



A comparison of patch connectivity measures using data on invertebrates in hollow oaks

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This study aimed at comparing six patch connectivity measures by fitting them to field data. We used occupancy data for eight beetle and two pseudoscorpion species from 281 hollow oaks in southeast Sweden. Species occupancy was modelled in relation to tree characteristics and one measure of patch connectivity at a time. For each connectivity measure we searched for the spatial scale that generated the best fit to field data. Connectivity measures that only include occupied patches provided better model fits than those that include all patches. When occupancy data are absent for surrounding habitat patches, information that reflects occurrence probabilities can be included in the connectivity measure. However, in this study incorporation of such information resulted in only a slight improvement of model fit. A frequently used connectivity measure based on the negative exponential function was relatively poor in explaining species' occurrence; for eight species out of nine a buffer measure was better. A better fit was obtained when the negative exponential function was modified to take into account that habitat patches may “compete” for the immigrants. The spatial scale with the best fit tended to be larger when we used connectivity measures in which dispersal sources are identified with lower precision. Thus, the outcomes from different multiple-scale studies are not directly comparable if the density of dispersal sources is not measured in the same way. Overall we conclude that buffer measures are useful, as they give good predictions and are easy to understand and use. If a biologically more realistic measure is needed, one that up-weights the closest patches should be used. Finally, the possibility that habitat patches may compete with each other for immigrants should be considered when selecting a connectivity measure.

Species persistence in fragmented landscapes depends on the possibility for migration between habitat patches (Baguette et al. 2000, Thomas 2000). The probability for immigration from surrounding patches is reflected in patch connectivity. Connectivity may be measured in many different ways. Some connectivity measures require detailed data on the movement of individuals, while others are simple estimates of the distance to the nearest neighbor (Calabrese and Fagan 2004). Patch connectivity measures that are intermediate regarding data requirements, such as buffer measures or measures based on the negative exponential function, have in many cases been found to be useful (Moilanen and Nieminen 2002). Buffer measures are simple to understand and use, but have been criticized because they are not based on realistic assumption about dispersal biology. Therefore, measures that up-weight the closest habitat patches, for instance by using the negative exponential function, have been recommended (Moilanen and Nieminen 2002).

Connectivity measures may either take into account all suitable habitat or occupied habitat only. The latter usually generates better predictions of species occupancy (Prugh 2009). However, obtaining field data on species

distribution is more time-consuming than obtaining data on habitat distribution. Consequently, habitat distribution measures are frequently used. The usefulness of such measures probably relies on how well habitat patches are identified.

Some connectivity measures assume that the number of immigrants to a patch is only a function of distances to and population sizes of the donor populations (e.g. in the incidence function model; Hanski et al. 1994). Seen from the donor population perspective, this means that the total number of successful emigrants is proportional to the number of surrounding habitat patches. This is a reasonable assumption for plants or fungi dispersing with seeds or spores, and perhaps also for some animals; however, the dispersal behavior of many animals may generate different migration ranges and rates in differently structured parts of landscapes (Kindvall 1999, Mennechez et al. 2004). One reason for this is the “shadow effect”, which results in a decreasing number of migrants from one particular patch to another particular patch, with an increasing number of habitat patches (Hein et al. 2004). In other words, if the number of migrants is limited and the migrants are able to search for suitable patches there will be more “competition”

for the migrants when there is more habitat close to the dispersal source. Therefore, an alternative is to modify the negative exponential function so the proportion of successful emigrants among all individuals per patch becomes constant among possible donor populations. If these emigrants are distributed among surrounding patches according to the negative exponential function, it implies that the probability for long-distance migration becomes higher in those parts of a landscape with a lower density of habitat patches. This would be the case when a certain proportion of individuals leave their natal habitat patch, and all emigrants eventually reach a new patch.

The aim of this study was to compare the fits of different patch connectivity measures to field data on presence/absence per tree of tree-inhabiting invertebrates. All species (eight beetles and two pseudoscorpions) that were frequent enough (present in at least ten trees) and predominantly occur in hollow oaks were analysed. Tree hollows are a relatively long-lasting habitat, and species associated with such habitats are generally expected to have a limited dispersal propensity (Southwood 1962). For one of the study beetles, *Osmoderma eremita*, a limited dispersal rate and range has been demonstrated by capture-recapture (Ranius and Hedin 2001) and telemetric (Hedin et al. 2008) studies. The study beetles fly between trees, while the pseudoscorpions move phoretically, i.e. they hitch-hike with other animals (Ranius and Wilander 2000). In the first analysis we used the simplest measure of patch connectivity, and for each subsequent analysis we used measures with successively more information thought to be relevant for the probability of occurrence. We hypothesised that patch connectivity would explain more of the observed occurrence pattern, the more biological realism that was included in the connectivity variable. We tested connectivity measures that have been used before, as well as measures that are used here for the first time.

Methods

Collecting field data

Connectivity reflects the potential for dispersal. In the present study we fitted connectivity measures to presence/absence data, because dispersal data are difficult to obtain, and dispersal is one of the main processes that affect occurrence patterns (Hanski 1994). Prugh (2009) obtained comparable results when connectivity measures were fitted to colonisation data and to occupancy data, which lends support to the use of occupancy data.

Five areas were surveyed, all in the province of Östergötland, southeast Sweden (Table 1). Data from three

of the areas have been used in a previous study (Ranius 2002), while data from two areas are used here for the first time. All potential host trees were identified, and for 32% of oaks presence/absence of beetle and pseudoscorpion species was assessed. Before the invertebrate survey, we identified potentially suitable trees by visiting sites with large or hollow trees. In Kättilstad, aerial photographs and an inventory of old oaks in forest land made by the regional forestry board in 1995 were used. In Sankt Anna, we used information from a survey by Johannesson (1996), and in Bjärka Säby a survey by Ranius and Hedin (2001). In Skärkind and Omberg we used a survey conducted by the County Administration Board including all large or hollow trees (Sandell 1999). In Omberg, Kättilstad and Bjärka Säby, oak was by far the dominant tree species among hollow trees. In Skärkind and Sankt Anna also trees of other species were hollow-bearing – birch, aspen, linden, and apple. However, our observations of these hollows indicated that the amount of wood mould they contain is generally low, which makes them poor habitat for the study species. Consequently, only oaks were sampled. We only analysed beetle and pseudoscorpion species that have been observed predominantly in hollows in oaks (>90% of the findings made in the hemiboreal region in Sweden, according to a database provided by the Swedish Species Information Centre, and Ranius and Wilander 2000).

When estimating patch connectivity, we used data on the position and diameter of every hollow oak within the study landscapes and 4-km wide buffer zones around these landscapes. We combined a tree survey by the County Administration Board (Sandell 1999) with information from our own field survey to obtain data on the position and diameter for all oaks estimated to have large amounts of wood mould. A previous study revealed a strong positive correlation between wood mould volume and size of the entrance hole (Ranius et al. 2009). Therefore, trees with entrance holes with diameters >10 cm were included unless, upon examining the hollow, we found the wood mould volume to be less than ca 2 litres. Trees with smaller entrance holes were assumed to have amounts of wood mould too small for the study species.

Sampling was done by taking eight litres of wood mould from a hollow in each tree (or the total volume, if less than eight litres was available). The wood mould was sieved, and spread out on a white sheet in the field. We examined the material for an hour, and then returned it to the hollow. Presence/absence of larvae, adults (both beetles and pseudoscorpions) or adult beetle body parts (elytra, pronotums, or heads) was recorded. There is a strong correlation between the occurrence of adult beetle body parts and live adult beetles (Ranius and Nilsson 1997). As most of the species records are based on body parts that may remain in

Table 1. Characteristics of the five study areas in the province of Östergötland, southeast Sweden, in which beetles and pseudoscorpions in hollow oaks were sampled.

Name	Coordinates (midpoints)	Size (km ²)	Hollow oaks km ⁻²	No. sampled trees	Sample year
Bjärka Säby	58°16'N, 14°45'E	1.3	79.2	46	2000
Kättilstad	58°04'N, 15°50'E	201.0	1.0	127	1996
Omberg	58°21'N, 14°39'E	22.5	11.7	41	2007
Sankt Anna	58°24'N, 16°52'E	32.7	6.3	26	1997–1998
Skärkind	58°28'N, 16°01'E	94.7	1.5	41	2007

the trees over several years, at least for these species the result is not sensitive to the fluctuations of population sizes or weather between years. We included hollows up to 5 m from the ground. Less than half of all entrance holes in oaks are situated higher than this (Ranius et al. 2009). In Omberg and Skärkind, hollows at the ground level were avoided, as they contain a smaller number of beetle species (Ranius 2002). In Kättistad and Bjärka Säby, we sampled as many hollow oaks as possible (61 and 46% of all hollow oaks, respectively), while in Omberg, Sankt Anna, and Skärkind, among trees in larger stands, a smaller number of trees was selected for sampling (14, 29 and 16% of all hollow oaks, respectively). All trees in smaller stands were selected, while in bigger stands trees were randomly selected. For each tree and sampled hollow, we measured characteristics that have been found to influence the occurrence of the inhabiting species (Ranius and Wilander 2000, Ranius 2002; Table 2).

Data analysis

First, we constructed generalized linear models with binomial distribution and a logit link function (logistic regression) for each species, using only the tree characteristics as predictors, to find the subset of tree characteristics affecting the distribution of each species (model name: TREE). We compared the models using Akaike's information criterion (AIC). The AIC value was calculated as $-2 \log\text{-likelihood} + 2k$, where k is the number of parameters in the logistic regression model plus the spatial scale parameter of the connectivity measure, as that was also estimated in the statistical test. We first tested each variable separately and when building the model, variables were added one by one in order of explained deviance, until we obtained the model with the lowest AIC value. To this model, we then added one patch connectivity variable at a time (Table 3). For each variable we scanned through spatial scales (i.e. r in eq. 1 for the buffer metrics and $1/\alpha$ in eq. 2 for the negative exponential function) within an interval from 25 to 2500 m, and identified the scale that generated the minimum residual deviance for the total model. Thus, we treated both r and $1/\alpha$ as free parameters. We did this separately for six different measures of patch connectivity. For each statistical model, we calculated the explained deviance (an analogue to R^2) and the AIC value. We compared each connectivity measure with the previously tested measure. A decrease in AIC >7 is taken to mean that the latter model has considerably more support in the data than the previous one.

The six patch connectivity measures (Table 3) were as follows. The first four measures are different kinds of buffer

measures, which imply that we summed the hollow trees within circles with radii equal to the scale r :

$$S_i = \sum_{j=1}^n A_j, \text{ for all } j \neq i \text{ and } d_{ij} < r \quad (1)$$

where A_j may reflect either the habitat available in tree j or the population size in tree j , d_{ij} is the distance between trees i and j , and n is the total number of hollow oaks within the buffer (radius r). In previous studies, various kinds of buffer measures have frequently been used (Moilanen and Nieminen 2002).

In the first, most simple, measure (model name: BUF TREE), $A_j=1$ for all hollow oaks. This is the only assumption possible when data on either habitat quality or habitat requirements is lacking, used e.g. by Holland et al. (2005).

Second, we estimated the invertebrate species occurrence probability for each surrounding tree based on tree size, and summed these probabilities for oaks within the circles (BUF DIAM). Occurrence probability was estimated using logistic regression models of species presence/absence for each invertebrate species on tree diameter; tree diameter was the only tree characteristic used here, because this was the only variable known for the oaks that were not sampled as well as those that were sampled. Thus, eq. (1) was used, with $A_j = \text{logit}(kD_j + m)$, where k is a coefficient, D_j is the tree diameter, and m is the intercept. Also in previous studies, the size of habitat fragments (Kurki et al. 2000) and habitat quality (Reunanen et al. 2002) have often been considered in buffer measures.

Third, in estimating connectivity of tree i , we also included the connectivity – measured as BUF TREE, i.e. the number of hollow oaks in a surrounding buffer – of each of the surrounding trees j (BUF CONN). Eq. (1) was used, with $A_j = \text{logit}(kD_j + qC_j + m)$, where k and q are coefficients, D_j is diameter of surrounding tree j , C_j is BUF TREE of surrounding tree j and m is the intercept. The logistic regression model was fitted to presence/absence data for each species. As far as we are aware, this connectivity measure has not been used before.

Fourth, we limited the summation of trees within the buffer to the hollow oaks actually occupied by each species. This was done using presence/absence data when available, and for the remaining trees the same probability of presence as in BUF DIAM was used (BUF PRES). Thus, if sampled, $A_j = p_j$, in which p_j represents presence (1) or absence (0) of species; otherwise $A_j = \text{logit}(kD_j + m)$. This type of connectivity measure has been used, for instance, by Prugh (2009).

Table 2. Measured characteristics of the sampled oaks and the hollows (one per tree) from which wood mould samples were taken.

Name	Description
Canopy cover	The vertical projection of foliage around the tree: <25% (0), 25–75% (1) or >75% (2).
Circumference	Trunk circumference 1.3 m above ground (in cm).
Entrance	Horizontal (0) or oblique/vertical (1).
Height	Distance between the ground and the entrance hole (in m).
Wood mould volume	The amount of wood mould divided into two categories: small (0), and large (1), with about 15 litres as a cut-off.

Table 3. The six patch connectivity measures used in this study. For detailed descriptions, see Methods.

Name	Description	Equation ¹
BUF TREE	The number of hollow oaks summed within circles.	$S_i = \sum_{j=1}^n A_j$, for all $j \neq i$ and $d_{ij} < r$ in which $A = 1$
BUF DIAM	Species' occurrence probability (based on tree diameter) for each hollow oak summed for all hollow oaks within circles.	$S_i = \sum_{j=1}^n A_j$, for all $j \neq i$ and $d_{ij} < r$ in which $A = \text{logit}(kD + m)$
BUF CONN	Species' occurrence probability (based on tree diameter and density of surrounding hollow oaks) for each hollow oak summed for all hollow oaks within circles.	$S_i = \sum_{j=1}^n A_j$, for all $j \neq i$ and $d_{ij} < r$ in which $A = \text{logit}(kD + nC + m)$
BUF PRES	Number of surveyed oaks that were occupied plus occurrence probabilities for oaks that were not surveyed, summed within circles.	$S_i = \sum_{j=1}^n A_j$, for all $j \neq i$ and $d_{ij} < r$ If surveyed, $A = 1$ if species present and $A = 0$ if absent. If not surveyed, $A = \text{logit}(kD + m)$
NEG EXP	Number of surveyed oaks that were occupied plus occurrence probabilities for oaks that were not surveyed, where each tree was given a different weight according to a negative exponential function of distance.	$S_i = \sum_{j=1}^n p_j \exp(-\alpha d_{ij})$, for all $j \neq i$ If surveyed, $p = 1$ if species present and $p = 0$ if absent. If not surveyed, $p = \text{logit}(kD + m)$
CONST EMIGR	Number of surveyed oaks that were occupied plus occurrence probabilities for oaks not surveyed but given different weights according to a negative exponential function and a correction factor that takes into account the competition for immigrants among trees, by making the proportion of successful emigrants in the population per tree constant among "donor" patches.	$S_i = \sum_{j=1}^n p_j \exp(-\alpha d_{ij}) c_j$, for all $j \neq i$ in which $c_j = 1 / \sum_{k=1}^n \exp(-\alpha d_{jk})$ If surveyed, $p = 1$ if species present and $p = 0$ if absent. If not surveyed, $p = \text{logit}(kD + m)$

¹ A = probability of occurrence per tree, C = connectivity measured as BUF TREE, D = tree diameter, d_{ij} = distance between patch i and j , n is the total number of hollow oaks, and k , q and m are coefficients/intercept in regression models.

For the first four measures only trees within the buffer distance were included in the connectivity calculations. For the fifth and sixth measures all occupied trees were included. The fifth measure used the same information as the fourth, but each potential source tree was weighted depending on its distance from the tree for which connectivity was being estimated (i.e. its potential importance as a dispersal source), according to a negative exponential function:

$$S_i = \sum_{j=1}^n p_j \exp(-\alpha d_{ij}), \text{ for all } j \neq i \quad (2)$$

where S_i = connectivity of tree i , p_j = probability of species occurrence in tree j , d_{ij} = distance between i and j , n = total

number of hollow oaks, and α is a parameter controlling the rate of decay (NEG EXP). Usually the area of the potential donor patch j would be used as a factor in this equation, because larger patches have larger populations and therefore more emigrants (Hanski 1994). For our study system tree diameter could potentially be used as a measure of habitat patch size. However, we did not do this because the only study on population sizes of invertebrates in hollow trees did not indicate any correlation between population size and tree diameter (Ranius et al. 2009). On the other hand, tree diameter is related with occupancy of several of the study species (Ranius 2002), which was the reason why we used tree diameter to estimate the probability of species occurrence. NEG EXP has been frequently used, especially in

Table 4. Frequency of occurrence of beetle (B) and pseudoscorpion (P) species (Freq.). Generalised linear model with binomial distribution and logit link function, obtained by including one predictor at a time until the AIC value was minimised. Tree characteristics are described in Table 2. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. $n = 281$.

Species	Freq. (%)	Canopy cover	Circumference	Entrance	Height	Wood mould volume
<i>Elater ferrugineus</i> (B)	6				0.60***	
<i>Procræus tibialis</i> (B)	35		0.004**			0.91*
<i>Ampedus hjorti</i> (B)	31		0.002	-0.51		
<i>Ampedus cardinalis</i> (B)	25	-0.89***		-0.99**	0.28**	1.3*
<i>Osmoderma eremita</i> (B)	37	-0.75**			0.19*	1.4***
<i>Liocola marmorata</i> (B)	4		0.004			
<i>Tenebrio opacus</i> (B)	15		0.009***		-0.27*	
<i>Allecula morio</i> (B)	37		0.004***	-0.69*	0.09	1.1**
<i>Larca lata</i> (P)	7		0.005*	-1.0		16.7
<i>Allochernes wideri</i> (P)	31				0.22*	0.91*

metapopulation studies (Moilanen and Nieminen 2002). NEG EXP implies that the migration rate from patch j to patch i is independent of the number of other patches surrounding patch j , and therefore that the total number of successful emigrants from patch j (to all other patches) increases with the number of patches surrounding j .

Sixth, we modified the function for NEG EXP (eq. 2) to take into account competition for immigrants among habitat patches (CONST EMIGR). This competition implies the number of successful migrants from one particular habitat patch to another particular patch may decrease the more other patches there are in the area surrounding the patches because emigrants are divided among the possible recipient patches. It will tend to make the migration distances shorter in those parts of the landscapes with many habitat patches (many patches in close proximity to a donor patch), in comparison to parts of the landscape with few habitat patches. As discussed above, this assumption may be appropriate for animals that actively search for patches. For each donor tree j , connectivity to recipients was estimated using eq. 2 with p set to 1. To obtain the same proportion of successful emigrants among all individuals in the population per tree from each donor tree j , we used a correction factor, c_j , which was estimated by dividing 1 by the value of connectivity to recipients for j . The higher value of c_j , the fewer are the recipients that the emigrants are divided between, and the more individuals are emigrating from the donor tree j to a certain recipient tree i . This is described by the following equation:

$$S_i = \sum_{j=1}^n p_j \exp(-\alpha d_{ij}) c_j, \text{ for all } j \neq i \quad (3)$$

with variables defined as in eq. (1) and $c_j = 1 / \sum_{k=1}^n \exp(-\alpha d_{jk})$. This modification of the negative exponential function has not been used in any previous study.

Previous studies have shown that connectivity measures may improve if the difference in resistance of intervening land cover ("matrix") is considered (Verbeulen et al. 2003). We did not include matrix resistance in any of the connectivity measures we tested, because we believe that pseudoscorpions and flying beetles are able to move over open areas, open stretches of water, and forests, and in our field sites there are no other obvious barriers. Statistical analyses were conducted using R 2.9.0 (R Development Core Team 2009).

Results

For seven species out of ten the model fit became considerably better ($\Delta AIC > 7$) when connectivity was included as a predictor, even when the most simple connectivity measure was used (BUF TREE; Table 5). For one species, *Liocola marmorata*, the relationship with connectivity was negative. This indicates that the relationship between species' occupancy and connectivity was governed by other factors than probability for immigration. Consequently, the species was excluded from further comparisons of connectivity measures. For most species,

the model fit increased slightly when information about the diameters of surrounding trees was included in the patch connectivity measure (BUF DIAM), but not when information about the density of hollow trees surrounding each potential donor tree was also included (BUF CONN; Table 5). For most species, model fit was slightly better when using a connectivity measure that included only occupied potential donor patches within a buffer (BUF PRES) instead of a connectivity measure using all potential donor patches within a buffer (BUF DIAM), and for two species this difference was considerable. Patch connectivity measures that weight the contributions of potential donor trees according to a negative exponential function (NEG EXP) did not have a considerably better fit for any species in comparison to the more simple approach of counting trees within buffers (BUF PRES) (Table 5). For seven species out of nine, a modification of the negative exponential function in which the competition for immigrants among recipient habitat patches was taken into account (CONST EMIGR) produced a better fit than the usual application of the negative exponential function (NEG EXP). For five species out of nine this modified function (CONST EMIGR) generated the best fit to the data (Table 5), but for no species this measure was considerably better ($\Delta AIC > 7$) than the second best measure.

The buffer radii that generated the strongest relationships were on average larger when the connectivity measure was one in which all hollow oaks were counted as potential donors (BUF TREE), in comparison to connectivity measures that considered only occupied oaks and probability of occupancy (BUF PRES, $p = 0.006$, paired t-test; Fig. 1).

Discussion

Patch connectivity is an important predictor of species occupancy for the invertebrate fauna specialised on tree hollows (Table 5). For the majority of the study species there was a positive relationship that considerably improved the model fit, but for one species (*Liocola marmorata*) the relationship was negative. This may be because it competes with *Osmoderma eremita*, and is a better disperser but a weaker competitor (Ranius 2002).

For several species, the model fit became considerably better using connectivity measures that identified potential dispersal sources with higher precision, i.e. by including information on species occurrence when identifying potential donor trees (Table 5). Other studies have also revealed a stronger relationship when connectivity measures include occupied patches rather than all patches (Johansson and Ehrlén 2003, Snäll et al. 2004, Prugh 2009). Thus, if possible, occupancy data should be collected in surrounding habitat patches in connectivity studies.

For many systems, it is very time-consuming to obtain data on occupancy in all surrounding habitat. When no occupancy data are available for surrounding habitat, it is possible to use characteristics of the surrounding habitat patches that reflect the probability of species occupancy to obtain better information about where the dispersal sources likely are. However, when we tested that approach, tree diameter of surrounding trees only generated a small

Table 5. Generalized linear models with species occurrence as dependent variables, and tree characteristics and patch connectivity measures as independent variables, ordered from the simplest measure to the measure thought to reflect dispersal biology most closely. ED is the explained deviance and AIC the Akaike information criterion value. An asterisk (*) indicates that the AIC value is considerably lower ($\Delta AIC > 7$) than the previously tested model (BUF DIAM is compared with BUF TREE, and so on, except BUF PRES, which is compared with BUF TREE). "TREE" is the model including tree characteristics alone (Table 4), while the other models include these tree characteristics and one connectivity measure each. The connectivity measures are summarized in Table 3. The best model for each species is in bold.

	TREE		BUF TREE		BUF DIAM		BUF CONN		BUF PRES		NEG EXP		CONST EMIGR	
	ED (%)	AIC	ED (%)	AIC	ED (%)	AIC	ED (%)	AIC	ED (%)	AIC	ED (%)	AIC	ED (%)	AIC
<i>Elater ferrugineus</i>	13.9	119.32	30.2	101.35*	31.0	100.38	30.2	101.48	25.8	107.33	24.1	109.58	33.4	97.15*
<i>Procerasus tibialis</i>	6.1	350.46	9.4	342.15*	9.6	341.56	9.1	343.44	9.8	340.80	9.1	343.30	9.9	340.39
<i>Ampedus hjorti</i>	2.4	344.59	6.7	333.44*	6.5	334.23	6.7	333.72	6.9	332.83	5.9	336.48	4.3	341.86
<i>Ampedus cardinalis</i>	11.7	289.14	15.4	281.38*	15.8	280.02	16.5	278.04	17.4	275.14	15.8	280.08	17.8	273.87
<i>Osmoderma eremita</i>	8.5	347.69	14.8	328.00*	14.9	327.81	13.7	332.32	16.9	320.27*	15.7	324.98	16.6	321.52
<i>Liocola marmorata</i>	2.8	88.05	18.8	78.22* neg										
<i>Tenebrio opacus</i>	14.2	206.70	26.2	182.52*	30.8	171.92*	28.1	178.06	34.3	163.71*	33.6	165.28	37.1	157.11*
<i>Allecula morio</i>	9.7	347.00	11.5	344.54	11.6	343.93	11.6	343.99	11.9	342.92	11.4	344.95	11.5	344.32
<i>Larca lata</i>	14.7	140.02	25.0	128.11*	26.2	126.21	21.9	132.91	27.2	124.69	30.2	120.08	27.5	124.30
<i>Allochemes wideri</i>	3.9	344.04	4.4	345.96	4.5	345.93	4.4	346.03	5.1	343.66	4.6	345.37	6.0	340.31

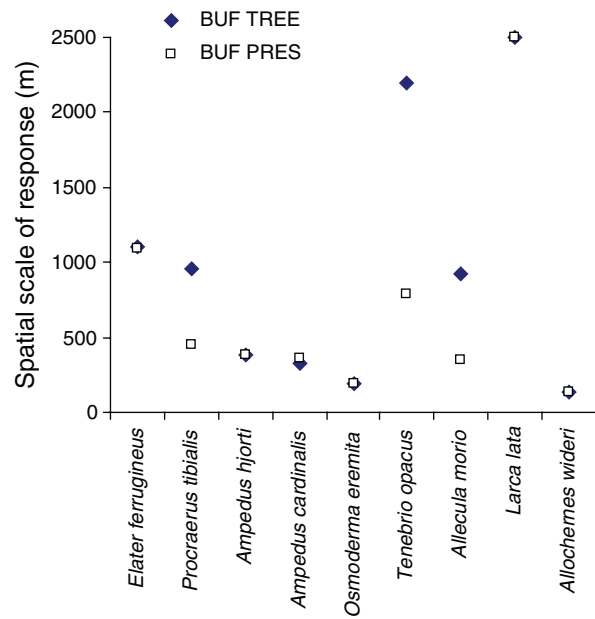


Figure 1. Radii that provided the best model fit (lowest AIC). Comparison between two buffer measures of connectivity, BUF TREE and BUF PRES ($p = 0.006$, paired t-test). Radii between 25 and 2500 m were tested.

improvement, while for most species the model fit became worse when the density of trees surrounding each of the potential donor trees was included. This means that the connectivity measure was not improved by up-weighting donor trees with high connectivity. This is consistent with our comparison of NEG EXP and CONST MIGR, which revealed that the connectivity measure may be improved by down-weighting donor trees with high connectivity (see below). An explanation for this is that there is a higher competition among trees for emigrating individuals from trees with a higher density of recipient trees surrounding them.

For most species, the goodness of fit was similar for BUF PRES and for NEG EXP, and that when there was a difference, the goodness of fit was generally higher for BUF PRES (Table 5). This is surprising because the degree to which the occurrence patterns are explained by patch connectivity should reflect how closely the connectivity measure reflects the dispersal pattern. Habitat density within a circle should only be the best connectivity measure in the rare case of a species with a distinct maximum dispersal distance equal to the circle radius. It is unlikely that there are any such distinct cut-off distances for any species; it is more likely that the probability of dispersal decreases with distance according to a continuous function. In fact, for one of our study species, the distribution of observed dispersal distances is close to a negative exponential function (Ranius 2006). The fact that the simpler measures appear to be adequate is advantageous because they are easier to understand and to use in landscape planning. At least for our study species, these simpler measures are clearly an acceptable approach when identifying areas of highest conservation value for hollow-dwelling invertebrates, even though they may be biologically less realistic.

For five study species out of nine, the best model fit was obtained with a function assuming the same rate of successful emigration for all inhabited potential donor trees, independent of the density of hollow trees surrounding them (CONST EMIGR), while a function with successful emigration rate proportional to the number of surrounding hollow trees (NEG EXP) generated the best fit for only one species (Table 5). The latter function has been used frequently, for instance in tools for metapopulation modelling such as the incidence function model (Hanski 1994). This type of function is reasonable (even though the negative exponential function is questionable for many species groups, see for instance Fitt et al. 1987, Clark et al. 1999, Baguette et al. 2000), for instance for dispersal of spores or seeds. This is because spores and seeds do not have any active dispersal behaviours; if deposited on a suitable substrate they may give rise to a colonisation, while all other seeds or spores are lost. Therefore, seen from the view of a donor population, the number of successful emigrants is proportional to the area of substrate in its surrounding area. Animal movement probably rarely works this way, and our results suggest that this includes most of our study species (Table 5). This is because the number of emigrating animals is limited, and their movements are affected by active behaviour. Therefore, the number of successful migrants from a particular habitat patch to another particular patch will probably decrease the more other habitat patches there are in the area, as these patches will compete for the migrating animals. This competition for migrating animals will also tend to make the migration ranges shorter in those parts of the landscapes with many habitat patches, in comparison to parts with few habitat patches. This can be taken into account in individual-based models (Kindvall 2004, Ovaskainen 2004). However, a big disadvantage with such models is that detailed data on movement behaviour are needed for parameterisation. In the present study, we tested a much less data-demanding model that takes into account competition for immigrants (CONST EMIGR). We had expected a priori that CONST EMIGR would fit the data best for at least one of our species, *Osmoderma eremita*, for which we had detailed dispersal information. This species occurs in small populations per tree, only a limited proportion of the individuals disperse, and those emigrants we have observed by telemetry have quickly and successfully moved from one tree to another suitable tree (Ranius 2006). These characteristics should produce a dispersal pattern that fits the assumption of competition among recipient trees for emigrants as represented in the CONST EMIGR connectivity measure.

We cannot yet say how general our CONST EMIGR result is. Previous tests of connectivity measures have mainly focused on butterflies (Moilanen and Nieminen 2002) and on animals that disperse by walking on the ground (Prugh 2009). Butterflies are visual searchers, while our study species and many other flying insects are at least partly olfactory searchers, which may generate different dispersal patterns (Hambäck and Englund 2005). Differences in dispersal patterns between animals and plants, and various groups of animals may affect how appropriate different connectivity measures are. Many flying insects may have similar dispersal patterns as the beetles in our study, which suggest that the better fit of the connectivity measure

CONST EMIGR with field data than the connectivity measure NEG EXP may be a fairly general result.

Using a measure of patch connectivity that counts all trees as potential donor trees (BUF TREE), the relationship between species occurrence and patch connectivity was strongest at a larger spatial scale in comparison to when we used a connectivity measure that counts only occupied trees within a buffer as potential donor trees (BUF PRES; Fig. 1). The reason for this may be that there are usually only a few trees in a small circle. This means that at smaller scales the variability in quality and occupancy among trees will generate a large deviation between the BUF TREE estimate and the actual occurrence of donor trees. Within a larger circle there are more trees, and therefore the differences among trees average each other out to a larger extent, resulting in similar values for BUF TREE and BUF PRES. Consistent with this explanation, the mean (across species) Pearson correlation coefficients between BUF TREE and BUF PRES for radii 25, 250 and 2500 m are: 0.69, 0.88, and 0.94, respectively. Consequently, a patch connectivity measure based on habitat rather than occupied habitat may be poor at reflecting the true connectivity at a smaller spatial scale, but quite reasonable at a larger spatial scale. For this reason, the spatial scale of patch connectivity that generates the strongest correlation with occupancy is not directly comparable between multiscale studies if the measure of donor habitat amount in the connectivity measures differs among studies; the more poorly the habitat amount measure reflects the availability of potential immigrants, the larger the spatial scale that will be identified as the most relevant one when identifying isolation effects.

Conclusion

This study shows that habitat amount within a circle is a useful connectivity measure; the model fit is not substantially lower for this measure than for other more complicated measures. An advantage with this measure is that it is easy to understand and use, e.g. in landscape planning.

If a biologically more realistic measure is needed, a measure that up-weights the closest patches should be used. In simulation models, dispersal is often modelled using the negative exponential function. For instance, in a textbook with population simulation models constructed with a software frequently used for this purpose (RAMAS-GIS), 14 models out of 22 (63%) were based on the negative exponential function (Akçakaya et al. 2004). In the great majority of these cases, there was no empirical support for the use of this function. Based on our results, we suggest that in several of these models, and likely in many other cases, biological realism would be improved if it were taken into account that habitat patches may compete with each other for a limited number of potential immigrants.

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