Research article

Supporting the planning of urban blue-green infrastructure for biodiversity: A multi-scale prioritisation framework

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1. Introduction

Anthropogenic pressures, particularly urban sprawl and agricultural intensification, are causing the degradation and fragmentation of natural habitats, resulting in declines of biodiversity and ecosystem services worldwide (Horváth et al., 2019). According to the 17th edition of the Global Risks Report (WEF, 2022), biodiversity loss ranks as the third most severe risk on a global scale over the next 10 years. Maintaining the composition and quality of such habitats, as well as their spatial arrangement and integration with semi-natural ones has therefore become a top priority concern to reduce biodiversity loss in human-dominated landscapes (Hodgson et al., 2009; Horváth et al., 2019). This involves prioritising what actions to take and where to take them, which is a timely concern that has been highlighted by many conservation experts (Dickman et al., 2015; Kukkala and Moilanen, 2013; Pascual-Hortal and Saura, 2006; Plisoff et al., 2020; Rudnick et al., 2012; Watson et al., 2016; Welch et al., 2020; Wilson et al., 2007).

Blue-Green Infrastructures (BGI) are emerging nature-based mitigation solutions by which urban planners can address the impact of urban growth and climate change while providing a wide range of ecosystem services (Bolliger and Silbernagel, 2020; Coutts and Hahn, 2015; Kabisch et al., 2016). For instance, the provision of structurally complex vegetated systems and/or wet habitats can increase the number and variety of niches and species (Davis et al., 2015; Le Lay et al., 2015).
functioning as ‘stepping stones’ (Saura et al., 2014) or blue-green corridors (Pauleit et al., 2020) for otherwise fragmented habitats (Lynch, 2019). BGI may not only support the dispersal of species, but also constitute transit and recreation areas for humans at the same time (LaPoint et al., 2015; Monteiro et al., 2020). In urban areas, the design of BGI for multiple functions is being actively sought (Hansen et al., 2019; Laforteza et al., 2013). Nevertheless, objectives of sustainable storm-water management and/or urban heat mitigation remain dominant considerations for BGI, whereas biodiversity conservation is often considered as a secondary benefit (Erickson, 2004; Lennon, 2015), tagged on as part of its ‘business case’ rather than a core planning requirement (Zhang et al., 2020). In fact, while those in charge of urban water management and heat mitigation are aware of the benefits of these systems as opposed to traditional grey infrastructure, there are still hurdles to overcome to take advantage of the full potential of BGI for biodiversity enhancement (Bauchin et al., 2016; Liao et al., 2017).

With limited funds available for biodiversity conservation, there is therefore a pressing need to come up with fully evaluated and consolidated methods available to conservation managers in order to allocate conservation resources in the most effective and efficient manner possible. However, considerable knowledge gaps remain in the context of applying quantitative spatially explicit methods and models that aim to better integrate multi-functional BGI for biodiversity in impacted environments. First, the regional representation of movement/connectivity across the landscape usually relies on circuit theory, which applies the concepts of electrical resistance and current density to evaluate the contributions of multiple dispersal pathways across the landscape (McRae et al., 2008). This widely accepted approach (Dickson et al., 2019; Peng et al., 2018) is usually applied within high resolution grid representations of the landscape, such as rasters. This can be computationally very intense, making it challenging for planners to test different scenarios, which is a crucial step in decision-making processes (Banks, 1993). Second, rasters and other square grid representations (e.g., Bach et al. (2020)) might not be best suited to model connectivity due to their constrained spatial geometry, as cells only share edges with four neighbours (de Sousa and Leiáo, 2018). To circumvent the effects of the limited spatial geometry, high resolution input data may be required which, in turn, increases the processing time of the analyses. Third, network analyses based on least-cost-paths and patch-based models (Galpern et al., 2011; Kong et al., 2010) identify unambiguous optimal routes to move between patches, but have the limitation of not giving information on how cost values are distributed over the landscape (Cushman et al., 2013). Yet, network approaches can support ecological restoration efforts in heavily fragmented landscapes through different metrics that describe flux, vulnerability, redundancy, and connected habitat area (Thompson et al., 2017). Fourth, the placement of the start and end points of movement, called focal nodes (Anantharaman et al., 2019), can be an additional modelling challenge. In regional-scale conservation planning, the focal nodes are commonly placed in ecologically meaningful locations to analyse movement patterns (e.g., inter-breeding sites connectivity) (Churko et al., 2020). While in local-scale planning (e.g., urban planning), due to the absence or limited presence of the species in a reduced spatial extent, focal nodes may be placed along the perimeter of the study area to characterise the potential landscape permeability regardless of the actual distribution of the species (Churko et al., 2020) (i.e., how the landscape matrix shapes the movement potential (Hall et al., 2021)). These challenges have led to ambiguity around circuit and network-based approaches, focal node placement (Churko et al., 2020; Hodgson et al., 2009), spatial extents, and resolutions (Galpern and Manseau, 2013). To our knowledge, there is currently no approach that leverages the strengths of circuit and network theories and the benefits of both regional and local-scale focal node placement to support the planning of urban ecological networks, particularly supported by BGI.

We aimed to generate a framework that supports the efficient and effective planning of BGI with a focus on urban areas. The framework prioritises local BGI interventions based on their contribution to maintaining the connectivity of the regional ecological network. By simplifying the inputs and reducing computational demands, the framework enhances accessibility for use and integration into urban planning efforts, ensuring alignment with ecological goals. To do so, we assess the performance of different spatial resolutions and representations to merge circuit theory with more rigorous post-processing network analysis in three guiding steps: (1) use circuit theory in coarse-resolution spatial grids to identify potential corridors at a regional scale to support essential dispersal processes, (2) use network metrics to assess the relative contribution of individual nodes in the regional ecological network and establish a priority rank for effective and efficient BGI implementations in highly impacted areas (i.e., urban areas) and (3) obtain highly spatially resolved outputs in selected local-scale priority areas identifying habitat restoration and protection needs for biodiversity enhancement.

2. Material and methods

2.1. Study area

Our study area spans across a rural-urban gradient encompassing 3,133 km² in the Swiss lowlands (Fig. 1). It covers the Cantons of Aargau (AG) and Zurich (ZH) with an elevation range between 264 m and 21,212 m (a.s.l.). Aargau (1,404 km²) has 213 municipalities scattered in communities across the landscape with an average population density of 490 inhabitants/km² (its largest city, Aarau has a population of 21,700). Zurich (1,729 km²) comprises 169 municipalities with an average population density of 900 inhabitants/km² mainly located in the major cities of Zurich and Winterthur. Zurich city has a population of more than 434,300 inhabitants (Confederation Suisse, 2022). Approximately 42.9% of the study area consists of meadows, pastures, and other agricultural land; forests occupy a 31.1%; urban settlements 22.2% (12.2% of impervious surfaces and 10% of urban green spaces); water bodies cover 3.8% and the remaining comprises wetlands, rocky surfaces, and rubble-sandy grounds. Regional parks, Ramsar and Emerald sites, alluvial zones, dry meadows, amphibian breeding sites of national importance, and protected ‘Pro Natura’ sites, are some of the major ecological infrastructures (Donati et al., 2022).

2.2. The methodological framework

An overview of our methodological approach is summarised in Fig. 2 and comprises three steps: (1) coarse analysis of landscape connectivity at the regional scale aiming at balancing computational time with representation accuracy of regional ecological movement, (2) network analysis of regional ecological movement to describe node importance and identify local priority locations that are critical to maintaining connectivity of regional corridors, and (3) local-scale connectivity analysis of priority locations and identification of BGI opportunities by interrogating which key environmental characteristics are favourable for design to strengthen connectivity.

2.3. Data sets for model input and validation of approach

Our analysis builds upon Donati et al. (2022), who identified distributions of amphibian biodiversity hotspots and landscape elements essential to amphibian movability at the regional scale by modelling inter-breeding sites connectivity using the amphibian breeding sites of national importance (Ryser et al., 2002) as focal nodes. Donati et al. (2022) carried out the analyses in Circuitscape (Julia implementation v5.0) (Anantharaman et al., 2019) at a resolution of 30m × 30m and using a high-performance cluster. In the present study, we selected four ecologically distinct amphibian species which were also characterised by having different movement patterns according to Donati et al. (2022): 1) Alytes obstetricans, 2) Bombina variegata, 3) Hyla arborea,
4) *Salamandra salamandra*. Resistance layers to amphibian movement (Chubaty et al., 2020) were computed by Donati et al. (2022) based on species distribution models (SDM) (Thuiller et al., 2016), and using a species-specific exponential decay function to strengthen the barrier effect of less favourable areas (Duflot et al., 2018).

2.4. Step 1: coarse analysis of landscape connectivity at the regional scale

2.4.1. Step 1a: spatial aggregation of resistance layers into squared and hexagonal grids

The extensive computational demands needed to perform fine-resolution regional circuit theory-based connectivity simulations on computers within reach of most practitioners hinders the widespread use of these models. To evaluate how much we could reduce computational demands while obtaining a good representation of the ecological movement patterns at the regional scale, we aggregated Donati et al. (2022)’s 30 m resolution resistance layers into squared and hexagonal spatial grids of a 300 × 300 m cell area (an area 100x larger). The aggregation was done using the median resistance value of the raster cells falling within each grid polygon (Fig. 2, Step 1a).

Hexagonal grids were introduced as they allow for a better representation of connectivity when compared to squared representations, especially in coarse grids (Birch et al., 2007). Their major advantage is that each hexagonal cell has six equidistant adjacent nearest neighbours (Birch et al., 2000), as opposed to squared grids, with only four (Childress et al., 1996; Holland et al., 2007). This translates into an increased choice of movement directions (Fig. 2, Step 1a) while maintaining roughly the same number of grid cells and computation time. Finally, the resistance layers in the 300 m squared and hexagonal grid configurations were converted into a spatial network structure, with nodes at the cell centroids and edges linking the adjacent neighboring cells (Fig. 2, Step 1a). Introducing the data as a network edge list allowed us to skip the network creation step in Circuitscape (McRae et al., 2008), which already saves significant processing time.

2.4.2. Step 1b: regional inter-breeding sites connectivity modelling using circuit theory

To model inter-breeding sites connectivity for all four amphibian species, we used Circuitscape (Python implementation v4.0.5) (McRae et al., 2008) in the pairwise calculation mode and the network input format. We performed two connectivity simulations per amphibian species using the aggregated resistance layers for both the square and hexagonal 300 m grids (Fig. 2, Step 1a). We defined the focal nodes (i.e., source locations) using the 271 amphibian breeding sites of national importance (Ryser et al., 2002) (Fig. 1), as assessed by Donati et al. (2022), to predict the maximal inter-breeding site movement potential of amphibians across the study area.

Single-species cumulative current output maps were normalised between 0 and 1 to enable comparative analyses. We then produced multi-species connectivity maps by aggregating the normalised cumulative current maps for every species and grid type (i.e., squares and hexagons). These multi-species maps accounted for the unique movement ecology of each species (Churko et al., 2020) and already served as a useful evaluation of connectivity to estimate which areas of the landscape would be highly connected (Fig. 2, Step 1b).

2.4.3. Validation of the coarse resolution outputs (validation of step 1)

We validated the outputs from our coarse 300 m resolution simulations based on multi-species results using as benchmark the 30 m connectivity maps from Donati et al. (2022). We compared the multi-species 300 m square grid current and the multi-species 300 m hexagonal grid current against the created Donati et al. (2022) multi-species 30 m raster current as well as against each other. We calculated the spatial correlation between layers using the Spearman rank correlation coefficient (ρs) (Zar, 2014). Based on Akoglu (2018), we interpreted the correlations as follows: null [0], weak (0, 0.25), moderate (0.25, 0.5), strong (0.5,
0.75], very strong (0.75, 1), and perfect [1]. For the validation of Step 1 we considered strong to perfect correlations as the criteria for agreement in the comparisons.

2.5. Step 2: Network analysis of regional outputs

Network models usually rely on patch-based representations of the landscape (Rayfield et al., 2011) instead of grid-based, and analyses are mostly centred around the concept of least-cost paths or optimal routes (Chubaty et al., 2020; Cushman et al., 2013). Here we built these networks upon the grid-based outputs of Circuitscape (i.e., the 300 m squared and hexagonal grids), which allowed us not only to describe the contribution of each habitat patch to connectivity but also evaluate the role of the landscape matrix between them, potentially finding other secondary corridors that could be missed in patch-based network analyses. The output of Circuitscape provided node and edge information of the network and magnitudes of current therein. Running Circuitscape in the network format allowed us to merge its circuit-theory-based connectivity results with analyses typically carried out in network connectivity models. To this end, we used the sfnetworks R package (van der Meer et al., 2022), which connects the functionalities of the tidygraph package (Pedersen, 2020) for network analysis and the sfpackage (Pebesma, 2018) for spatial data science.

Fig. 2. Overview of the three-step methodological approach.
2.5.1. Steps 2c and 2e: selection of network metrics and node contribution to connectivity

Selecting a network metric presents a challenge to researchers, as Galpern et al. (2011) counted more than 40 metrics among the studies reviewed. Drawing upon Estrada and Bodin (2008), Galpern et al. (2011), Kupfer (2012), Minor and Urban (2008), and Rayfield et al. (2011), we selected a representative set of network metrics and classified them into those that: (a) characterise the overall network connectivity, (b) assess node contribution to connectivity at the regional scale, (c) assess node importance for connectivity at the local scale, and (d) assess network cohesion. A summary and description of the ecological relevance of the eight selected network metrics are presented in Table 1.

2.5.2. Step 2b: edge-thresholding experiments to subset ecological corridors

The overall regional network initially consisted of a single component (i.e., set of mutually reachable nodes). Due to its grid structure, all the nodes had the same degree (except those along the perimeter). This hindered the computation of the network metrics of node importance at the local scale (Table 1c) and metrics of network cohesion (Table 1d), as these metrics investigate relationships with neighboring nodes with different degrees or differences in components. An additional step was therefore required to increase the number of components and the variability in node degrees, which we accomplished by subsetting only the nodes and edges with high enough currents to be considered ecological corridors. The current threshold was estimated by an adaptation of the edge-thinning technique, originally described by Keitt et al. (1997). We designed a simple analysis in which edges below a certain threshold of current (derived from the Circuitscape outputs) were removed and the resultant connected sub-networks were then identified. We subsequently computed this number of sub-networks (i.e., number of components), mean order (i.e., number of nodes) of the components, and network diameter (Brooks, 2006). We then increased the value of this threshold iteratively and recalculated network metrics. By plotting each of these threshold values against the mentioned metrics, a critical threshold was identified at the value associated with the highest connectivity change (Galpern et al., 2011). In accordance with Elliot et al. (2014), we basied our thresholds on the specific distribution of the data. In short, we iteratively subset the edges with a current (C) equal or higher than the mean current (C̄) plus an increasing number (x = {0, 4}) of standard deviations (σ), denoted by Eqn. (1).

\[ C \geq C̄ + x \cdot \sigma \]  

(1)

The outcome was an ecologically meaningful binarisation of the network describing what was considered as an ecological corridor and what was not, rather than deciding on a pseudo-random percentile not objectively grounded on connectivity changes.

2.5.3. Validation of the network representations

The network analyses of the two grid representations (squares and hexagons) at 300 m resolution could lead to disagreement due to their different network topologies (i.e., different node degrees). To validate the network representations used in Step 2, we proceeded to analyse the correlations between the betweenness centrality maps obtained for each type of grid. Betweenness was chosen among other metrics as it is the only node-specific metric that analyses connectivity over the entire regional network (Table 1b). Moreover, according to Ray and Burgman (2006), and McNeil et al. (2006), the calculation of the shortest paths, which is the underlying principle of the betweenness, is most likely to benefit from a change from a rectangular to a hexagonal grid. Seeing an almost perfect agreement between cumulative current maps of the two grid shapes (discussed later in Section 3.1.2, Table 2), here we only considered a “very strong” to “perfect” correlation (Section 2.4.3) as the criteria to acknowledge congruence between the square- and the hexagonal-grid networks. Lower correlation values would justify the choice of a hexagonal representation over a squared grid, eventually accepting a slightly higher demand on computational demands.

2.5.4. Step 2f: prioritisation of urban areas for BGI implementation

We aggregated network metric values into a single weighted index for the identification of the most relevant nodes for connectivity. To this end, some indices have previously been developed (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Villégé et al., 2008), yet they are all meant to be applied in networks based on habitat patches and not applicable to grid-based networks. We propose a weighted combination of node metrics of node importance at both the regional (Table 1b) and at the local scale (Table 1c). For the assignment of weights, we computed the Spearman’s corregor and performed a cluster analysis to find groups of highly correlated network metrics. After normalising the values of each metric between 0 and 1, the cluster analysis was used to assign equal weights to every cluster of metrics, as

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**Table 1**

<table>
<thead>
<tr>
<th>Scope</th>
<th>Metric</th>
<th>Description</th>
<th>Ecological relevance</th>
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<tbody>
<tr>
<td>a) Overall network connectivity</td>
<td>Diameter</td>
<td>Measures the length of the longest shortest path between any two nodes in the network (Bum et al., 2000).</td>
<td>The higher the diameter, the slower is the movement through the network (Minor and Urban, 2008).</td>
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<tr>
<td>b) Node contribution to connectivity at the regional scale</td>
<td>Betweenness</td>
<td>Measures how frequently a node lies on the shortest path between any two nodes in the whole network (Luke, 2015).</td>
<td>A node with a high betweenness has a crucial function due to its position of control over the flow of information in the network (Kolaczek and Gaßt, 2015). The spatial distribution of nodes with high betweenness delineates the backbones for maintaining regional ecological connectivity. Depending on the habitat quality, high degree nodes may be highly transited areas (Minor and Urban, 2008). Highly clustered nodes imply access to a fair amount of nearby nodes and facilitate organism dispersal (Bodin et al., 2006).</td>
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<tr>
<td>c) Node contribution to connectivity at the local scale</td>
<td>Node degree</td>
<td>Measures the number of edges adjoining a node and is an indicator of accessibility (Kupfer, 2012).</td>
<td>It provides a characterisation of the susceptibility of the network to perturbations. A high value of the metric indicates more resistance to fragmentation and higher robustness of the corridor (Melian and Bascompte, 2002). The bigger the component the more nodes will be mutually reachable (Minor and Urban, 2008).</td>
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<td></td>
<td>Local clustering coefficient</td>
<td>Measures the average fraction of the node’s neighbours that are connected to each other (Minor and Urban, 2008).</td>
<td>It provides a characterisation of the susceptibility of the network to perturbations. A high value of the metric indicates more resistance to fragmentation and higher robustness of the corridor (Melian and Bascompte, 2002). The bigger the component the more nodes will be mutually reachable (Minor and Urban, 2008).</td>
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<td>Compartamentalisation</td>
<td>Also known as connectivity correlation (Melian and Bascompte, 2002), measures the relationship between the node degree and the average node degree of its neighbours (Minor and Urban, 2008).</td>
<td>It provides a characterisation of the susceptibility of the network to perturbations. A high value of the metric indicates more resistance to fragmentation and higher robustness of the corridor (Melian and Bascompte, 2002). The bigger the component the more nodes will be mutually reachable (Minor and Urban, 2008).</td>
</tr>
<tr>
<td></td>
<td>Component’s order</td>
<td>A component is a set of nodes that are connected to each other but separated from the rest of the network. Its order describes the quantity of nodes that pertain to it.</td>
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<td></td>
<td>Cut-nodes and cut-edges</td>
<td>Tree structures in the network by which all nodes are connected with the minimum number of edges and the minimum total cost (Jalali et al., 2016).</td>
<td>Cut nodes and edges occupy critical locations to preserve connectivity (van der Meer et al., 2022). They represent weak spots against disturbances, so the robustness of the network depends directly on them (Albert et al., 2000). They represent arterial corridors (Luo and Wu, 2021), and are therefore important in maintaining regional ecological integrity (Zhao et al., 2019).</td>
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<td></td>
<td>Minimum Spanning Trees (MST)</td>
<td>Tree structures in the network by which all nodes are connected with the minimum number of edges and the minimum total cost (Jalali et al., 2016).</td>
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opposed to a simple average. This way, we were able to mitigate the cross-correlation effects between metrics and avoid over-weighting of certain ecological aspects that could be explained by more than a single metric. The index was computed for every node as a measure of importance to support both the regional and local connectivity.

Owing to the critical role of cut-nodes in maintaining the connectivity of the network (Table 1d), and the relevance of BGI to enhance biodiversity in urban and other human-impacted landscapes, a top-priority node in the present study followed 3 conditions:

a) must be a ‘cut-node’ (Table 1d).
b) located in urban areas, selected based on the majoritarian land-use in every node’s grid cell.
c) with a high priority index; the greater the value, the higher the priority.

2.6. Step 3: local-scale connectivity analysis of priority locations

2.6.1. Step 3g: selection of top-priority locations and connectivity modelling in the surroundings

For the actual planning of urban BGI solutions, a more detailed resolution is needed to capture intra-urban variability in morphology (e.g., Bach et al. 2018). To illustrate this step, we selected the top-two priority nodes as assessed in Section 2.5.4. We first applied a buffer of 2 km around the nodes’ centroid to capture its surroundings over an area of 12.5 km². This distance was selected because the diameter of the buffering circle (4 km) represents the maximum dispersal distance of Hyla arborea (Trochet et al., 2014), the species with the highest dispersal distance among those selected. Moreover, it is a large enough extension to include representative urban structures and landscape features, while being relatively small to allow for detailed planning and feasible computation. This reduction in scale enabled us to perform local-scale connectivity modelling placing the focal nodes along the perimeter of the buffering circles, as not enough ecologically relevant sites were found within. This then allowed us to model high-resolution permeability for the areas that were identified in Steps 1 and 2 as the most crucial ones for connectivity support at the regional scale (Fig. 2, Step 3g). Perimeter effects can impact local-scale connectivity when placing focal nodes along the perimeter. Koen et al. (2014) found that a buffer >20% of the study area width was sufficient to remove the effects of node placement on current density. We reduced perimeter effects by choosing circle-shaped areas and, since the geometrical distance from a focal node to any other focal node through the centroid was equal, only the outer 20% of the area should be considered with caution.

For urban planning purposes, at this scale, resistance needs to be defined either based on detailed cadastral data and expert judgments (see e.g., Churko et al. 2020) or from regional SDMs. In our case, as we had access to data of the latter and for consistency purposes, local-scale connectivity modelling was carried out at a 10 m resolution applying the same resistance transformation function to Donati et al. (2022)’s SDMs (see Section 2.3.2). This was the finest available resolution based on the SDM inputs, three times more detailed than the simulations by Donati et al. (2022), which could only be handled by a high-performance computing cluster. A total of 126 focal nodes were placed every 100 m along the perimeter and circuit theory-based connectivity was modelled in Circuitscape, now using the raster format input. We simulated all four species and, once normalised, combined their output into multi-species current maps.

2.6.2. Step 3h: consideration of environmental variables for BGI design

We used 14 environmental variables identified as important for amphibian whole-life cycle environmental predictors (Donati et al., 2022) and were used to describe the local environment for BGI design. These included topographic, hydrologic, edaphic, vegetation, land-use derived, and movement-ecology related predictors (SM Table S1). We extracted their values within each of the regional grid cells featuring the highest cumulative currents computed in Step 1b. To achieve this, we further restricted the edge threshold (see Section 3.2.2) by two additional standard deviations. This procedure was carried out for the 300 m hexagonal grid representation and the original 30 m rasters of Donati et al. (2022) and served additionally as a method of comparison and validation of our coarse setup. We observed the ranges and distributions of the variables and computed the peak values of the density distributions as a proxy of preference of every variable for species movement. These regional-scale peak values where then compared to the median value at the grid cell of our selected local-scale top-priority nodes. Large differences of the latter compared to the regional peak values would then provide guidance of what features (e.g., use of vegetation, provision of soil moisture) of suitable BGI technologies and design could contribute to enhance species movement in the area.

3. Results & discussion

3.1. Step 1: coarse analysis of landscape connectivity at the regional scale

3.1.1. Regional inter-breeding sites connectivity modelling using circuit theory

The multi-species inter-breeding sites connectivity maps highlight amphibian movement patterns along the major waterways, namely the Reuss, the Aare, and the Rhein (Fig. 3a). Other corridors are found across...
the landscape, with notable variation between species (see Supplementary material – SM Fig. S1 for single-species results). Alytes obstetricans can potentially disperse broadly over Aargau, being favoured by forest edges, and with less prominent corridors in the surroundings of Zurich, which could explain the absence of observations in that area. Bombina variegata shows similar preference and emphasis on the river network, highlighting less diffuse pathways. The dispersal of Hyla arborea appears more restricted, with narrow corridors along the Aare and the Reuss and along the shorelines of the lake Greifensee, areas with variable soil moisture. Salamandra salamandra exhibits more predicted movement across artificial landscapes, with relatively high currents inside the Zurich agglomeration. Although the species is widespread across the study area, this has to be interpreted with caution as an indicator of potential movement. In fact, Salamandra salamandra is the species with the lowest dispersal capability (Trochet et al., 2014) and its connectivity could be compromised in the long term if we fail in specific: wet-forest habitats, which constitute its core habitats (Manenti et al., 2009). Overall, the coarse analysis of landscape connectivity at the regional scale identified forest edges, waterways, wet forest habitats, and soils with variable moisture as essential landscape elements for amphibian dispersal. Despite using coarser resolution data, such landscape elements were highlighted in agreement with (Donati et al., 2022).

3.1.2. Validation of the coarse resolution outputs

To validate the coarse resolution outputs from Step 1, the Spearman rank correlation coefficient (\( \rho_s \)) between cumulative current maps is presented in Table 2a. The coarser setups perform relatively well when compared to reference 30 m rasters by Donati et al. (2022), yielding correlation coefficients of nearly 0.7, indicating a strong agreement (Akoglu, 2018). Following our acceptance criteria (Section 2.4.3), the 300 m resolutions are considered similar enough to the reference case and accepted for the analysis. The downside of a coarser resolution is found to be much less severe than initially anticipated. Visually, we can confirm very strong agreement in the location of high current corridors (SM Fig. S2). Moreover, the spatial distribution of the cumulative currents between the two grid representations (i.e., squares and hexagons) is almost perfectly correlated, with a Spearman’s correlation coefficient of 0.961.

### 3.2. Step 2: Network analysis of regional outputs

#### 3.2.1. Node contribution to connectivity at the regional scale

By computing the single- and multi-species betweenness centralities (Table 1b) we identify the nodes located most frequently on the shortest path between any other two nodes in the network. Results highlight the most traversed nodes and illustrate what we refer to as the ‘backbones’ of the regional connectivity network. The rivers Reuss, Aare and Rhein are the main landscape features that support these routes. However, not all backbone branches are associated with water features, especially the secondary ones. For instance, all species exhibit a movement preference between the Reuss to the Zurich area, crossing through more terrestrial habitats towards the Limmat river (in the case of Hyla arborea) or the Zurich lake (in the case of Alytes obstetricans, Bombina variegata, and Salamandra salamandra). More detailed pathways are illustrated in SM Fig. S3. On the multi-species betweenness map (Fig. 3b) we observe that the cities of Zurich, Winterthur, Aarau and Brugg contribute notably to the backbone structure, highlighting the important and needed integration of BGI in these and other urban areas to protect and facilitate species dispersal through artificial environments.

#### 3.2.2. Validation of the network representations

To validate the use of the network representations from Step 2 in subsequent analyses, Table 2b shows the comparison of the network metrics at the regional scale (i.e., betweenness centrality) for the two different grid shapes (squares and hexagons). Even though their almost complete agreement in the cumulative currents (Table 2a, \( \rho_s = 0.961 \)), divergence in the betweenness centrality metric (Table 2b, \( \rho_s = 0.737 \)) highlights the potential limitation of movement directions in a coarse square grid network as opposed to a hexagonal one. According to our criteria of interpretation (Section 2.5.3), and due to their similar computation times (Section 3.4), the square 300 m network representation is not accepted for further analyses. We therefore focus the rest of our approach on the hexagonal grid representation to minimise the effect of data aggregation on movement opportunities.

#### 3.2.3. Edge-thresholding experiments to subset ecological corridors

By performing edge thresholding experiments (Fig. 4) in the single- and multi-species networks, we find an agreement between all the three assessed metrics on showing the greatest change in the connectivity at the threshold value that included only edge currents equal or higher

<table>
<thead>
<tr>
<th>Validation</th>
<th>Layer 1</th>
<th>Layer 2</th>
<th>Spearman coeff. ( \rho_s )</th>
<th>Interpretation$^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) STEP 1: Circuit theory Normalised cumulative current</td>
<td>Raster 30 m (Donati et al., 2022)</td>
<td>Hexagons 300 m</td>
<td>0.692</td>
<td>Strong (accepted)</td>
</tr>
<tr>
<td></td>
<td>Raster 30 m (Donati et al., 2022)</td>
<td>Squares 300 m</td>
<td>0.685</td>
<td>Strong (accepted)</td>
</tr>
<tr>
<td></td>
<td>Hexagons 300 m</td>
<td>Squares 300 m</td>
<td>0.961</td>
<td>Very strong (accepted)</td>
</tr>
<tr>
<td>b) STEP 2: Network analysis Betweenness centrality</td>
<td>Hexagons 300 m</td>
<td>Squares 300 m</td>
<td>0.737</td>
<td>Strong (not accepted)</td>
</tr>
</tbody>
</table>

* The criteria of interpretation of the correlation coefficients are detailed in Section 2.4.3 (for Step 1) and Section 2.5.3 (for Step 2).
than the mean current plus one standard deviation ($C \geq \bar{C} + \sigma_C$). This is therefore the most adequate and ecologically relevant threshold to subset the nodes and edges of the networks conforming the ecological corridors.

3.2.4. Node contribution to connectivity at the local scale

Although having disaggregated the regional grid-based and single-component network into ecological corridors with multiple components (Section 3.2.3), we can still observe some effects of the precedent topology on the metrics of node contribution to connectivity at the local scale (Table 1c), the clearest being node degree and compartmentalisation limited to six. The local clustering coefficient highlights closed triangles within thin and fragile corridors, where organisms can have access to an increased number of nearby nodes. Potentially highly transited and robust areas, characterised by high compartmentalisation values, are found along the Aare, the Rhein, and the Reuss. Indeed, these three rivers, together with the Limmat, form the biggest connected component in the area, the rest being notably smaller.

3.2.5. Network cohesion: identification of cut-nodes and minimum spanning trees

We used the ecological corridors network subset (Section 3.2.2) to identify cut-nodes, cut-edges, and compute the minimum spanning trees (MST) (Table 1d). We identified *Salamandra salamandra* as the species with the highest proportion of cut-nodes over the total number of nodes (0.46), followed by *Hyla arborea* (0.44), *Alytes obstetricans* (0.43), and *Bombina variegata* (0.38). Despite the high order (i.e., total number of nodes) of some of these corridor components, the presence of almost half of them being critical nodes compromises the connectivity of the ecological corridors in the long term. Eventually, urban development projects where a cut-node is located could transform its land use into barrier structures, leading to fragmentation of the ecological corridor into disconnected network components. These critical areas should imperatively be managed and protected against anthropogenic impacts, promoting the restoration of its surrounding habitats and the creation of alternative blue (i.e., aquatic) – green (i.e., terrestrial) corridors or ‘stepping stone’ habitats for redundancy (Grant et al., 2019). Minimum spanning trees (MST), on their side, can provide useful insights to support the planning and location of BGI in the local scale (Fig. 5).

3.2.6. Index of prioritisation of urban areas for BGI implementation

The hierarchical clustering dendrogram and the graph of fusion level values representing the correlations and pairwise dissimilarities between the network metrics, are presented in SM Fig. S4. From its interpretation, the best cutting level (Borcard et al., 2018) was found to be at a height of 0.6, obtaining two different clusters of similar metrics. Interestingly, one included the only metric of connectivity at the regional scale (Tables 1b and i.e., betweenness centrality), and the other grouped the metrics of connectivity at the local scale (Tables 1c and i.e., node degree, local clustering coefficient, compartmentalisation, and component order). We considered the regional and local scales of equal importance to connectivity in human-dominated landscapes. The priority index was therefore computed as a weighted average assigning 50% of the weight to the regional scale metrics and 50% equally (12.5% each) to the ensemble of metrics at the local scale.

3.3. Step 3: local-scale connectivity analysis of priority locations

3.3.1. Selection of top-priority locations and connectivity modelling in the surroundings

Fig. 5 shows two examples of top-ranked priority nodes and their surroundings. We overlaid the regional-scale coarse ecological corridor networks (Section 2.5) on the 10 m resolution multi-species local-scale connectivity cumulative current maps (Section 2.6.1), illustrating the node metrics, cut-nodes and cut-edges, and minimum spanning trees (MST). These examples highlight that high resolution current corridors can occur along specific streets, urban parks, small creeks and/or peri-urban agricultural field edges. Moreover, network features indicate the contribution of those areas to ecological connectivity at the regional scale. The planning of multi-functional BGI in these locations should not

![Mean order of components](image1)

![Network diameter](image2)

![Number of components](image3)

Fig. 4. Edge thresholding experiments for the selection of a meaningful threshold for ecological corridors subset. Grey lines represent the network metrics of overall network connectivity for the species-specific threshold values, and the blue line illustrates the average between the 4 species and the multi-species scenario. The selected threshold represents the biggest change in connectivity observed and is highlighted in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
only consider biodiversity in multi-criteria assessments but perhaps assign to it a greater weight than other ecosystem services (e.g., stormwater management).

The top-ranked priority area (Fig. 5a) includes the municipalities of Brugg (12,738 inhabitants), Umiken (1,069 inhabitants) and Riniken (1,482 inhabitants). Its high priority index of 0.81 is, in part, due to its excellent contribution to the regional scale inter-breeding sites connectivity (Table 1b), with a normalised betweenness value of 0.99. To minimise the impacts of fragmentation to the regional ecological network, it is crucial to ensure movement permeability by creating additional blue-green corridors or ‘stepping stone’ habitats, and removing all possible barriers. In this regard, the railway for the IR36 line becomes a particular point of conflict, together with the urban areas of Brugg and Umiken. Small scale mitigations could also prove effective, such as implementing track deflectors. At the local scale, the contribution of this node to connectivity (Table 1c) is also notable, with a node degree of 4, a normalised local clustering coefficient of 0.5, and compartmentalisation of 0.55, making it part of the biggest component of the ecological corridors. Concerning the permeability of movement, particularly high currents are found along the riverbanks of the Aare, hence BGI solutions might focus attention on the restoration of riparian corridors employing soft bioengineering techniques to provide heterogeneous micro-habitats while preventing excessive geomorphic degradation, especially along the outer edge of the river bend. Other corridors contributing to species movement across the region include forest edges at the interface with agricultural fields, and more diffuse corridors along green areas and urban creeks.

The second top-rated node (Fig. 5b) is an excellent example of a location that could almost go unnoticed when considering only circuit theory-based connectivity analyses for decision-making. Yet, the network analysis points it out as the second most critical urban area in the regional ecological network. Even if the surroundings do not show the highest current, the regional movement of the species directly depends on this narrow and fragile sequence of cut-nodes and cut-edges along the Rhine river, that would fragment the biggest ecological corridor component of the network if degraded. A normalised betweenness of 0.75 confirms its crucial position of control over the flow of organisms in the region. Indeed, this location would benefit in greater measure from BGI interventions by being effective and efficient, compared to other areas with higher current but lower contribution in the network.

3.3.2. Consideration of environmental variables for BGI design

The ranges and value distributions of the environmental variables at the regional highest current corridors (C ≥ C + 3σ, see Fig. 4), representing the potentially most favourable areas, are presented in Fig. 6. As observed, both the 30 m raster and our 300 m hexagonal representation show very similar density distributions of the environmental variables within the mentioned highest current corridors, with almost a perfect agreement in their peak values.

These regional-scale values can now be compared to the environmental characteristics at the selected top-priority nodes, to target specific measures for habitat enhancement. Hereby we illustrate the procedure focusing only on the top-ranked priority node (Fig. 5). We observed good agreement between the local-scale median value at the top node and the regional-scale peak value of the vegetation height, the distance to water, to forests, to roads and to rock-gravel-sand features. However, the NDVI index in the surroundings of our top-node could be improved to enhance species movement (e.g., by increasing the vegetation cover and reducing plant stress), as well as implementing specific BGI solutions to increase the soil moisture variability (e.g., by implementing bioretention swales), decrease the runoff coefficient (e.g., by removing impervious surfaces), and decrease the slope (e.g., by restoring river banks with soft slopes and vegetated stabilisation techniques). Some other values like the level of urbanisation might be more difficult to modify, hence the importance of BGI to mitigate their negative effects.
be attributed to specific land management practices, or even ownership. The number of squared and hexagonal grids. While both scenarios had almost the exact same number of nodes, the number of edges of the hexagonal grid-based networks was 50% higher than the reference squared-grids. The number of focal nodes and focal pairs was also higher, though in a lesser extent. This would potentially represent the urban areas better in the output maps showing more diverse and accurate flow directionality.

3.4. Overview of the simulation setups and computation times design

To minimise the computational time while maximising the quality of our outputs, we compared the circuit theory-based simulations of the squared and hexagonal grids. While both scenarios had almost the exact same number of nodes, the number of edges of the hexagonal grid-based networks was 50% higher than the reference squared-grids. The number of focal nodes and focal pairs was also higher, though in a lesser extent. In spite of this significant increase in the amount of information (an accumulated +58.52%), the running times only took, on average, 12.5% longer than the squared grids, making it safe to say that the hexagonal representation provided a much better input quality over computation time ratio, a non-negligible benefit when using fairly coarse resolutions. This can be appreciated in the output maps showing more diverse and accurate flow directionality.

3.5. Limitations and future work

Two major limitations exist relating to ecological representation, specifically: (a) resistance transformations assuming that animal movement behaviour reflects similar factors to habitat suitability, which may not always be the case (Bolliger and Silbernagel, 2020; Zeller et al., 2012); (b) the consideration of maximal dispersal potential by describing all breeding sites (i.e., focal nodes) as mutually reachable, meaning unlimited time and generations for the colonisation of new potential habitats (Bolliger and Silbernagel, 2020). In relation to this, it would be interesting to test different setups of the focal nodes, for instance from the occupied suitable habitats. Another interesting improvement would be to test Dirichlet tessellations of the landscape, based on land use, cadastre map or similar, from which the aggregation of the SDMs would be done. The network would then be built placing the nodes inside each polygonal feature and the edges linking all the adjacent neighbours. This would potentially represent the urban areas better by providing finer-resolutions in heterogeneous areas while maintaining less detail where is not needed. Additionally, each network node could be attributed to specific land management practices, or even ownership. As a result, future work including exploratory modelling techniques could benefit from this enhancement to assess the impact of different BGI solutions on biodiversity within detailed urban planning alternatives (e.g., Bach et al. (2015)). The spatial simplification and effectiveness of the approach also enables its integration with other spatial models, such as those for planning BGI for other ecosystem services (e.g., UrbanBEATS (Bach et al., 2020)), or as a driver for future urban development dynamics (e.g., UrbanSim (Waddell, 2002)). Furthermore, through the network approach, it also provides a foundation piece for constructing broader social-ecological networks to model governance challenges related to sustainable ecosystem management (e.g., Bodin et al. (2016); Janssen et al. (2006)).

4. Conclusions

In this study we demonstrate the use of a three-step approach to identify priority locations within urban areas where BGI can support and enhance regional ecological networks: (1) coarse regional analysis of landscape functional connectivity, (2) network analysis of regional outputs, and (3) fine-scale structural connectivity analysis of priority locations. Circuit theory or network theory approaches by themselves can support the location of effective BGI opportunities, where species movement will occur with the highest probability. However, there is no guarantee that these locations would benefit the most from BGI interventions to support the movement of the species in the region. For instance, those locations could already be ecological infrastructure protected against human disturbances, or secondary corridors with limited contribution in the region. By strategically implementing circuit theory at different scales and ecologically-relevant network metrics, we can identify priority locations according to their contribution to connectivity, the cohesion and robustness of the network, which is crucial when enhancing biodiversity. It ultimately allows us to obtain fine resolution outputs at strategic locations while optimising computational demands. This approach significantly simplifies circuit theory-based simulations for BGI planning purposes by adopting alternative spatial representations and coarser resolutions and enhances exploratory modelling possibilities for practitioners. By being both effective and efficient, these human-impacted locations could benefit the most from the implementation of BGI and potentially provide the highest benefit.
over cost ratio to support ecological connectivity in the region. For instance, in our identified priority node, analyses have shown that selecting BGI options that specifically target vegetation cover, quality and soil moisture retention present the greatest opportunity in creating conditions suitable for regional biodiversity enhancement. Our approach demonstrates how we can make more informed decisions and adopt specific design solutions for biodiversity within multi-functional BGI planning procedures, rather than just considering biodiversity as a secondary benefit inherent of these.

Author contributions

Francesc Molné: Conceptualization, Methodology, Software, Validation, Investigation, Data curation, Writing - Original Draft, Writing - review & editing, Visualization; Giulia Francesca Azzurra Donati: Conceptualization, Methodology, Software, Validation, Investigation, Data curation, Supervision, Writing - review & editing; Janine Boliger: Conceptualization, Methodology, Funding acquisition, Writing - review & editing; Manuel Fischer: Conceptualization, Methodology, Funding acquisition, Writing - review & editing; Max Maurer: Conceptualization, Funding acquisition, Writing - review & editing; Peter Marcus Bach: Conceptualization, Methodology, Validation, Investigation, Supervision, Funding acquisition, Writing - review & editing.

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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

We have uploaded the data to an open-access online repository (EnviDat). We have a provisional and reserved doi while the data is being reviewed: https://doi.org/10.16904/envidat.386

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Appendix A. Supplementary data

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