Functional connectivity as an indicator for patch occupancy in grassland specialists

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ABSTRACT

Habitat specialists living in metapopulations are sensitive to habitat fragmentation. In most studies, the effects of fragmentation on such species are analyzed based on Euclidean inter-patch distances. This approach, however, ignores the role of the landscape matrix. Recently, therefore, functional distances that account for the composition of the landscape surrounding the habitat patches have been used more frequently as indicators for patch occupancy. However, the performance of functional and non-functional connectivity measures in predicting patch occupancy of such species has never been compared in a multi-specialists approach.

Here we evaluate the effect of habitat connectivity on the patch occupancy of 13 habitat specialists from three different insect orders (Auchenorrhyncha, Lepidoptera, Orthoptera) in fragmented calcareous grasslands. In order to calculate functional distances we used four different sets of resistance values and rankings. We then modelled species' occurrence using both Euclidean and functional (based on least-cost modelling) inter-patch distances as predictors.

We found that functional connectivity measures provided better results than the non-functional approach. However, a functional connectivity measure that was based on very coarse land-cover data performed even better than connectivity measures that were based on much more detailed land-use data.

In order to take into account possible effects of the landscape matrix on patch occupancy by habitat specialists, future metapopulation studies should use functional rather than Euclidean distances whenever possible. For practical applications, we recommend a 'simple approach' which requires only coarse land-cover data and in our study performed better than all other functional connectivity measures, even more complex ones.

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1. Introduction

Land-use change is believed to be the major driver of terrestrial biodiversity loss (Foley et al., 2005; Jetz et al., 2007; Sala et al., 2000). Over the last 150 years, in particular, semi-natural habitats have suffered a severe decline in area due to land-use intensification, abandonment and afforestation (Baur et al., 2006; van Swaay, 2002; WallisDeVries et al., 2002). As a consequence, calcareous grasslands are currently threatened and are therefore protected under the Habitats Directive of the European Union (European Commission, 2007). As these habitats harbour a unique and often very diverse flora and fauna, their destruction has resulted in a rapid loss of species, which still continues (Fahrig, 2003; Kleijn et al., 2011; Krauss et al., 2010; Sang et al., 2010). An interlinked effect of habitat loss is an increase in spatial isolation of the remaining habitat patches (Fahrig, 2003), which can itself contribute to declines of species (Krauss et al., 2003; Roesch et al., 2013).

High extinction rates can particularly be observed for habitat specialists, as they are known to be more sensitive to land-use change than habitat generalists (Brueckmann et al., 2010; Oeckinger et al., 2012). Many highly specialized species build metapopulations, i.e., the regional population consists of several local subpopulations (Biedermann, 2000; Carlsson and Kindvall, 2001; Eichel and Fartmann, 2008; Hanski and Thomas, 1994;
that are inter-connected by migrating individuals (Baguette, 2003; Hill et al., 1996; Schmitt et al., 2006; Zalewski, 2004). Metapopulations have a dynamic population structure that is characterized by local extinctions and recolonizations. The higher the isolation of a subpopulation, the more prone to extinction it becomes and the less likely it is to be re-established (Appelt and Poethke, 1997; Carlsson and Kindvall, 2001; Hanski et al., 1994; Kindvall and Ahlen, 1992; Krauss et al., 2004). In the long-term, this can lead to extinction of the whole metapopulation (van Strien et al., 2011). Consequently, species living in metapopulations are highly affected by habitat fragmentation.

A well-established method for measuring the degree of isolation of populations is Hanski’s connectivity index (Hanski, 1999). It yields better results than other connectivity measures such as percentage habitat cover or distance to the next suitable habitat (e.g. Brueckmann et al., 2010; Moilanen and Nieminen, 2002). The index uses the distances of the focal patch to the occupied patches in the surrounding area, the size of the occupied patches in the surroundings and the average dispersal distance of the focal species. Although this approach has proven useful in several studies (e.g. Anthes et al., 2003; Binzenhofer et al., 2008; Carlsson and Kindvall, 2001; Krauss et al., 2004), when based on Euclidean distances it ignores the landscape matrix. This matrix represents the structural configuration of the landscape between the focal patch and the patches in the surrounding (Ricketts, 2001). The major effects of the matrix on the accessibility of a patch have already been shown by several studies dealing with the concept of functional connectivity (e.g. Richard and Armstrong, 2010; Watts and Handley, 2010; review by Sawyer et al., 2011; Sutcliffe et al., 2003). Functional connectivity has also been established as an indicator for landscape fragmentation (Hernández et al., 2015) and uses functional (least-cost) rather than Euclidean distances. While most of the studies that adopt this functional approach focus on landscape ecology (i.e. landscape connectivity, least-cost corridors and/or migration zones), functional connectivity is rarely analyzed in the context of metapopulation ecology (i.e. patch connectivity). In addition, the few studies that investigate the influence of functional connectivity on species’ occurrence deal with single species rather than groups of species, which is why the results are often not applicable to other species (cf. Doerr et al., 2011).

Functional distances can be calculated using least-cost modelling. This method assigns a specific resistance value to each land-cover type in the matrix (Adriaensen et al., 2003; Chardon et al., 2003). Land-cover types favouring dispersal are allocated lower resistance values than those that hinder movement (Kraemer et al., 2012). In least-cost modelling, the length of a potential dispersal corridor is traded off against the sum of the resistance values encountered along that corridor. Hence, the functional distance describes the accumulated cost that is demanded of an individual to cover the least costly path between two habitat patches.

Even though Hanski’s index is widely used in metapopulation ecology (see above), to our knowledge it has only once been combined with least-cost modelling: Verbylen et al. (2003) achieved good results with this method. However, the authors emphasize a need for further research, especially with regard to resistance values.

This study presents a multi-species approach using 13 species from three different insect orders (Auchenorrhyncha, Lepidoptera, Orthoptera). We modelled species’ occurrences using the classical approach (based on Euclidean inter-patch distances) on the one hand and the functional approach (based on least-cost modelling) on the other hand. We tested four different sets of resistance values and rankings for the functional approach. In each case, habitat connectivity was calculated using Hanski’s index. Specifically, the following questions were addressed:

(1) Does the functional approach lead to better results than the classical approach?
(2) Which method of assigning resistance values and rankings to land-cover types has the highest explanatory power?
(3) Which approach of modelling habitat connectivity is most suitable in practical applications?

### 2. Material and methods

#### 2.1. Study organisms

As study organisms we chose four Auchenorrhyncha (*Batracomorphus irroratus*, *Goniagnathus brevis*, *Kosswigianella exigua*, *Neophilaenus albipennis*), six butterfly (*Argynnis aglaja*, *Cupido minimus*, *Erynnis tages*, *Hesperia comma*, *Melitaea aurelia*, *Satyrium spini*) and three Orthoptera species (*Metrioptera brachyptera*, *Phaneroptera falcata*, *Stenobothrus lineatus*) (Table 1). Due to their high sensitivity to environmental changes, the three groups are well-suited for ecological studies (Auchenorrhyncha: Achtziger et al., 2014; Nickel and Hildebrandt, 2003; butterflies: Fartmann et al., 2013; Orthoptera: Fartmann et al., 2012). All study organisms

<table>
<thead>
<tr>
<th>Table 1</th>
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<tr>
<td>Study organisms and their developmental stages searched for during the study period (April to September).</td>
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<tr>
<th>Study organisms</th>
<th>Study period</th>
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<tbody>
<tr>
<td></td>
<td>Late April</td>
</tr>
<tr>
<td>(a) Auchenorrhyncha</td>
<td></td>
</tr>
<tr>
<td>Batracomorphus irroratus</td>
<td></td>
</tr>
<tr>
<td>Goniagnathus brevis</td>
<td>Adult</td>
</tr>
<tr>
<td>Kosswigianella exigua</td>
<td>Adult</td>
</tr>
<tr>
<td>Neophilaenus albipennis</td>
<td>Adult</td>
</tr>
<tr>
<td>(b) Lepidoptera</td>
<td></td>
</tr>
<tr>
<td>Argynnis aglaja</td>
<td></td>
</tr>
<tr>
<td>Melitaea aurelia</td>
<td>Adult/egg</td>
</tr>
<tr>
<td>Cupido minimus</td>
<td>Adult/egg</td>
</tr>
<tr>
<td>Erynnis tages</td>
<td>Adult/egg</td>
</tr>
<tr>
<td>Hesperia comma</td>
<td>Adult/egg</td>
</tr>
<tr>
<td>Satyrium spini</td>
<td></td>
</tr>
<tr>
<td>(c) Orthoptera</td>
<td></td>
</tr>
<tr>
<td>Phaneroptera falcata</td>
<td>Nymph</td>
</tr>
<tr>
<td>Stenobothrus lineatus</td>
<td>Nymph</td>
</tr>
<tr>
<td>Metrioptera brachyptera</td>
<td>Nymph</td>
</tr>
</tbody>
</table>
calcareous grasslands within the study area (n = 89) were surveyed (Eichel and Fartmann, 2008; Poniatowski and Fartmann, 2008, 2010). Patches were regarded as discrete when they were isolated from the nearest neighbouring patch by more than 50 m of non-habitat, such as forest, improved grassland or arable fields (Kraemer et al., 2012; Poniatowski and Fartmann, 2010; Stuhldreher and Fartmann, 2014). In the case of species that are known to depend on particular host plants (all studied Auchenorrhyncha and butterfly species), only potentially suitable patches (i.e. patches where the host plant was present) were used for the statistical analyses.

2.4. Species sampling

From the end of April to the beginning of September 2010, all 89 calcareous grassland patches in the study area were sampled five times (end of April, end of May, end of June, end of July/start of August and start of September) (Table 1). By doing so we made sure that for each of our study species one visit coincided with the time of year when its detectability is highest. The time spent searching per species varied with the structural heterogeneity of a particular patch. We defined seven structural types that differed with respect to vegetation height and cover (cf. Poniatowski and Fartmann, 2008) and searched for 0.5 h in each of the structural types that were present in a patch. The presence of the butterfly species was assessed by searching for adults, larvae or eggs (Table 1). A sweep net was used to sample the Auchenorrhyncha and Orthoptera species living in the herb layer. Bare soil and host plants growing there were searched visually to detect geophilic/epigeic species. In order to avoid the results being biased by weather conditions, all sampling of the adult stages was done on dry, sunny days with low wind speed. A patch was classified as occupied if at least three adults or one larva/egg were detected.

2.5. Connectivity

For each of our study organisms, we calculated the patch connectivity from each focal patch to all neighbouring patches within a radius of 2 km around the focal patch in which the species was present (potential source populations, cf. Brueckmann et al., 2010). A patch was considered to be a focal patch if the host plant of the specific species was present (Auchenorrhyncha, butterflies). In the case of the polyphagous Orthoptera, all patches were used for the analysis.

For each of the focal patches, connectivity $I_i$ was calculated using Hanski’s index (Hanski, 1999) modified according to Moilanen and Nieminen (2002):

$$I_i = \sum_{1 \neq j} \exp(-\alpha \cdot d_{ij}) \cdot A_j^b,$$

where $A_j$ is the size (in $m^2$) of the neighbouring calcareous grassland patch and $d_{ij}$ is the distance (in km) between the neighbouring patch $j$ and the focal patch $i$. For the scaling parameter $b$, we chose $b = 0.5$, as the ratio of patch edge to patch area decreases with $b^{0.5}$ when the patch size increases (Moilanen and Nieminen, 2002). The parameter $\alpha$ is scaling the effect of distance to migration ($1/\alpha$ is the average migration distance of a species). Average migration distances were determined by reviewing elementary literature on species’ dispersal: Auchenorrhyncha ($1/\alpha = 0.1$ km; Biedermann, 1997), butterflies ($A. aglaja$ and $H. comma$: $1/\alpha = 2$ km, all other species: $1/\alpha = 1$ km; Gutierrez et al., 1999; Gutierrez, 2005; Settele et al., 1999; Zimmermann et al., 2009), Orthoptera ($P. falcata$ and $S. lineatus$: $1/\alpha = 0.5$ km, $M. brachyptera$: $1/\alpha = 0.1$ km; Ingrisch and Köhler, 1998). Larger values of the connectivity index $I$ indicate better connectivity (and lower isolation) than smaller values. To

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**Figure 1.** Study area, the Lower Diemel Valley in central Germany (inlay), and the 89 study patches. Ten patches (white circles) were situated within a 2-km range of adjacent calcareous grassland patches of the Middle Diemel Valley and were therefore only used for calculating the isolation of some of the 79 remaining patches (grey circles).

**Table 1.** Connectivity values of local connectivity indices for 89 study patches in the study area.
2. **Functional connectivity**: This procedure is based on the functional distances (least-cost paths) from the focal patch to occupied patches in the surrounding area (Fig. 2b). Functional distances were measured using the cost-distance tool in ArcGIS 10.0 (Adriaensen et al., 2003; Chardon et al., 2003). How costly a potential dispersal corridor depends on its length and on the characteristics of the matrix that an animal has to cross when moving from one patch to another. We therefore generated a cost-grid (resolution 5 m × 5 m), which included all relevant land-cover types in the study area. The structure of the landscape matrix was derived from land-use data from the real estate cadastre information system (ALKIS). In ALKIS, the type of land-use is documented for every single parcel of land at a scale of 1:5000. Additionally, we added all calcareous grasslands to this dataset. Land-cover types favouring dispersal of grassland specialists were allocated lower resistance values than those that hinder movement (Kraemer et al., 2012, Table 2). Because we had no data about how the different land-cover types affect species dispersal in detail, four functional connectivity measures with different resistance values were calculated (Table 2). For all approaches it was assumed that the step from a habitat to a non-habitat is the greatest (at least four times more difficult than the step from one type of non-habitat to another, Table 2, cf. Kraemer et al., 2012), since most habitat specialist individuals are usually very sedentary (Stamps et al., 1987):

(a) **Habitat/non-habitat approach (HAB)**: The habitat/non-habitat approach only distinguished between habitat and non-habitats: non-habitats were assumed to have a resistance value eight times greater than habitats, as they strongly limit inter-patch movement of habitat specialists.

(b) **Simple approach (SIM)**: In addition to the categories “habitat” and “non-habitat”, the simple approach distinguished between two non-habitat types: the high-growing non-habitats (e.g. forest) had a resistance value eight-times greater than habitats. Low-growing non-habitats (e.g. mesic grassland) had a resistance value only four times higher than habitats, as they were assumed as more suitable for inter-patch movements.

(c) **Conservative approach (CON)**: The conservative approach considered all the important land-cover types in the study area (seven categories of non-habitats, Table 2). The categories were ordered by their resistance for species’ dispersal based on our own field observations (cf. Driessen et al., 2007; Verbeylen et al., 2003). A calcareous grassland specialist, for instance, probably disperses more easily through mesic grassland than arable land, and arable land again is easier to move through than settlements and forests. However, the conservative approach assumed that it makes little

![Fig. 2. Map section of the study area. (a) Non-functional connectivity (EUC): the arrow denotes the shortest Euclidean edge-to-edge distance from patch A to patch B. (b) Functional connectivity (SIM: simple approach): the arrow denotes the least-cost path from patch A to patch B.](image)

illustrate the influence of the landscape matrix on patch occupancy of the model organisms, two approaches were compared:

1. **Non-functional connectivity (EUC)**: For this calculation the distance \( d_{ij} \) enters the formula as the Euclidean distance from the focal patch to the neighbouring patch. Thus, the non-functional approach does not take into account the varying structure of the matrix (Fig. 2a).

<table>
<thead>
<tr>
<th>Land-cover type</th>
<th>Connectivity</th>
<th>Non-functional</th>
<th>Functional</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>EUC</td>
<td>HAB</td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Calcareous grassland</td>
<td>2%</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Non-habitat</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesic grassland</td>
<td>15%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cemetery, garden, park</td>
<td>2%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arable land</td>
<td>43%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lane, railway, river</td>
<td>6%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Road</td>
<td>2%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubbery</td>
<td>1%</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Forest, settlement</td>
<td>30%</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2

Assumed resistance values of the land-cover types in the five connectivity measures. The proportion of the land-cover types is shown in brackets. EUC: approach based on Euclidean distance; HAB: Habitat/non-habitat approach; SIM: simple approach; CON: conservative approach; DUP: duplicative approach (for details see Section 2.5).


Table 3

Results of generalized linear models (GLM): relationship between patch occupancy (binomial response variable) and the five connectivity measures. (a) Species whose patch occupancy was significantly related to at least one of the five connectivity measures. (b) Species whose patch occupancy was not significantly related to any of the connectivity measures. For each connectivity measure the Z values and the level of significance are shown. Non-funct.: non-functional; Pre.: presence (occupied patches); Abs.: absence (unoccupied patches); N: total number of potentially suitable patches;Freq.: frequency of patch occupancy (%); EUC: approach based on Euclidean distance; HAB: habitat/non-habitat approach; SIM: simple approach; CON: conservative approach; DUP: duplicative approach (for details see Section 2.5); A: Auchenorrhyncha; L: Lepidoptera; D: Orthoptera; **P<0.01, *P<0.05, \(*P<0.1, n.s.: not significant.

<table>
<thead>
<tr>
<th>Study organisms</th>
<th>Patch occupancy</th>
<th>Connectivity</th>
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<tbody>
<tr>
<td></td>
<td>EUC</td>
<td>HAB</td>
</tr>
<tr>
<td>(a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Goniaspithus brevis (A)</td>
<td>30</td>
<td>43</td>
</tr>
<tr>
<td>Kosswigliella exigua (A)</td>
<td>12</td>
<td>67</td>
</tr>
<tr>
<td>Hesperia comma (L)</td>
<td>52</td>
<td>27</td>
</tr>
<tr>
<td>Melitaea aurelia (L)</td>
<td>42</td>
<td>30</td>
</tr>
<tr>
<td>Satyrium spin (L)</td>
<td>25</td>
<td>30</td>
</tr>
<tr>
<td>Stenobotthus lineatus (O)</td>
<td>58</td>
<td>21</td>
</tr>
<tr>
<td>Metroptera brachyptera (O)</td>
<td>37</td>
<td>42</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neophaeula albipennis (A)</td>
<td>66</td>
<td>13</td>
</tr>
<tr>
<td>Bacraomorphus irroratus (A)</td>
<td>9</td>
<td>10</td>
</tr>
<tr>
<td>Cupido minimus (L)</td>
<td>18</td>
<td>4</td>
</tr>
<tr>
<td>Erynnis tages (L)</td>
<td>55</td>
<td>20</td>
</tr>
<tr>
<td>Argynnis afago (L)</td>
<td>27</td>
<td>49</td>
</tr>
<tr>
<td>Phaneropta falcata (O)</td>
<td>41</td>
<td>38</td>
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3. Results

In seven of our 13 study organisms, patch occupancy was significantly related to at least one of the five connectivity measures (Table 3a). For the remaining six species no significant correlations between patch occupancy and patch connectivity were detected (Table 3b).

For the seven species that were affected by connectivity, we detected generally different results between species groups (Table 3a): while the occurrence of butterflies was significantly correlated to all functional connectivity measures in three species and to non-functional connectivity in two species, Auchenorrhyncha and Orthoptera were less affected by functional connectivity. In Auchenorrhyncha, non-functional connectivity had a significant effect on patch occupancy of two species, while functional connectivity played a minor role. The only significant correlation in functional connectivity to Auchenorrhyncha was a positive relationship between patch occupancy of K. exigua and the conservative approach. In Orthoptera, patch occupancy of two species was significantly related to non-functional as well as simple functional connectivity. Furthermore, the occurrence of S. lineatus was correlated to the conservative approach.

For all species, the explanatory power of the models (AUC values) differed significantly between the non-functional and the simple functional approach, while there were no differences between the non-functional and the other three functional connectivity approaches (Fig. 3). Of the functional connectivity measures, the simple approach had the best performance. However, we detected no significant differences in model performance between the four functional connectivity measures.

4. Discussion

Our study showed that functional connectivity is a good indicator for patch occupancy in grassland specialists and provided clearly better results than non-functional connectivity; i.e., the landscape matrix had an effect on the patch occupancy. This is in line with some other authors, who concluded that least-cost models predict species’ occurrence better than models using Euclidean distance (Chardon et al., 2003; Sutcliffe et al., 2003; Verbeelen et al., 2003).
A weak point of least-cost modelling is that the resistance values are often based on expert judgement and not on empirical studies. They are therefore subject to some uncertainty (Johnson and Gillingham, 2004; Rayfield et al., 2010). As a consequence, least-cost modelling has recently been combined with radio-tracking data (e.g. Driezen et al., 2007; Richard and Armstrong, 2010). However, this method is very time-consuming, especially when several species are being considered. Our results showed that expert-based least-cost modelling in combination with Hanski’s index represent a robust tool to analyze patch occupancy, even without empiric data on the dispersal behaviour of the focal species. When doing so, it is essential to follow a transparent procedure (Sawyer et al., 2011). In this context three points are of special relevance (cf. Rayfield et al., 2010):

1. The number of land-cover types in the matrix must be known as a prerequisite for points 2 and 3. However, our study showed that a coarse separation of the matrix into low- and high-growing land-cover types (simple approach) provided the best results, at least for stenotopic species living in calcareous grasslands.

2. In order to consider the effect of the different land-cover types on the dispersal behaviour of the species, the rank of all land-cover types according to their suitability for dispersal must be specified adequately. If available, field or experimental data should be used (e.g. Graham, 2001; O’Brien et al., 2006). Otherwise, ranking based on transparent expert judgement also represents a useful approach, as has been shown by this and several other studies (e.g. Chardon et al., 2003; Kraemer et al., 2012; Rabinowitz and Zeller, 2010; Verbeeyen et al., 2003). Species living in forests, for example, disperse more easily and with lower risk of mortality through plantations, shrubland and hedgerows than through arable land and meadows (cf. Chardon et al., 2003; Richard and Armstrong, 2010; Verbeeyen et al., 2003). In our case, the reverse is true. The fact that the functional approach performed better than the non-functional one shows that dispersal of many of our study species was obviously hindered by shrubs and forests (cf. Ries and Debinski, 2001; Roland et al., 2000; Schmitt et al., 2000).

3. The resistance values reflect the effort a species must invest to disperse through a certain land-cover type. Consequently, the relative cost of the land-cover types must be quantified by assigning appropriate numerical cost values. If empiric data is not available, a comparison of different model outputs can be used to assess the robustness of the projections (Sawyer et al., 2011). Generally, we assume that a specialized animal prefers to stay within its breeding habitat and is usually unwilling to cross the habitat border (cf. Stamps et al., 1987). However, if the animal decides to migrate, its dispersal behaviour may be influenced by the composition of the landscape matrix in four different ways. These are represented by the four approaches of calculating functional connectivity that were tested in this study: (i) the habitat/non-habitat approach, which simply differentiates between habitat and the unfavourable matrix; (ii) the simple approach, in which movements of dispersing individuals are solely influenced by the vertical structure of the land-cover types, with low-growing vegetation (e.g. mesic grassland) being easier to cross than tall structures (e.g. forest); (iii) the conservative approach, in which each land-cover type has its own effect on dispersal behaviour, but the differences are small; and (iv) the duplicative approach, in which the differences between the land-cover types are remarkable. The duplicative approach assumes that land-cover types such as mesic grassland are easy to move through, whereas others such as shrubland and forest represent an obstacle.

Since the occurrence of our study organisms was best predicted by the simple approach, we conclude that the matrix has only a moderate effect on dispersal behaviour, as otherwise the conservative or the duplicative approach would have led to better results.

Although the relationship between patch occupancy and connectivity was generally positive in most of the study species, it was not statistically significant in some species. This may be accounted for by their mobility. On the one hand, the mobility of small species such as *N. albipennis*, *B. irroratus* and *C. minimus* is probably so low that they fail to reach most of the other suitable patches in the study area, especially if the host plant is present in only a small fraction of the patches (which was the case for the monophagous *B. irroratus* and *C. minimus*). Previous metapopulation studies on *N. albipennis* (Biedermann, 2000, 2004) and *C. minimus* (Binzenhofer et al., 2008), which found significant effects of connectivity on patch occupancy, were conducted at a much smaller spatial scale. In these studies, patches were regarded as discrete when being only 5 and 10 m, respectively, apart. In contrast, we defined a minimum of 50 m for patch separation. On the other hand, highly mobile species may have no difficulties in colonizing other habitat patches, especially if the overall degree of habitat fragmentation is rather low and if their host plants occur in virtually every patch (either is true for our study area). Hence, the occurrence of some relatively mobile of our study species may be more strongly influenced by other factors such as patch size and habitat quality (which were not considered in the here presented paper) than by connectivity. This is probably the case for the small but mobile butterfly *E. tago* (cf. Gutierrez et al., 1999), the highly mobile butterfly *A. aglaja* (cf. Zimmermann et al., 2009) and the long-winged bush-cricket *P. falcata* which has recently expanded its range in several parts of Europe (e.g. Boelme et al., 2011; Handke et al., 2011; Kocarek et al., 2008).

5. Conclusions

Although least-cost modelling depends on expert judgement, we showed that the performance of metapopulation models can be improved when combining Hanski’s index with functional distance. It is therefore essential to consider the role of the landscape matrix for patch occupancy by habitat specialists in future metapopulation studies. For practical applications, we recommend the simple approach which requires only coarse land-cover data that are easier to obtain than detailed information on the landscape matrix and
in which the spatial analyses are less time-consuming. Moreover, in our study the simple approach performed better than all other functional connectivity measures, even more complex ones.

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