-use planning. *Landscape and Urban Planning, 124*, 140–150. https://doi.org/10.1016/j.landurbplan.2013.12.012

Galpern, P., Manseau, M., & Fall, A. (2011). Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. *Biological Conservation, 144*(1), 44–55. https://doi.org/10.1016/j.biocon.2010.09.002

Gelot, S., & Bigard, C. (2021). Challenges to developing mitigation hierarchy policy: Findings from a nationwide database analysis in France. *Biological Conservation, 263*, Article 109343. https://doi.org/10.1016/j.biocon.2021.109343

GIBOP. (2023). *Global Inventory of Biodiversity Offset Policies (GIBOP) (International Union for Conservation of Nature, The Biodiversity Consultancy, Durrel Institute of Conservation & Ecology).* https://portals.iucn.org/offsetpolicy/.

Hanski, I. K. (1998). Home ranges and habitat use in the declining flying squirrel Pteromys volans in managed forests. *Wildlife Biology, 4*(1), 33–46. https://doi.org/10.2981/wlb.1998.013

Hanski, I. K., & Selonen, V. (2009). Female-biased natal dispersal in the Siberian flying squirrel. *Behavioral Ecology, 20*(1), 60–67. https://doi.org/10.1093/beheco/arn115

Hirvonen, K. (2018). *Siberian flying squirrel and children: The use of urban green space. Master of Science thesis.* University of Jyväskylä. (In Finnish with English summary).

Hurme, E., Mönkkönen, M., Sippola, A.-L., Ylinen, H., & Pentinsaari, M. (2008). Role of the Siberian flying squirrel as an umbrella species for biodiversity in northern boreal forests. *Ecological Indicators, 8*(3), 246–255. https://doi.org/10.1016/j.ecolind.2007.02.001

Hyvärinen, E., Juslén, A. K., Kemppainen, E., Uddström, A., & Liukko, U.-M. (2019). Suomen lajien uhanalaisuus 2019—Punainen kirja: The 2019 Red List of Finnish Species. *Ympäristöministeriö & Suomen.* ympäristökeskus.

Ipbes. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *Zenodo*. https://doi.org/10.5281/zenodo.5517154

Jongman, R. H. G., Kulvik, M., & Kristiansen, I. (2004). European ecological networks and greenways. *Landscape and Urban Planning, 68*(2–3), 305–319. https://doi.org/10.1016/s0169-2046(03)00163-4

Kiesecker, J. M., Copeland, H., Pocewicz, A., & McKenney, B. (2010). Development by design: Blending landscapelevel planning with the mitigation hierarchy. *Frontiers in Ecology and the Environment, 8*(5), 261–266. https://doi.org/10.1890/090005

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 in Australia. *Biological Conservation, 192*, 513–521. https://doi.org/10.1016/j.biocon.2015.08.017

Lepczyk, C. A., Aronson, M. F. J., Evans, K. L., Goddard, M. A., Lerman, S. B., & Macivor, J. S. (2017). Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. *BioScience, 67*(9), 799–807. https://doi.org/10.1093/biosci/bix079

B. Madsen N. Carroll K. Moore Brands State of Biodiversity Markets Report: Offsets and Compensation Programs Worldwide (Forest Trends - Ecosystem Marketplace) 2010 https://www.forest-trends.org/publications/state-of-biodiversity-markets/.

Mäkeläinen, S., de Knegt, H. J., Ovaskainen, O., & Hanski, I. K. (2016). Home-range use patterns and movements of the Siberian flying squirrel in urban forests: Effects of habitat composition and connectivity. *Movement Ecology, 4*(1), 5. https://doi.org/10.1186/s40462-016-0071-z

Moilanen, A., & Kotiaho, J. S. (2018). Fifteen operationally important decisions in the planning of biodiversity offsets. *Biological Conservation, 227*(July), 112–120. https://doi.org/10.1016/j.biocon.2018.09.002

Mönkkönen, M., Juutinen, A., Mazziotta, A., Miettinen, K., Podkopaev, D., Reunanen, P., Salminen, H., & Tikkanen, O.-P. (2014). Spatially dynamic forest management to sustain biodiversity and economic returns. *Journal of Environmental Management, 134*, 80–89. https://doi.org/10.1016/j.jenvman.2013.12.021

Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., … Hendrickx, F. (2020). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology, 26*(3), 1196–1211. https://doi.org/10.1111/gcb.14934

Rubio, L., & Saura, S. (2012). Assessing the importance of individual habitat patches as irreplaceable connecting elements: An analysis of simulated and real landscape data. *Ecological Complexity, 11*, 28–37. https://doi.org/10.1016/j.ecocom.2012.01.003

Santangeli, A., Wistbacka, R., Hanski, I. K., & Laaksonen, T. (2013). Ineffective enforced legislation for nature conservation: A case study with Siberian flying squirrel and forestry in a boreal landscape. *Biological Conservation, 157*, 237–244. https://doi.org/10.1016/j.biocon.2012.09.012

Saura, S., Estreguil, C., Mouton, C., & Rodríguez-Freire, M. (2011). Network analysis to assess landscape connectivity trends: Application to European forests (1990–2000). *Ecological Indicators, 11*(2), 407–416. https://doi.org/10.1016/j.ecolind.2010.06.011

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 and Urban Planning, 83*(2–3), 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*(3), 523–537.

Sawyer, S. C., Epps, C. W., & Brashares, J. S. (2011). Placing linkages among fragmented habitats: Do least-cost models reflect how animals use landscapes? *Journal of Applied Ecology, 48*(3), 668–678. https://doi.org/10.1111/j.1365-2664.2011.01970.x

Selonen, V., & Hanski, I. K. (2003). Movements of the flying squirrel Pteromys volans in corridors and in matrix habitat. *Ecography, 26*(5), 641–651. https://doi.org/10.1034/j.1600-0587.2003.03548.x

Selonen, V., & Hanski, I. K. (2004). Young flying squirrels (Pteromys volans) dispersing in fragmented forests. *Behavioral Ecology, 15*(4), 564–571. https://doi.org/10.1093/beheco/arh049

Selonen, V., Hanski, I. K., & Mäkeläinen, S. (2012). Predictors of long-distance dispersal in the Siberian flying squirrel. *Evolutionary Ecology, 26*(6), 1361–1369. https://doi.org/10.1007/s10682-012-9569-z

Selonen, V., Hanski, Ii. K., & Stevens, P. C. (2001). Space use of the Siberian flying squirrel Ptevomys volans in fragmented forest landscapes. *Ecography*, *24*(5), 588–600. Doi: 10.1111/j.1600-0587.2001.tb00493.x.

Selonen, V., & Mäkeläinen, S. (2017). Ecology and protection of a flagship species, the Siberian flying squirrel. *Hystrix, the Italian Journal of Mammalogy, 28*(2), 134–146. https://doi.org/10.4404/hystrix-28.2-12328

Tannier, C., Bourgeois, M., Houot, H., & Foltête, J.-C. (2016). Impact of urban developments on the functional connectivity of forested habitats: A joint contribution of advanced urban models and landscape graphs. *Land Use Policy, 52*, 76–91. https://doi.org/10.1016/j.landusepol.2015.12.002

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. *Journal of Environmental Management*, *241*(October 2018), 439–449. https://doi.org/10.1016/j.jenvman.2019.02.031.

Tarabon, S., Bergès, L., Dutoit, T., & Isselin-Nondedeu, F. (2019). Maximizing habitat connectivity in the mitigation hierarchy. A case study on three terrestrial mammals in an urban environment. *Journal of Environmental Management, 243*, 340–349. https://doi.org/10.1016/j.jenvman.2019.04.121

Tarabon, S., Calvet, C., Delbar, V., Dutoit, T., & Isselin-Nondedeu, F. (2020). Integrating a landscape connectivity approach into mitigation hierarchy planning by anticipating urban dynamics. *Landscape and Urban Planning, 202*. https://doi.org/10.1016/j.landurbplan.2020.103871

Tournant, P., Afonso, E., Roué, S., Giraudoux, P., & Foltête, J.-C. (2013). Evaluating the effect of habitat connectivity on the distribution of lesser horseshoe bat maternity roosts using landscape graphs. *Biological Conservation, 164*, 39–49. https://doi.org/10.1016/j.biocon.2013.04.013

United Nations. (2019). *World Urbanization Prospects 2018: Highlights* (s (ST/ESA/SER.A/421)). Department of Economic and Social Affairs, Population Division.

Urban, D., & Keitt, T. (2001). Landscape connectivity: A graph-theoretic perspective. *Ecology, 82*(5), 1205–1218.

Wistbacka, R., Orell, M., & Santangeli, A. (2018). The tragedy of the science-policy gap – Revised legislation fails to protect an endangered species in a managed boreal landscape. *Forest Ecology and Management, 422*, 172–178. https://doi.org/10.1016/j.foreco.2018.04.017

Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology, 27*(6), 777–797.