Trading connectivity improvement for area loss in patch-based biodiversity reserve networks

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Abstract

Development pressure on biodiversity reserve networks in densely populated countries may lead to the decision to compensate for biotope loss by improving connectivity. Such a decision makes sense, if creation of new biotopes takes too long and if improving population exchange is a conservation target of the reserve network. To explore the impact of such decisions, we analyse four compensation scenarios. The scenarios vary in how strong loss and compensation is locally fixed. The reserve network was modelled as a graph where biotope patches are represented by nodes and connectivity corresponds to edges along which animals migrate from patch to patch. Connectivity improvement was modelled as a reduction of edge lengths. Ecological equivalence is measured by metapopulation capacity as defined by Hanski and Ovaskainen (2000). Localised modifications were analysed with eigenanalysis. Modifications spread over the whole component were analyzed with a linear regression model which uses the total biotope area and the length of the minimal spanning tree as input. Our results show that both general connectivity improvement and clearly localised connectivity improvement can be efficient compensation measures for area loss. Local measures best focus on connectivity improvement between the largest patches. For Switzerland’s dry grassland reserve network, we found that in general, for half of the patches it is possible to compensate an area loss of 100 m² by a connectivity improvement equivalent to an edge length reduction of less then 3 m. Our results show that connectivity improvement is a valuable compensation alternative to creation of new patches.

1. Introduction

Biodiversity loss was identified as one of the greatest ongoing challenges worldwide at the Rio Convention (UNEP, 1992). Patch-based reserve networks are important tools for decreasing or even stopping biodiversity loss in fragmented landscapes (Margules and Pressey, 2000; Margules and Sarkar, 2007; Noon et al., 2009; Pressey et al., 2007). A typical patch-based reserve network consists of a number of biodiversity-rich biotope patches embedded in a matrix of low biodiversity value. The patches are usually under strict protection, whereas the matrix is much less regulated. Establishing patch-based reserve networks should guarantee that inside patches target-species populations have a high probability for long-time survival. Since survival probability is enhanced by migration of individuals between patches, high matrix-permeability is important if survival within patches is threatened (Steffan-Dewenter and Tscharntke, 2002).

Several countries have issued guidelines on how to manage threats to protected patches in a reserve network. The guidelines generally follow a mitigation hierarchy (Quétier and Lavorel, 2011): If possible, threat should be avoided. If not possible, damage should be minimised, and if any residual impacts exist, biodiversity loss should be compensated by an equivalent biodiversity gain, preferably in the neighbourhood of the loss (Rundcrantz and Skärbäck, 2003; Quétier and Lavorel, 2011; Kägi et al., 2002). Compensation may involve protecting new areas (creating new patches or enlarging the size of existing ones), improving the quality of existing patches or enhancing the connectivity between patches (Etienne, 2004).

Under certain circumstances compensation by enhancing connectivity between patches can be the most efficient compensation approach. It is especially efficient if the time needed to establish new high-quality patches is long. For example, newly created calcareous grasslands need more than a century until they develop an acceptable quality (Fagan et al., 2008; Zobel et al., 1996). Furthermore, this approach is efficient if target species can profit from increased metapopulation dynamics. For example, pollinators (bumblebees, bees and other hymenopteras), insects as part of the food-chain (grasshoppers) and many charismatic species (butterflies, crickets) can profit from connectivity (van Swaay, 2002). Connectivity improvement is also an attractive approach if it is more cost-efficient to improve matrix permeability than to establish a new patch in the neighbourhood.
A reliable method for measuring ecological equivalence of biodiversity loss and gain is then a basis for compensation. However, there is still a lack of such methods (Quétié and Lavorel, 2011). We propose a method for assessing ecological equivalence of biodiversity loss due to reduced patch area and biodiversity gain due to connectivity improvement. The method is appropriate for general assessments, when little is known about the local situation. If detailed knowledge about threatened species’ ecological needs and about matrix properties exists, compensation scenarios can be compared by more sophisticated approaches (e.g. circuit theory (McRae et al., 2008)) that use individual-based simulations of migration paths.

Metapopulation capacity (MC; Hanski and Ovaskainen, 2000) is an appropriate indicator for assessing ecological equivalence. The indicator is derived from metapopulation dynamics theory in fragmented landscapes and takes patch properties and landscape context into account. Furthermore, it enables the quantification of the effect of small changes in network geometry on biodiversity (Hanski, 2004). MC may be viewed as the “total amount of suitable habitat in the landscape” or as the “carrying capacity” for a local population (Moilanen and Hanski, 2006). Alternative measures for assessing ecological equivalence are based on composition of the species pool (Dalang and Hersperger, 2010), the area (Allen and Feddema, 1996), or on conservation targets adapted to specific conservation problems (Pressey et al., 2004; Cabeza and Moilanen, 2004). However, MC has the advantage of aggregating patch sizes and inter-patch distances into one single measure.

We estimate compensation need (CN) for a real existing reserve network with high ecological variability. CN is defined as the reduction of the distance between two patches that is ecologically equivalent to an area loss of 100 m². The definition uses two simple assumptions: The ability of a patch to harbour a population is assumed to be equal to patch area, and connectivity between patches is assumed to be equal to the Euclidian distance between patches.

In applied compensation projects, localised and non-localised area loss and connectivity improvement are common. For example, the construction of a building or road causes a localised loss, the design of stepping-stones causes a localised gain, and a change of mowing or mulching (Römermann et al., 2009) or small-scaled heterogeneity increasing (Braschler et al., 2009) causes a non-localised loss or a non-localised gain. We therefore analyse in four scenarios (Table 1) the effect of localised and non-localised area loss, and of localised and non-localised connectivity improvement.

Compensation guidelines often demand “on-site” compensation, referring to compensation within a neighbourhood (Mckenney and Kiesecker, 2010). No general definition of neighbourhood exists. However, it is expected that the definition of neighbourhood affects the CN. We therefore investigate how two different thresholds for defining neighbourhood influence CN.

Specifically, we studied the following five questions using the data of the dry grassland inventory of Switzerland (for details see Section 2.1):

1. How must the connectivity between two patches be improved to compensate for a loss of 100 m² within one patch, with loss and compensation in the same neighbourhood? (Section 3.1).
2. How does the definition of neighbourhood influence CN? (Section 3.2).
3. How can MC be estimated by a regression based on network descriptors? (Section 3.3).
4. How do CNs differ, if computed for localised versus non-localised loss and compensation? (Section 3.4).
5. How can the method used to answer question (1) be simplified so it is easy to use in practice? (Section 3.5).

2. Materials and methods

2.1. Study area and dry grassland data set

The dry grassland inventory of Switzerland is the basis of a biodiversity conservation project run by the Federal Office for the Environment (FOEN). The goal of the FOEN-project is to establish and maintain a network of dry grassland patches with management contracts between government and farmers. The inventory gained official status in 2010 (SBR, 2010). It describes 13,531 biotope patches varying in size from 488 m² to 1.1 km² (mean: 1.8 ha, median: 0.9 ha), adding up to 250 km² (0.6% of Switzerland). Half of the patches belong to the Mesobromion (Dalang and Hersperger, 2010), which corresponds to EUNIS type E1.262B, characterised as “mesophile calcareous grasslands of the French and Swiss Jura and adjacent areas” by the pan-European habitat type classification (EEA, 2010). The inventory methodology is described in detail in Eggemberg et al. (2001) and summarised in Dalang and Hersperger (2010). Additional information about the project is available on the Internet site www.bafu.admin.ch/tww. Data is stored at FOEN and at the Datacenter Nature and Landscape (geonet.wsl.ch/geonetwork, search term “DNL”).

Swiss dry-grassland-inventory data is suitable for conducting this research because (1) area and quality of calcareous grasslands decrease as a consequence of agricultural intensification, the abandonment of traditional agricultural practice (Diacon-Bolli et al., submitted for publication), and the spread of human settlements (Monteiro et al., 2011). In a topographically structured landscape this degradation results in fragmentation, where species-rich biotopes persist only in peripheral areas. (2) Mobile and small animals, such as butterflies, bees and orthopterans have a high biodiversity in grasslands (van Swaay, 2002), and have therefore been the focus of several biodiversity conservation programs (Europe: ECE, 2007; Switzerland: SBR, 2010). (3) In order to solve real world planning problems, such as compensation and connectivity issues (Kägi et al., 2002; BAFU, 2011), it is worthwhile to use data with realistic variability. Models based on simulated data can hardly yield good solutions for complex real world problems. Though they might be better for studying theoretical questions.

2.2. Patch-based network model

We modelled the landscape as an interconnected network of biotope patches. Such networks can be represented with mathematical graphs (Bunn et al., 2000), in which the nodes correspond to biotope patches and the edges to connectivity between patches (Fig. 1). The dynamics of a metapopulation can be described by extinction and colonisation processes. We made the following assumptions: patch size indicates the quality of a patch for the survival of a species and that the larger the patch, the better the chances that a species would survive; and inter-patch distance corresponds inversely with movement permeability in the matrix. Therefore, biotope loss was expressed as a decrease in patch area. Compensation was expressed as decreased inter-patch distance. Patch sizes and inter-patch distances were measured in metric units.

2.3. Cutting the network in components

Generally, the larger the distance between patches, the smaller the population exchange between them, and consequently the smaller the MC of the network. Therefore, omitting large edges results in a small underestimation of MC. We excluded in the basic compensation problem edges longer than 1 km because a 1 km-threshold was used to quantify the “degree of aggregation” in
the Swiss dry grassland inventory (Dalang, 2001). The same threshold had, for example, been observed for the butterfly *Plebejus argus* L. (*Lycraenidae*), which is found only in patches within 1 km of other populated patches (Thomas et al., 1992).

Components were constructed in three steps using the R-packages *tripack* (Renka et al., 2009) and RBGL (Carey et al., 2011): (1) The minimal spanning tree (MST) was constructed (Fig. 1). This is the shortest graph that connects all patches of the network. Figuratively, the MST can be viewed as the “backbone” of connectivity along which animals migrate. (2) Then the MST edges longer then the cutting-threshold were removed. (3) Then, all components along which animals migrate. (2) Then the MST edges longer then the cutting-threshold were removed. (3) Then, all components along which animals migrate.

The effect of the threshold on CN values was analysed by comparing the CN4 values (see Section 2.4) for the patch-edge pairs of the 1 km-components with the CN4 values for the same pairs computed with the 2 km-components.

The change in MC caused by small changes in the transition matrix \( T \) can be approximated by a Taylor approximation polynomial. We restricted it on the first derivatives \( t_{jk} = \frac{\partial C}{\partial t_{jk}} \) of the Perron root \( C \) with respect to the entries \( t_{jk} \) of the transition matrix \( T \). The derivative of the Perron root yields a transition matrix with the Perron root equal to one, so that the population remains constant over time. The larger the value of the Perron root, the smaller the probability that the metapopulation will die out. Therefore it seems reasonable to interpret the Perron root as the carrying capacity of a component (Hanski and Ovaskainen, 2000).

The vectors of occupation probabilities \( p(t) \) or, without matrix notation, as

\[
p_i(t + 1) = A_i \sum_{j \neq i} e^{-\alpha_{jk}} \cdot A_k p_j(t)
\]

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\[
p_i(t + 1) = A_i \sum_{j \neq i} e^{-\alpha_{jk}} \cdot A_k p_j(t)
\]
matrix with the Perron root as diagonal elements, where all other elements are set to zero.

To compute edge-length reduction needed to compensate a given MC loss, we first estimate the change needed in the transition matrix by a Taylor approximation. Afterwards, this change was transformed by Eq. (1) in edge length reduction.

2.6. Regression model

The MC of a component can be estimated reliably by the regression equation

\[
\log_{10} C = b + a \log_{10} A + s \log_{10} S.
\]

MC C is positively correlated with component’s area A, and negatively correlated with MST length S; so, \(a > 0\) and \(s < 0\). Transformations of the Eq. (2) shows that multiplying the area by \(x\) corresponds to the multiplication of MST length by \(x^{-0.5}\); whereby MC does not change. We will use the quotient \(-a/s\), which is always positive, to characterise the regression models.

2.7. Approximation by singular value decomposition

For scenario S4, the CN4 value is different for each patch/edge pair. A simple approximation for CN4 is therefore desirable, if this approach should be used in practice. A CN4 value can be approximated by the product of a patch-specific factor and an edge-specific factor. Singular value decomposition UDV\(^T\) of matrix W is therefore appropriate (svd-function of R-package base: R Development Core Team (2011), Gentle (2007)), where W is the matrix with patches as rows, edges as columns and CN4 values \(w_{jk}\) as entries. \((j)\) means a patch and \((j)k\) means the MST-edge between patches \(j\) and \(k\). U and V are orthogonal matrices, D is a diagonal matrix and superscript \(T\) indicates transposition. The first column of matrix U multiplied by the square root of the first entry (the largest one) of diagonal matrix D gives the patch-specific compensation factors \(u_k\) and the first column of matrix V multiplied by the same square root gives the edge-specific compensation factors \(v_k\). Thus \(u_k v_k \approx w_{jk}\). Because \(w_{jk}\) is measured in meter units, square root of meter (m\(^{0.5}\)) is the most appropriate unit for the factors \(u_k\) and \(v_k\).

2.8. Example

To illustrate how the model works, we describe CN in more detail for a component near Andermatt (Fig. 2, Table 2, bold lines and white dots in Fig. 6, Annex). The total biotope area of the component is 19.3 ha, the MST length is 2.53 km, and the MC is 21.7. The component consists of eight patches, and the MST consists of seven edges. These means there are 56 patch/edge combinations. The following data uses the model with 643 components, as described in Section 3.3. \(CN_1\) is 3.6 m, \(CN_2\) is between 1.9 m and 6.1 m (median = 3 m), \(CN_3\) is between 3 m and 343 m (median = 89 m), and \(CN_4\) is between 1.5 m and 521 m (median = 86 m). The difference between \(CN_4\) and the product of the two factors is always <6.1 m. The factors were used to code the patch grey-scale and edge width in Fig. 2b. The darker the shading of a patch, the larger is its contribution to the component’s MC, and the larger is the CN to compensate for the size reduction and the larger is the patch-specific factor. Analogously, the wider the mapped edge, the larger is its contribution to the component’s MC, the smaller is the length reduction required to compensate for the area loss, and the smaller is the edge-specific factor.

The most valuable patch in the example is no. 8 (large \(CN_2\), large patch-specific factor), which means that a large edge length reduction is required to compensate for an area loss. This is due to the geometrical arrangement because patch no. 8 is, together with patch no. 6, part of the large hotspot in the eastern part of the component. Patch no. 8 has a larger \(CN_2\) than patch no. 6, even though its area is smaller. The smaller patch of a pair is more sensitive than the larger one because pairs of equal-sized patches have a higher MC than non-equal-sized patches. Therefore, the most valuable MST edge (small \(CN_3\), small edge-specific factor) is the edge between patches no. 6 and 8, because the edge length reduction to compensate for the area loss is smallest for this edge. Patch no. 7 forms a second, less prominent hotspot that complements the eastern hotspot. This patch and the adjoining MST edge 3–7 are characterised by the fact that their CN\(_4\) factors are influenced only marginally by changes in the mobility parameter \(x\).

3. Results

The data set of all components with more then one patch consists of 980 components with 6688 patches and 240,402 patch/MST-edge pairs. The total biotope area A of the components varies from 0.18 ha to 534 ha (median = 8.0 ha), MST length S from 60 m to 91 km (median = 1.1 km), and MC from 0.003 to 3594 (median = 57). Pearson correlations between the log-transformed measures are 0.97 between area and MC, 0.71 between area and MST length, and 0.58 between MST length and MC.

3.1. CN for scenario S4

Scenario S4 (Table 1) gives the most detailed insights into the relationship between patch area loss and connectivity improvement. It is characterised by a localised patch size reduction and by a localised edge size reduction. For 50% of the patches minimal \(CN_4\) is <2.2 m (point A in Fig. 3). For 54% of the patches \(CN_4\) is <100 m for half of the MST edges within the same component (point B). For 99% of the patches \(CN_4\) is <100 m for at least one edge (point C), and for 26% of the patches (point D) \(CN_4\) is <100 m for all MST edges within the same component.

3.2. Influence of neighbourhood-parameterisation on CN

The influence of neighbourhood-parameterization depends on the spatial arrangement of the patches. For 70% of the pairs, the 2 km-value is larger than the 1 km-value. The quotient between both values varies in the range between 0.99 and 1.56 (25%–75%-quantiles, median: 1.01).

It is not obvious how the cutting-threshold influences the \(CN_4\) values. The causality becomes much clearer if we focus at a single component. We analyse therefore a 2 km-component that is composed of three 1 km-components (Fig. 4). The quotient between the 2 km-value and the 1 km-value is in the range between 0.1 and 1.2 (median = 2.57), and for 80% of the pairs the 2 km-value is larger then the 1 km-value. The addition of a 1 km-component to a component used for MC calculation increases the connectivity for nearby patches, increases the value for metapopulation survival and increases therefore their CN to compensate area loss. For example, if the large 1 km-component B (Fig. 4) is added to component A, its influence on patches of group A2 is strong because patches are small, have a peripheral position within component A and are next to component B. On the other hand, patches of group A1 are weakly influenced by component B because the patches are small, have a peripheral position within component A and are far away from component B. Component B (marked with circles in Fig. 4) does not profit from the two others 1 km-components A and C, resulting in small differences between the CN-values, because component B has itself a large MC.

3.3. Regression between component descriptors and MC

MC can be estimated for the 980 components by a regression model (Eq. (2)) with parameters \(b = -0.985 \pm 0.013\) (standard
error), \(a = 1.897 \pm 0.013\), \(s = -0.454 \pm 0.017\) and \(R^2 = 0.97\). The quotient \(a/s\) becomes \(4.17 \pm 0.2\) (whereby the range is calculated with the two standard errors). The largest residuals are found for the 337 components with two patches and the nine components with \(P_{63}\) patches (Fig. 5). Using log-transformed data, the Pearson correlation between the variable are 0.97 (between MC and area), 0.65 (number of patches and area) and 0.90 (number of patches and MST-length).

If components with two patches were excluded, a truncated data set with 643 components, 6014 patches and 239,728 pairs of patch/MST-edge results. The regression parameters change to \(b = 0.931 \pm 0.013\), \(a = 1.955 \pm 0.014\), \(s = 0.703 \pm 0.020\) and \(R^2 = 0.978\). The quotient \(a/s\) is now 2.78 \(\pm 0.1\). This is clearly less then the quotient computed with the non-truncated data. The computation of CN for scenarios S1, S2 and S3 use this truncated data set.

### 3.4. Comparing the four CN

The comparison of the four scenarios (Fig. 6) shows the quotient between the maximal and minimal CN values of a component (= length of the grey lines in Fig. 6). It increases from scenarios where only one modification step is localised (scenarios S2 and S3) to scenario S4 where both modification steps are localised.

![Fig. 2](https://example.com/fig2.png)

(a) Density distribution of the 643 components in Switzerland, where the darker the shading, the higher the density. The triangle shows the component mapped in detail in (b). (b) Map of a dry grassland component near Andermatt (coordinate system WGS84 (www.epsg.org): 46°38'N, 8°36'E; CH1903: 690,000/166,000; 1800 m a.s.l.1). Each patch is mapped as a circle. Its area is equal to the area of the patch (delineated with a fine line). The shading of the circle represents the patch-specific compensation factor (light = small factor, dark = large factor, see Table 2). Edges of the MST are shown. The thickness of the edge represents the edge-specific compensation factor (thin line = large factor, thick line = small factor). CN is therefore small (large) for light patch / thick edge (dark patch / thin edge) combinations. See Table 2 for an example. The diagram is printed on a 1:25,000 Swiss topographic map (©2007, www.swisstopo.ch).

### Table 2

Compensation needs for component Andermatt.

<table>
<thead>
<tr>
<th>MST edges</th>
<th>From patch no: to patch no</th>
<th>Length (m)</th>
<th>CN(_1) (m)</th>
<th>Factor (m(^{1/2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1:2</td>
<td>240</td>
<td>179</td>
<td>13.37</td>
<td></td>
</tr>
<tr>
<td>1:3</td>
<td>476</td>
<td>307</td>
<td>22.72</td>
<td></td>
</tr>
<tr>
<td>2:6</td>
<td>294</td>
<td>26</td>
<td>1.97</td>
<td></td>
</tr>
<tr>
<td>3:4</td>
<td>149</td>
<td>343</td>
<td>25.32</td>
<td></td>
</tr>
<tr>
<td>3:7</td>
<td>620</td>
<td>89</td>
<td>6.70</td>
<td></td>
</tr>
<tr>
<td>5:8</td>
<td>442</td>
<td>60</td>
<td>4.49</td>
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<tr>
<td>6:8</td>
<td>304</td>
<td>3</td>
<td>0.22</td>
<td></td>
</tr>
</tbody>
</table>

Patches

<table>
<thead>
<tr>
<th>No</th>
<th>Area (ha)</th>
<th>(CN_2) (m)</th>
<th>Factor (m(^{1/2}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.54</td>
<td>4.1</td>
<td>14.96</td>
</tr>
<tr>
<td>2</td>
<td>0.83</td>
<td>3.1</td>
<td>11.70</td>
</tr>
<tr>
<td>3</td>
<td>0.76</td>
<td>1.9</td>
<td>7.66</td>
</tr>
<tr>
<td>4</td>
<td>1.27</td>
<td>2.9</td>
<td>11.07</td>
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<td>1.03</td>
<td>2.5</td>
<td>9.85</td>
</tr>
<tr>
<td>6</td>
<td>0.89</td>
<td>4.5</td>
<td>16.12</td>
</tr>
<tr>
<td>7</td>
<td>5.11</td>
<td>2.2</td>
<td>8.67</td>
</tr>
<tr>
<td>8</td>
<td>2.87</td>
<td>6.1</td>
<td>20.76</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Patch/edge combinations</th>
<th>(CN_4) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>200.6</td>
</tr>
<tr>
<td>2</td>
<td>341.8</td>
</tr>
<tr>
<td>3</td>
<td>29.1</td>
</tr>
<tr>
<td>4</td>
<td>377.3</td>
</tr>
<tr>
<td>5</td>
<td>99.5</td>
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<tr>
<td>6</td>
<td>66.5</td>
</tr>
<tr>
<td>7</td>
<td>3.3</td>
</tr>
<tr>
<td>8</td>
<td>6.8</td>
</tr>
</tbody>
</table>

Compensation needs (CNs) for patch/edge combinations can be approximated by the product of a patch-specific and an edge-specific factor. Data for the component mapped in Fig. 2 are given. Example (in bold): Reducing the largest patch (no. 6) by 100 m\(^2\) can be compensated for by reducing the edge length between patches 3 and 7 by approximately 16.12 m\(^{1/2}\) times 6.7 m\(^{1/2}\) = 108.9 m. The eigenvalue method gives a CN\(_4\) of 108.8 m.
The quotient is $\leq 10$ for 73% of the CN values in scenario S2, for 38% in S3, and for 27% in S4. The medians (circles) of $CN_3$ are $\sim 7.8$ times (median) larger than the medians of $CN_2$.

Scenario S1 (x-axes of Fig. 6a and b) is characterised by non-localised patch size reduction and by non-localised edge length reduction. In 50% of the components, an area loss of 100 m$^2$ can be compensated by an MST length reduction of <3.9 m, and for all components by a reduction of <87 m. For components with a total area of 1 ha, 10 ha and 100 ha, $CN_1$ is $\sim 25$ m, $\sim 4$ m and $\sim 1.5$ m, respectively.

Scenario S2 (y-axes of Fig. 6a and c) is characterised by a localised patch size reduction and a non-localised edge length reduction. For 50% of the patches, MC loss can be compensated for by a MST length reduction of <3 m, and for all patches, $CN_2$ is <159 m. For half of the components, the largest $CN_2$ is <3.7 times larger than the smallest $CN_2$, and for 90% of components, this factor is <87.

Scenario S3 (y-axes of Fig. 6b and d) is characterised by a non-localised patch size reduction and by a localised edge length reduction. For 50% of the components, half of the MST edges have $CN_3$ <42 m. For all components, there is at least one MST edge with $CN_3$ < 203 m.

3.5. Simplification of $CN_4$

It is appropriate to approximate $CN_4$ as a product of a patch-specific and an edge-specific factor (see Section 2.7). This approximation facilitates a separate analysis of patches and edges and is
thus easier to use for practical applications. It works particularly well for small components. In 90% of the components with three to six patches, the difference between the approximation and the CN⁴ is <10 m for all patch/edge combinations. For components with 7–10 patches, this is only the case for 30% of the components. The patch-specific factor is highly correlated with CN², i.e. for 80%

Fig. 5. Residuals of the regression model (Eq. (1)) fitted with the data set of 980 components. The y-axis gives the residuals, the x-axes of (a) and (b) give the input variable used for the regression and x-axis of (c) gives the number of patches. Black dots mark 2-patch components. They are excluded for the truncated data set shown in Fig. 6. Crosses mark components with >63 patches.

Fig. 6. Each panel (a–d) shows a comparison of the CN values of two scenarios from Table 1. Each dot and each line represents one of the 643 components with >2 patches. Dots mark the singular CN¹ value of the components and the medians of CN², CN³ and CN⁴ respective to components. Lines mark the min–max range for one value of the CN pairs. Data for the component shown in Fig. 2 and Table 2 are emphasised and labelled with arrows. Measures marked with double arrows are shown in two panels.

of the components, $R^2 > 0.95$. And the edge-specific factor is highly correlated with $CN_{N}$, i.e. for 95% of the components, $R^2 > 0.99$.

4. Discussion

Our CN estimates refer to four land-change scenarios (Table 1). Scenario S1 concerns projects where neither area reduction nor connectivity improvement is spatially localised to one patch or one edge. Examples are loss in quality caused by changes in the management regime and connectivity improvements by introducing structural elements such as hedges (Dipner et al., 2010). In the context of our study, this scenario is of practical relevance because a new planning tool (priority areas or “Vorranggebiete”) promoting such connectivity improvements has been introduced in recent legislation on biodiversity conservation (SBR, 2010). Our results show that, for instance, 1% area loss can be compensated by a 3% MST length reduction. Therefore, a small percentage of area loss of a compact component with large total area needs only a small connectivity improvement as compensation. But for a component with small MC (large MST and small total area), $CN_1$ is considerably larger.

Scenario S2 concerns compensation projects where one patch is reduced in size (e.g. in an infrastructure development project), and where the resulting loss is compensated by improving non-localised connectivity. Such development projects are quite frequent in a densely populated country like Switzerland. For calcareous grasslands, which take a long time to develop from a low-quality into a high-quality habitat, ecological improvements over the whole matrix are appropriate, e.g. by optimising the mowing regime (Römermann et al., 2009; Braschler et al., 2009) or promoting structural elements such as piles of stones or hedges (Eggenberg et al., 2001). Our results show that $CN_2$ strongly depends on a patch’s size and position within the component. Therefore, it makes sense to localise the destruction of a patch so that the resulting MC loss is minimised.

Scenario S3 stands for compensation projects where area loss is distributed over the whole component and where compensation is spatially focused on improving the connectivity between two selected patches. Such a distributed loss may be caused by extinction debt (Kuussaari et al., 2009), referring to delayed extinction because species composition has not reached equilibrium after the biotope has been fragmented. Extinction debt can be identified when e.g. vegetation is degraded but butterfly biodiversity is still relatively high (Sang et al., 2010). As an immediate measure, compensation may be implemented by creating a stepping stone that improves migration between patches. Within half a century (Zobel et al., 1996), this stepping stone may develop into dry grassland of high quality. Our results show that creating biotope patches of mediocre quality as stepping stones is most effective at localities where it improves population exchange with large patches.

Scenario S4 concerns compensation projects where an area in one patch becomes partially lost (as in scenario S2), and compensation is focused (as in scenario S3) on one edge. This constellation arises, e.g. outside priority areas where property rights do not allow substantial connectivity improvement. This situation is covered by the Swiss law on biotope conservation (SBR, 1966; Kägi et al., 2002) that requires an “adequate compensation” if a patch is damaged. In principle, biotope loss should be compensated for by the creation of new biotopes. But connectivity improvement is also an option. We see from our results that the localisation of destruction and compensation has a much stronger influence on $CN_1$ than in scenario S2. Thus, compensation following this scenario is more effective than in the other scenarios.

We found that the MC of a component can be estimated reliably by a regression equation that takes the component’s total area and MST length as input. The regression equation was used to estimate CN in scenarios with non-localised modifications. The parameters of the regression equation are strongly influenced by components with only two patches. Because the distinction between localised and non-localised modification makes little sense for two-patch components, scenarios S1, S2 and S3 are based on components with >2 patches. The coefficient of determination of the regression equation was quite strong, but no causal connection with the field methodology was evident. We therefore assume that the regression is a general feature of components in a patch-based biotope network. It would be interesting to study this feature further with a particular focus on fractal geometry (Etienne, 2004; Li, 2000).

The observations made on the example component near Andermatt (Fig. 2, Table 2) fit the rules of thumb proposed by Etienne (2004) quite well: “(1A) Enlarge the largest patch if one must choose to increase patch size by a fixed percentage (relative change). (1B) Enlarge the smallest patch if one must choose to increase patch size by a fixed amount of area (absolute change). (2) Reduce the (effective) distance between the two largest patches if one must choose among any pair of patches.” In the example component, two hotspots are most important: one in the east with patches no. 6 and no. 8 at the centre, and one in the west with the isolated patch no. 7. Etienne’s rules must be applied to each hotspot rather than to the entire component. Rule (1A) applies to patches nos. 6 and 7, rule (1B) to patch no. 3, and rule (2) only to the eastern hotspot where the two largest patches, nos. 6 and 8, are located.

Our model has used very simple assumptions about the species-specific parameters: (1) immigration and emigration rates to and from patches are assumed to be proportional to patch size; (2) migration paths are assumed to be straight lines between the patch centres; (3) permeability is assumed to be equal everywhere in the matrix; and (4) dispersion was modelled simply as an exponential function. We defined components as patch groups with intra-patch distances ≤1 km. The choice of the optimal threshold distance depends on legal demands, ecological needs of the target species and landscape characteristics (topology, land cover). For our case study, a threshold of 1 km seems reasonable. In the presentation of the results, we focused on the edges of the MST because the regression analysis indicated that MST contains the most relevant edges of a component. For the eigenvalue calculation, however, all edges were taken into account.

Ecological characteristics of a species, such as the dependence of the mobility on matrix quality or its sensitivity to patch disturbance (Frank, 2004), can be incorporated into the model by replacing Euclidian distance by functional distance, which models the behaviour of a species along the migration path from patch to patch (Tischendorf and Fahrig, 2000), and by replacing metric patch area by functional area, which models the behaviour of a species inside patches. One way to do this is to generalise the definition of the transition matrix (Drechsler et al., 2003), for example by enlarging parameter $a$ of the dispersion function – $e^{ax}$, which reduces MC (Moilanen and Hanski, 2006). Ecologically this means that the matrix between biotope patches is less permeable for a species with a high $a$. CN grows with increased $a$ because edges become ecologically longer and dispersion declines exponentially with increasing distance. In calcareous grasslands where insects are very important for conservation, we still know too little about the parameters that determine the threatened species groups. It would help if better data about population dynamics were available.

Many interesting questions about compensation problems in patch-based reserve networks remain. Future research should address especially the following issues: (1) Optimal choice for connectivity improvement depends on ecological characteristics of target species (single species or multi-species approach), geometrical characteristics of the network, permeability of the matrix, etc. A
typology of network components based on these characteristics can give new insights into biodiversity reserve networks and can be used to build and analyze simulated networks. (2) The interior of a patch can be described by gradients. An alternative to the approach studied in this paper is therefore to enhance the survival probability of populations by improving connectivity within the patch. To analyze such a scenario, landscape can be modeled as a grid, and circuit theory (McRae et al., 2008) can be applied. (3) Compensation in the Swiss dry grassland network has been studied with indicators for ecological equivalence being MC of a component (this study) or the plant species set of the lost patches (Dalang and Hersperger, 2010). For more flexible solutions, it would be helpful to combine the two approaches and to study the increase in biotope diversity in the network.

Both a general improvement of the matrix and clearly localized connectivity improvement can be efficient measures for compensating for area loss. Which alternative should be favored will depend upon the geometry of the components. If localized measures are favored, it is crucial to plan carefully where improvement measures should take place, since connectivity improvement generally works best near large biotope patches.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bioso.2012.01.042.

References


Annex

Algorithm for computation of compensation needs

1. Notations

Terminology of compensation transaction: The state of a component at beginning is modified by area loss. This leads to the intermediate state. Compensation by MST-length reduction follows. This leads to the state at the end of the transaction.

\[ A \] Total area of component’s patches.

\[ S \] Length of component’s MST.

\[ C \] MC of a component.

\[ A_j, B_j \] Area of patch \( j \) before respectively after loss.

\[ s_{jk} \] Distance between patches \( j \) and \( k \).

\[ a, b, s \] Parameters of the regression equation.

\[ \alpha \] Parameter for scaling the effect of distance.

\[ T, M \] Transition matrix of a component at beginning respectively after localised area loss.

\[ t_{jk}, m_{jk} \] Entries of transition matrices \( T \) and \( M \).

\[ t'_{jk}, m'_{jk}, T', M' \] Derivatives of \( C \) respective to the entries \( t_{jk} \) etc. (e.g. \( t'_{jk} = \partial C/\partial t_{jk} \)) and matrices of the derivatives.

\[ q_A, q_C, q_S \] Quotient (Area at beginning)/(Area at intermediate state). Analogous for MC (index \( C \)) and MST-length (\( S \)). \( q_A > 1, q_C > 1, q_S = 1 \).

\[ d_C, d_S \] Difference (MC at beginning)-(MC at intermediate state). Analogous for MST-length (\( S \)). \( d_C > 0, d_S = 0 \).

\[ q^*_C, q^*_S \] Quotient (MC at intermediate state)/(MC at end). Analogous for MST-length (\( S \)). \( q^*_C < 1, q^*_S > 1 \).

\[ d^*_C, d^*_S, d^*_m \] Difference (MC at intermediate state)-(MC at end). Analogous for MST-length (\( S \)) and entry of transition matrix (\( m \)). \( d^*_C > 0, d^*_C < 0, d^*_S > 0, d^*_S < 0, d^*_m < 0 \).

\( CN_1, CN_2, CN_3, CN_4 \) Compensation need for scenarios S1, S2, S3 and S4.

\[ W, w_{ijk} \] Matrix of \( CN_d \) values with patches \( i \) as rows and edges \( jk \) (i.e. edge between patches \( j \) and \( k \)) as columns, \( w_{ijk} \) are the entries of matrix \( W \).

\[ D \] Square root of largest entry in matrix \( D \) (see section 2.7 about single value decomposition).

\[ u_i \] Patch-specific factor for patch \( i \).

\[ v_{jk} \] Edge-specific factor for edge between patches \( j \) and \( k \).
2. Preparatory steps

2.1 Components of the whole network were identified by
• computing the Delaunay triangulation using R-package *tripack* (Renka et al., 2009),
• computing the MST using function *mstree.kruskal* of R-package *RBGL* (Carey et al., 2011),
• deleting all edges $\geq 1$ km from the MST,
• identifying all connected components using function *connectComp* of R-package *RBGL*.

2.2 For each component with $>1$ patch, MC $C$ was computed by
• computing the transition matrix $T$. It is a symmetric $n$-by-$n$ matrix with entries $t_{jk} = A_j \cdot A_k \cdot e^{-\alpha s_{jk}}$ for $j \neq k$ and $t_{kk} = 0$ for $j = k$, with $\alpha = 1$.
• $C$ is the largest eigenvalue (the “Perron root”) of matrix $T$.
  $C = Perron(T)$; in R-syntax: `eigen(T)$values[1]`.

2.3 For the sample of components with $>2$ patches, parameters $b$, $a$ and $s$ of the linear regression

$$\log_{10} C = b + a \cdot \log_{10} A + s \cdot \log_{10} S$$

were estimated.

3. Computing MC-loss and compensation

3.1 Non-localised loss. MC loss $q_C$ and $d_C$ of a component with area $A$ and MC $C$, caused by a non-localised area loss of 100 m$^2$.

$$q_A = A/(A - 100 \text{ m}^2); \quad q_C = q_A^a; \quad d_C = C - C/q_C$$

3.2 Localised loss. MC loss $q_c$ and $d_c$ of a component with MC $C$ patch areas $A_j$ and inter-patch distances $s_{jk}$, caused by localised area loss of 100 m$^2$ on patch $p$.

$$B_i = A_i \text{ for } i \neq p \text{ and } B_i = A_i - 100 \text{ m}^2 \text{ for } i = p.$$ 

$$m_{jk} = B_j \cdot B_k \cdot e^{-\alpha s_{jk}} \text{ for } j \neq k \text{ and } m_{jk} = 0 \text{ for } j = k, \text{ with } \alpha = 1.$$ 

$$q_C = C / Perron(M); \quad d_C = C - C/q_C.$$ 

3.3 Non-localised compensation. Non-localised MST length reduction $d_S$ needed to compensate MC loss $d_C$ of a component with MC $C$ and MST-length $S$:

$$d^*_C = -d_C; \quad q^*_C = (C+d^*_C)/C; \quad q^*_S = q^*_C^{1/s}; \quad d^*_S = S - S/q^*_S.$$ 

3.4 Localised compensation. MST length reduction $q^*_S$ and $d^*_S$ of edge between patches $j$ and $k$
needed to compensate MC loss $d_C$ of a component. For scenario S3, transition matrix $M$ is approximated by $T$. The elements of $M$ and $M'$ corresponding to edge $jk$ are denoted as $m$ and $m'$. 

\[ d^*C = -d_C; \quad d^*_m = \frac{1}{2} \cdot d^*_C / m'; \quad d^*_S = \ln(m - d^*_m) - \ln(m) \]

Proof of the third formula: According to paragraph 2.2 there is $t_{jk} = A_i \cdot A_k \cdot \exp(-\alpha s_{jk})$ for $j \neq k$. Replacing $m = t_{jk}, s = s_{jk}$ and $\alpha = 1$, we get $s = \ln A_i + \ln A_k - \ln m$ for intermediate state and $s_E = \ln A_i + \ln A_k - \ln m_E$ for end state (marked by index E). There is $d^*_S = s - s_E$ and $d^*_m = m - m_E$ (see paragraph 1). It follows $d^*_S = \ln m_E - \ln m = \ln(m - d^*_m) - \ln m$.

4. Computing $CN_1$, $CN_2$, $CN_3$ and $CN_4$ with an example

Parameters used by all scenarios for component “Andermatt” (Figure 2, Table 2):

- $A = 19.30498$ ha; $C = 21.73717$; $S = 2.526439$ km; $a = 1.95498$; $1/s = -1.422009$. 

4.1 Scenario S1 (non-localised loss and non-localised compensation).

For component “Andermatt” (Figure 2 and Table 2) there is

Loss (formulas of 3.1): $q_A = 1.000518; q_C = 1.001013; d_C = 0.02200739$;

Compensation (formulas of 3.3): $q^*_C = 0.9989876; q^*_S = 1.001441; d^*_S = 0.003636501$ km; $CN_1 = d_S \approx 3.64$ m.

4.2 Scenario S2 (localised loss and non-localised compensation).

For patch 6 of component “Andermatt” there is

Loss (formulas of 3.2): $A_6 = 5.894108$ ha; $B_6 = 5.884108$ ha; $Perron(M) = 21.71005$;

$q_C = 1.001249; d_C = 0.02712224$;

Compensation (formulas of 3.3): $q^*_C = 0.9987523; q^*_S = 1.001777; d^*_S = 0.004481455$ km; $CN_2 = d_S \approx 4.48$ m.

4.3 Scenario S3 (non-localised loss and localised compensation).

For the edge between patches 3 and 7 of component “Andermatt” there is

Loss (formulas of 3.1): as in 4.1;

Compensation (formulas of 3.4): $m' = 0.05632848; m = 2.09341; d^*_m = -0.1953487$;

$d^*_S = 0.08921529$ km; $CN_3 \approx 89.2$ m.

4.4 Scenario S4 (localised loss and localised compensation).

For patch 6 and the edge between patches 3 and 7 of component “Andermatt” there is

Loss (formulas of 3.2): as in 4.2;

Compensation (formulas of 3.4): $m' = 0.05637815; m = 2.09341; d^*_m = -0.2405385$;

$s_{37} = 0.6203112$ km; $d^*_S = 0.1087672$ km; $CN_4 \approx 108.8$ m.

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5. Single value decomposition.

For the example described in 4.4 there is

\[ w_{637} = 108.7672 \text{ m}; \]

\[ D = 37.48444 \quad \text{in R-syntax: } \sqrt{\text{svd}(W)[1]} \]
\[ u_6 = 16.12454 \text{ m}^{\frac{1}{2}} \quad \text{in R-syntax: } \text{abs}(D \times \text{svd}(W)[6,1]) \]
\[ v_{37} = 6.695245 \text{ m}^{\frac{1}{2}} \quad \text{in R-syntax: } \text{abs}(D \times \text{svd}(W)[5,1]) \]

("5" indicates the edge between patches 3 and 7)

\[ u_6 \cdot v_{37} = 107.9577 \text{ m}. \]