

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

Assu Gil-Tena, Jean Nabucet, Cendrine Mony, Julie Abadie, S. Saura, Alain Butet, Françoise Burel, Aude Ernoult

▶ 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

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

2	TITLE PAGE
3	
4	Woodland bird response to landscape connectivity in an agriculture-dominated landscape: a functional
5	community approach
6	
7	Running title: Woodland bird response to connectivity
8	
9	Assu Gil-Tena ^{1,2,3*} , Jean Nabucet ⁴ , Cendrine Mony ¹ , Juliet Abadie ¹ , Santiago Saura ⁵ , Alain Butet ¹ ,
10	Françoise Burel ¹ , Aude Ernoult ¹
11	
12	1 Observatoire des Sciences de l'Univers de Rennes, UMR CNRS 6553 ECOBIO, Université de Rennes
13	1-UEB, Avenue du général Leclerc, 35042, Rennes cedex (France).
14	2 Forest Sciences Center of Catalonia. Ctra. Sant Llorenç de Morunys km 2. 25280, Solsona (Spain).
15	3 Centre for Ecological Research and Forestry Applications, Bellaterra Campus of Universidad
16	Autónoma de Barcelona, Edifici C, 08193, Cerdanyola del Vallès (Spain).
17	4 Climat et Occupation du Sol par Télédétection, UMR COSTEL. Place du Recteur Henri Le Moal,
18	35043, Rennes (France).
19	5 ETSI Montes, Universidad Politécnica de Madrid, Ciudad Universitaria, s/n. 28040, Madrid (Spain).
20	
21	phone: +34 973481752 / fax: +34 973481392
22	E-mail address: assu.gil@ctfc.cat
23	*Corresponding author.
24	
25	
26	
27	

- 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 ± 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 processes, and for biodiversity conservation, is widely acknowledged (Crooks and Sanjayan 2006, 66 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 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. 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 (m²)] 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

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
- 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
- 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
- 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
- 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
- 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;

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
- through the connections of patch *k* with all other patches in the landscape (when *k* is either the starting or
- ending patch of that connection or flux). dF^* is given by:

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

where p_{ij}^* is the maximum product probability of all possible paths between two patches, *i* and *j*, in the landscape, including direct and non-direct (facilitated by other intermediate patches functioning as

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

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
- 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

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

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

- 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
- habitat patches (including both sampled and unsampled woodlands and forests within the study area)

were calculated with Graphab 1.0 software (Foltête et al. 2012; http://thema.univ-

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_{ii}) (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

- graph), because it considers maximum product probabilities (direct and non-direct dispersal between twopatches).
- 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
- extent considered was 5 km (429 woodlands and forests; Fig 1). Considering a larger spatial extent than
- the target one (e.g., Armorique ZA in this study) has been suggested as adequate when computing graph-
- based connectivity measures such as dF^* which do not take into account patch area (Pascual-Hortal and
- Saura 2007). The land-use map showing the different extents was obtained in the same manner as for the

295 Armorique ZA extent, using the same aerial photography and satellite imagery.

Figure 3 provides a schematic representation of the various factors that were considered in the

- 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, $p \le 0.05$; 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 $(\Delta AICc \le 2)$ 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 ($\Delta AICc = 0$), 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

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

al. 2011, Carranza et al. 2012, Decout et al. 2012), as well as for plants at the community level (Muratetet al. 2013).

501 ot al. 2015).

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 ≤ 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

- and the habitat availability concept (Saura and Rubio 2010) should be particularly adequate as integrative
 analytical tools that operationally consider as many different factors as possible that influence population
 viability.
- 489

490 ACKNOWLEDGEMENTS

- 491 Thanks to Regis 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).
- 499
- 500 REFERENCES
- 501 Adriaensen F., J.P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck and E. Matthysen. 2003.
- 502 The application of 'least-cost' modelling as a functional landscape model. Landscape Urban Plan. 64:
- 503 233-247.
- 504
- Baker, L. 2007. Effect of corridors on the movement behavior of the jumping spider *Phidippus princeps*(*Araneae, Salticidae*). Can. J. Zool. 85: 802-808.
- 507
- 508 Batáry, P., A. Kovács-Hostyánszki, C. Fischer, T. Tscharntke and A. Holzschuh. 2012. Contrasting effect
- 509 of isolation of hedges from forests on farmland vs. woodland birds. Community Ecol. 13(2): 155-161.
- 510
- 511 Baum, K.A., K.J. Haynes, F.P. Dillemuth and J.T. Cronin. 2004. The matrix enhances the effectiveness of
- 512 corridors and stepping stones. Ecology 85(10): 2671-2676.
- 513

514	Bennett, A., K.R. Crooks and M. Sanjayan. 2006. The future of connectivity conservation. In: K.R.
515	Crooks and M. Sanjayan (eds.), Connectivity Conservation. Cambridge Univ. Press, New York. pp. 676-
516	694.
517	
518	Benton, T.G., J.A. Vickery and J.D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the
519	key? Trends Ecol. Evol. 18: 182-188.
520	
521	Bibby, C.J., N.D. Burgess and D.A. Hill. 1992. Bird Census Techniques. Cambridge Univ. Press,
522	Cambridge.
523	
524	Bunn, A.G., D.L. Urban and T.H. Keitt. 2000. Landscape connectivity: A conservation application of
525	graph theory. J. Environ. Manage. 59: 265-278.
526	
527	Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical
528	information-theoretical approach. Springer-Verlag, New York.
529	
530	Carranza, M.L., E. D'Alessandro, S. Saura and A. Loy. 2012. Connectivity providers for semi-aquatic
531	vertebrates: the case of the endangered otter in Italy. Landscape Ecol. 27: 281-290.
532	
533	Cleland, E.E. 2012. Biodiversity and ecosystem stability. Nat. Educ. Knowl. 3(10): 14.
534	
535	Cook, W.M., K.T. Lane, B.L. Foster and R.D. Holt. 2002. Island theory, matrix effects and species
536	richness patterns in habitat fragments. Ecol. Lett. 5: 619-623.
537	
538	Crooks K.R. and M. Sanjayan (eds.). 2006. Connectivity conservation. Cambridge Univ. Press, New
539	York.
540	
541	Damschen, E.I., N.M. Haddad, J.L. Orrock, J.J. Tewksbury and D.J. Levey. 2006. Corridors increase
542	plant species richness at large scales. Science 313: 1284-1286.

543 544 Davies, Z.G. and A.S. Pullin. 2007. Are hedgerows effective corridors between fragments of woodland 545 habitat? An evidence-based approach. Landscape Ecol. 22: 333-351. 546 547 Decout, S., S. Manel, C. Miaud and S. Luque. 2012. Integrative approach for landscape-based graph 548 connectivity analysis: a case study with the common frog (Rana temporaria) in human-dominated 549 landscapes. Landscape Ecol. 27: 267-279. 550 551 Donald, P.F., R.E. Green and M.F. Heath, M.F. 2001. Agricultural intensification and the collapse of 552 Europe's farmland bird populations. P. Roy. Soc. B-Biol. Sci. 268: 25-29. 553 554 Ewers, R.M. and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat 555 fragmentation. Biol. Rev. 81: 117-142. 556 557 Fall, A., M.J. Fortin, M. Manseau and D. O'Brien. 2007. Spatial graphs: Principles and applications for 558 habitat connectivity. Ecosystems 10: 448-461. 559 560 Filippi-Codaccioni, O., V. Devictor, Y. Bas, J. Clobert and R. Julliard. 2010. Specialist response to 561 proportion of arable land and pesticide input in agricultural landscapes. Biol. Conserv. 143: 883-890. 562 563 Fischer, C., A. Flohre, L.W. Clement, P. Batáry, W.W. Weisser, T. Tscharntke and C. Thies. 2011. Mixed 564 effects of landscape structure and farming practice on bird diversity. Agric. Ecosyst. Environ. 141: 119-565 125. 566 567 Fischer, J. and D.B. Lindenmayer. 2006. Beyond fragmentation: the continuum model for fauna research 568 and conservation in human-modified landscapes. Oikos 112: 473-480. 569 570 Foltête, J.C., C. Clauzel and G. Vuidel. 2012. A software tool dedicated to the modelling of landscape 571 networks. Environ. Modell. Softw. 38: 316-327.

- 573 Fuller, R.J., D.E. Chamberlain, N.H.K. Burton and S.J. Gough. 2001. Distributions of birds in lowland
- 574 agricultural landscapes of England and Wales: How distinctive are bird communities of hedgerows and
- 575 woodland? Agric. Ecosyst. Environ. 84: 79-92.
- 576
- 577 Fuller, R.J., S.A. Hinsley and R.D. Swetnam. 2004. The relevance of non-farmland habitats, uncropped
- areas and habitat diversity to the conservation of farmland birds. Ibis 146: 22-31.
- 579
- 580 Gaston, K.J., R.G. Davies, C.D.L. Orme, V.A. Olson, G.H. Thomas, T.S. Ding, P.C. Rasmussen, J.J.
- 581 Lennon, P.M. Bennett, I.P.F. Owens and T.M. Blackburn. 2007. Spatial turnover in the global avifauna.
- 582 Proc. R. Soc. Biol. Sci. 274: 1567-1574.
- 583
- 584 Gil-Tena, A., R. Lecerf and A. Ernoult. 2013. Disentangling community assemblages to depict an
- 585 indicator of biological connectivity: A regional study of fragmented semi-natural grasslands. Ecol. Indic.
- 58624: 48-55.
- 587
- 588 Gilbert-Norton, L., R. Wilson, J. R. Stevens and K.H. Beard. 2010. A meta-analytic review of corridor
- 589 effectiveness. Conserv. Biol. 24: 660-668.
- 590
- 591 Gregory, R.D., A. van Strien, P. Vorisek, A.W.G. Meyling, D.G. Noble, R.P.B. Foppen and D.W.
- 592 Gibbons. 2005. Developing indicators for European birds. Philos. T. R. Soc. B. 360: 269-288.
- 593
- 594 Gurrutxaga, M., L. Rubio and S. Saura. 2011. Key connectors in protected forest area networks and the
- 595 impact of highways: A transnational case study from the Cantabrian Range to the Western Alps (SW
- 596 Europe). Landscape Urban Plan. 101: 310-320.
- 597
- 598 Haas, C.A. 1995. Dispersal and use of corridors by birds in wooded patches on an agricultural landscape.
- 599 Conserv. Biol. 9: 845-854.
- 600

601 Hinsley, S.A., R.A. Hill, R.J. Fuller, P.E. Bellamy and P. Rothery. 2009. Bird species distributions across 602 woodland canopy structure gradients. Community Ecol. 10: 99-110. 603 604 Houet, T., T.R. Loveland, L. Hubert-Moy, C. Gaucherel, D. Napton, C.A. Barnes and K. Sayler. 2010. 605 Exploring subtle land use and land cover changes: a framework for future landscape studies. Landscape 606 Ecol. 25: 249-266. 607 608 Hoyle, M. and F.S. Gilbert. 2004. Species richness of moss landscapes unaffected by short-term 609 fragmentation. Oikos 105: 359-367. 610 611 Jongman, R.H.G., M. Külvik and I. Kristiansen. 2004. European ecological networks and greenways. 612 Landscape Urban Plan. 68: 305-319. 613 614 Kadoya, T. 2009. Assessing functional connectivity using empirical data. Popul. Ecol. 51: 5-15. 615 616 Kindlmann, P. and F. Burel. 2008. Connectivity measures: a review. Landscape Ecol. 23: 879-890. 617 618 Laitila, J. and A. Moilanen. 2013. Approximating the dispersal of multi-species ecological entities such 619 as communities, ecosystems or habitat types. Ecol. Model. 259: 24-29. 620 621 Lennon, J.J., P. Koleff, J.J.D. Greenwood and K.J. Gaston. 2001. The geographical structure of British 622 bird distributions: diversity, spatial turnover and scale. J. Anim. Ecol. 70: 966-979. 623 624 Ludwig, M., H. Schlinkert, A. Holzschuh, C. Fischer, C. Scherber, A. Trnka, T. Tscharntke and P. Batáry. 625 2012. Landscape-moderated bird nest predation in hedges and forest edges. Acta Oecol. 45: 50-56. 626 627 Magurran, A. E. 2009. Measuring Biological Diversity. Oxford: Blackwell. 628 629 McRae, B.H. 2006. Isolation by resistance. Evolution 60: 1551-1561.

630	
631	Moilanen, A. 2011. On the limitations of graph-theoretic connectivity in spatial ecology and conservation.
632	J. Appl. Ecol. 48: 1543-1547.
633	
634	Muratet, A., R. Lorrillière, P. Clergeau and C. Fontaine. 2013. Evaluation of landscape connectivity at
635	community level using satellite-derived NDVI. Landscape Ecol. 28: 95-105.
636	
637	Ockinger, E. and H.G. Smith. 2008. Do corridors promote dispersal in grassland butterflies and other
638	insects? Landscape Ecol. 23: 27-40.
639	
640	Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P.
641	Solymos, M.H.H. Stevens and H. Wagner. 2013. vegan: Community Ecology Package. R package
642	version 2.0-10. http://CRAN.R-project.org/package=vegan
643	
644	Paradis, E., S.R. Baillie, W.J. Sutherland and R.D. Gregory. 1998 Patterns of natal and breeding dispersal
645	in birds. J. Anim. Ecol. 67: 518-536.
646	
647	Paradis E., J. Claude and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R
648	language. Bioinformatics 20: 289-290.
649	
650	Pascual-Hortal, L. and S. Saura. 2007. Impact of spatial scale on the identification of critical habitat
651	patches for the maintenance of landscape connectivity. Landscape Urban Plan. 83: 176-186.
652	
653	Peach, W.J., S.R. Baillie and D.E. Balmer. 1998. Long-term changes in the abundance of passerines in
654	Britain and Ireland as measured by constant effort mist-netting. Bird Study 45: 257-275.
655	
656	Price, B., C.A. McAlpine, A.S. Kutt, S.R. Phinn, D.V. Pullar and J.A. Ludwig. 2009. Continuum or
657	discrete patch landscape models for savanna birds? Towards a pluralistic approach. Ecography 32: 745-
658	756.

659

- 660 Ralph, C.J., G.R. Geupel, P. Pyle, T.E. Martin and D.F. DeSante. 1993. Handbook of field methods for
- 661 monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Albany, CA: Pacific Southwest Research Station,
- 662 Forest Service, U.S. Department of Agriculture.
- 663
- 664 Rayfield, B., M.J. Fortin and A. Fall. 2010. The sensitivity of least-cost habitat graphs to relative cost

665 surface values. Landscape Ecol. 25: 519-532.

- 666
- 667 Rösch, V., T. Tscharntke, C. Scherber and P. Batáry. 2013. Landscape composition, connectivity and
- fragment size drive effects of grassland fragmentation on insect communities. J. Appl. Ecol. 50: 387-394.
- 669
- 670 Sala, O.E., F.S. Chapin III, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F.
- 671 Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff,
- 672 M.T. Sykes, B.H. Walker, M. Walker and D.H. Wall. 2000. Global biodiversity scenarios for the year
- 673 2100. Science 287: 1770-1774.
- 674
- 675 Sauer, J.R., J.E. Hines and J. Fallon. 2004. The North American Breeding Bird Survey, results and
- analysis 1966-2003. Version 2004.1. Laurel, MD: USGS Patuxent Wildlife Research Center.
- 677
- 678 Saura, S. and L. Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in
- 679 landscape conservation planning: comparison with existing indices and application to a case study.
- 680 Landscape Urban Plan. 83: 91-103
- 681
- 682 Saura, S. and L. Rubio. 2010. A common currency for the different ways in which patches and links can
- 683 contribute to habitat availability and connectivity in the landscape. Ecography 33: 523-537.
- 684
- 685 Saura, S. and J. Torné. 2009. Conefor Sensinode 2.2: A software package for quantifying the importance
- of habitat patches for landscape connectivity. Environ. Modell. Softw. 24: 135-139.
- 687

- 688 Shanahan, D.F., C. Miller, H.P. Possingham and R.A. Fuller. 2011. The influence of patch area and
- 689 connectivity on avian communities in urban revegetation. Biol. Conserv. 144: 722-729.
- 690
- 691 Smith, A., N. Koper, C.M. Francis and L. Fahrig. 2009. Confronting collinearity: comparing methods for
- disentangling the effects of habitat loss and fragmentation. Landscape Ecol. 24: 1271-1285.
- 693
- 694 Sutherland, G.D., A.S. Harestad, K. Price and K.P. Lertzman. 2000. Scaling of natal dispersal distances in
- terrestrial birds and mammals. Conserv. Ecol. 4 (1), 16, http://www.consecol.org/vol4/iss1/art16.
- 696
- 697 Taylor, P.D., L. Fahrig, K. Henein and G. Merriam. 1993. Connectivity is a vital element of landscape
- 698 structure. Oikos 68: 571-573.
- 699
- 700 Taylor, P.D., L. Fahrig and K.A. With. 2006. Landscape connectivity: a return to the basics.
- 701 In: K.R. Crooks and M. Sanjayan (eds.), Connectivity Conservation. Cambridge University
- 702 Press, New York. pp. 29-43.
- 703
- 704 Tellería, J.L. and T. Santos. 1995. Effects of forest fragmentation on a guild of wintering passerines: the
- role of habitat selection. Biol. Conserv. 71: 61-67.
- 706
- 707 Urban, D. and T. Keitt. 2001. Landscape connectivity: a graph-theoretic perspective. Ecology 82 (5):708 1007 1010
- 708 1205-1218.
- 709
- 710 Vannier, C. 2012. Analyse spatiale de structures paysagères en contexte agricole bocage. Cybergeo:
- 711 European Journal of Geography, Environment, Nature, Landscape: 607. Available at
- 712 <u>http://cybergeo.revues.org/25354?lang=en</u>.
- 713
- 714 Venables, W.N. and B.D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New
- 715 York. ISBN 0-387-95457-0.
- 716

- 717 Verboom, J., A. Schotman, P. Opdam and J.A. J. Metz. 1991. European Nuthatch Metapopulations in a
- 718 Fragmented Agricultural Landscape. Oikos 61: 149-156.
- 719
- 720 Watts, K., A.E. Eycott, P. Handley, D. Ray, J.W. Humphrey and C.P. Quin. 2010. Targeting and
- 721 evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic
- focal species and least-cost networks. Landscape Ecol. 25: 1305-1318.
- 723
- Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia 50: 296-302.

725 TABLES

- Table 1. Friction values used to model landscape matrix permeability based on the vertical structure of the
- 127 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

729			
730			
731			
732			
732			
733			
734			
/35			
736			
737			
738			
739			
740			
741			
742			
743			
744			
745			
746			
740			
748			
740			
749			
/50			
/51			
752			
753			
754			
755			
756			
757			
758			
759			
760			
761			
762			
763			
764			
765			
765			
700			
/0/			
/68			
/69			

770 771	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	Species richness	12.00	21.00	15.48	2.35
community 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

- 795 796
- Table 3. Significant models of the factors behind woodland bird proportional similarity and abundance.
- A backward step-wise variable selection was performed for each model in which woodland size was
- 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

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).
- 831
- 832

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



- 855
- Figure 2. Increasingly ranked relative maximum abundance of the bird species pool of the woodlands in
- the study area. Bird species occurrence in the sampled woodlands (n = 25) is also shown. For each species
- 858 recorded and all the sampled woodlands of the study area, the relative maximum abundance (%) was
- 859 computed from the sum of the maximum abundance for each species during the three visits in the
- 860 breeding season regarding the sum of the maximum abundance for all the species. Geometric mean natal
- 861 dispersal (km) according to Paradis et al. (1998) is shown in brackets when available.



863

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

	- Type of graph	- Complete graph (C)
		- Minimum planar graph (mpg)
Connectivity assessment	- Type of distance	- Euclidean distance (Eu)
through graph theory		- Effective distance (Ef)
	- Spatial scale	- Grain: 2 and 10 m (2m / 10m)
		- Extent: 3 and 5 km (3km / 5km)

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





- 900
- 901
- 902
- 903
- 904
- 905
- 906

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

