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TITLE PAGE

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ABSTRACT

Over the last 30 years, ecological networks have been deployed to reduce global biodiversity loss by enhancing landscape connectivity. Bird species dwelling in woodland habitats that are embedded in agriculture-dominated landscapes are expected to be particularly sensitive to the loss of connectivity. This study aimed to determine the role of landscape connectivity in woodland bird species richness, abundance, and community similarity in north-east Brittany (north-west France). An exhaustive woodland selection protocol was carried out to minimize the effects of woodland size on the response variables. Connectivity of the woodland and forest network in the study area was evaluated using graph-theory, accounting for matrix permeability, and a characteristic median natal dispersal distance at the community level based on the bird species pool recorded in the sampled woodlands. Information-theoretic model selection, controlling for woodland size in all the cases, depicted the response of woodland birds at the community level to the connectivity of agriculture-dominated landscapes.

On average, the sampled woodlands (n = 25) contained 15.5 ± 2.4 bird species, with an abundance of 25.1 ± 3.9, and had highly similar bird communities (species composition and proportion); eight species represented 57% of total abundance and were present in at least 22 woodlands. The performance of models improved when using effective, rather than Euclidean, interpatch distances in the connectivity assessment. Landscape connectivity was only significantly related to similarity of proportional species composition. Large woodlands contained communities with more similar species proportions in an inhospitable agricultural landscape matrix than in a more permeable one. Woodland size was the most relevant factor determining species abundance, indicating that the bird population sizes are primarily proportional to the local habitat availability. Connectivity in relation to landscape matrix permeability did not seem to induce the flow of woodland-dependent bird species that are dominant in the community but rather of matrix-dwelling bird species that are less dependent on woodland patch area. In conclusion, both habitat conservation and restoration (i.e., amount and quality), in combination with permeable landscape structures (such as heterogeneous land cover mosaics), are advocated for community level conservation strategies.

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INTRODUCTION

Land-use change has major impacts on the structure of communities (Sala et al. 2000), and might also influence ecosystem stability (resistance and resilience to environmental changes) (Cleland 2012). Since the 1980s, multi-scale ecological networks have been successfully deployed at the political and societal level, with the aim to reduce the rates of biodiversity declines in human-modified ecosystems (Jongman et al. 2004). Dispersal is recognized as a key ecological process for community composition and diversity (Kadoya 2009), and is largely dependent on landscape connectivity. Landscape connectivity represents the degree to which a given landscape facilitates or impedes the movement of organisms among habitat resources (Taylor et al. 1993). Therefore, the relevance of landscape connectivity for many ecological processes, and for biodiversity conservation, is widely acknowledged (Crooks and Sanjayan 2006, Kindlmann and Burel 2008). Different types of connectors among habitats (e.g., corridors, stepping stones) or the permeability of the landscape will allow the movement, or flow, of organisms, and sustain ecological processes that are fundamental for biodiversity persistence in ecosystems dominated and fragmented by human activities (Bennett et al. 2006).

More empirical data are needed to understand the influence of connectivity beyond the population level (Laitila and Moilanen 2013, Muratet et al. 2013). Previous studies have mostly focused on single species, and obtained contradictory results depending on the type of connector or species being considered (Hoyle and Gilbert 2004, Damschen et al. 2006, Baker 2007, Ockinger and Smith 2008). Yet, the outstanding importance of implementing corridors to protect biodiversity is universally agreed upon (Gilbert-Norton et al. 2010). However, species-specific responses to connectivity make difficult the deployment of effective planning schemes aimed at preserving overall biodiversity. Multi-species response to connectivity is rarely considered (but see Gil-Tena et al. 2013, Muratet et al. 2013) and accurate sampling protocols at the suitable scale are needed to obtain reliable data about the response of biological diversity to connectivity (e.g., controlling for other masking effects, such as patch area and edge effects; Smith et al. 2009).

The quantification of landscape connectivity represents a major and evolving challenge because landscape characteristics and species dispersal capabilities must be inferred (Taylor et al. 2006), since it is very difficult to measure species dispersal directly (Sutherland et al. 2000). A more permeable landscape matrix is expected to promote dispersal (Baum et al. 2004; Rösch et al. 2013). Landscape elements

composed of different types of permeable land cover have the potential to enhance connectivity and, ultimately, biodiversity in highly human modified systems (Watts et al. 2010), particularly from a community perspective (Gilbert-Norton et al. 2010). This interpretation advocates for a functional approach of landscape connectivity assessments rather than using connectivity measures that obviate species dispersal capabilities and/or matrix permeability (i.e., structural connectivity; Taylor et al. 2006, Kindlmann and Burel 2008). Hence, new improved connectivity methods have been recently developed that allow landscape connectivity pattern to be analyzed through graph theory indices, as well as from a species-specific (more functional) perspective by considering the dispersal capacity of species (Saura and Pascual-Hortal 2007, Saura and Torné 2009, Saura and Rubio 2010, Foltête et al. 2012). In addition, increasing awareness about the need to account for the capability of species to traverse different types of land covers in landscape connectivity assessment has led to the promotion of related analytical methodologies such as least-cost path modeling (Adriaensen et al. 2003, Rayfield et al. 2010, Gurrutxaga et al. 2011). Without excluding some level of uncertainty in matrix permeability modeling (McRae 2006, Rayfield et al. 2010), these methodological advances, combined with more functional analytical approaches, provide an opportunity to incorporate less biased criteria based on connectivity assessment in ecological network deployment.

In agriculture-dominated regions subject to protracted management, such as those in Europe, woodlands and forests represent semi-natural habitats, with a high degree of fragmentation, despite supporting a significant number of animal and plant species. Increasing agricultural intensification since 1960s has favored more open landscapes that are dominated by increasingly larger crop areas, resulting in the further loss of semi-natural habitats and associated components, which has had a consequent negative impact on farmland biodiversity (Benton et al. 2003). Hedgerows are a potential supplementary habitat for some woodland species in agriculture-dominated landscapes (Fuller et al. 2001, Davies and Pullin 2007). Yet, as a consequence of agricultural intensification and the associated landscape homogenization over the last century, the length of the hedgerow network surrounding crop fields, which characterizes the countryside of many European regions, has been also decreasing. Hedgerows have a recognized role as corridors for certain species (Haas 1995, Gilbert-Norton et al. 2010); hence, dispersal among woodland patches may be hampered due to reduced landscape matrix permeability among isolated woodlands.

In this study, we analyze the effect of landscape connectivity on bird alpha diversity, abundance and community similarity in the woodlands of the agriculture-dominated landscape of north-east Brittany in north-west France. We specifically assessed connectivity of the woodland and forest network in the study area through graph theory and matrix permeability modeling techniques, because they allowed for a functional landscape connectivity assessment. The role of connectivity may vary with woodland size since the presence of individuals and species in smaller woodlands may be more dependent on landscape connectivity than in larger ones (Rösch et al. 2013). Hence, an exhaustive selection protocol was carried out to minimize the effects of woodland size on the response variables. We explicitly tested factors that were likely to influence the landscape connectivity analysis, and the matrix permeability assessment, such as spatial grain and extent, and interpatch distance type (Euclidean or effective) (Fall et al. 2007, Pascual-Hortal and Saura 2007, Moilanen 2011). In addition, we also tested whether matrix permeability improved the modeling of bird alpha diversity, abundance, and bird community similarity. We expect a positive response of woodland bird community to landscape connectivity, with richer and more similar communities in more permeable landscapes, without ruling out the likely interaction with woodland size.

MATERIALS AND METHODS

Study area

The study area encompassed the Armorique *Zone Atelier* (Armorique ZA; ca., 13000 ha), which is located in NE Brittany, and is integrated in the LTER (Long Term Ecological Research) international network. Brittany is part of the Armorican Massif, which is composed of shale and granite bedrock, with loess deposits on the northern coast. The climate is oceanic, and the landscape is dominated by agriculture (with forested areas covering just 12% of the region), and is strongly influenced by intensive farming devoted to dairy cows, pigs, and poultry. The Armorique ZA is mainly a set of countryside agrosystems that have an extensive hedgerow network, a marshy region to the east in the Couesnon Valley, and the Villecartier forest to the south (Fig. 1). The typical landscape structure (or *bocage*) shows an increasing density gradient from north to south, with a denser hedgerow network in the southern Armorique ZA.

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Woodland selection and conceptual landscape model adopted

The initial land-use map that was used to determine which woodlands would be sampled in the Armorique ZA was obtained from a photointerpretation of aerial photography (French National Institute of Geographic and Forest Information) in combination with object based and remote sensing aerial classification by Rapideye satellite data collected during 2010. Six land-use categories were identified: crops, seminatural grasslands, managed grasslands, woodlands and forests, urban areas (e.g., villages), and water bodies. Moors and heathlands were not mapped because they are very rare in the region. The hedgerow network and roads were identified from the vector geographic database BDTopo® (2003–2006), which was produced by the French National Institute of Geographic and Forest Information.

To select woodlands for sampling, all woodlands that were separated by less than 25 m from the edges were first grouped as a single unique woodland area. As a result, 143 woodland and forest habitats (woodlands smaller than forests) were identified in the *Armorique* ZA. The average forest patch size is 2 ha. To minimize the size and edge effects on the response variables characterizing bird community, homogeneous woodland sample selection was conducted [woodland size ranged from 1 ha to 8 ha, with woodland compactness [perimeter (m) /size (m^2)] being set below the median (i.e., 0.04)]. Twenty-five woodlands (Fig. 1) were selected based on their naturalness and forest management homogeneity, which was confirmed through preliminary winter fieldwork. Habitat descriptors of the 25 selected woodlands were recorded, including descriptions of their age, canopy cover, and tree species richness. Woodland age was determined from ancient land cover maps (1862) and orthophotography in 1952, 1974, 1985, 1996, and 2004. We measured canopy cover and tree species richness in six 14×5 m squares placed in the core (3) and edges (3) of each woodland. Woodland core was defined as the central area 25 m from the edge (trees with diameter at the breast height greater than 10 cm). It was not possible to consider other habitat descriptors linked to forest management in the woodlands after telephone interviews with the owners, because of lack of data precision (all of the sampled woodlands were private, and managed to obtain firewood).

According to Fischer and Lindenmayer (2006) different conceptual landscape models can be applied to explain wildlife distributions (e.g., the fragmentation and the continuum model). The conceptual landscape model adopted for studying the bird community dwelling in woodlands of the agriculture-dominated landscape in NE Brittany was the fragmentation model. The fragmentation model assumes

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that: (1) there is a clear contrast between the human-defined habitat patches (woodlands) and areas outside the patches (agricultural landscape matrix); (2) the considered species within the woodland bird communities have similar habitat requirements (e.g., species nesting in woodlands); and (3) the landscape pattern is a good indicator of multiple interacting processes and for this reason we tested the role of landscape connectivity on bird community response.

Bird data collection

Bird species occurrence and abundance were estimated in each woodland using the point-count method (Bibby et al 1992, Ralph et al 1993). This method is similar to the North American Breeding Bird Survey and the British Constant Effort Sites Scheme (Sauer et al. 1997, Peach et al. 1998). A 5-min point count was conducted in the morning by the same observer (R.M.) approximately at the center of each woodland, under calm weather conditions, and all individual bird species that were seen or heard within a 100-m fixed radius were recorded. A hundred meter radius corresponds to the maximum distance where the greater bird species may be contacted in forest (Bibby et al., 1992), most species being detected in a circle of 50 meters centered on the counting point. Despite considering the most compact woodlands, variations in shape irregularity and size (1-8 ha) of the 25 selected woodland patches made distance from point count centers to woodland edges was about 75 m. When necessary, point count boundaries were established in order to record only birds inside woodlands (i.e., excluding open-country birds). Therefore, we assume that our protocol did not induce an excessive edge effect bias to estimate abundance and the compositional indices of the woodland bird communities from the smallest to the largest patches because woodland core and edges were well covered by the point count surface in all the cases, and particularly considering that woodlands were visited 3 times during the breeding season (April, May and June).
The species that were selected for analysis in this study were those that were characteristic of the woodlands in the region. Consequently, we excluded *Pica pica*, *Columba oenas*, and raptors (*Buteo buteo*) from the analysis. *Pica pica* is a farmland species rarely nesting inside woodlands, and *Columba oenas* is extremely rare in wood patches of our study area, recording only one case of presence without certainty of nesting. We remove *Buteo buteo* from data as its detection was more random than most of the singing passerine species and because the species often leaves wood patches at observers' arrival.

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For the sampled woodlands, we calculated: bird species richness and the total species maximum abundance across three visits during the breeding season. For each species in the sampled woodlands, maximum abundance (hereafter termed abundance) was computed from the number of visual and sound contacts with a species during each point count.

Similarity measures of the woodland bird community

We computed two different measures of community similarity. The first measure is based on traditional measures of spatial turnover, which are derived from three matching/mismatching components: continuity (the total number of species shared by two areas), gain (the number of species present in an area but absent from the focal area), and loss (the number of species present in the focal area but absent from the other area) (Gaston et al. 2007). For this study, we used the modified Simpson's index of beta diversity [a dissimilarity measure, D ($S = 1 - D$)], which quantifies the relative magnitude of the gains and losses of a given species [min(gain, loss)/(min(gain, loss) + continuity)] (Lennon et al. 2001). This measure allowed us to determine the true differences in species composition among sites (hereafter termed composition similarity), separating the influence on species composition due to local richness gradients (i.e., nestedness).

The other measure of similarity indicated the overlap among sampled woodlands in terms of proportional species composition (hereafter termed proportional similarity). The Morisita-Horn similarity index was computed because of its robustness against species richness, although it is highly sensitive to the abundance of the most abundant species (Wolda 1981, Magurran 2009). The index is presented as:

Proportional similarity = $2\Sigma(an_i * bn_i) / [(da + db)*(Na*Nb)]$,

where Na and Nb are the total number of individuals in site A and B, respectively, an_i and bn_i are the total number of individuals of ith species in site A and B, respectively, and da and db are $\Sigma an_i^2 / Na^2$ and $\Sigma bn_i^2 / Nb^2$, respectively.

Both similarity measures were computed from the corresponding dissimilarity matrices by the "vegan" package (Oksanen et al. 2013) in *R* (http://www.r-project.org). For each sampled woodland, we averaged the similarity values in comparison to the remaining sampled woodlands in the study area.

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Landscape connectivity assessment

From the land-use map and the hedgerow and road network, the landscape connectivity of the sampled woodlands was computed by graph theory using Conefor 2.6 (Saura and Torné 2009; http://www.conefor.org). Our connectivity measure for a given woodland patch k (dF^*_k) assessed the percentage of total dispersal flux among all woodland and forest patches in the landscape that occurs through the connections of patch k with all other patches in the landscape (when k is either the starting or ending patch of that connection or flux). dF^* is given by:

$$dF_k^* = \frac{\sum_{i=1, i\neq k}^{n-1} p_{ik}^*}{\sum_{i=1}^{n} \sum_{j=1, i\neq j}^{n} p_{ij}^*},$$

where p^*_{ij} is the maximum product probability of all possible paths between two patches, i and j, in the landscape, including direct and non-direct (facilitated by other intermediate patches functioning as stepping stones) dispersal between the two patches (Saura and Pascual-Hortal 2007).

The direct dispersal probabilities p_{ij} between habitat patches were computed by a negative exponential function of interpatch distance, which has been used in many published studies (Bunn et al. 2000, Urban and Keitt 2001, Saura and Pascual-Hortal 2007, Gurrutxaga et al. 2011). The interpatch distance was calculated as the Euclidean and effective distance between all woodland and forest patches in the study area. The decay rate of this negative exponential function was determined by the value of the median natal dispersal distance characteristic of the bird community recorded during the sampling period in the woodlands of the study area (Fig. 2), corresponding to $p_{ij} = 0.5$.

For these species, the geometric mean natal dispersal distances were extracted from the bird ringing data of the British Trust of Ornithology (Paradis et al. 1998). Data from Paradis et al. (1998) were available for 67% of the recorded bird species, and the median natal dispersal distance characteristic of the bird community in the woodlands of the study area was 1.3 km.

The Euclidean and effective (considering landscape matrix permeability) distances between each pair of habitat patches (including both sampled and unsampled woodlands and forests within the study area) were calculated with Graphab 1.0 software (Foltête et al. 2012; http://thema.univ-fcomte.fr/productions/graphab/). The effective distances between each pair of woodlands or forests

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(including sampled and unsampled habitats) were calculated as the accumulated cost along the least cost paths throughout friction surfaces (Adriaensen et al. 2003) (see Table 1). Although birds fly and are less sensitive to matrix permeability, in the connectivity assessment we specifically considered the matrix impedance of this agriculture-dominated landscape. Permeable landscape structures may encompass different types of landscape elements, such as stepping stones or heterogeneous land cover mosaics, which are more permeable for species movements (Baum et al. 2004, Rösch et al. 2013). Uncertainty is usually associated with the friction values for different land cover types (Rayfield et al. 2010); however, the friction values and habitat classification of this study were based on Watts et al. (2010), according to the degree of ecological modification of the vertical structure of different land cover types that might affect birds in woodlands. The study by Watts et al. (2010) was conducted in a similar agricultural context in the UK. In our case, the friction values correspond to a mathematical exponential function, with a maximum friction threshold of 50, which were very similar to those of Watts et al. (2010) based on expert criteria. Like Gurrutxaga et al. (2011), the characteristic median natal dispersal distance of the sampled bird community in the study area was multiplied by the statistical median value of resistance in the friction surface (Table 1). The result indicated the effective distance (accumulated cost) threshold corresponding to a 0.5 dispersal probability between nodes (p_{ij}) (Saura and Pascual-Hortal 2007).

The type of graph that is used might influence the computation of the connectivity metrics, and the understanding of the identified connectivity network (Fall et al. 2007), particularly when considering large spatial extents, fine spatial grains, and a large set of habitat patches or nodes. For instance, a complete graph, with paths between every pair of patches, provides a good ecological representation; however, it poses challenges for computational processing and visualization, particularly for planning purposes. In comparison, the minimum planar graph (Fall et al. 2007) is a spatial generalization of Delaunay triangulation in which only neighboring patches can be linked, and provides a reasonable approximation of the complete graph, while facilitating the visualization and comprehension of the connectivity network. In this study, we tested whether the use of a complete graph versus a minimum planar graph affects the modeling performance of community bird diversity, and abundance. For this purpose, we used Graphab 1.0, which allows different types of graph architectures to be computed. Hence, *dF** is adequate for testing the effect of the type of graph (complete graph *vs* minimum planar

graph), because it considers maximum product probabilities (direct and non-direct dispersal between two patches).

The effects of scale issues, such as spatial grain and extent, on the connectivity analysis are rarely considered in studies that rank landscape elements by their contribution to overall landscape connectivity (but see Pascual-Hortal and Saura 2007, Gil-Tena et al. 2013). In this study, spatial grain and extent was constrained by computational limitations. The finest spatial grain that was used to compute landscape connectivity was 2 m, which forced us to consider a maximum spatial extent of 3 km around the *Armorique* ZA (355 woodlands and forests; Fig. 1). In comparison, at a spatial grain of 10 m, the spatial extent considered was 5 km (429 woodlands and forests; Fig 1). Considering a larger spatial extent than the target one (e.g., Armorique ZA in this study) has been suggested as adequate when computing graph-based connectivity measures such as *dF** which do not take into account patch area (Pascual-Hortal and Saura 2007). The land-use map showing the different extents was obtained in the same manner as for the Armorique ZA extent, using the same aerial photography and satellite imagery.

Figure 3 provides a schematic representation of the various factors that were considered in the connectivity assessment using graph theory, in addition to the corresponding abbreviations of the nomenclature [also see the summary statistics of the connectivity values of the sampled woodlands (n = 25) in Table 2].

Data analysis

Ordinary Least Squares (OLS) regression was used to model bird species richness, species abundance, and the similarity in species composition (composition similarity) and in proportional species composition (proportional similarity) as a function of landscape connectivity. In all regression analyses, woodland characteristics (age, averaged canopy cover, and tree species richness) were also considered, and woodland size was always retained in the model due to differences in the size of the sampled woodlands (Table 2). In addition, the interaction between landscape connectivity and woodland size was tested in order to check if woodland bird community response to landscape connectivity depends on woodland size. A backward step-wise OLS model selection was performed to adjust the final OLS model. We checked the variance inflation factors in the OLS models, which were always under 1.4, indicating the absence of strong linear dependencies among the independent variables. To compare alternative *a*

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priori models, we used the information-theoretic model comparison approach based on second-order Akaike's Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002). All the statistical analyses were performed with the "MASS" package (Venables and Ripley 2002) in *R*. Spatial autocorrelation in the response variables and model residuals was checked through Moran's *I* by means of the "ape" package in *R* (Paradis et al. 2004).

RESULTS

In the 25 sampled woodlands, 30 bird species were recorded. On average, the sampled woodlands contained 15.48 bird species, with a mean abundance of 25.1 (Table 2). The bird species assemblages of the sampled woodlands also had highly similar species composition and proportional species composition (average values of 0.86 and 0.88, respectively) (Table 2). Eight bird species were found in almost all the sampled woodlands (*Phylloscopus collybita*, *Fringilla coelebs*, *Troglodytes troglodytes*, *Sylvia atricapilla*, *Columba palumbus*, *Erithacus rubecula*, *Turdus merula*, and *Cyanistes caeruleus* were present in at least 22 woodlands) and had a relative maximum abundance greater than 5% (5-11%, 57% in total), whereas the remaining 22 species were less frequent and abundant (10 species with less than 1% relative maximum abundance) (Fig. 2). Spatial autocorrelation in the bird community response variables was not significant ($p>0.05$, results not show).

Greater variability was obtained in the patch-level connectivity metric that did not take matrix resistance into account compared to that using the effective distances among woodlands and forests of the Armorique ZA (Fig. 4). This result was consistent across the two spatial extents that were considered (3 and 5 km). Connectivity values tended to be greater for the smallest spatial extent (i.e., 3 km). Similar patterns were observed in the sampled woodlands (n = 25; Table 2). For the sampled woodlands, we recorded similar connectivity measurements depending on the type of spatial resolution (2 and 10 m) and the type of graph (complete graph and minimum planar graph) (Wilcoxon test, $p > 0.05$). However, we demonstrated that spatial extent and the type of interpatch distance (Euclidean or effective) had a significant effect (Wilcoxon test, $p \leq 0.05$; results not shown).

The models of species richness and composition similarity were not significant ($p > 0.05$), whereas the models of proportional similarity and abundance were significant. The modeling of proportional similarity improved when the permeability of the agricultural matrix was taken into account in the

connectivity assessment, because all of the best regression models according to AICc were those that considered effective distances, rather than Euclidean distances (Table 3). In the best regression models (ΔAICc $\leq$ 2) for similarity in the proportion of bird species composition (proportional similarity), about 20% of the variability was explained (adjusted-R^2, Table 3). These models indicated that woodland size and connectivity accounting for matrix permeability had a similar influence on proportional similarity; woodland size positively influenced proportional similarity, whereas connectivity negatively influenced proportional similarity (Table 3). According to the best regression model (ΔAICc = 0), when woodland size remained constant, one unit increment in connectivity (CEf2m3km) decreased proportional similarity by 0.29 units, whereas 1 ha woodland increased proportional similarity by 0.007 units (Fig. 5). The model predicting species abundance had a determination coefficient of 0.18 (p = 0.02), and showed that bird abundance was only positively associated with woodland size (p = 0.02) (Table 3). Bird abundance nearly increased by 1 unit (0.987) with each 1 ha increment in woodland size. In any case, the interaction between landscape connectivity and woodland size nor spatial autocorrelation in model residuals were significant (p>0.05, results not show).

DISCUSSION

This study confirmed the relevance of using effective distances (i.e., considering the landscape matrix heterogeneity) for graph-based connectivity assessments aimed at explaining woodland bird community composition in an agriculture-dominated landscape. The agricultural matrix of the study area was dominated by crops and grasslands (Fig. 1); thus, more reliable measures were obtained when taking matrix permeability into account. We hypothesize that this result would be even more prominent for non-flying species, such as mammals, as previously shown at the species and population level (Gurrutxaga et al. 2011, Carranza et al. 2012, Decout et al. 2012), as well as for plants at the community level (Muratet et al. 2013).

Results did not support our main hypothesis, regarding the positive effect of connectivity on the response variables. The relatively small sample size (n = 25) might have influenced model significance (e.g., species richness and composition similarity). The alternative best models for species richness using the AICc approach were marginally significant (model p-value $\leq$ 0.1, with an adjusted-R^2 about of 0.16), and were not always conclusive regarding the positive effect of landscape connectivity (results not shown). In

revegetated urban patches in Australia, connectivity was shown to be the main factor explaining bird species richness, because more colonizers were able to reach more available habitat area (Shanahan et al. 2011). In agriculture-dominated landscapes, the disruption of matrix-dwelling species (e.g., species less dependent on woodland patch area to breed) cannot be excluded (Fuller et al. 2001, Ewers and Didham 2006), and might, ultimately, increase species richness in woodlands. The lack of model adjustment for the similarity of species composition might be related to the fact that bird communities in small woodlands might be similar to those of hedgerows (Fuller et al. 2001). In the Armorique ZA, hedgerow density increases from north to south, ranging from approximately 44 to 115 m/ha, respectively, with a total length of 575 km (Vannier 2012). This spatial heterogeneity in hedgerow density might prevent direct responses in composition similarity from being determined. In this study, we only controlled for the effect of woodland size (e.g., on species richness), because the influence of hedgerows was considered in the connectivity assessment when accounting for matrix permeability. In the specific case of composition similarity, a control for the influence of the hedgerow network would be preferred, but is not feasible at the extent of the current analysis, if woodland size is also considered. In addition, the assumptions taken when we selected the fragmentation model as landscape conceptual model may affect the obtained lack of landscape connectivity importance (Price et al. 2009). On the one hand, it is possible that the community-level approach might have masked some relationships, due to differences in the recorded species ecological traits (Ewers and Didham 2006, Batáry et al. 2012). On the other hand, averaged canopy cover of the selected woodlands finally ranged from 38 % to 91 % (with Q2 = 68 % and IQR = 20). This may affect woodland bird community composition, particularly the species more associated with more open canopy covers which are more sensitive to canopy closure (e.g. *Phyllocopus trochilus, Sylvia borin, Prunella modularis*; Hinsley et al. 2009), although canopy cover was not significant in any computed model.

Our most outstanding result was the negative effect of connectivity on the similarity of proportional species composition, which was only obtained when considering landscape matrix heterogeneity. This negative influence of connectivity on proportional species composition, together with the positive association with woodland size, might indicate that large woodlands contain more similar bird communities in an inhospitable matrix compared to those in a more permeable agricultural landscape matrix. Although the effect of landscape connectivity may be modulated by the amount of habitat (Rösch

et al. 2013), in this study the interaction between landscape connectivity and woodland size was not significant. This result may be partially due to the low size range of the selected woodlands and the focus on the smallest woodlands. Less dominant woodland bird species in the community (see Fig. 2) but highly dependent on landscape connectivity due to their sensitivity to woodland fragmentation in agriculture-dominated landscapes [e.g., *Sitta europaea* (Verboom et al. 1991)] or other specialists such as *Regulus ignicapilla* less dependent on woodland size (Tellería and Santos 1995), may contribute to community dissimilarity in permeable landscapes. Enhanced agricultural landscape matrix permeability might also produce an overlap between woodland bird species and matrix-dwelling species (Cook et al. 2002), which ultimately produces different proportions in the species composition of bird species that are typical of woodlands in the study area. Moreover, competition processes with species that have wider habitat breadths must be considered, as this phenomenon might also contribute to increase community dissimilarity. Competition and interactions with other species might be different at habitat edges compared to the interior, although the landscape context might buffer interspecific relationships (Ewers and Didham 2006). Therefore, we hypothesize that bird species that are less dependent on woodlands in agriculture-dominated landscapes are above all positively influenced by matrix permeability (Fuller et al. 2001, Batáry et al. 2012).

Assuming that edge effect biases on bird counts were negligible because woodland core and edges were fairly covered by the point count surface in all the cases (see details in the *Bird data collection* subsection in *Material and Methods*), woodland size was the only variable positively correlated with species abundance. This significant positive association supports the findings of Shanahan et al. (2011), who found that greater patch area, as well as connectivity, caused bird abundance to increase by expanding the habitat available to species that were already established in revegetated urban patches. In agriculture-dominated landscapes, small woodlands tend to have greater extents of edges, which might ultimately cause greater reproductive failure, due to increased exposure to potential nest predation (Ludwig et al. 2012); thus, negatively influencing bird abundance. The lack of association between landscape connectivity and bird abundance when using matrix permeability also suggests that a more permeable matrix does not moderate the edge effects on woodland species. This finding contradicts with previous literature (see Ewers and Didham 2006), but might indicate that abundant woodland bird species in the community are more sensitive to woodland size in agriculture-dominated landscapes compared to

agricultural landscape matrix permeability. For instance, Batáry et al. (2012) found that woodland bird species are more abundant at the forest edges, but are less abundant in hedges, while the inverse association was obtained for farmland birds.

Landscape connectivity influences the immigration and emigration of species, but does not affect other mechanisms that influence population dynamics, such as births and deaths, which are related to habitat availability or quality (Moilanen 2011). If woodland size is the main predictor of bird abundance in woodlands in agriculture-dominated landscapes, with connectivity appearing to be more related to the flow of less dominant or dependent bird woodland species, then rescue effects modulated by immigration might be hampered for bird species that are more dependent on woodlands in small and isolated woodlands. Therefore, more insights are needed into the role of landscape permeability to promote population viability according to species ecological traits (Davies and Pullin 2007). In addition, most of the measures favoring woodland bird species will not equally affect farmland birds, which are indeed more threatened than woodland birds, with significant declining population trends (Gregory et al. 2005) because of agricultural intensification (Donald et al. 2001). Whereas some specialist farmland birds need large extensions of open-habitat characterized by low intensity crop systems (Filippi-Codaccioni et al. 2010, Fischer et al. 2011), other farmland birds use woodlands as complementary habitats (Fuller et al. 2004). Particularly in the latter case, negative environmental changes affecting woodland birds will also negatively impact on farmland bird communities, such as the hedgerow removal, and the implementation of highly demanding crops with large patch size (e.g., maize; Houet et al. 2010) in the characteristic *bocage* landscape structure of the study area. New improved graph-based connectivity indices might help integrate and identify the different ways in which landscape elements contribute to habitat availability and connectivity (i.e., inter- and intrapatch connectivity; Saura and Rubio 2010). Results for different types of species with contrasted habitat requirements (e.g., woodland and farmland birds in agricultural landscapes) may be incorporated into decision support tools for landscape planning purposes. Apart from considering the immigration and emigration component of habitat use, these connectivity metrics also take into account the value of local resources in each patch to determine the effective amount of habitat that may be reached by a given species, with both aspects being integrated in a single analytical framework (Saura and Rubio 2010). Nevertheless, the sampling methodology used to monitor bird species dwelling in woodlands prevented us from being able to simultaneously consider other factors that

also affect the mechanisms involved in population viability because relatively small woodlands were sampled compared to the rest of the study area.

Our results also showed that computing connectivity through maximum probability indices, such as *dF**, could be accelerated by using minimum planar graphs (Fall et al. 2007). For the sampled woodlands, the different spatial extents in the connectivity assessment did not affect the modeling of the response variables. This finding might be partly due to a much larger extent than the study area being taken into account from the onset of the connectivity assessment, as recommended by Pascual-Hortal and Saura (2007). In any case, the spatial grain, which largely reduces the computational times required for connectivity assessments, had an effect with respect to the modelling approach and the magnitude of connectivity among the woodlands and forests in the study area (but see Pascual-Hortal and Saura 2007).

Conclusions

Identifying how landscape connectivity affects wildlife communities is a major concern, particularly with respect to global change, requiring the development of research strategies that obtain robust inferences. In this study, we demonstrated that connectivity assessment through graph-based methodologies that allow the ecological traits of species to be taken into account (e.g., habitat preferences and dispersal capacities) might represent a relatively unbiased technique for the deployment of ecological networks. These analytical advances are fundamental for the establishment of effective permeable landscape structures aimed at enhancing dispersal. The existing landscape matrix is fundamental for holistically preserving the biodiversity (e.g., at the community level) of agriculture-dominated landscapes. A combination of different landscape conceptual models beyond discrete habitat patches within a less inhabitable matrix might help optimize the community level approach (Price et al. 2009). In addition, new solutions have been recently developed for approximating multi-species community level dispersal (Laitila and Moilanen 2013). However, viable populations depend on both processes influenced by landscape connectivity (emigration and immigration) and habitat availability and quality (births and deaths). Therefore, these factors must also be incorporated into the analyses of management plans for the deployment (design and identification) of ecological networks, and particularly for specialist habitat species, for which landscape matrix permeability does not necessarily enhance the flow of individuals. For this purpose, new improved connectivity measures that are based on a combination of graph theory

and the habitat availability concept (Saura and Rubio 2010) should be particularly adequate as integrative analytical tools that operationally consider as many different factors as possible that influence population viability.

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TABLES

Table 1. Friction values used to model landscape matrix permeability based on the vertical structure of the land uses (see also Watts et al. 2010) in which the values corresponded to an exponential function with a maximum friction threshold of 50.

	Land cover type	*Friction value*
Decreasing permeability ↓	Woodlands and forests ≥ 1 ha	1
	Hedgerows and woodlands < 1 ha	2.57
	Semi-natural and managed grasslands	6.84
	Crops	18.4
	Water bodies and watercourses	18.4
	Artificial lands (urban areas and roads)	50

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Table 2. Summary statistics of the response variables characterizing woodland bird communities, the connectivity values according to the factors considered for connectivity assessment, and the other factors describing the sampled woodlands (n = 25). min: minimum value, max: maximum value, std: standard deviation. In order of appearance, the abbreviation of the connectivity metric indicates the type of graph computed (Complete and minimum planar graph, C and mpg, respectively), the consideration or not of the matrix heterogeneity [i.e., effective (Ef) or Euclidean (Eu) distances among forests and woodlands], the spatial resolution of the friction surface (2 and 10 m) and the spatial extent considered around the study area where the woodlands were sampled (3 and 5 km). * Information is not available for two woodlands.

		min	max	mean	Std
Descriptors of woodland bird community	Species richness	12.00	21.00	15.48	2.35
	Abundance	18.00	32.50	25.14	3.90
	Composition similarity	0.73	0.88	0.82	0.05
	Proportional similarity	0.74	0.86	0.82	0.03
Connectivity	CEf2m3km	0.52	0.67	0.60	0.04
	mpgEf2m3km	0.52	0.68	0.60	0.04
	CEf10m3km	0.53	0.68	0.61	0.04
	mpgEf10m3km	0.53	0.69	0.61	0.04
	CEu2m3km	0.39	0.86	0.64	0.11
	mpgEu2m3km	0.39	0.86	0.64	0.11
	CEu10m3km	0.38	0.87	0.64	0.12
	mpgEu10m3km	0.38	0.87	0.64	0.12
	CEf10m5km	0.44	0.56	0.51	0.04
	mpgEf10m5km	0.44	0.56	0.51	0.04
	CEu10m5km	0.32	0.73	0.55	0.09
	mpgEu10m5km	0.32	0.73	0.55	0.10
Habitat factors	Woodland size (ha)	1.13	8.01	2.97	1.81
	Age (years)*	10.00	150.00	83.04	51.30
	Tree species richness	3.00	14.00	10.04	2.73
	Averaged canopy cover (%)	38.33	90.83	64.60	15.26

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795
796
797 Table 3. Significant models of the factors behind woodland bird proportional similarity and abundance.
798 A backward step-wise variable selection was performed for each model in which woodland size was
799 always retained to avoid bias due to the different size of the sampled woodlands (1 – 8 ha). In the case of
800 the proportional similarity model, the independent variables were standardised to compare their respective
801 magnitude of influence. See abbreviations regarding the connectivity metric in Fig. 3. * p≤0.05, **
802 p≤0.01 and *** p≤0.001. Absence of significant spatial autocorrelation of model residuals was checked
803 through Moran's *I* (*p*>0.05).

Response variable	Parameter	Intercept and Estimate	AICc	adjusted-R^2	Model *p*
Proportional similarity		0.817***	-105.28	0.20	0.03
	woodland size	0.013*			
	CEf2m3km	-0.013*			
Proportional similarity		0.817***	-105.26	0.20	0.03
	woodland size	0.013*			
	mpgEf2m3km	-0.013*			
Proportional similarity		0.817***	-105.08	0.20	0.03
	woodland size	0.013*			
	CEf10m5km	-0.013*			
Proportional similarity		0.817***	-104.97	0.19	0.04
	woodland size	0.013*			
	CEf10m3km	-0.013*			
Proportional similarity		0.817***	-104.93	0.19	0.04
	woodland size	0.013*			
	mpgEf10m5km	-0.012*			
Proportional similarity		0.817***	-104.85	0.19	0.04
	woodland size	0.013*			
	mpgEf10m3km	-0.012*			
Proportional similarity		0.817***	-102.41	0.06	0.12
	woodland size	0.009*			
Abundance		22.21***		0.18	0.02
	woodland size	0.987*			

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FIGURE CAPTIONS

Figure 1. Geographic location of the study area (north-east Brittany in north-west France) (left) and representation of the land uses in the study area (*Armorique* ZA) and the sampled woodlands (dots; *n* = 25) within the different extents used to compute connectivity measures (right). The land uses shown correspond to the categories of the friction values (see Table 1).

Figure 2. Increasingly ranked relative maximum abundance of the bird species pool of the woodlands in the study area. Bird species occurrence in the sampled woodlands (*n* = 25) is also shown. For each species recorded and all the sampled woodlands of the study area, the relative maximum abundance (%) was computed from the sum of the maximum abundance for each species during the three visits in the breeding season regarding the sum of the maximum abundance for all the species. Geometric mean natal dispersal (km) according to Paradis et al. (1998) is shown in brackets when available.

Figure 3. Factors considered in the connectivity assessment through graph theory. Abbreviations in brackets comprise the nomenclature of the connectivity measure and represent, in order of appearance, the type of graph computed (C / mpg), the consideration or not of the matrix heterogeneity (Eu / Ef), the spatial grain of the friction surface (2m / 10 m) and the spatial extent considered around the study area where the woodlands were sampled (3km / 5km).

Figure 4: Boxplot of the connectivity values according to the different factors considered to compute graph-based connectivity in the 143 woodlands and forests (≥ 1 ha) within the study area (the thickest edge represented in Fig. 1). See abbreviations regarding the connectivity metric in Figure 3.

Figure 5. Response curves of the top regression model according to the AICc approach for similarity in terms of proportional species composition (Table 3). Independent variables were not standardised and each time the unrepresented predictor [connectivity (CEf2m3km) above and woodland size below, respectively] was set constant (mean value).

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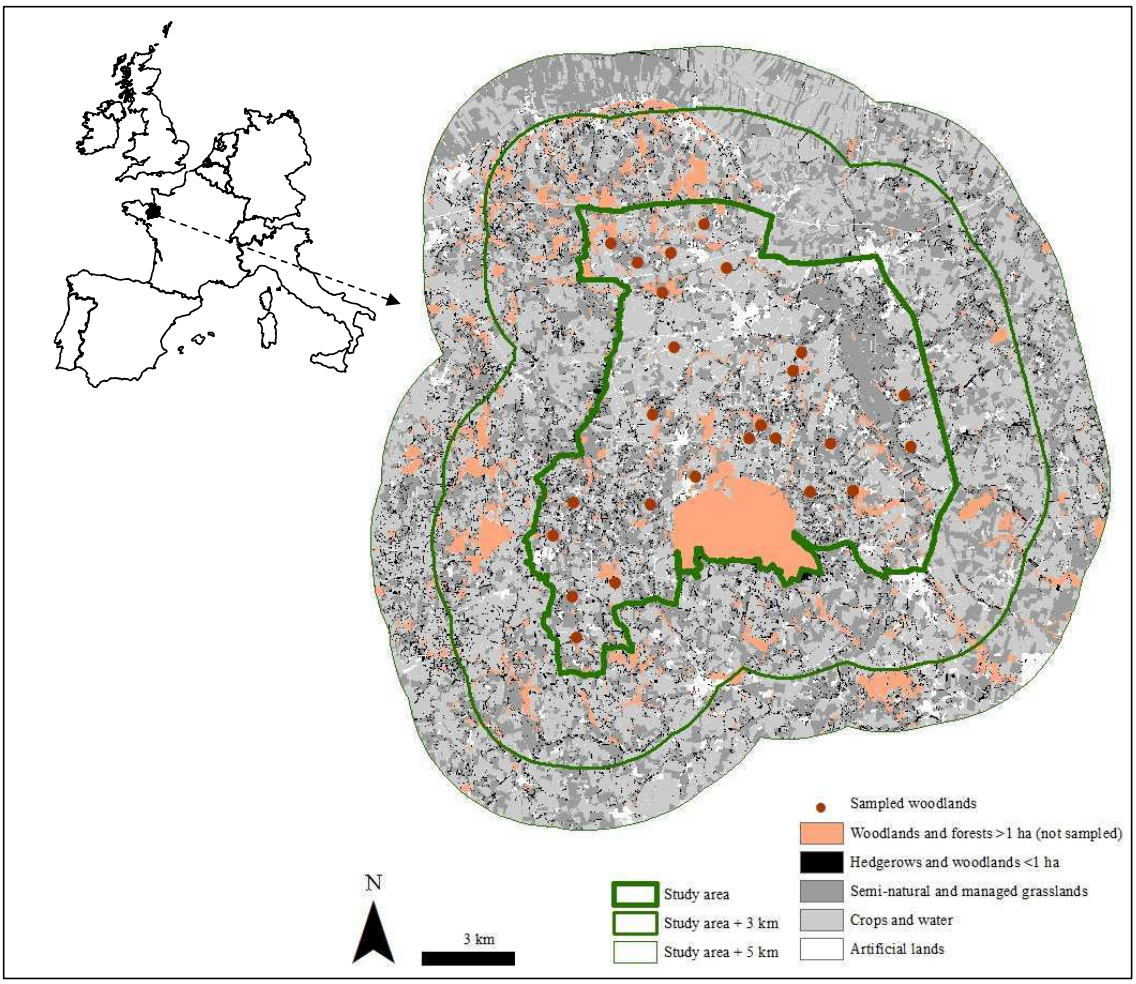

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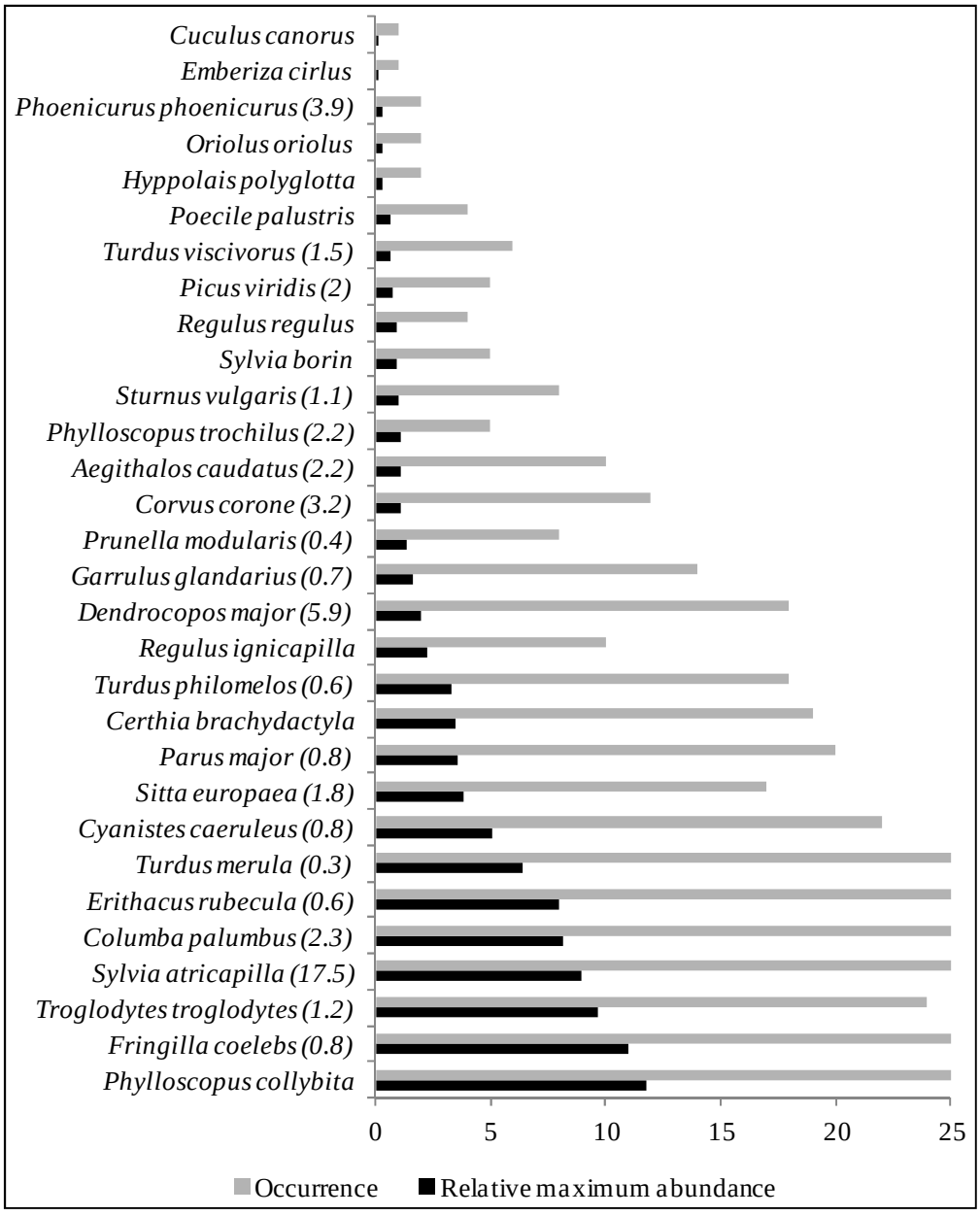

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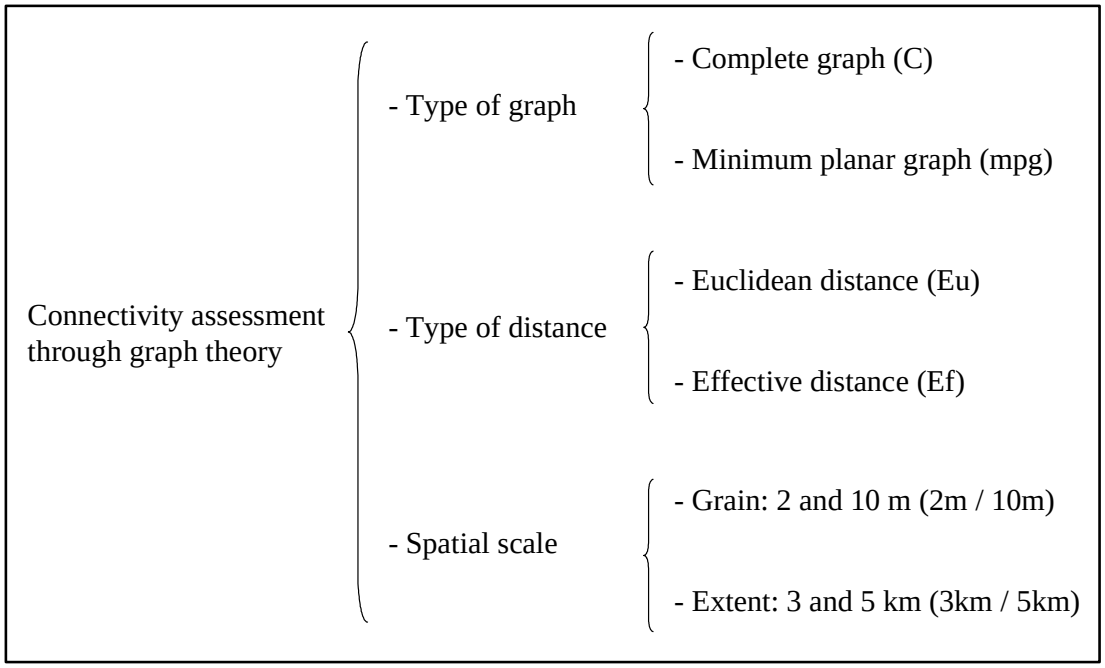

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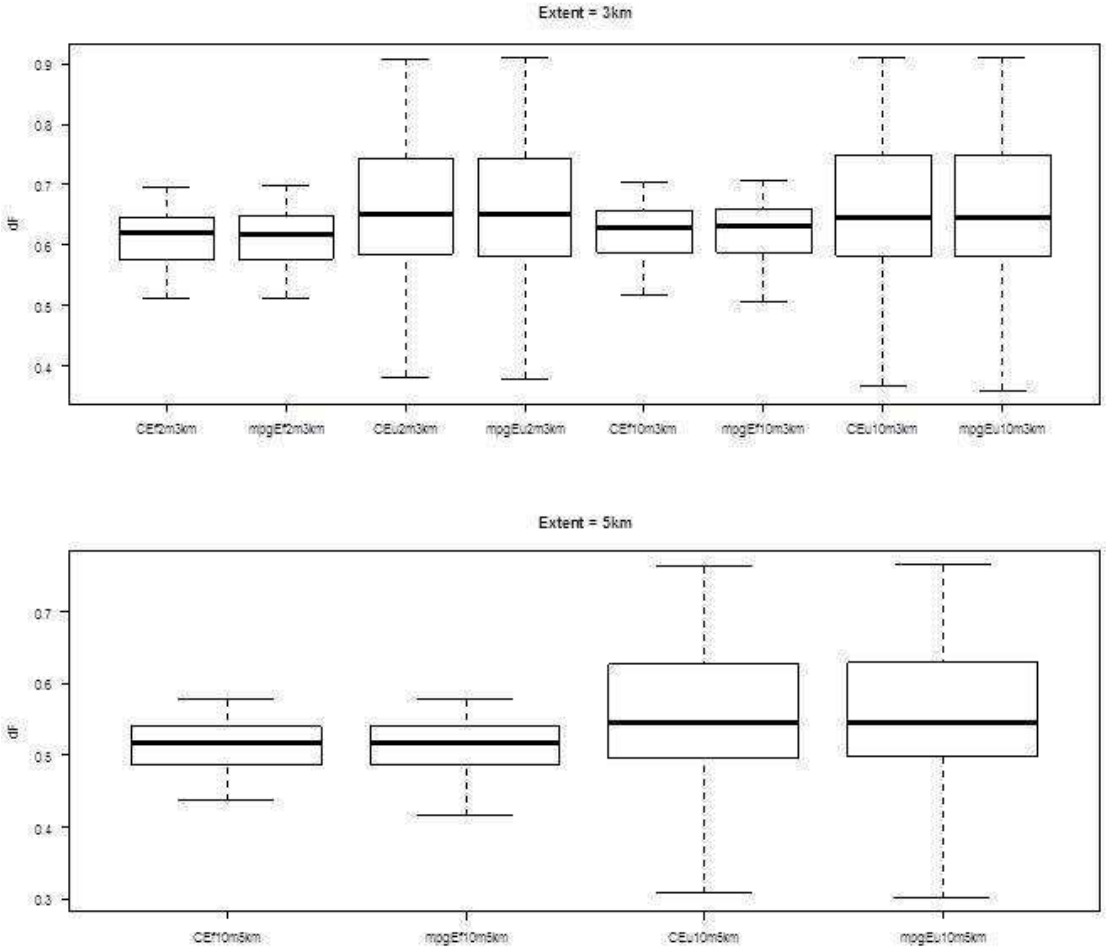

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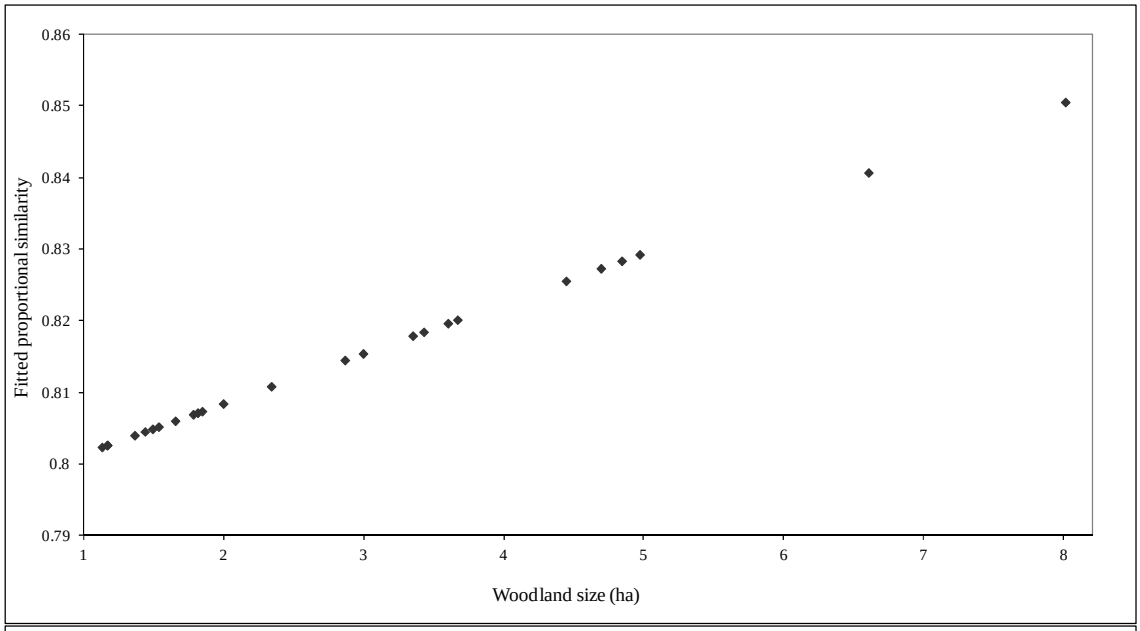

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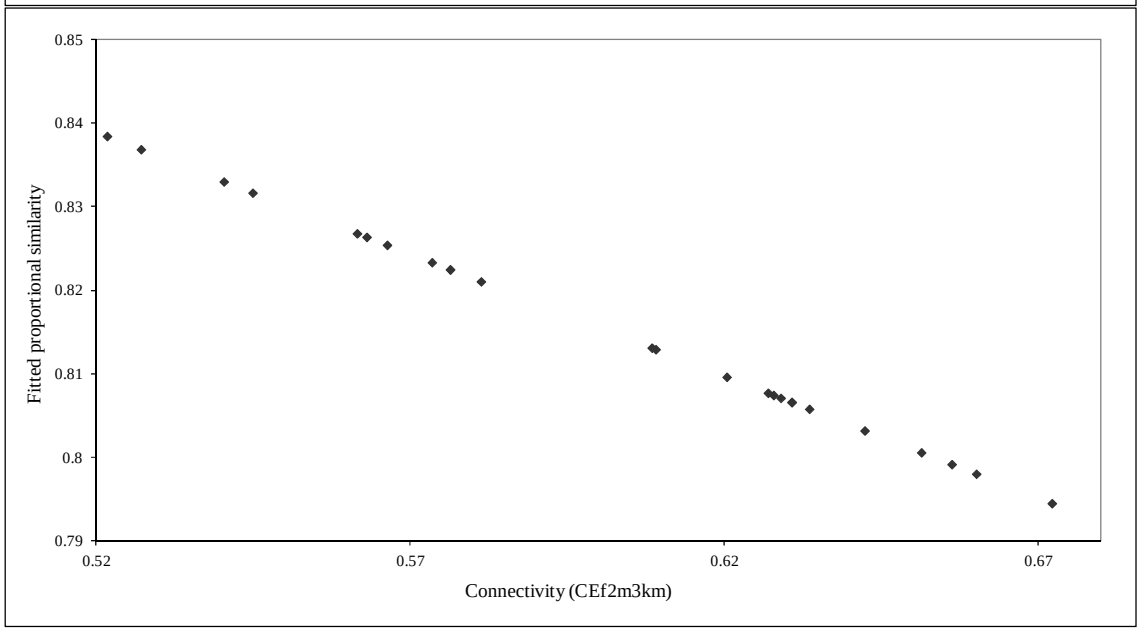

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