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STRUCTURAL VERSUS FUNCTIONAL HABITAT CONNECTIVITY MEASURES TO EXPLAIN BIRD DIVERSITY IN FRAGMENTED ORCHARDS

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ABSTRACT

Habitat connectivity plays a paramount role in the biodiversity of fragmented landscapes. Commonly, connectivity is measured using simple structural metrics, e.g. Euclidean distances between habitat patches. Recently, functional measures such as cost-distance metrics have been proposed. Cost-distance metrics account for behavioural aspects of investigated organisms. They weight the habitats of the investigated landscape according to specific cost values, and model the optimal dispersal corridor according to these values. This study investigated i) if structural or functional connectivity measures explain biodiversity in a focal habitat better and ii) if the appropriateness of the measure differs between patch and landscape scale. We mapped the landscapes within a 500 m radius around 30 fragmented traditional orchards (focal patch). Connectivity measures were based on either Euclidean distances (structural) or cost-distances (functional) to other suitable habitat patches. Birds were used as biodiversity indicators. For analysis, we calculated species richness and total abundance of all species with a preference for woody habitats. In addition, abundances of four wood-preferring bird species were also examined individually. Linear models were created using stepwise forward selection. The relative performance of structural and functional connectivity measures was scale dependent. Structural metrics explained more variance at the patch scale whereas functional metrics explained more variance at the landscape scale. We conclude that simple structural metrics can be used to investigate local or small-scale effects on bird diversity but that investigations of landscape scale connectivity should consider behavioural aspects by using more complex functional metrics. The comparison between group and single species showed that not all individual species behave similarly to group results. Whilst the use of organism groups must be treated with caution, it is certainly worthy of future study.

Key words: Biodiversity, birds, cost distance analysis, fragmentation, landscape metrics, spatial scale

INTRODUCTION

Connectivity has important effects on dispersal and metapopulation dynamics, and hence species persistence in fragmented landscapes (With 2004). It is defined as the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993) through a background matrix of less suitable habitat types (Forman and Godron 1986). Therefore, connectivity is influenced both by the physical location of habitat patches as well as by characteristics of the surrounding habitat matrix (Baskent and Jordan 1995). Furthermore, it can define the status of the fragmentation process in a landscape (Tischendorf and Fahrig 2000a). There are two main types of connectivity: i) structural connectivity which describes the physical relationships between habitat patches such as inter-patch distances based on Euclidean units (Keitt et al. 1997) and ii) functional connectivity which accounts for organism's behavioural response to both the landscape structure and the landscape matrix (Tischendorf and Fahrig 2000b; Taylor et al. 2006).

As a consequence, and because no single measure can be applied to all ecological situations, a great variety of connectivity measures have been used in landscape connectivity research (Goodwin 2003). Frequently, structural connectivity is calculated using the Euclidean shortest distance (Kindlmann and Burel 2008). Structural connectivity metrics are easy to apply (Taylor et al. 2006), require less data than functional metrics (Magle et al. 2009) and avoid the potential complications of movement behaviour (Goodwin 2003). Therefore, they are more often applied than functional connectivity measures. However, Tischendorf and Fahrig (2000b) insist that measures of connectivity should be based on the organism's movement through a landscape; otherwise they may not be ecologically meaningful (Goodwin 2003). Cost-distance modelling is a functional approach that can identify species movements and dispersal within the landscape (Bunn et al. 2000; Adriaensen et al. 2003; Schneider and Fry 2005; Driezen et al. 2007). With this approach more realistic functional connectivity measures can be developed. Cost-distance modelling accounts for the effect of the landscape structure and matrix on organism movements by influencing the modelled species dispersal and immigration through the assignment of species specific so-called cost values to different land-use types in the landscape (Adriaensen et al. 2003). In doing so, least-cost paths, which represent the most economical way to reach a point in the landscape from a defined source, can be calculated to predict organism movements and therefore the functional connectivity of an investigated landscape for the specific organism.

Most studies are limited to a single connectivity metric, thus, Kindlmann and Burel (2008) have called for studies comparing different connectivity measures. Since connectivity measurements may be used as a basis for decision making (Calabrese and Fagan 2004), it should be clearly investigated whether simple structural or complex functional metrics perform best in describing biodiversity for certain landscapes. Only a few studies like Chardon et al. (2003) or Magle et al. (2009) have compared structural and functional connectivity metrics. Both reported a better performance of functional measures.

However, the scale at which the different measurements are applied needs to be adapted to the species in question. The spatial scale must account for the dispersal and movement capabilities of the species, which in turn forms the basis of the species specific landscape connectivity (Keitt et al. 1997). For example, effects of habitat connectivity on different taxonomic groups have been observed to vary at the patch and landscape scale (Bailey et al. 2010, in press) probably because different processes predominate at these scales (Wiens 1989). Furthermore, animal movements will differ at diverse spatial scales depending on their use of various parts of the landscape (e.g., for foraging and breeding) or through their

sequential use of different habitats to find temporally varying resources (Mac Nally and Horrocks 2000; Pope et al. 2000). Hence, a comparison of structural and functional connectivity metrics at different spatial scales offers the possibility to evaluate i) which measure is more informative to compass certain species connectivity and ii) if the appropriateness of the metric differs with scale. Previously, metric appropriateness has been observed to be sensitive to changes of thematic scale as well as spatial resolution and extent (e.g. Bailey et al. 2007; Wu et al. 2002).

In this paper structural and functional connectivity metrics are compared as indicators of the diversity and abundance of wood-preferring birds at a patch (relation between the focal site and only its nearest neighbouring patch) and landscape scale (relation between the focal site and all surrounding patches within a 500 m radius) in 30 traditional Swiss orchards. Birds were chosen as they are a typical traditional fruit and nut orchard biodiversity indicator (Herzog et al. 2005; Kleijn et al. 2006). Furthermore, habitat connectivity is important in bird conservation (Haas 1995; Desrochers and Hannon 1997) and as birds differ greatly in the extent to which they actually disperse (Böhning-Gaese et al. 1998), testing their specific connectivity at two distinct spatial scales could be informative. As species traits strongly influence species responses to fragmentation (Bennett et al. 2004; Ewers and Didham 2006), we grouped the birds according to their use of woody habitat as their main resting area. This group is referred to as wood-preferring in the text. Previously, Wiens et al. (2002) have suggested that the identification of functional species groups based on landscape structure response may be a useful conservation management tool.

Typically, cost-distance analysis examines movements of only one species through the landscape (see e.g. Chardon et al. 2003; Driezen et al. 2007) because assigning resistance / cost values is a species specific challenge (Adriaensen et al. 2003). In the present study, we examined the applicability of cost-distance analysis on a group of wood-preferring bird species. The use of a species trait group instead of analysing single species could render cost-distance modelling more generally applicable. Furthermore, a variety of different species could be analysed in one step to evaluate the connectivity of a certain landscape more generally. This is one of the first studies attempting a species group approach. Group results were compared to the four most common single species in the study sites to examine whether connectivity metrics can be applied to groups of species with similar habitat requirements.

MATERIALS AND METHODS

Site selection

The study was undertaken in North Eastern Switzerland (cantons Thurgau and St. Gallen) in landscapes which are characterised by mature high-stem apple orchards with mown or grazed underlying meadows. Orchards were selected that were between 0.5 and 1.7 ha in size, had an elevation less than 650 m above sea level and a maximum slope of 20 %. Orchards bordering towns, villages and large roads or surrounded by large areas of forest were excluded from the selection process. Orchards represent a combination of woody and open grassy habitat. Therefore all similar semi-open woody habitats (woodland edge, hedgerows, tree lines, other high-stem orchards, solitary trees) were mapped within a 500 m radius of these orchards. The share of habitats in the 30 selected landscapes ranged between 4.0 and 45.7 %. Subsequently, additional land use classes other than semi-open habitats (Table 1) were defined within the orchards 500 m surrounding. A 500 m investigation radius was chosen as landscape scale because wood-preferring birds are known to be

sensitive to even small gaps of 50 m between their habitat patches and territories (Desrochers and Hannon 1997). Furthermore, Schweiger et al. (2005), Billeter et al. (2008), Schmidt et al. (2008) and Bailey et al. (2010, in press) found that 500 m represents an intermediate scale at which the investigated species respond to landscape composition in Europe. Additionally, given the fine resolution of our analysis (0.5 m grain size), study areas can be considered as landscapes with a relatively small extent and fine scale relative to the studied bird movements.

Site selection process as well as site properties are given by Bailey et al. (2010, in press) in more detail.

Table 1: Bird group cost values

First column - categorised land use types; second column - cost values assigned for the wood-preferring birds.

Land use types	Cost values wood-preferring birds
Focal orchard, Other fruit and nut orchards, Treelines, Woodland and forest habitat, Woodland edge	1
Shrub plantations, Solitary trees	3
Heathland, Scrub, Hedgerows	5
Intensive orchards, Unpaved roads	8
Quarry/pit, Railway, Vineyards	10
Rotational grassland	12
Paved roads, Permanent grassland, Wetlands	15
Buildings, Arable	17

Study organisms

Three bird surveys were carried out in each of the 30 orchards during the early morning (05:30 – 09:30) between April and June 2007 according to the mapping scheme of the Swiss Ornithological Institute (www.vogelwarte.ch) to obtain information about the number of species and the number of territories of breeding birds within the studied orchards. For each orchard, the three surveys were combined to determine the number of bird territories. Due to the variation in the orchard sizes it was necessary to correct bird species richness for orchard area using linear regression, whereas the number of territories, i.e. bird abundance, was corrected to territories per hectare.

Bird species were then grouped according to their relation to woody habitats. Woodland-dependent species are primarily associated with woodland or forest habitat for regular daily activities (i.e. foraging, roosting and nesting) and seldom observed in modified environments (Radford et al. 2005). Our woodland-dependent species were identified a priori following Glutz von Blotzheim (1997) and Zwygart (1983). We analysed only species that rest predominately in woody habitats. These included *Certhia brachydactyla*, *Dendrocopos major*, *Ficedula hypoleuca*, *Fringilla coelebs*, *Garrulus glandarius*, *Musicapa striata*, *Parus caeruleus*, *Parus major*, *Parus palustris*, *Picus viridis*, *Regulus ignicapillus*, *Sitta europaea*, *Sylvia atricapilla*, *Turdus merula*, *Turdus philomelos* and

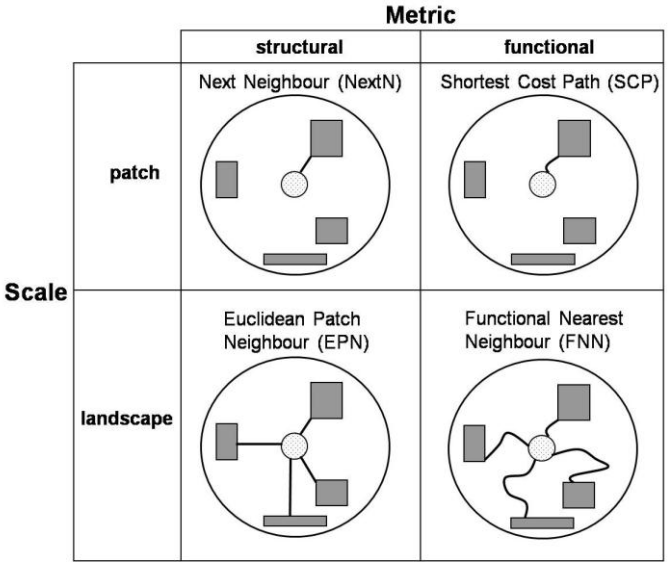
Turdus viscivorus. Thus, species such as *Carduelis carduelis*, *Carduelis chloris*, *Columba palumbus*, *Corvus corone*, *Emberiza citrinella*, *Lanius collurio*, *Passer montanus*, *Pica pica*, and *Sturnus vulgaris* were excluded because they are open land species that utilize woody structures mostly for nesting. The species *Buteo buteo*, *Milvus milvus*, *Motacilla alba*, *Passer domesticus* and *Phoenicurus ochruros* were removed from the list and analyses, because they lack suitable nesting sites in the orchards and were only recorded in the field for integrity reasons. Such grouping allowed the same cost values to be set to the various land use types for all bird species within the wood-preferring bird group (see below). The four most abundant bird species within this group were *Parus major* (36 territories), *Fringilla coelebs* (31 territories), *Parus caeruleus* (29 territories) and *Turdus merula* (13 territories). To compare the multi-species group approach to a single species approach, single species were analysed in the same way as the bird group which means that connectivity metrics were calculated with equal assumptions as the group metrics, i.e. same cost values and suitable orchard surrounding habitat patches.

Connectivity metrics

Four connectivity metrics were calculated at both the patch and landscape scale (Figure 1). All four metrics represented continuous gradients of increasing distance to the next neighbour patch or the average distance to every suitable habitat in the 500 m surrounding landscape. The structural connectivity metrics Next Neighbour (NextN) and Euclidean Patch Neighbour (EPN) were opposed to the functional connectivity measures Shortest Cost Path (SCP) and Functional Nearest Neighbour (FNN).

Fig. 1: Tested connectivity metrics

Schematic figures show focal orchard (spotted circle) and other suitable habitat patches (grey rectangles) within the 500 m surrounding radius (large circle). The corresponding connectivity metrics (in meters; averaged across the orchard sites and for EPN and FNN also averaged within each orchard site) are represented by black lines.



Structural metrics: NextN and EPN were measured manually within ArcGIS 9.2 (ESRI). NextN (patch scale) represents the shortest Euclidean distance (in metres) from the focal

orchard boundary to the next nearest suitable habitat patch. EPN (landscape scale) is the average Euclidean distance (in metres) from the focal orchard boundary to every suitable habitat in the 500 m surrounding landscape.

Functional metrics: Following Broquet et al. (2006), the choice of the cost values characterising birds' movement abilities across our landscapes was based on existing knowledge of wood-preferring bird biology. For example *Turdus merula* only rests in and moves through woody habitat. Even under semi-natural conditions it prefers mature forest stands and avoids uncovered areas such as arable or grassland (Glutz von Blotzheim 1997). Other study species like *Parus major* and *Parus caeruleus* also depend on mature woodland habitat and show reduced dispersal between isolated woody habitat patches embedded in a matrix of agricultural land (Matthysen et al. 2001). Although these species can also be observed within residential areas, a group of several mature trees is essential for them (Glutz von Blotzheim 1997). According to bird biology landscape cost values were then assigned to all land use types within the study sites for the cost-distance analysis. These values were arbitrarily chosen and range theoretically between 1 (representing suitable habitat e.g. forest and woodland) and 20 (barrier) in this study. The relational assignment of these values to the different land use types resulted in cost values from 1 to 17 as no direct barrier to bird movement was obtained within the study landscapes (Table 1). SCP and FNN were then calculated in ArcGIS 9.2 using cost distance and cost path tools in Spatial Analyst. Path-cost values were calculated by multiplying the cost value of each cell by the cell resolution (here 0.5 m). Diagonal movements were accounted for by additionally multiplying by the square root of 2. Thus, one cell in the land use map (0.5 x 0.5 m) with a cost value of 10 represents a path-cost value of 5 (metres), implying that the cost of moving through this cell is equivalent to moving through 5 metres of source habitat (cost value = 1). Cost-distance raster and related least-cost paths were calculated for the orchards using the cost values for the wood-preferring birds. The resultant attribute tables contained the specific path-cost values. The value of the path with the least cost to the nearest suitable habitat patch (in a functional manner) represents SCP (patch scale). FNN (landscape scale) was calculated by averaging all path costs to all suitable habitat patches and represents the average functional distance from the focal orchard to suitable patches in the landscape.

Data analysis

Linear models using stepwise forward selection of explanatory variables according to Akaike's Information Criterion (AIC) were run in R (R Development Core Team 2006) using the library MASS (Venables and Ripley 2002). Bird species richness and abundance were the dependent variables whereas the connectivity metrics were the explanatory variables. The connectivity metrics were transformed beforehand to reach normality ($\log10(x+1)$). Bird data were not transformed as the corresponding residuals were well distributed within the Quantile-Quantile plots. Separate models were created to investigate species richness and territory number of all wood-preferring birds as well as the number of territories of the four most common single bird species. To avoid intercorrelations between the connectivity measures, we allowed only one connectivity metric to enter each model. The R values were compared to identify which of the connectivity metrics explained the most variance in species richness (bird group) and number of territories (bird group, single bird species).

RESULTS

Study sites are structurally characterised by values of NextN ranging between 0.5 m and 277 m with an average distance of 60 m whereas EPN values ranged between 149 m and 334 m with an average of 259 m. Cost-distance measures delineate the studied orchards with a minimum value of 0.5 m and a maximum value of 3875 m for SCP with an average of 863 m whereas FNN values ranged between 583 m and 4875 m with an average functional distance of 2153 m.

Both bird species richness and abundance showed significant negative correlations with the connectivity metrics regardless of scale, the structural or functional nature of the indicator, group or singular species (Table 2). As expected, fewer species and territories were found in orchards that were further away from other woody habitats (patch isolation), and in landscapes in which distances between woody habitat patches were generally high (landscape isolation). The only exception was *Fringilla coelebs*, for which there resulted no significant correlation.

Table 2: Correlations (R values) between bird species number (bird group) and number of bird territories (bird group, single species) with functional and structural connectivity measures. (***) significant at $p < 0.001$; (**) significant at $p < 0.01$; (*) significant at $p < 0.05$; (.) trend at $p < 0.05$ to 0.1; (-) connectivity metric did not improve model fit according to AIC.

	Patch scale		Landscape scale	
	Structural metric	Functional metric	Structural metric	Functional metric
	NextN	SCP	EPN	FNN
Bird group: Species richness	-0.62***	-0.57***	-0.26 .	-0.45**
Bird group: abundance	-0.5**	-0.46**	-	-0.37*
Fringilla coelebs	-	-	0.28 .	-
Parus major	-0.43*	-0.36*	-	-0.27 .
Parus caeruleus	-0.37*	-0.44**	-0.42*	-0.32*
Turdus merula	-0.38*	-0.36*	-	-0.27 .

At the patch scale both NextN and SCP correlated significantly with the bird group species and territory number. The structural indicator NextN explained more variance (species 38%, territories 25%) than the functional SCP (species 32%, territories 21%). In contrast, at the landscape scale, only the functional metric FNN correlated significantly with group species richness (explained variance 20%) and the number of territories (explained variance 14%).

Except *Fringilla coelebs*, all tested single bird species were significantly and negatively correlated with two or more connectivity metrics. This was particularly the case at the patch

scale where NextN explained more of the species variance (18% *P. major*, 14% *T. merula*) than SCP (13% *P. major*, 13% *T. merula*). Contrarily, for *P. caeruleus* more variance was explained by SCP (19%) than by NextN (13%). At the landscape level, significant correlations were obtained only for *P.caeruleus* with structural EPN accounting for 17% of the explained variance and functional FNN for 10% of the explained variance.

DISCUSSION

Birds responded significantly to the connectivity metrics at both the patch and landscape scale whereby more variance was generally explained at the patch level. All significant correlations were negative, i.e. species richness or abundance increased with decreased structural or functional distance to other suitable habitats.

Structural vs. functional connectivity metrics

The significant negative correlations of patch scale connectivity metrics with bird species richness and abundance support previous findings. For example, Radford and Bennett (2007) found that greater structural connectivity promotes larger woodland-dependent bird populations in Australian agricultural landscapes, and that local isolation had clear negative effects on forest birds. Ward (2005) found that many migratory bird species decline in peripherally isolated populations as they are susceptible to changes in connectivity through fragmentation which affects the population's immigration rates. Desrochers and Hannon (1997) in an investigation of gap crossing decisions by forest songbirds, observed forest birds twice as likely to travel through (only) 50 m of woodland than through 50 m of open land to reach a defined destination. They concluded that although woodland birds are potentially highly mobile, local connectivity is very important to maintain viable populations (see also Awade and Metzger 2008). Bélisle & Desrochers (2002) and Gillies and Clair (2008) concluded from their data, that forest dwelling birds prefer to move along forested corridors for interpatch movements in a fragmented landscape.

Based on these findings we would expect functional metrics to better explain the bird species richness and abundance we observed in our focal orchards than non-specific structural metrics. However, focussing on the patch scale, the structural metric Next Neighbour explained slightly more variance of bird species and territory number than the equivalent functional metric Shortest Cost Path. This indicates that the simple Euclidean metric (NextN) provides equal or even slightly better information about the local connectivity for wood-preferring birds than the functional one (SCP). This contrasts with previous studies that have compared structural and functional connectivity metrics (e.g. Magle et al. 2009; Chardon et al. 2003). These studies found that functional connectivity metrics performed better than structural metrics. However, both studies were restricted to the landscape scale and did not test other spatial scales. Our results question whether the use of complex and time-consuming functional metrics is beneficial for investigations of sensitivity to local habitat isolation. Based on our results at the patch scale, simple structural connectivity metrics suffice for the investigation of highly mobile species such as birds. Certainly, this is a topic worthy of further investigation for biological groups of different mobility.

In contrast to our findings at the patch scale, at the landscape scale, only the functional metric Functional Nearest Neighbour significantly explained the bird group species richness and territory number. This underpins conclusions by e.g. Magle et al. (2009), Driezen et al. (2007), Stevens et al. (2006) and Verbeylen et al. (2003), who found that cost-distance measurements represent organism dispersal more effectively than structural Euclidean distances (for prairie dogs, hedgehogs, toads, red squirrel respectively). Our

results suggest that functional connectivity should be investigated when studying the connectivity of suitable habitat at a landscape scale. The frequently used structural metrics may lead to misinterpretations and could underplay the relative importance of spatial configuration. The use of simple Euclidean metrics at the landscape and regional scale should be re-considered. Hence, functional connectivity measures may provide more meaningful and realistic results providing better instruments for conservation management decisions.

Multi-species approach vs. single species for cost-distance analyses

Cost-distance analyses usually investigate single species as assigning cost values is normally a species specific challenge (Adriaensen et al. 2003). Detailed biological knowledge of the species is required (especially dispersal and habitat preference). If cost-distance analysis could be applied for species groups, this could allow the development of more generic indicators which might be more readily applied. However, in such applications differences between individual species can not be accounted for, which might blur the results. Nevertheless, *Parus major* and *Turdus merula* matched the group results at the patch scale and almost at the landscape scale (trend to significance). *Parus caeruleus* in contrast, was better explained by functional SCP (patch scale) and structural EPN (landscape scale) although NextN and FNN were also significant for this species. This suggests that the cost values set for the group are more appropriate for some species than others. This is because certain species match more closely the investigated trait of the group. For example, *Fringilla coelebs* was not significantly correlated with the connectivity metrics, potentially as it is less wood-preferring. Greegan and Osborne (2005) found *Fringilla coelebs* to more readily cross open land than woodland. Thus, the cost values for the open habitat types may differ considerably from the values used for the entire bird group (Table 1). Clearly, when examined individually, not all species behave similarly to the group. Thus, group results must be treated with caution as some species better match the considered trait than others. Nevertheless, using organism groups according to particular life history traits is an interesting area of future connectivity research (see for example Ewers and Didham 2006).

CONCLUSIONS

The appropriateness of structural and functional connectivity measures appears to be scale-dependent in this study. Simple structural measures seem more suitable to examine patch scale connectivity (or fragmentation / isolation) phenomena. Complex functional metrics appear promising to investigate landscape scale connectivity. Thus, structural measures could suffice for local or small scale investigations of habitat isolation and could be easily included in long-term monitoring programs, providing early-warning signals. However, landscape-scale investigations may benefit from the inclusion of more complex functional metrics as they can be expected to generate more realistic, ecologically meaningful results which are representative of the relevant importance of spatial configuration. Here, we focused our investigation on the patch and landscape scale. The appropriateness of structural and functional connectivity metrics for a progressive gradient of spatial scales, for example by using different buffers widths around the focal patch, would be an interesting topic for further research. Grouping species according to particular traits increases the wider applicability of both structural and functional connectivity measures. It is an exciting area worthy of future investigation.

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REFERENCES

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

Awade, M., Metzger, J.P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology*, 33: 863-871.

Bailey, D., Billeter, R., Aviron, S., Schweiger, O. & Herzog, F. (2007). The influence of thematic resolution on metric selection for biodiversity monitoring in agricultural landscapes. *Landscape Ecology*, 22: 461-473.

Bailey, D., Schmidt-Entling, M.H., Eberhardt, P., Herrmann, J., Hofer, G., Kormann, U. & Herzog, F. (2010). Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. *Journal of Applied Ecology* (in press).

Baskent, E.Z., Jordan, G.A. (1995). Characterizing spatial structure of forest landscapes. *Canadian Journal of Forest Research*, 25: 1830-1849.

Bélisle, M., Desrochers, A. (2002). Gap-crossing decisions by forest birds: An empirical basis for parameterizing spatially-explicit, individual-based models. *Landscape Ecology*, 17: 219-231.

Bennett, A.F., Hinsley, S.A., Bellamy, P.E., Swetnam, R.D. & Mac Nally, R. (2004). Do regional gradients in land-use influence richness, composition and turnover of bird assemblages in small woods? *Biological Conservation*, 119: 191-206.

Billeter, R., Liira, J., Bailey, D., Bugter, R., Arens, P., Augenstein, I., Aviron, S., Baudry, J., Bukacek, R., Burel, F., Cerny, M., De Blust, G., De Cock, R., Diekötter, T., Dietz, H., Dirksen, J., Dormann, C., Durka, W., Frenzel, M., Hamersky, R., Hendricky, F., Herzog, F., Klotz, S., Koolstra, B., Lausch, A., Le Coeur, D., Maelfait, J.P., Opdam, P., Roubalova, M., Schermann, A., Schermann, N., Schmidt, T., Schweiger, O., Smulders, M.J.M., Speelmans, M., Simova, P., Verboom, J., Van Wingerden, W.K.R.E., Zobel, M. & Edwards, P.J. (2008). Indicators for biodiversity in agricultural landscapes. A pan-European study. *Journal of Applied Ecology* 45: 141-150.

Böhning-Gaese, K., González-Guzmán & Brown, H.J. (1998). Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evolutionary Ecology*, 12: 767-783.

Broquet, T., Ray, N., Petit, E., Fryxell, J.M. & Burel, F. (2006). Genetic isolation by distance and landscape connectivity in the American marten (Martes americana). *Landscape Ecology*, 21: 877-889.

Bunn, A.G., Urban, D.L. & Keitt, T.H. (2000). Landscape connectivity: A conservation application of graph theory. *Journal of Environmental Management*, 59: 265-278.

Calabrese, J.M., Fagan, W.F. (2004). A comparison-shoppers's guide to connectivity metrics. *Frontiers in Ecology and the Environment*, 2(10): 529-536.

Chardon, J.P., Adriaensen, F. & Matthysen, E. (2003). Incorporating landscape elements into a connectivity measure. A case study for the Speckled wood butterfly *(Pararge aegeria L.)*. *Landscape Ecology*, 18: 561-573.

Desrochers, A., Hannon, S.J. (1997). Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology*, 11: 1204-1210.

Driezen, K., Adriaensen, F., Rondinini, C., Doncaster, P. & Matthysen, E. (2007). Evaluating least-cost model predictions with empirical dispersal data: A case-study using radiotracking data of hedgehogs *(Erinaceus europaeus)*. *Ecological Modelling*, 209: 314-322.

Ewers, R.M., Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, 81: 687-699.

Forman, R.T.T., Godron, M. (1986). *Landscape Ecology*, Cambridge University Press, Cambridge.

Gillies, C.S., Clair, C.C.S. (2008). Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, Volume: 105, Issue: 50, pp. 19774-19779.

Glutz von Blotzheim, U.N. (1997). *Handbuch der Vögel Mitteleuropas*. Band 11-14, Passeriformes. Aula-Verlag, Wiesbaden.

Goodwin, B.J. (2003). Is landscape connectivity a dependent or independent variable*?* *Landscape Ecology*, 18: 687-699.

Goodwin, B.J., Fahrig, L. (2002). How does landscape structure influence landscape connectivity. *Oikos*, 99: 552-570.

Greegan, H.P., Osborne, P.E. (2005). Gap-crossing decisions of woodland songbirds in Scottland: an experimental approach. *Journal of Applied Ecology*, 42: 678-687.

Haas, C.A. (1995). Dispersal and use of corridors by birds in wooded patches on an agricultural landscape. *Conservation Biology*, 9: 845-854.

Herzog, F., Dreier, S., Hofer, G., Marfurt, C., Schüpbach, B., Spiess, M. & Walter, T. (2005). Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes. *Agriculture, Ecosystems & Environment*, 108: 189-204.

Keitt, T.H., Urban, D.L. & Milne, B.T. (1997). Detecting critical scales in fragmented landscapes. *Conservation Ecology* (1/1). Retrieved May 2009, from http://www.consecol.org/vol1/iss1/art4/

Kindlmann, P., Burel, F. (2008). Connectivity measures. A review. *Landscape Ecology*, 23: 879-890.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marhsall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006). Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, 9: 243-254.

Mac Nally, R., Horrocks, G. (2000). Landscape-scale conservation of an endangered migrant: the Swift Parrot *Lathamus discolor* in its winter range. *Biological Conservation*, 92: 335-343.

Magle, S.B., Theobald, D.M. & Crooks, K.R. (2009). A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. *Landscape Ecology*, 24: 267-280.

Matthysen, E., Adriaensen, F. & Dhondt, A.A. (2001). Local recruitment of great and blue tits (*Parus major, P. caeruleus*) in relation to study plot size and degree of isolation. *Ecography*, 24: 33-42.

Pope, S.E., Fahrig, L. & Merriam, H.G. (2000). Landscape complementation and metapopulation effects on leopard frog populations. *Ecology*, 81: 2498-2508.

R Development Core Team (2006). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. Retrieved 2009-10-15, from http://www.R-project.org.

Radford, J.Q., Bennett, A.F. (2007). The relative importance of landscape properties for woodland birds in agricultural environments. *Journal of Applied Ecology*, 44: 737-747.

Radford, J.Q., Bennett, A.F. & Cheers, G.J. (2005). Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, 124: 317-337.

Schmidt, M.H., Thies, C., Nentwig, W. & Tscharntke, T. (2008). Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography*, 35: 157-166.

Schneider, C., Fry, G. (2005). Estimating the consequences of land-use changes on butterfly diversity in a marginal agricultural landscape in Sweden. *Journal of Nature Conservation*, 13: 247-256.

Schweiger, O., Maelfait, J.P., van Wingerden, W., Hendrickx, F, Billeter, R., Speelmans, M., Augenstein, I., Aukema, B.; Aviron, S., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Frenzel, M., Herzog, F., Liira, J., Roubalova, M. & Bugter R. (2005). Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organisational levels and spatial scales. *Journal of Applied Ecology*, 42: 1129-1139.

Stevens, V.M., Verkenne, C., Vandewoestijne, S., Wesselingh, R.A. & Baguette, M. (2006). Gene flow and functional connectivity in the natterjack toad. *Molecular Ecology*, 15: 2333-2344.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 68: 571-573.

Taylor, P.D., Fahrig, L. & With, K.A. (2006). Landscape connectivity. A return to the basics. *Conservation Biology*, 14: 29-43.

Tischendorf, L., Fahrig, L. (2000a). How should we measure landscape connectivity? *Landscape Ecology*, 15: 633-641.

Tischendorf, L., Fahrig, L. (2000b). On the usage and measurement of landscape connectivity. *Oikos*, 90: 7-19.

Venables, W.N., Ripley, B.D. (2002). *Modern Applied Statistics with S.* Springer, New York.

Verbeylen, G., De Bruyn, L., Adriaensen, F. & Matthysen, E. (2003). Does matrix resistance influence red squirrel *(Sciurus vulgaris* L. 1758) distribution in an urban landscape? *Landscape Ecology*, 18: 791-805.

Ward, M.P. (2005). The role of immigration in the decline of an isolated migratory bird population. *Conservation Biology*, 19: 1528-1536.

Wiens, J.A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3: 385-397.

Wiens, J.A., Van Horne, B. & Noon, B.R. (2002). Integrating landscape structure and scale into natural resource management. In: Liu, J., Taylor, W.W. (Eds.): *Integrating Landscape Ecology into Natural Resource Management*. pp. 23-67. Cambridge University Press, Cambridge,

With, K.A. (2004). Metapopulation dynamics: perspectives from landscape ecology. In: Hanski, I., Gaggiotti, O. (Eds.): *Ecology, Genetics and Evolution of Metapopulations.* pp. 23-44. Academic Press, San Diego.

Wu, J., Shen, W., Sun, W. & Tueller, P.T. (2002). Empirical patterns of the effects of changing scale on landscape metrics. *Landscape Ecology*, 17: 761-782.

Zwygart, D. (1983). Die Vogelwelt von Nieder- und Hochstammobstkulturen des Kantons Thurgau. *Der Ornithologische Beobachter*, 80: 89-104.