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### ► To cite this version:

Assu Gil-Tena, Jean Nabucet, Cendrine Mony, Julie Abadie, S. Saura, et al.. Woodland bird response to landscape connectivity in an agriculture-dominated landscape: a functional community approach. *Community Ecology*, 2014, 15 (2), pp.256 - 268. 10.1556/ComEc.15.2014.2.14 . hal-01090613

**HAL Id: hal-01090613**

**<https://univ-rennes.hal.science/hal-01090613>**

Submitted on 3 Dec 2014

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2 TITLE PAGE

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4 Woodland bird response to landscape connectivity in an agriculture-dominated landscape: a functional  
5 community approach

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7 Running title: Woodland bird response to connectivity

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28 Keywords: alpha diversity, Brittany, community similarity, CONEFOR, ecological networks,

29 GRAPHAB, landscape matrix permeability, spatial scale

30

31 ABSTRACT

32 Over the last 30 years, ecological networks have been deployed to reduce global biodiversity loss by

33 enhancing landscape connectivity. Bird species dwelling in woodland habitats that are embedded in

34 agriculture-dominated landscapes are expected to be particularly sensitive to the loss of connectivity. This

35 study aimed to determine the role of landscape connectivity in woodland bird species richness,

36 abundance, and community similarity in north-east Brittany (north-west France). An exhaustive woodland

37 selection protocol was carried out to minimize the effects of woodland size on the response variables.

38 Connectivity of the woodland and forest network in the study area was evaluated using graph-theory,

39 accounting for matrix permeability, and a characteristic median natal dispersal distance at the community

40 level based on the bird species pool recorded in the sampled woodlands. Information-theoretic model

41 selection, controlling for woodland size in all the cases, depicted the response of woodland birds at the

42 community level to the connectivity of agriculture-dominated landscapes.

43 On average, the sampled woodlands ( $n = 25$ ) contained  $15.5 \pm 2.4$  bird species, with an abundance of  $25.1$

44  $\pm 3.9$ , and had highly similar bird communities (species composition and proportion); eight species

45 represented 57% of total abundance and were present in at least 22 woodlands. The performance of

46 models improved when using effective, rather than Euclidean, interpatch distances in the connectivity

47 assessment. Landscape connectivity was only significantly related to similarity of proportional species

48 composition. Large woodlands contained communities with more similar species proportions in an

49 inhospitable agricultural landscape matrix than in a more permeable one. Woodland size was the most

50 relevant factor determining species abundance, indicating that the bird population sizes are primarily

51 proportional to the local habitat availability. Connectivity in relation to landscape matrix permeability did

52 not seem to induce the flow of woodland-dependent bird species that are dominant in the community but

53 rather of matrix-dwelling bird species that are less dependent on woodland patch area. In conclusion, both

54 habitat conservation and restoration (i.e., amount and quality), in combination with permeable landscape

55 structures (such as heterogeneous land cover mosaics), are advocated for community level conservation

56 strategies.

57 INTRODUCTION

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

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

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

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

102 In agriculture-dominated regions subject to protracted management, such as those in Europe, woodlands  
103 and forests represent semi-natural habitats, with a high degree of fragmentation, despite supporting a  
104 significant number of animal and plant species. Increasing agricultural intensification since 1960s has  
105 favored more open landscapes that are dominated by increasingly larger crop areas, resulting in the  
106 further loss of semi-natural habitats and associated components, which has had a consequent negative  
107 impact on farmland biodiversity (Benton et al. 2003). Hedgerows are a potential supplementary habitat  
108 for some woodland species in agriculture-dominated landscapes (Fuller et al. 2001, Davies and Pullin  
109 2007). Yet, as a consequence of agricultural intensification and the associated landscape homogenization  
110 over the last century, the length of the hedgerow network surrounding crop fields, which characterizes the  
111 countryside of many European regions, has been also decreasing. Hedgerows have a recognized role as  
112 corridors for certain species (Haas 1995, Gilbert-Norton et al. 2010); hence, dispersal among woodland  
113 patches may be hampered due to reduced landscape matrix permeability among isolated woodlands.

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

128

## 129 MATERIALS AND METHODS

### 130 *Study area*

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

140

141

142

143 *Woodland selection and conceptual landscape model adopted*

144 The initial land-use map that was used to determine which woodlands would be sampled in the  
145 Armorique ZA was obtained from a photointerpretation of aerial photography (French National Institute  
146 of Geographic and Forest Information) in combination with object based and remote sensing aerial  
147 classification by Rapideye satellite data collected during 2010. Six land-use categories were identified:  
148 crops, seminatural grasslands, managed grasslands, woodlands and forests, urban areas (e.g., villages),  
149 and water bodies. Moors and heathlands were not mapped because they are very rare in the region. The  
150 hedgerow network and roads were identified from the vector geographic database BDTopo® (2003–  
151 2006), which was produced by the French National Institute of Geographic and Forest Information.  
152 To select woodlands for sampling, all woodlands that were separated by less than 25 m from the edges  
153 were first grouped as a single unique woodland area. As a result, 143 woodland and forest habitats  
154 (woodlands smaller than forests) were identified in the *Armorique* ZA. The average forest patch size is 2  
155 ha. To minimize the size and edge effects on the response variables characterizing bird community,  
156 homogeneous woodland sample selection was conducted [woodland size ranged from 1 ha to 8 ha, with  
157 woodland compactness [perimeter (m) /size (m<sup>2</sup>)] being set below the median (i.e., 0.04)]. Twenty-five  
158 woodlands (Fig. 1) were selected based on their naturalness and forest management homogeneity, which  
159 was confirmed through preliminary winter fieldwork. Habitat descriptors of the 25 selected woodlands  
160 were recorded, including descriptions of their age, canopy cover, and tree species richness. Woodland age  
161 was determined from ancient land cover maps (1862) and orthophotography in 1952, 1974, 1985, 1996,  
162 and 2004. We measured canopy cover and tree species richness in six 14×5 m squares placed in the core  
163 (3) and edges (3) of each woodland. Woodland core was defined as the central area 25 m from the edge  
164 (trees with diameter at the breast height greater than 10 cm). It was not possible to consider other habitat  
165 descriptors linked to forest management in the woodlands after telephone interviews with the owners,  
166 because of lack of data precision (all of the sampled woodlands were private, and managed to obtain  
167 firewood).

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

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

177

#### 178 *Bird data collection*

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



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

204

#### 205 *Similarity measures of the woodland bird community*

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

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

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

221 where  $Na$  and  $Nb$  are the total number of individuals in site  $A$  and  $B$ , respectively,  $an_i$  and  $bn_i$  are the total  
222 number of individuals of  $i$ th species in site  $A$  and  $B$ , respectively, and  $da$  and  $db$  are  $\sum an_i^2 / Na^2$  and  $\sum bn_i^2$   
223  $/ Nb^2$ , respectively.

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

227

228

229 *Landscape connectivity assessment*

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

$$236 \quad dF_k^* = \frac{\sum_{i=1, i \neq k}^{n-1} p_{ik}^*}{\sum_{i=1}^n \sum_{j=1, i \neq j}^n p_{ij}^*},$$

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

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

247 For these species, the geometric mean natal dispersal distances were extracted from the bird ringing data  
248 of the British Trust of Ornithology (Paradis et al. 1998). Data from Paradis et al. (1998) were available for  
249 67% of the recorded bird species, and the median natal dispersal distance characteristic of the bird  
250 community in the woodlands of the study area was 1.3 km.

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

255 (including sampled and unsampled habitats) were calculated as the accumulated cost along the least cost  
256 paths throughout friction surfaces (Adriaensen et al. 2003) (see Table 1). Although birds fly and are less  
257 sensitive to matrix permeability, in the connectivity assessment we specifically considered the matrix  
258 impedance of this agriculture-dominated landscape. Permeable landscape structures may encompass  
259 different types of landscape elements, such as stepping stones or heterogeneous land cover mosaics,  
260 which are more permeable for species movements (Baum et al. 2004, Rösch et al. 2013). Uncertainty is  
261 usually associated with the friction values for different land cover types (Rayfield et al. 2010); however,  
262 the friction values and habitat classification of this study were based on Watts et al. (2010), according to  
263 the degree of ecological modification of the vertical structure of different land cover types that might  
264 affect birds in woodlands. The study by Watts et al. (2010) was conducted in a similar agricultural context  
265 in the UK. In our case, the friction values correspond to a mathematical exponential function, with a  
266 maximum friction threshold of 50, which were very similar to those of Watts et al. (2010) based on expert  
267 criteria. Like Gurrutxaga et al. (2011), the characteristic median natal dispersal distance of the sampled  
268 bird community in the study area was multiplied by the statistical median value of resistance in the  
269 friction surface (Table 1). The result indicated the effective distance (accumulated cost) threshold  
270 corresponding to a 0.5 dispersal probability between nodes ( $p_{ij}$ ) (Saura and Pascual-Hortal 2007).  
271 The type of graph that is used might influence the computation of the connectivity metrics, and the  
272 understanding of the identified connectivity network (Fall et al. 2007), particularly when considering  
273 large spatial extents, fine spatial grains, and a large set of habitat patches or nodes. For instance, a  
274 complete graph, with paths between every pair of patches, provides a good ecological representation;  
275 however, it poses challenges for computational processing and visualization, particularly for planning  
276 purposes. In comparison, the minimum planar graph (Fall et al. 2007) is a spatial generalization of  
277 Delaunay triangulation in which only neighboring patches can be linked, and provides a reasonable  
278 approximation of the complete graph, while facilitating the visualization and comprehension of the  
279 connectivity network. In this study, we tested whether the use of a complete graph versus a minimum  
280 planar graph affects the modeling performance of community bird diversity, and abundance. For this  
281 purpose, we used Graphab 1.0, which allows different types of graph architectures to be computed.  
282 Hence,  $dF^*$  is adequate for testing the effect of the type of graph (complete graph vs minimum planar

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

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

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

300

### 301 *Data analysis*

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

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

317

## 318 RESULTS

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

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

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

341 connectivity assessment, because all of the best regression models according to AICc were those that  
342 considered effective distances, rather than Euclidean distances (Table 3). In the best regression models  
343 ( $\Delta\text{AICc} \leq 2$ ) for similarity in the proportion of bird species composition (proportional similarity), about  
344 20% of the variability was explained (adjusted- $R^2$ , Table 3). These models indicated that woodland size  
345 and connectivity accounting for matrix permeability had a similar influence on proportional similarity;  
346 woodland size positively influenced proportional similarity, whereas connectivity negatively influenced  
347 proportional similarity (Table 3). According to the best regression model ( $\Delta\text{AICc} = 0$ ), when woodland  
348 size remained constant, one unit increment in connectivity (CEf2m3km) decreased proportional similarity  
349 by 0.29 units, whereas 1 ha woodland increased proportional similarity by 0.007 units (Fig. 5). The model  
350 predicting species abundance had a determination coefficient of 0.18 ( $p = 0.02$ ), and showed that bird  
351 abundance was only positively associated with woodland size ( $p = 0.02$ ) (Table 3). Bird abundance nearly  
352 increased by 1 unit (0.987) with each 1 ha increment in woodland size. In any case, the interaction  
353 between landscape connectivity and woodland size nor spatial autocorrelation in model residuals were  
354 significant ( $p > 0.05$ , results not show).

355

## 356 DISCUSSION

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

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

370 revegetated urban patches in Australia, connectivity was shown to be the main factor explaining bird  
371 species richness, because more colonizers were able to reach more available habitat area (Shanahan et al.  
372 2011). In agriculture-dominated landscapes, the disruption of matrix-dwelling species (e.g., species less  
373 dependent on woodland patch area to breed) cannot be excluded (Fuller et al. 2001, Ewers and Didham  
374 2006), and might, ultimately, increase species richness in woodlands. The lack of model adjustment for  
375 the similarity of species composition might be related to the fact that bird communities in small  
376 woodlands might be similar to those of hedgerows (Fuller et al. 2001). In the Armorique ZA, hedgerow  
377 density increases from north to south, ranging from approximately 44 to 115 m/ha, respectively, with a  
378 total length of 575 km (Vannier 2012). This spatial heterogeneity in hedgerow density might prevent  
379 direct responses in composition similarity from being determined. In this study, we only controlled for the  
380 effect of woodland size (e.g., on species richness), because the influence of hedgerows was considered in  
381 the connectivity assessment when accounting for matrix permeability. In the specific case of composition  
382 similarity, a control for the influence of the hedgerow network would be preferred, but is not feasible at  
383 the extent of the current analysis, if woodland size is also considered. In addition, the assumptions taken  
384 when we selected the fragmentation model as landscape conceptual model may affect the obtained lack of  
385 landscape connectivity importance (Price et al. 2009). On the one hand, it is possible that the community-  
386 level approach might have masked some relationships, due to differences in the recorded species  
387 ecological traits (Ewers and Didham 2006, Batáry et al. 2012). On the other hand, averaged canopy cover  
388 of the selected woodlands finally ranged from 38 % to 91 % (with Q2 = 68 % and IQR = 20). This may  
389 affect woodland bird community composition, particularly the species more associated with more open  
390 canopy covers which are more sensitive to canopy closure (e.g. *Phylloscopus trochilus*, *Sylvia borin*,  
391 *Prunella modularis*; Hinsley et al. 2009), although canopy cover was not significant in any computed  
392 model.

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

399 et al. 2013), in this study the interaction between landscape connectivity and woodland size was not  
400 significant. This result may be partially due to the low size range of the selected woodlands and the focus  
401 on the smallest woodlands. Less dominant woodland bird species in the community (see Fig. 2) but  
402 highly dependent on landscape connectivity due to their sensitivity to woodland fragmentation in  
403 agriculture-dominated landscapes [e.g., *Sitta europaea* (Verboom et al. 1991)] or other specialists such as  
404 *Regulus ignicapilla* less dependent on woodland size (Tellería and Santos 1995), may contribute to  
405 community dissimilarity in permeable landscapes. Enhanced agricultural landscape matrix permeability  
406 might also produce an overlap between woodland bird species and matrix-dwelling species (Cook et al.  
407 2002), which ultimately produces different proportions in the species composition of bird species that are  
408 typical of woodlands in the study area. Moreover, competition processes with species that have wider  
409 habitat breadths must be considered, as this phenomenon might also contribute to increase community  
410 dissimilarity. Competition and interactions with other species might be different at habitat edges  
411 compared to the interior, although the landscape context might buffer interspecific relationships (Ewers  
412 and Didham 2006). Therefore, we hypothesize that bird species that are less dependent on woodlands in  
413 agriculture-dominated landscapes are above all positively influenced by matrix permeability (Fuller et al.  
414 2001, Batáry et al. 2012).

415 Assuming that edge effect biases on bird counts were negligible because woodland core and edges were  
416 fairly covered by the point count surface in all the cases (see details in the *Bird data collection* subsection  
417 in *Material and Methods*), woodland size was the only variable positively correlated with species  
418 abundance. This significant positive association supports the findings of Shanahan et al. (2011), who  
419 found that greater patch area, as well as connectivity, caused bird abundance to increase by expanding the  
420 habitat available to species that were already established in revegetated urban patches. In agriculture-  
421 dominated landscapes, small woodlands tend to have greater extents of edges, which might ultimately  
422 cause greater reproductive failure, due to increased exposure to potential nest predation (Ludwig et al.  
423 2012); thus, negatively influencing bird abundance. The lack of association between landscape  
424 connectivity and bird abundance when using matrix permeability also suggests that a more permeable  
425 matrix does not moderate the edge effects on woodland species. This finding contradicts with previous  
426 literature (see Ewers and Didham 2006), but might indicate that abundant woodland bird species in the  
427 community are more sensitive to woodland size in agriculture-dominated landscapes compared to



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

431 Landscape connectivity influences the immigration and emigration of species, but does not affect other  
432 mechanisms that influence population dynamics, such as births and deaths, which are related to habitat  
433 availability or quality (Moilanen 2011). If woodland size is the main predictor of bird abundance in  
434 woodlands in agriculture-dominated landscapes, with connectivity appearing to be more related to the  
435 flow of less dominant or dependent bird woodland species, then rescue effects modulated by immigration  
436 might be hampered for bird species that are more dependent on woodlands in small and isolated  
437 woodlands. Therefore, more insights are needed into the role of landscape permeability to promote  
438 population viability according to species ecological traits (Davies and Pullin 2007). In addition, most of  
439 the measures favoring woodland bird species will not equally affect farmland birds, which are indeed  
440 more threatened than woodland birds, with significant declining population trends (Gregory et al. 2005)  
441 because of agricultural intensification (Donald et al. 2001). Whereas some specialist farmland birds need  
442 large extensions of open-habitat characterized by low intensity crop systems (Filippi-Codaccioni et al.  
443 2010, Fischer et al. 2011), other farmland birds use woodlands as complementary habitats (Fuller et al.  
444 2004). Particularly in the latter case, negative environmental changes affecting woodland birds will also  
445 negatively impact on farmland bird communities, such as the hedgerow removal, and the implementation  
446 of highly demanding crops with large patch size (e.g., maize; Houet et al. 2010) in the characteristic  
447 *bocage* landscape structure of the study area. New improved graph-based connectivity indices might help  
448 integrate and identify the different ways in which landscape elements contribute to habitat availability and  
449 connectivity (i.e., inter- and intrapatch connectivity; Saura and Rubio 2010). Results for different types of  
450 species with contrasted habitat requirements (e.g., woodland and farmland birds in agricultural  
451 landscapes) may be incorporated into decision support tools for landscape planning purposes. Apart from  
452 considering the immigration and emigration component of habitat use, these connectivity metrics also  
453 take into account the value of local resources in each patch to determine the effective amount of habitat  
454 that may be reached by a given species, with both aspects being integrated in a single analytical  
455 framework (Saura and Rubio 2010). Nevertheless, the sampling methodology used to monitor bird  
456 species dwelling in woodlands prevented us from being able to simultaneously consider other factors that

457 also affect the mechanisms involved in population viability because relatively small woodlands were  
458 sampled compared to the rest of the study area.  
459 Our results also showed that computing connectivity through maximum probability indices, such as  $dF^*$ ,  
460 could be accelerated by using minimum planar graphs (Fall et al. 2007). For the sampled woodlands, the  
461 different spatial extents in the connectivity assessment did not affect the modeling of the response  
462 variables. This finding might be partly due to a much larger extent than the study area being taken into  
463 account from the onset of the connectivity assessment, as recommended by Pascual-Hortal and Saura  
464 (2007). In any case, the spatial grain, which largely reduces the computational times required for  
465 connectivity assessments, had an effect with respect to the modelling approach and the magnitude of  
466 connectivity among the woodlands and forests in the study area (but see Pascual-Hortal and Saura 2007).

467

#### 468 *Conclusions*

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

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

489

#### 490 ACKNOWLEDGEMENTS

491 Thanks to Régis Morel (*Bretagne Vivante*) who has carried out the bird censuses and Doriane Moisan  
492 who helped in woodland inventories. We also want to thank two anonymous reviewers and Péter Batáry  
493 for improving a previous version of this manuscript. This work has received a financial support from the  
494 project DIVA 3 - AGRICONNECT (*Continuités écologiques dans les paysages agricoles*) funded by the  
495 *Ministère de l'Ecologie et du Développement Durable* (France). This work was also framed within the  
496 DECOFOR (AGL2009-07140) project (Spanish Government and the European fund for regional  
497 development). Rapideye imagery was furnished by GEOSUD. A. Gil-Tena was funded by the *Ministerio*  
498 *de Educación (Programa Nacional de Movilidad de RRHH, Plan Nacional de I+D+i 2008-2011, Spain)*.

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724 Wolda, H. 1981. Similarity indices, sample size and diversity. *Oecologia* 50: 296-302.

725 TABLES

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

|                           | <i>Land cover type</i>                   | <i>Friction value</i> |
|---------------------------|--|-----------------------|
| 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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 771 Table 2. Summary statistics of the response variables characterizing woodland bird communities, the  
 772 connectivity values according to the factors considered for connectivity assessment, and the other factors  
 773 describing the sampled woodlands ( $n = 25$ ). min: minimum value, max: maximum value, std: standard  
 774 deviation. In order of appearance, the abbreviation of the connectivity metric indicates the type of graph  
 775 computed (Complete and minimum planar graph, C and mpg, respectively), the consideration or not of  
 776 the matrix heterogeneity [i.e., effective (Ef) or Euclidean (Eu) distances among forests and woodlands],  
 777 the spatial resolution of the friction surface (2 and 10 m) and the spatial extent considered around the  
 778 study area where the woodlands were sampled (3 and 5 km). \* Information is not available for two  
 779 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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Table 3. Significant models of the factors behind woodland bird proportional similarity and abundance.

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A backward step-wise variable selection was performed for each model in which woodland size was

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always retained to avoid bias due to the different size of the sampled woodlands (1 – 8 ha). In the case of

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the proportional similarity model, the independent variables were standardised to compare their respective

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magnitude of influence. See abbreviations regarding the connectivity metric in Fig. 3. \*  $p \leq 0.05$ , \*\*

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$p \leq 0.01$  and \*\*\*  $p \leq 0.001$ . Absence of significant spatial autocorrelation of model residuals was checked

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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*                 |         |                 |           |

804 FIGURE CAPTIONS

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

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

816

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

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

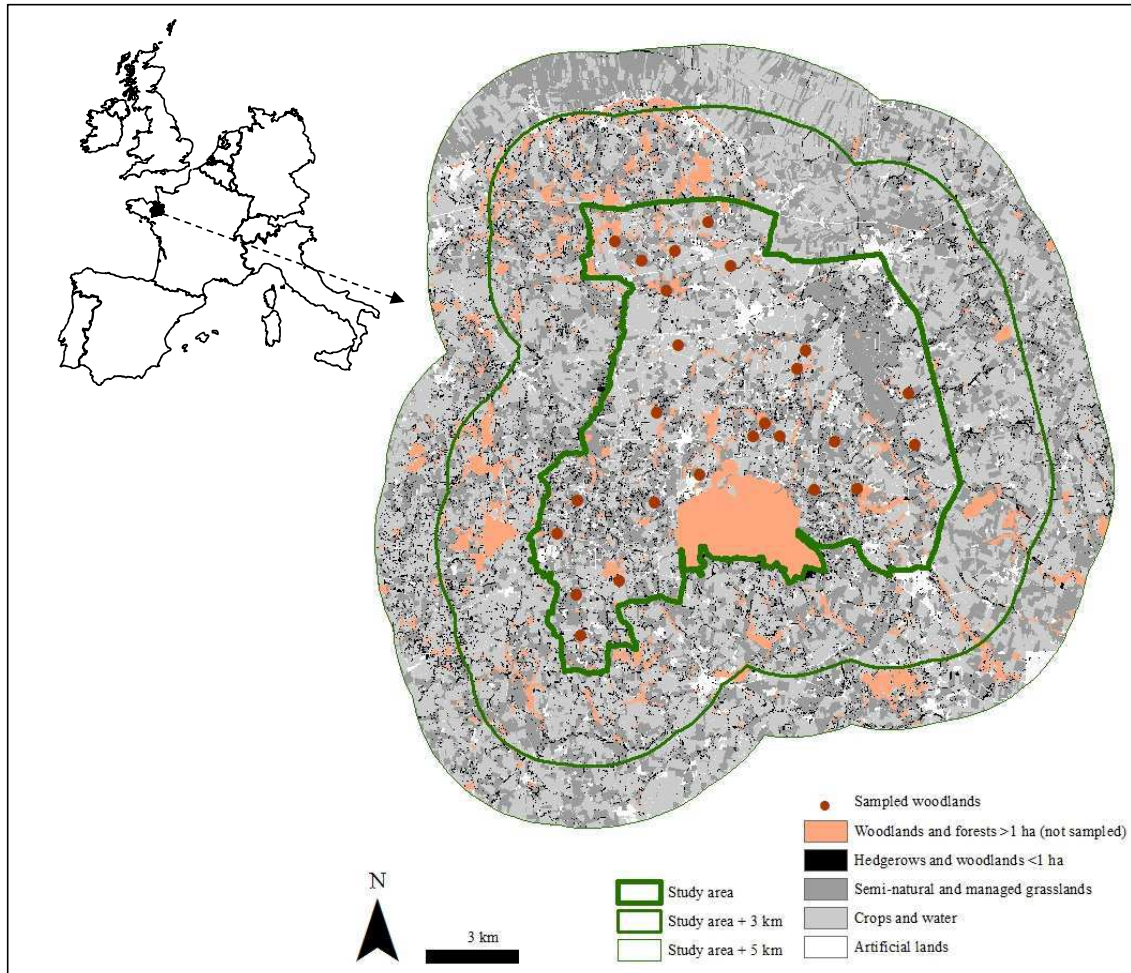
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827 Figure 5. Response curves of the top regression model according to the AICc approach for similarity in  
828 terms of proportional species composition (Table 3). Independent variables were not standardised and  
829 each time the unrepresented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

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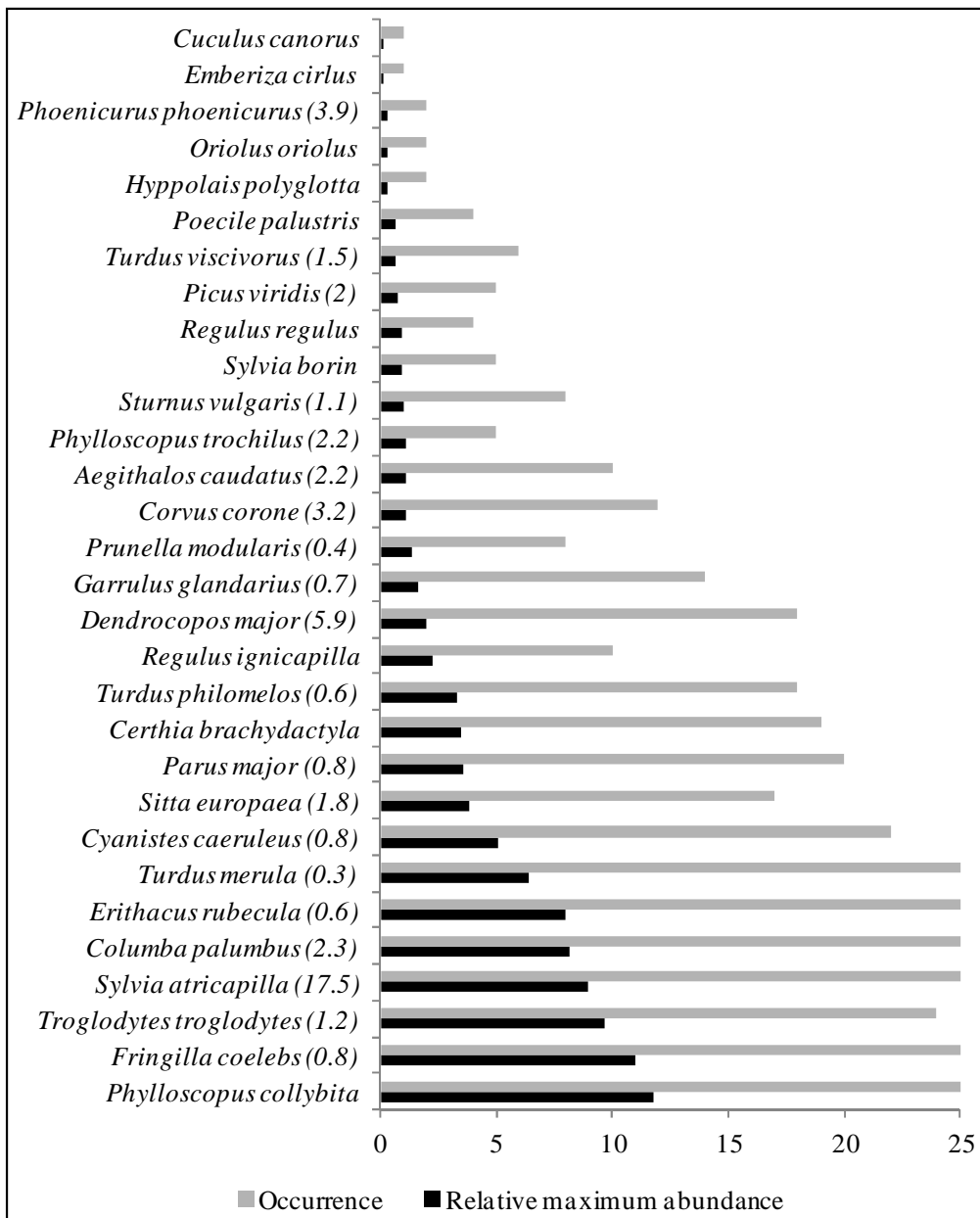
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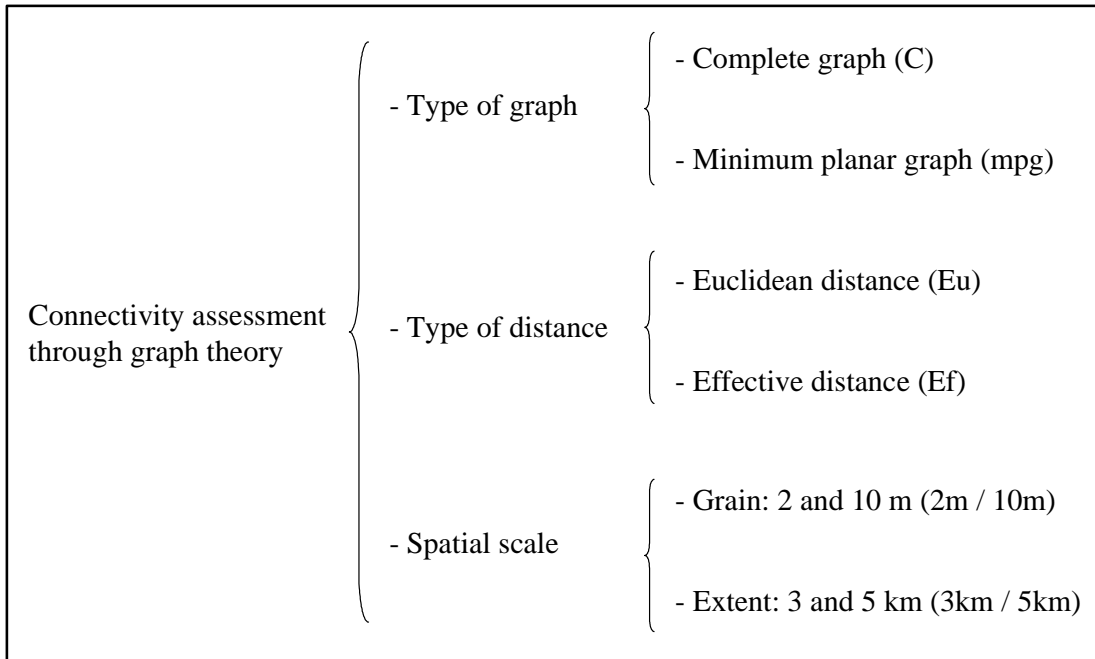


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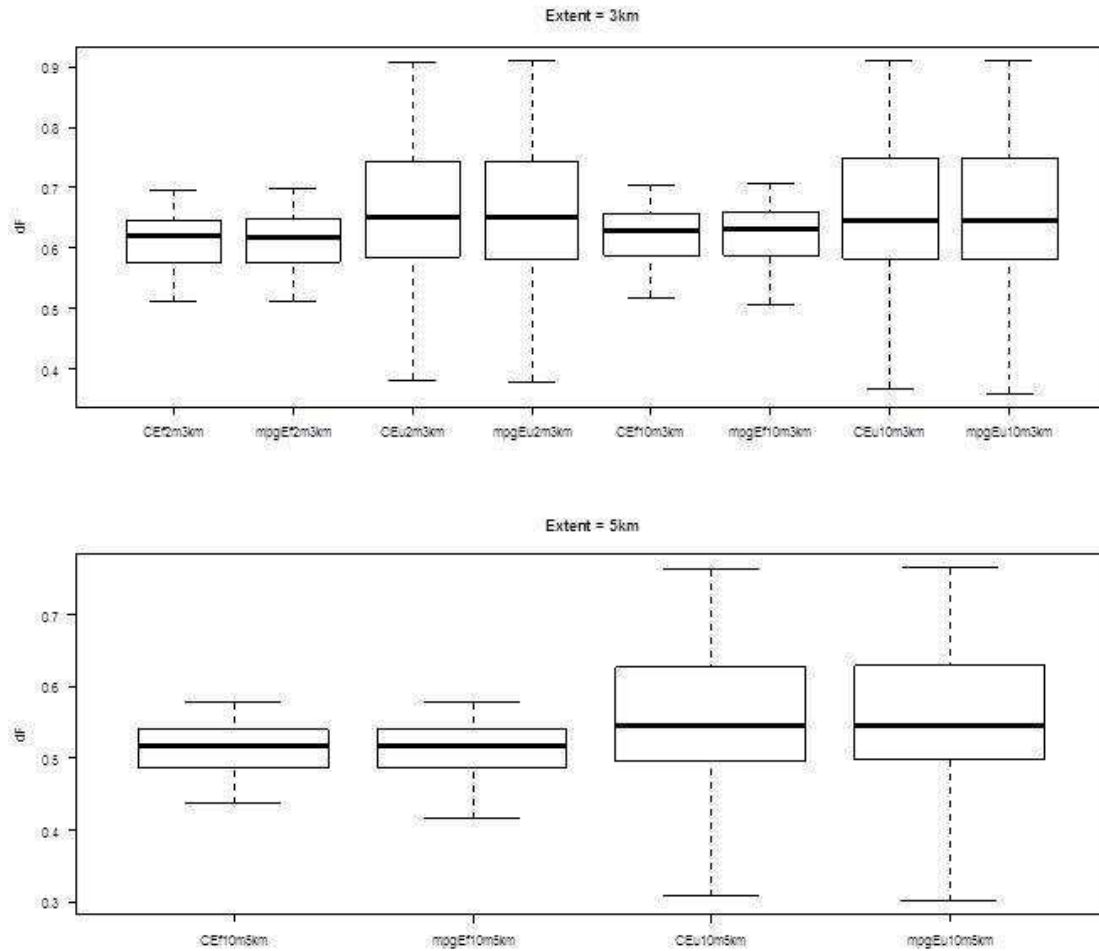
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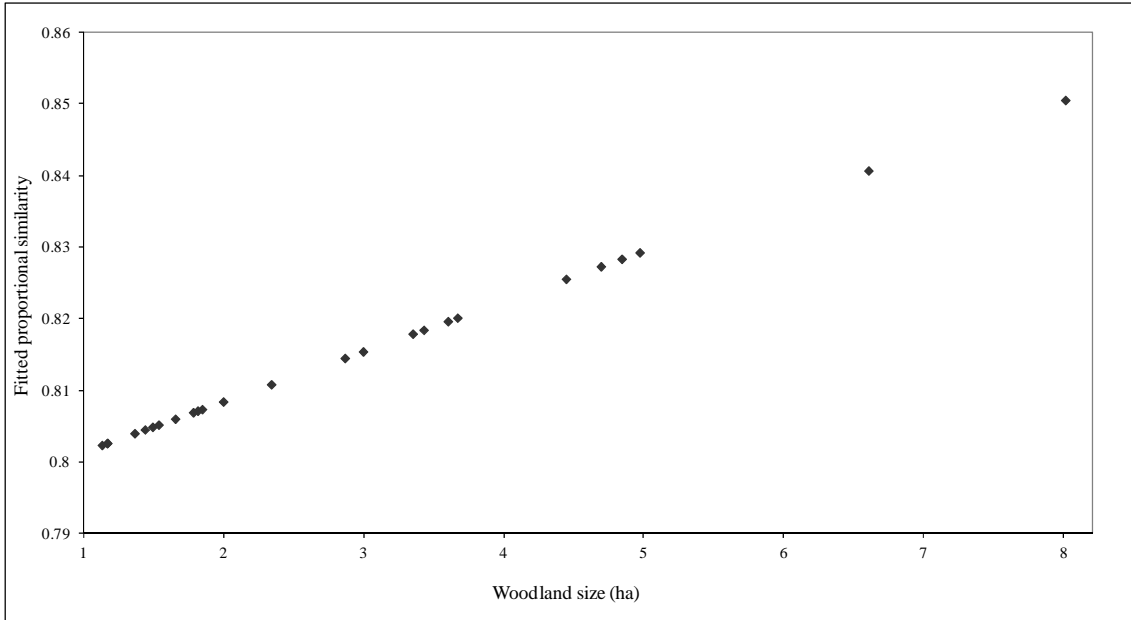
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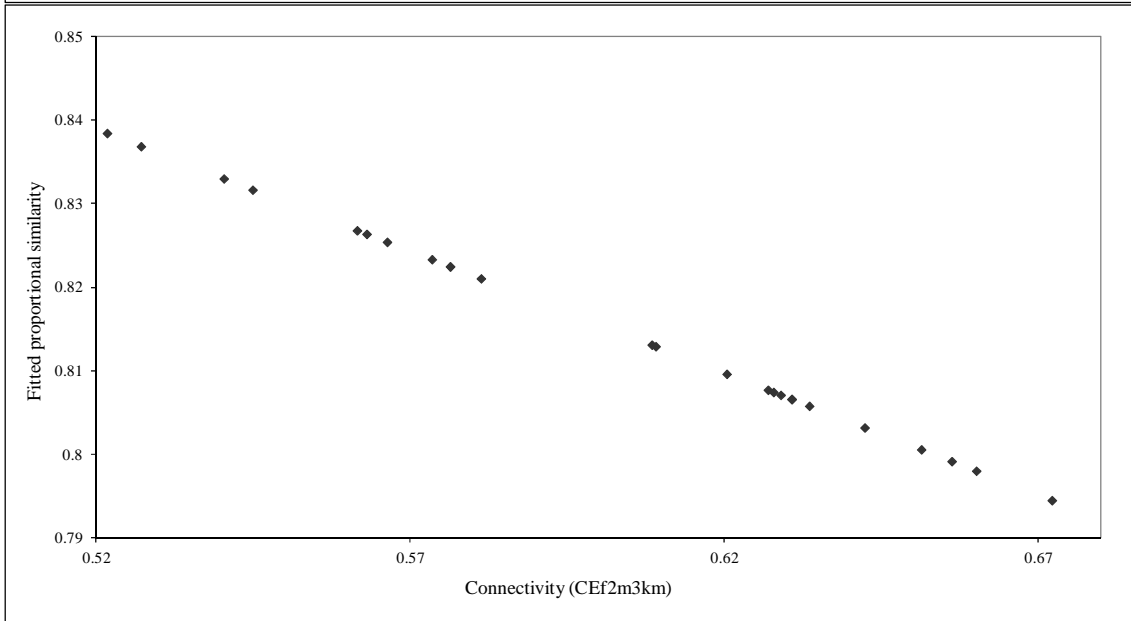


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