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

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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 ± 2.4 bird species, with an abundance of 25.1

44   ± 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.

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   Villecartier 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.

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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^2)] 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(gain, loss)/(min(gain, loss) + 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 = $2\Sigma(an_i * bn_i) / [(da + db)*(Na*Nb)]$,

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 ith species in site A and B, respectively, and da and db are $\Sigma an_i^2 /Na^2$ and Σbn_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^* is given by:

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

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-

254   fcomte.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* ≤ 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   (ΔAICc $\leq$ 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 (ΔAICc = 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. *Phyllocopus 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

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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.

	Land cover type	*Friction value*
	Woodlands and forests ≥ 1 ha	1
	Hedgerows and woodlands < 1 ha	2.57
Decreasing permeability ↓	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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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*			

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).

809

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).

822

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 (≥ 1 ha) within the study area (the thickest

825   edge represented in Fig. 1). See abbreviations regarding the connectivity metric in Figure 3.

826

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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834   representation of the land uses in the study area (*Armorique* ZA) and the sampled woodlands (dots; *n* =

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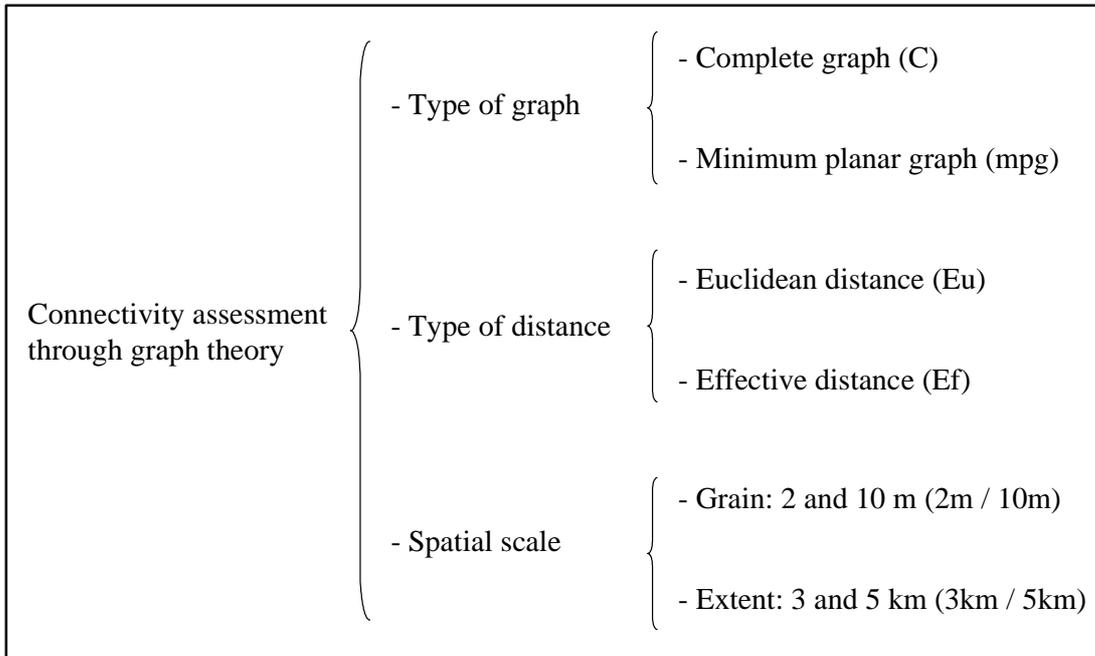844
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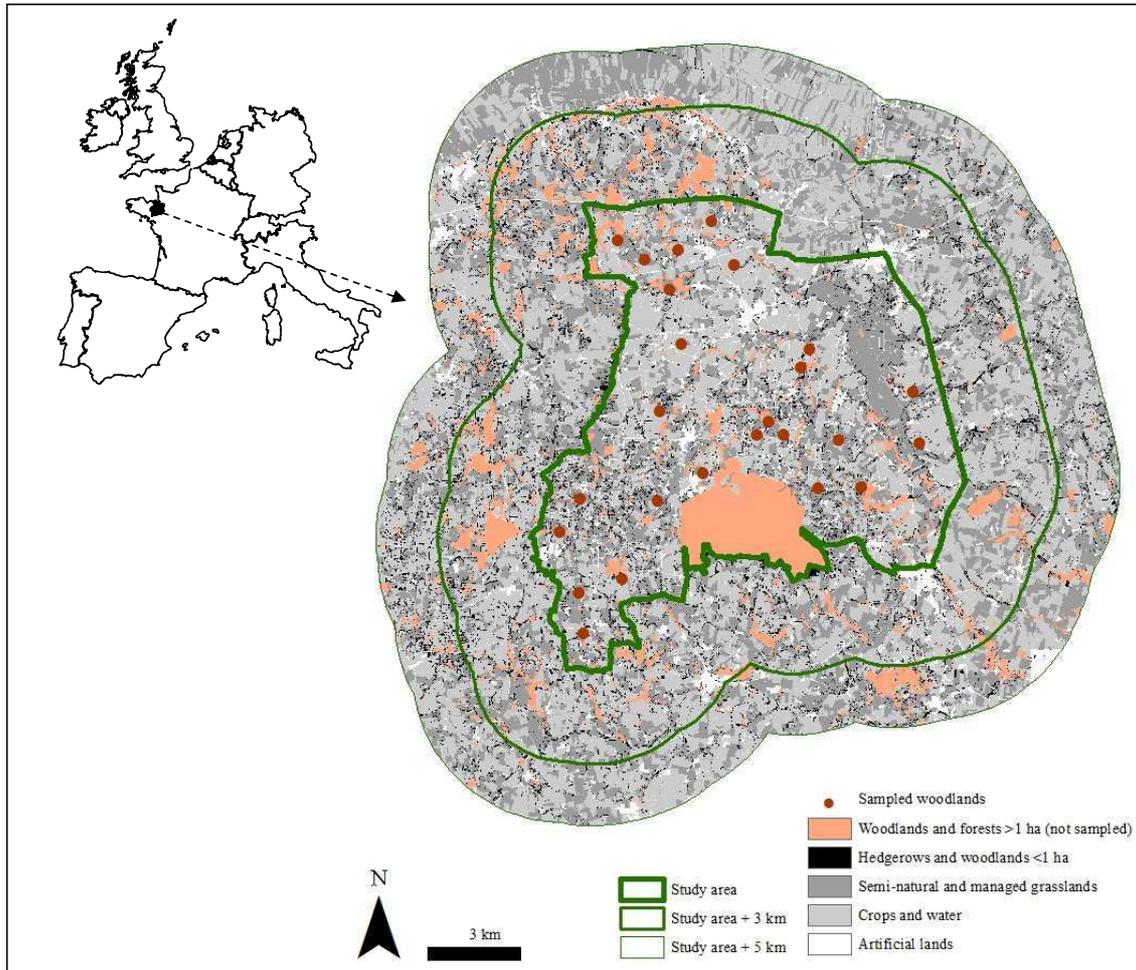
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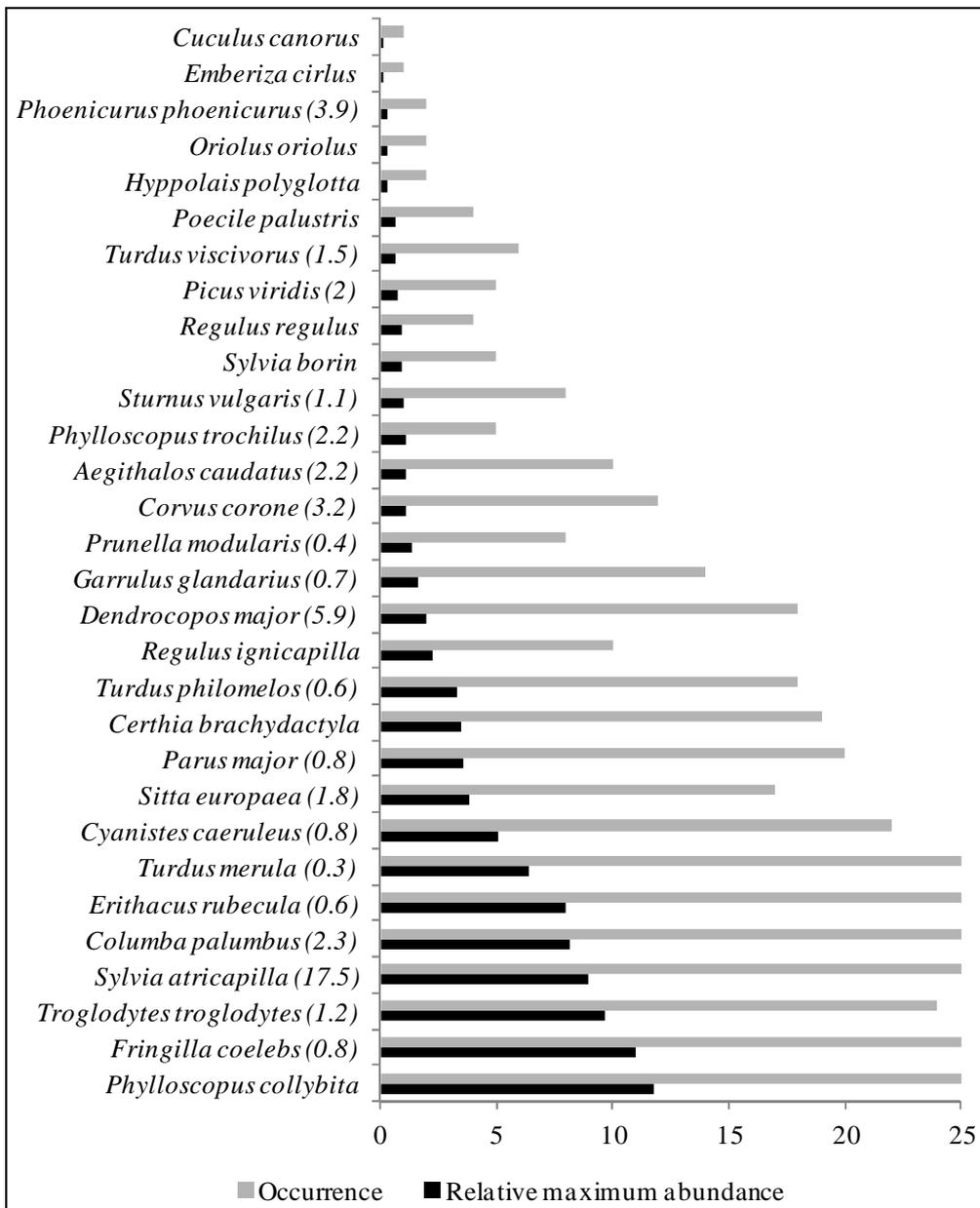

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867   spatial grain of the friction surface (2m / 10 m) and the spatial extent considered around the study area

868   where the woodlands were sampled (3km / 5km).

Connectivity assessment through graph theory

- Type of graph
  - Complete graph (C)
  - Minimum planar graph (mpg)

- Type of distance
  - Euclidean distance (Eu)
  - Effective distance (Ef)

- Spatial scale
  - Grain: 2 and 10 m (2m / 10m)
  - Extent: 3 and 5 km (3km / 5km)

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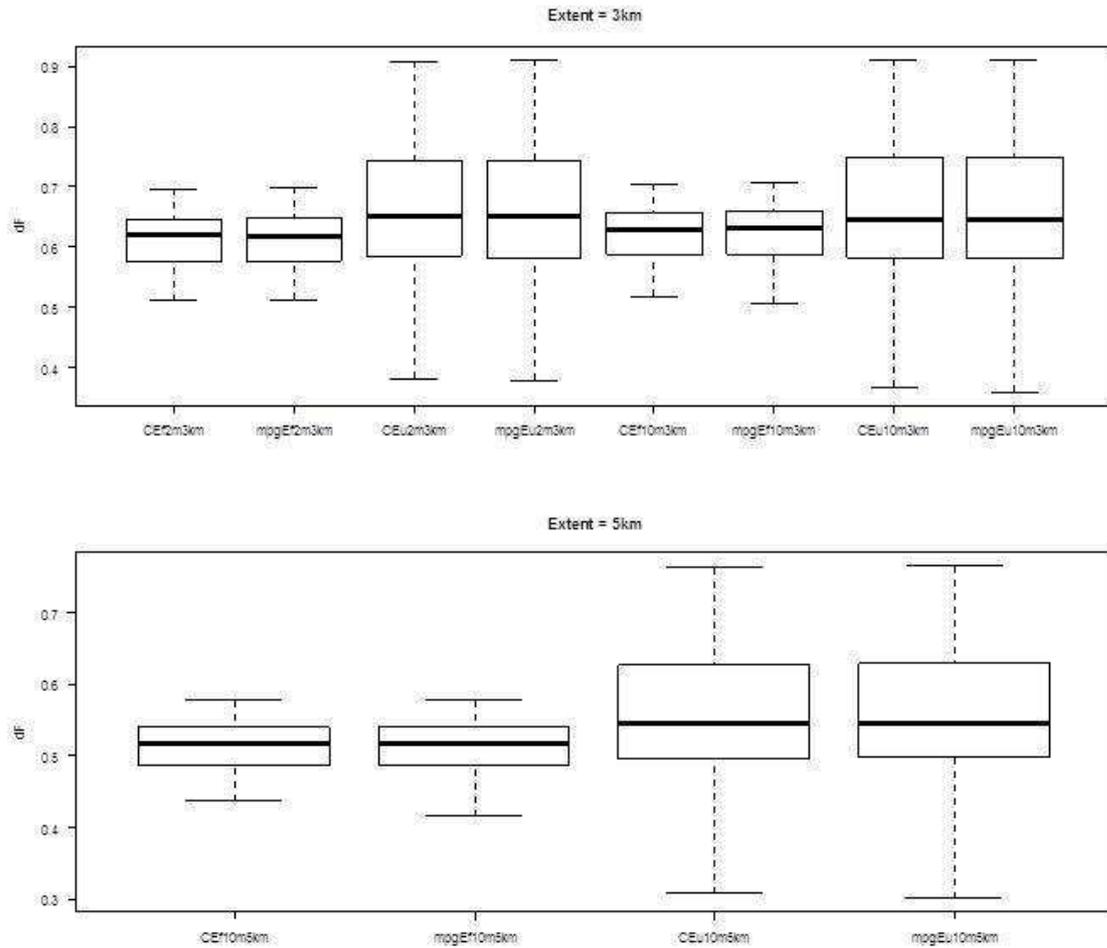
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