# *Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: forest management implications*

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# Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: forest management implications

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**Abstract** Woodpecker species have significantly expanded their ranges in the last decades of the twentieth century in Mediterranean Europe, which seems to be closely related to forest maturation following large-scale decline in traditional uses. Here we assess the explicit role of forest landscape connectivity in the colonization of the Great Spotted Woodpecker (*Dendrocopos major*) and the Black Woodpecker (*Dryocopus martius*) in Catalonia (NE Spain). For this purpose we combined data on breeding bird atlas (10 × 10 km; 1980–2000) and forest inventories (c. 1 × 1 km, 2000). Forest connectivity was measured through graph theory and habitat availability metrics (inter- and intra-patch connectivity) according to species median natal dispersal distances. The best regressions from a set of alternative models were selected based on AICc. Results showed that connectivity between areas of mature forests [diameter at breast height (dbh) $\geq$ 35 cm] affected Black Woodpecker colonization events. The probability of colonization of the Great Spotted Woodpecker was greater at localities near the sources of colonization in 1980 and with a high connectivity with other less developed forest patches (dbh $<$ 35 cm). The spatial grain at which landscape connectivity was measured influenced the model performance according to the species dispersal abilities, with the species with the lower mobility (*D. major*) responding better to the forest connectivity patterns at finer spatial scales. Overall, it seems that both species could expand further in European Mediterranean forests in upcoming years but at slower rates if landscape connectivity according to species requirements does not continue to increase. Hence, a proactive and adaptive management should be carried out in order to preserve these species while considering the related major impacts of global change in Mediterranean Europe.

**Keywords** Conefor · Forest habitat dynamics · Forest landscape management · Functional connectivity · Global change · Spatial grain · Species dispersal

## Introduction

Mediterranean ecosystems appear to be particularly susceptible to the impacts of global change (Lavorel et al. 1998) due to their high exposure to human activities (Blondel 2006) and sensitivity to climatic conditions (Peñuelas et al. 2002). Large-scale interplaying factors

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such as climate and land-use changes could have synergistic impacts on current biodiversity patterns (Sala et al. 2000; Barbet-Massin et al. 2012) and Mediterranean forests appear to be one of the most threatened habitats (de Dios et al. 2007; Metzger et al. 2008) with predicted deleterious effects on their biodiversity (Moreira and Russo 2007). Nevertheless, forest maturation and afforestation after large-scale decline in agricultural activity are considered as probable causes for recent forest bird expansions in Mediterranean Europe (Preiss et al. 1997; Sirami et al. 2007; Gil-Tena et al. 2009, 2010).

Dispersal is fundamental for species colonization at large scales (the so-called range expansion) (e.g. Hengeveld 1994; Sutherland et al. 2000; Tittler et al. 2009) allowing species immigration and establishment in new habitat areas. Landscape connectivity [i.e. the degree to which the landscape facilitates or impedes the movement of organisms across the existing habitat resources (modified from Taylor et al. 1993)] largely influences the occurrence of effective and successful dispersal events. Therefore, the relevance of landscape connectivity for many ecological processes, such as range expansion and for biodiversity conservation, is widely acknowledged (Crooks and Sanjayan 2006; Kindlmann and Burel 2008). Nevertheless, connectivity in its strict sense only refers to the immigration and emigration component of spatial population-dynamics and not to species regional population size, resilience or persistence (Moilanen 2011). Immigration and emigration are key aspects in range expansion processes, so that connectivity may have a potential role as modulator of species range changes associated with climate warming (Taylor et al. 1993; Opdam and Wascher 2004).The outstanding importance of managing forest landscape connectivity is reflected in a large number of international and national initiatives, political agreements and legislations (e.g. Improved Pan-European Indicators for Sustainable Forest Management, Spanish law 42/2007, Spanish Forest Plan (2002), the Spanish Strategy for the Conservation and Sustainable Use of Biological Diversity (1999), and the EU Directive 92/43). New improved connectivity methods have been developed which will allow to analyse the landscape connectivity pattern and, therefore, to apply the related results to improve forest management (Saura and Rubio 2010). In this framework, landscape connectivity analysis can be computed by means of habitat availability (reachability) indices based on graph-theory. These indices present an improved performance compared to other existing network connectivity indices and are particularly suited for landscape conservation planning and monitoring applications (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007) because they can evaluate the different ways in which patches can contribute to habitat availability and connectivity in the landscape (i.e. inter- and intra-patch connectivity; Saura and Rubio 2010). In particular, not only the immigration and emigration component of habitat use is considered but also the value of local resources in each patch to determine the effective amount of habitat that can be reached by a given species, with both aspects integrated in a single analytical framework (Saura and Rubio 2010).

The range expansion of the Black Woodpecker *Dryocopus martius* and the Great Spotted Woodpecker *Dendrocopos major* in the Mediterranean region of Catalonia (NE Spain) over 20 years (1980–2000) has been significantly related to widespread forest maturation, while the expansion of other woodpeckers such as the Lesser Spotted Woodpecker *Dendrocopos minor* is mainly attributed to the development and maturation of localised riverside poplar plantations (Estrada et al. 2004). During this period, the Black Woodpecker and the Great Spotted Woodpecker have expanded their range by 109 and 48 %, respectively (Estrada et al. 2004). In this region, the Black Woodpecker nests in trees with a diameter at breast height (dbh) $\geq$ 35 cm, while the Great Spotted Woodpecker can build its nest in smaller trees (dbh $\geq$ 14–16.5 cm) (Camprodon et al. 2007). Both woodpecker species prefer forests with considerable amounts of dead wood either as a nesting site or as a feeding substrate. These species play a key functional role in forest ecosystems through forest trophic chain regulation (e.g. predation of insects) and as ecosystem engineers due to the supply of dwelling sites for other forest birds, small mammals or bats in the case of their nesting holes (Sekercioglu 2006; Whelan et al. 2008). In addition, like other woodpecker species, they could be considered as umbrella or focal species for helping the conservation of other species dependent on similar habitats (Edman et al. 2011; Roberge et al. 2008). Therefore, disentangling the processes mediating woodpeckers' range expansion (and the particular role of forest connectivity) is crucial since they could also influence and indicate the fate of other taxa (Donald and Fuller 1998; Wenny et al. 2011). Eventually, management of the landscape connectivity patterns could be incorporated into regional forest planning schemes in order to preserve biodiversity.

Current rates of regional forest maturation have been hypothesised to favour bird species colonization in Mediterranean regions in which the landscape structure enhances dispersal through increased connectivity (Gil-Tena et al. 2010) but no explicit test has been conducted. This study assessed the role of forest landscape connectivity in the recent colonization of the Great Spotted Woodpecker and the Black Woodpecker in Catalonia (NE Spain). For this purpose, data on breeding bird atlas (10 × 10 km; 1980–2000) and forest inventories (c. 1 × 1 km, 2000) were considered. We implemented a functional landscape perspective by considering the effect on woodpecker colonization of habitat availability and connectivity according to three different forest maturation thresholds. The definition of the different forest maturation thresholds depended on the forest structure development in terms of basal area in relation with the habitat requirements for the two woodpecker species (minimum dbh of the nesting trees) and to applicable forestry criteria. The landscape connectivity of the forest structure was computed considering median natal dispersal distances and separately quantifying intra- and interpatch connectivity (Pascual-Hortal and Saura 2006; Saura and Rubio 2010). Two different spatial grain resolutions according to the data and computational limitations were tested in order to determine if they could influence the relationship between range expansion and forest connectivity, eventually being species-specific in terms of species dispersal capacities. Our main hypothesis explaining woodpeckers' colonization relies on the crucial role of forest habitat connectivity and availability, besides the recognized influence of the distance to the colonization source (Brotons et al. 2005, 2008). We expect the most specialized woodpecker in terms of nesting requirements (i.e. Black Woodpecker) to respond to interpatch connectivity of the most developed forest maturation threshold, while being less sensitive than the Great Spotted Woodpecker to the spatial grain considered for computing connectivity, due to its greater natal dispersal capacities (Pascual-Hortal and Saura 2007). Furthermore, we did not expect that intrapatch connectivity would play a dominant role in modelling woodpecker colonizations given the intermediate dispersal abilities of the analysed species compared to the distribution of forest habitats in the study area (Saura and Rubio 2010).

## Methods

### Study area

Catalonia (NE Spain, Fig. 1) is a climatically and topographically heterogeneous region covering 32,107 km$^2$. It includes a variety of habitat types comprising mountainous areas in the Pyrenees (up to 3,143 m) and inland chains, extensive interior and predominantly agricultural plains as the *Plana de Lleida*, and a long coastline of about 300 km along the Mediterranean Sea. The climate is mainly Mediterranean temperate, with maritime influence on the coast and a cold influence in the Pyrenees. About 38 % of Catalonia is covered by forests and about one hundred forest tree species are found in this region. Approximately 90 % of the total number of trees belongs to the 14 most common species (mainly *Pinus* spp. and *Quercus* spp.) (Gracia et al. 2000–2004).

The most common forest management practices in the region are those of moderate intensity, such as thinning and selective cutting. In some cases, these practices have increased biodiversity in the understory and canopy of forests compared to unmanaged stands or intensively managed forests, as predicted by the intermediate disturbance hypothesis (Torras and Saura 2008; Torras et al. 2012). Nevertheless, most forest owners in Catalonia have commonly implemented high-grading, especially in uneven aged stands. These practices consisted in harvesting the best and biggest trees in the forest, not allowing the stand to reach more advanced development stages (Torras et al. 2012). As a result of the past harvesting treatments and the fire occurrences that traditionally affected Catalan forests, the average stand age of most forest typologies is under 50 years (Gracia et al. 2000–2004). Nevertheless, Catalan forests have significantly aged during the last years of the twentieth century, according to the Spanish National Forest Inventory data (Ministerio de Medio Ambiente 2006). In the study area, the spatial pattern of forest maturation is similar throughout the region, whereas other forest dynamics and associated perturbations such as the increases in afforested areas and fire impact appeared to occur mainly as patchy processes (Gil-Tena et al. 2009).

### Changes in the woodpeckers' range

Data on changes in the ranges of woodpeckers were gathered from the Catalan Breeding Bird Atlases (CBBA; Estrada et al. 2004). The CBBA data are derived from a series of large-scale surveys covering the whole extent of Catalonia during two different periods: 1975–1983 (Atlas1) and 1999–2002 (Atlas2). A total of 385 × 10 × 10 km UTM squares were surveyed for each of the different time periods. The field work was conducted from March to July by volunteers who recorded evidence of occurrence or breeding either by sound or sight. To control for variation in sampling effort between atlases, we used estimates of effective sampling effort as a covariable in our analyses. Analyses of range changes were only carried out on the 309 × 10 × 10 km UTM squares for which changes in sampling effort could be obtained (Estrada et al. 2004).

For each woodpecker species and atlas square, we categorised the recorded changes in occurrence between Atlases as: colonization (present in Atlas2 but not in Atlas1), extinction (present in Atlas1 but not in Atlas2), maintenance (present in both periods) and absence (absent in both periods). This information was valuable for generating the response variable (colonization vs. absence) as well as one independent variable measuring the hypothetical nearest distance to the colonization source in 1980 (species presence in Atlas1). In this latter case, for each atlas square where woodpeckers had expanded or were absent, we computed the distance (km) to the nearest atlas square where the species was present in Atlas1.

The inclusion of zeroes that result from observations outside the environmental range of a species [i.e. naughty noughts (Austin and Meyers 1996)] was minimized in order to avoid giving positive predictions where the species

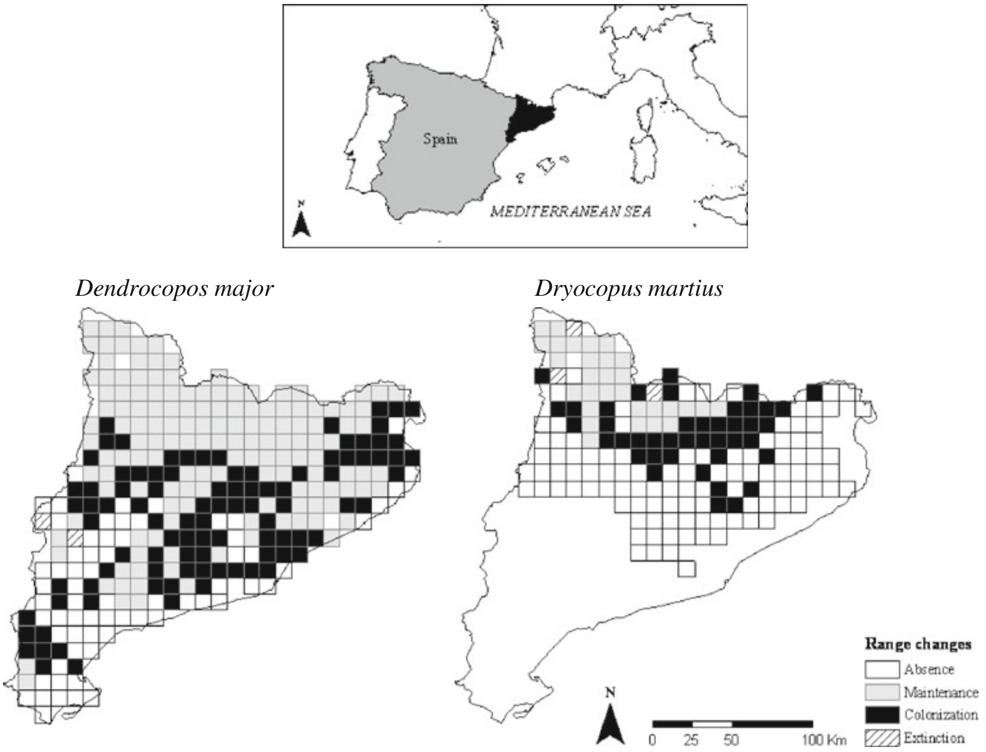


**Fig. 1** Location of the study area [Catalonia (NE Spain); *marked in black* in the *upper box*] and range expansion of woodpecker species during the period between bird atlases (1980–2000)

is known to be absent. In this sense, we filtered the Atlas data for the Black Woodpecker, as this is an expanding species which is absent from many regions of southern Catalonia, but there could be areas of potential habitat within its environmental range where the species has not yet arrived (see Fig. 1). This procedure avoided the inclusion of all Atlas squares where the Black Woodpecker was undetected as an indication of zero expansion (see also Melles et al. 2011). Our filter was based on climatic units inside the environmental ranges of the Black Woodpecker in Atlas2. The climatic units were previously defined in Catalonia through climatic variables (Moré et al. 2005) derived from the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al. 2005).

### Forest structure descriptors

Data on forest structure were gathered from the Third Spanish National Forest Inventory (NFI3; Ministerio de Medio Ambiente 2006). In Catalonia, the field work was carried out from 2000 to 2001 with a sampling density of about one NFI plot for every 1 km$^2$ of forest lands (i.e. 10,585 plots). The size of the NFI plots varied depending on tree dbh, ranging from a plot radius of 5 m for trees with a dbh between 75 and 125 mm up to a maximum radius of 25 m for trees with a dbh of at least 425 mm.

Basal area (m$^2$/ha) was computed at the NFI plot level according to three forest maturation thresholds based on dbh thresholds that considered species requirements for breeding as well as applicable forestry criteria. These three maturation thresholds were: "dbh $\geq$ 7.5 cm" which considered all tally trees, "dbh $\geq$ 20 cm" which accounted for trees from small timber trees in forestry terms and "dbh $\geq$ 35 cm" for trees from middle timber trees in forestry terms. To calculate basal area, we considered dead tally trees together with the living trees since they could be feeding and nesting resources. It is noteworthy that in the NFI3 in Catalonia there was no specific methodology for dead wood assessment (discriminating dead wood types and decay stages), which prevented us from assessing the possible role of dead wood supply on woodpecker colonization.

### Forest connectivity

Landscape connectivity of forest structure (basal area according to the three maturation thresholds) was computed through graph theory and habitat availability metrics (inter- and intrapatch connectivity) using Conefor 2.6 (Saura and Torné 2009), available at www.conefor.org. Due to computational limitations, we could not calculate connectivity at the spatial resolution of the NFI3 [i.e. at the plot level (c. 1 × 1 km)], which was not really necessary considering the Atlas data spatial resolution (10 × 10 km). Therefore, for the connectivity analysis, measures of forest structure were respectively averaged using a regular UTM grid at 2 × 2 and 5 × 5 km. This resulted in the following number of samples per maturation threshold: in the case of 2 × 2 km $n = 4{,}461$ for dbh $\geq$ 7.5 cm, $n = 4{,}145$ for dbh $\geq$ 20 cm and $n = 2{,}516$ for dbh $\geq$ 35 cm; in the case of 5 × 5 km $n = 1{,}104$ for dbh $\geq$ 7.5 cm, $n = 1{,}063$ for dbh $\geq$ 20 cm and $n = 868$ for dbh $\geq$ 35 cm.

Our connectivity measures were based on the Probability of Connectivity (PC; see Saura and Pascual-Hortal 2007 for a detailed description). PC is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable one from the other (interconnected) given a set of $n$ habitat patches and the links (direct connections) between them (Saura and Pascual-Hortal 2007). We computed the PC index with basal area as the attribute of the habitat patches (cells).

The PC metric, compared with other habitat availability metrics based on binary networks such as the Integral Index of Connectivity [IIC (Pascual-Hortal and Saura 2006, 2008)], allows focusing on the amount and number of individuals flowing in the landscape rather than on the study of long-term mixing of populations provided by a few successful dispersing individuals as is the case for the IIC metric (Bodin and Saura 2010). In fact, Awade et al. (2012) have shown that PC was more effective than IIC in explaining the occurrence patterns of forest birds in the Atlantic rainforests of Brazil, while the opposite was found by Neel (2008) for the case of genetic diversity patterns at the landscape scale.

The direct dispersal probabilities $p_{ij}$ between habitat patches (cells) were computed here through a negative exponential function of interpatch distance, as in many other studies (Bunn et al. 2000; Urban and Keitt 2001; Saura and Pascual-Hortal 2007; Gurrutxaga et al. 2011). The rate of decay of this negative exponential function was determined by the value of the median dispersal distance for each of the analysed species, corresponding to $p_{ij} = 0.5$. The interpatch distance was calculated as the Euclidean distance between the centroids of the UTM cells analysed (2 × 2 or 5 × 5 km):

$$p_{ij} = \mathrm{e}^{-kd_{ij}},$$

where $k$ is a constant and $d_{ij}$ is the distance between centroids.

In the case of the Black Woodpecker, the median natal dispersal distance was set to 16.25 km according to Christensen (2002) and the median values of observed mean dispersal distances between unpaired females ($22.1 \pm 4.0$, $n = 24$) and unpaired males ($10.4 \pm 2.9$, $n = 12$). This value was also supported by expert criteria (G. Gorman, personal communication). In the case of the Great Spotted Woodpecker, the median natal dispersal was set to 5.88 km ($n = 15$), which was the geometric mean natal dispersal distance extracted from the bird ringing data of the British Trust of Ornithology (Paradis et al. 1998).

The relative ranking of landscape elements by their contribution to overall landscape connectivity according to a certain index (here PC) can be obtained by calculating the importance of each individual element (Urban and Keitt 2001; Pascual-Hortal and Saura 2006) as the absolute difference (varPC) between the index value when the landscape element is present in the landscape and the index value after removal of that landscape element (e.g. after a certain habitat patch loss). In the case of the probability of connectivity metric, Saura and Rubio (2010) showed that varPC can be partitioned in three fractions (varPCintra, varPCflux, varPCconnector) in order to distinguish the different ways in which a patch can contribute to habitat connectivity and availability in the landscape. varPCintra represents the contribution of a patch in terms of intrapatch connectivity (amount and/or quality of habitat resources existing within that patch). varPCintra is fully independent from the way the patch may be connected to other patches, thus it does not depend on the dispersal distance of the focal species and would remain the same even if the patch was completely isolated. In order to quantify interpatch connectivity we considered the fraction varPCflux, which measures the amount of dispersal flux that might be expected to reach a particular forest habitat patch from all the other forest habitat areas in the landscape. Finally, a third fraction measures the contribution of a patch or link to the connectivity between other habitat patches different from itself (varPCconnector), as a connecting element or stepping stone between them. However, a permanent colonization in a given habitat area (as detected in the breeding bird atlas surveys) can only be explained by the local habitat characteristics of the colonized habitat site (intra) or by the amount of flux expected to arrive to that site as the final destination of the dispersal fluxes (flux), and not by the use of that site as a connecting element that ultimately directs the colonizers to other habitat patches further apart (connector). Therefore, hereafter we focus only on varPCintra and varPCflux for modelling the factors behind the colonization events of the woodpecker species.

## Data analysis

In order to carry out statistical analyses at the scale at which the atlas data were available (10 × 10 km), measures of basal area and forest interpatch and intrapatch connectivity for different maturation thresholds were averaged at 10 × 10 km for each of the spatial grain resolutions (2 × 2 and 5 × 5 km), forest maturation thresholds (dbh $\geq$ 7.5 cm, dbh $\geq$ 20 cm and dbh $\geq$ 35 cm) and woodpecker species (*D. major* and *D. martius*) (see Table 1). Independent variables were standardised to zero means and unit variances to eliminate the effects of differences in the measurement scale. Multicollinearity problems among the predictors of colonization events were avoided through excluding strong correlated variables in the same model (Spearman's $\text{rho} > 0.8$), particularly among the variables describing basal area and connectivity of the same or among similar forest maturation thresholds (e.g. $\text{dbh} \geq 7.5$ cm and $\text{dbh} \geq 20$ cm). In addition, in regressions (see below) we checked that variance inflation factors (VIF) were always under the desired threshold for logistic regressions of 2.5 (Allison 1999) which indicates the absence of strong linear dependencies among predictors.

We used generalized linear models with a binomial error distribution (McCullagh and Nelder 1989) to model the colonization events (against non-occupation ones) of the two woodpecker species based on the occurrence in both bird atlases as a function of the distance to the colonization source (species presence in 1980), the basal area and forest interpatch and intrapatch connectivity for different maturation thresholds. For each woodpecker species and both spatial grain resolutions, different models were developed considering or not biologically meaningful (and statistically possible) interactions (Table 2). We used the information-theoretic model comparison approach based on Akaike's Information Criterion (AIC), comparing alternative a priori models through second-order AIC corrected for small sample sizes (AICc) (Burnham and Anderson 2002). In our analysis, models were considered to have a substantial level of empirical support if $\Delta\text{AICc} < 4$ (Burnham and Anderson 2002). In all the computed models, we considered sampling effort differences and performed a backward stepwise selection procedure based on AIC and significant variables at $p = 0.05$.

For each top regression model ($\Delta\text{AICc} < 4$), we calculated the area under the curve (AUC) of a receiver operating characteristic plot (ROC) to assess the probability that a model will correctly distinguish a true maintenance and a true colonization event drawn at random. AUC values and their respective 95 % confidence intervals were computed following a block cross-validation with 10 % of

**Table 1** Summary statistics [mean and coefficient of variation (CV)] of forest structure [basal area ($G$ in m$^2$/ha)] and its intrapatch and interpatch connectivity (varPCintra and varPCflux, respectively in absolute values) according to three different forest maturation thresholds ($\text{dbh} \geq 7.5$ cm, $\text{dbh} \geq 20$ cm and $\text{dbh} \geq 35$ cm)

| Spatial grain | Species | | dbh ≥ 7.5 cm | | | dbh ≥ 20 cm | | | dbh ≥ 35 cm | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | *G* | varPCintra | varPCflux | *G* | varPCintra | varPCflux | *G* | varPCintra | varPCflux |
| 2 × 2 km | *D. major* | Mean | 11 | 187 | 16,828 | 6 | 79 | 5,333 | 3 | 18 | 611 |
| | | CV | 59 | 85 | 103 | 79 | 141 | 107 | 80 | 175 | 139 |
| 5 × 5 km | *D. major* | Mean | 10 | 158 | 3,674 | 6 | 62 | 1,216 | 3 | 15 | 206 |
| | | CV | 64 | 93 | 90 | 76 | 161 | 99 | 83 | 212 | 116 |
| 2 × 2 km | *D. martius* | Mean | 15 | 318 | 213,243 | 8 | 113 | 62,270 | 3 | 25 | 7,787 |
| | | CV | 36 | 63 | 49 | 48 | 92 | 58 | 66 | 120 | 69 |
| 5 × 5 km | *D. martius* | Mean | 11 | 205 | 18,860 | 7 | 98 | 5,974 | 3 | 21 | 695 |
| | | CV | 47 | 78 | 103 | 53 | 79 | 125 | 69 | 120 | 223 |

The reported values corresponded to those computed at 10 × 10 km (spatial grain of the bird atlas data)

**Table 2** Possible models for the factors behind the colonization of woodpecker species

| Model | Formula |
|---|---|
| Distance to colonization source | $D$ |
| Distance to colonization source + habitat availability of the maturation threshold $i$ | $D \times G_i$ |
| Distance to colonization source × habitat availability of the maturation threshold $s$ × intrapatch connectivity of the maturation threshold $t$ | $D \times G_s \times \text{varPCintra}_t$ |
| Distance to colonization source × habitat availability of the maturation threshold $s$ × interpatch connectivity of the maturation threshold $t$ | $D \times G_s \times \text{varPCflux}_t$ |

The considered factors were the variation in sampling effort between atlases, the distance to the colonization source ($D$), the forest structure [basal area ($G_i$)] and its intra and interpatch connectivity ($\text{varPCintra}_i$ and $\text{varPCflux}_i$, respectively) according to three different forest maturation thresholds ($i$; 7.5: $\text{dbh} \geq 7.5$ cm; 20: $\text{dbh} \geq 20$ cm and 35: $\text{dbh} \geq 35$ cm). $s$ and $t$ indicated the different forest maturation thresholds which can be considered in the same model due to multicollinearity constraints (if $s$ is $\text{dbh} \geq 7.5$ cm or $\text{dbh} \geq 20$ cm then $t$ is $\text{dbh} \geq 35$ cm and if $s$ is $\text{dbh} \geq 35$ cm then $t$ is $\text{dbh} \geq 7.5$ cm or $\text{dbh} \geq 20$ cm) sample units left out each time (10 blocks) due to the reduced sample size at 10 × 10 km ($n = 147$ for *D. martius* and $n = 161$ for *D. major*) that can strongly influence AUC values. Despite existing more conservative criteria, we considered a model fair if $0.7 < \text{AUC} < 0.8$, good if $0.8 < \text{AUC} < 0.9$ and excellent if $0.9 < \text{AUC} < 1$ (Thuillier 2007) since we were more interested in inferential modelling than in model building. Statistical analyses were computed in *R* (http://www.r-project.org).

Spatial autocorrelation in model residuals was checked through Moran's *I* coefficients computed at 20 and 14 distance classes for *D. major* and *D. martius*, respectively, with a spatial lag of 15 km which encompassed the immediate neighbours (up to eight according to the atlas sampling). The significance of the autocorrelation coefficients was assessed through 999 permutations. The software Passage v.2 was used for exploring spatial autocorrelation (Rosenberg and Anderson 2011).

## Results

Our measures of landscape connectivity at different spatial grains allowed us to detect that for the species with a smaller natal dispersal distance (Great Spotted Woodpecker) the finest spatial grain (2 × 2 km) models were ranked as top regression models in the AIC framework ($\Delta\text{AICc} < 4$; Table 3, see Table 4 in Appendix 1), whereas this was not the case for the Black Woodpecker, since the top regression models included both types of spatial grains.

As stated before, multicollinearity problems among the independent variables of the same maturation threshold (basal area, intra- and interpatch connectivity) forced us to choose the candidate variables for each model (see Table 2) and, for instance, the models considering interpatch connectivity of a developed maturation threshold (e.g. dbh ≥ 35 cm) could only consider the basal area from the less developed maturation threshold (e.g. dbh ≥ 7.5 cm or dbh ≥ 20 cm).

When analysing the probability of colonization of the Great Spotted Woodpecker, the first top regression model ($\Delta\text{AICc} < 2$; Table 3 and see Table 4 in Appendix 1) had a Nagerkelke $R^2$ of 0.46 and relatively good predictive capacity ($\text{AUC} = 0.79 \pm 0.04$; Table 3). This model showed that the colonization probability of the Great Spotted Woodpecker was smaller away from the colonization source. The effect of interpatch connectivity of the less developed maturation threshold (dbh ≥ 7.5 cm) was positive but depended on the forest structure of the more developed maturation threshold (dbh ≥ 35) (Table 3). Both the distance to the colonization source and interpatch connectivity of the dbh ≥ 7.5 cm maturation threshold (log odds = −0.78 and log odds = 1.56, respectively) seemed to be equally important for the probability of colonization once the former interaction was taken into consideration (log odds = −0.75). The generalist character of the Great Spotted Woodpecker allowed the species to colonize localities not necessarily with more mature forests but well connected in terms of interpatch connectivity of all tally trees regardless of their size (Fig. 2a). Results from the second top regression model for the Great Spotted Woodpecker ($\Delta\text{AICc} < 4$, Nagerkelke $R^2 = 0.44$, $\text{AUC} = 0.78 \pm 0.04$; Table 3; see Table 4 in Appendix 1) roughly agreed with the former ones but now with the

**Table 3** Top regression models ($\Delta\text{AICc} < 4$) for the factors behind the colonization of woodpecker species

| Spatial grain | Species | Model | Null deviance | AICc | Nagerkelke $R^2$ | AUC ± 95 % CI |
|---|---|---|---|---|---|---|
| 2 × 2 km | *D. major* | $1.07 - 0.05\text{SE} - 0.78D + 0.08G_{35} + 1.56\text{varPCflux}_{7.5} - 0.75G_{35} \times \text{varPCflux}_{7.5}$ | 217.19 | 163.58 | 0.46 | 0.79 ± 0.04 |
| 2 × 2 km | *D. major* | $1.05 - 0.06\text{SE} - 0.87D + 0.21G_{35} + 1.33\text{varPCflux}_{20} - 0.72G_{35} \times \text{varPCflux}_{20}$ | 217.19 | 166.84 | 0.44 | 0.78 ± 0.04 |
| 5 × 5 km | *D. martius* | $-1.42 + 0.59\text{SE} - 0.86D + 2.58G_{7.5} + 0.52\text{varPCflux}_{35} - 0.92D \times G_{7.5} + 0.20D \times \text{varPCflux}_{35} - 1.4G_{7.5} \times \text{varPCflux}_{35} - 4.52D \times G_{7.5} \times \text{varPCflux}_{35}$ | 175.89 | 98.05 | 0.69 | 0.91 ± 0.03 |
| 2 × 2 km | *D. martius* | $-1.47 + 0.51\text{SE} - 1.45D + 1.75G_{7.5} + 0.53\ \text{varPCflux}_{35} - 1.28D \times \text{varPCflux}_{35}$ | 175.89 | 101.41 | 0.64 | 0.88 ± 0.03 |

Models were ordered by increasing values of AICc (AIC corrected for small sample sizes). The considered factors were the distance to the colonization source ($D$) and the forest structure [basal area ($G_i$)] and its interpatch connectivity in terms of area-weighted dispersal flux ($\text{varPCflux}_i$) according to three different forest maturation thresholds (*i* 7.5: dbh ≥ 7.5 cm; 20: dbh ≥ 20 cm and 35: dbh ≥ 35 cm). The effects on range expansion were described using generalized linear models (colonization vs. absence). In all the cases differences in sampling effort between atlases were considered (SE) and a backward stepwise selection process was used. AUC was computed following a block cross-validation with 10 % of sample units left out each time (10 blocks) due to the reduced sample size at 10 × 10 km ($n = 147$ for *D. martius* and $n = 161$ for *D. major*)

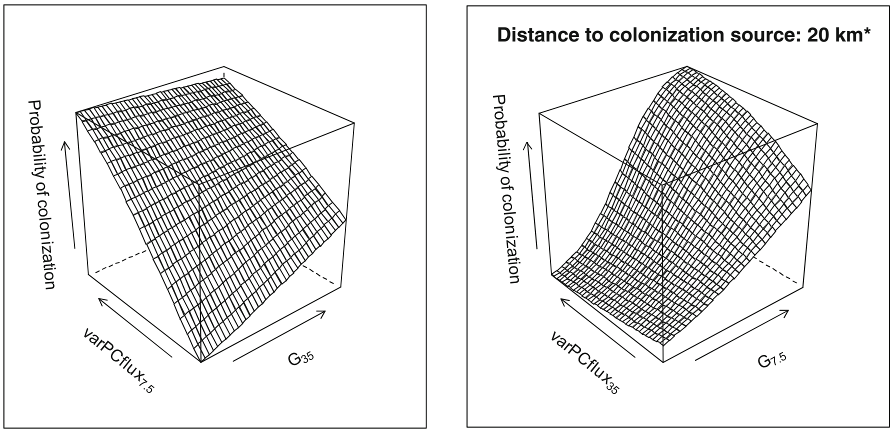
**Table 4** Alternative models for the factors behind the colonization of woodpecker species, ordered by increasing values of AICc (AIC corrected for small sample sizes)

| Spatial grain | Response | Formula | AICc |
|---|---|---|---|
| 2 × 2 | *D. major* | $D, G_{35}, \text{varPCflux}_{7.5}, G_{35} \times \text{varPCflux}_{7.5}$ | 163.58 |
| 2 × 2 | *D. major* | $D, G_{35}, \text{varPCflux}_{20}, G_{35} \times \text{varPCflux}_{20}$ | 166.84 |
| 5 × 5 | *D. major* | $D, G_{35}, \text{varPCflux}_{7.5}, G_{35} \times \text{varPCflux}_{7.5}$ | 168.08 |
| 5 × 5 | *D. major* | $D, G_{35}, \text{varPCflux}_{20}, G_{35} \times \text{varPCflux}_{20}$ | 171.12 |
| 2 × 2 | *D. major* | $D, G_{20}, \text{varPCintra}_{35}, G_{20} \times \text{varPCintra}_{35}$ | 171.53 |
| 2 × 2 | *D. major* | $D, G_{35}, \text{varPCintra}_{20}, G_{35} \times \text{varPCintra}_{20}$ | 172.71 |
| 5 × 5 | *D. major* | $D, G_{20}, \text{varPCflux}_{35}, G_{20} \times \text{varPCflux}_{35}$ | 173.03 |
| 2 × 2 | *D. major* | $D, G_{7.5}$ | 173.64 |
| 5 × 5 | *D. major* | $D, G_{20}, \text{varPCintra}_{35}, G_{2} \times \text{varPCintra}_{35}$ | 175.97 |
| 5 × 5 | *D. major* | $D, G_{7.5}, \text{varPCflux}_{35}, G_{1} \times \text{varPCflux}_{35}$ | 177.32 |
| 5 × 5 | *D. major* | $D, G_{7.5}, \text{varPCintra}_{35}, G_{7.5} \times \text{varPCintra}_{35}$ | 177.69 |
| 5 × 5 | *D. major* | $D, G_{7.5}$ | 178.62 |
| 5 × 5 | *D. major* | $D, G_{35}, \text{varPCintra}_{20}, D \times G_{35}, G_{35} \times \text{varPCintra}_{20}$ | 178.94 |
| 2 × 2 | *D. major* | $\mathrm{D} \times G_{20}$ | 179.35 |
| 2 × 2 | *D. major* | $D, G_{35}$ | 181.08 |
| 5 × 5 | *D. major* | $D, G_{20}$ | 185.77 |
| 5 × 5 | *D. major* | $D, G_{35}$ | 188.55 |
| 2 × 2/5 × 5 | *D. major* | $D$ | 197.88 |
| 5 × 5 | *D. martius* | $D \times G_{7.5} \times \text{varPCflux}_{35}$ | 98.05 |
| 2 × 2 | *D. martius* | $D, G_{7.5}, \text{varPCflux}_{35}, D \times \text{varPCflux}_{35}$ | 101.41 |
| 5 × 5 | *D. martius* | $D \times G_{35} \times \text{varPCflux}_{7.5}$ | 106.15 |
| 5 × 5 | *D. martius* | $D \times \mathrm{G}_{35} \times \text{varPCintra}_{7.5}$ | 110.10 |
| 2 × 2 | *D. martius* | $D \times G_{35} \times \text{varPCflux}_{20}$ | 110.23 |
| 2 × 2 | *D. martius* | $D, G_{20}, \text{varPCflux}_{35}, D \times \text{varPCflux}_{35}$ | 110.42 |
| 2 × 2 | *D. martius* | $D, G_{7.5}$ | 110.49 |
| 5 × 5 | *D. martius* | $D \times G_{7.5} \times \text{varPCintra}_{35}$ | 110.71 |
| 5 × 5 | *D. martius* | $D, G_{7.5}$ | 112.25 |
| 5 × 5 | *D. martius* | $D, G_{20}$ | 114.60 |
| 2 × 2 | *D. martius* | $D, G_{20}$ | 119.42 |
| 2 × 2 | *D. martius* | $D, G_{35}$ | 131.89 |
| 5 × 5 | *D. martius* | $D, G_{35}$ | 136.60 |
| 2 × 2/5 × 5 | *D. martius* | $D$ | 140.38 |

The considered factors were the distance to the colonization source ($D$) and the forest structure [basal area ($G_i$)] and its intra and interpatch connectivity (varPCintra$_i$ and varPCflux$_i$, respectively) according to three different forest maturation thresholds ($i$ 7.5: dbh ≥ 7.5 cm; 20: dbh ≥ 20 and 35: dbh ≥ 35 cm). The effects on range expansion were described using generalized linear models (colonization vs. absence). In all the cases differences in sampling effort between atlases were considered (results not shown) and a backward stepwise selection process was used. When interactions were significant, only the results corresponding to the greater order terms were shown but all the corresponding lower-order terms were considered in the model

interpatch connectivity of the dbh ≥ 20 cm maturation threshold (Table 3; see Fig. 3a in Appendix 2). In this model, the importance of interpatch connectivity of the dbh ≥ 20 cm maturation threshold (log odds = 1.33) was lower than that of distance to the colonization source (log odds = −0.87) when considering the interaction between the former and the basal area of the dbh ≥ 35 cm maturation threshold (log odds = −0.72; Table 3).

In the case of the Black Woodpecker, the first top regression model according to the AICc framework (ΔAICc < 2; Table 3 and see Table 4 in Appendix 1) obtained a Nagerkelke $R^2$ of 0.69 and had an excellent performance in terms of prediction capacity (AUC = 0.91 ± 0.03; Table 3). According to this model, the effect of interpatch connectivity of the dbh ≥ 35 cm maturation threshold on probability of colonization of the Black Woodpecker depended on the basal area of all tally trees regardless of their size (dbh ≥ 7.5 cm) and the distance from the source of colonization in 1980 (Table 3). Within the (median) range of natal dispersal movements (20 km), the probability of colonization of the Black Woodpecker was usually high due to increasing interpatch connectivity in terms of mature forests (dbh ≥ 35 cm) and secondly because of the increasing basal area of the dbh ≥ 7.5 cm maturation threshold, while further (60 km) colonization events were more probable at localities with increasing basal area of the dbh ≥ 7.5 cm maturation threshold. At the intermediate distance from the colonization source (40 km), the triple interaction depicted a transition state (Fig. 2b). The second top regression model for the Black Woodpecker (ΔAICc < 4, Nagerkelke $R^2 = 0.64$, AUC = 0.88 ± 0.03; Table 3 and see Table 4



**(a)** *Dendrocopos major* **(b)** *Dryocopus martius*

*Dryocopus martius* (continued)

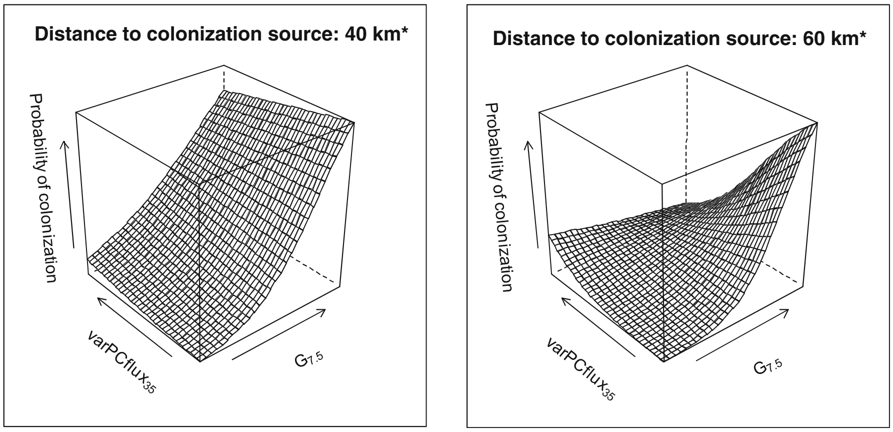


**Fig. 2** Response surface of probability of colonization to the interaction terms for the first top regression models according to the AICc framework ($\Delta$AICc < 2, see Table 3). Probability of colonization was calculated using the mean values of the rest of explanatory variables. The interquartile range of the explanatory variables was shown (see Table 1). *Asterisk* distance to the colonization source according to the first second and third quartiles, respectively. $G_i$ basal area; varPClux$_i$ interpatch connectivity in terms of area-weighted dispersal flux; $i$ forest maturation thresholds (7.5: dbh $\geq$ 7.5 cm and 35: dbh $\geq$ 35 cm)

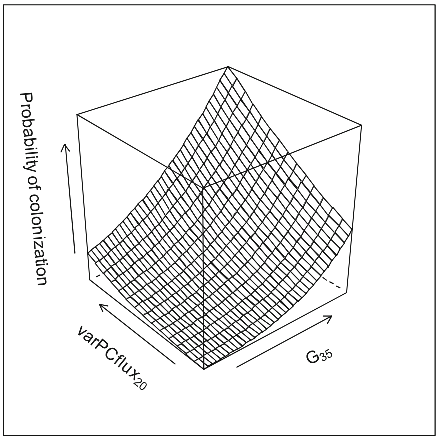
in Appendix 1) indicated that the probability of colonization was higher in those localities with a greater basal area of the dbh $\geq$ 7.5 cm maturation threshold and also depended on the interaction between the distance to the source of colonization and interpatch connectivity of the dbh $\geq$ 35 cm maturation threshold (Table 3), the probability of colonization being greater in the closest localities to the colonization source and with a greater interpatch connectivity of the more developed maturation threshold (see Fig. 3b in Appendix 2). The importance of distance to the colonization source (log odds $= -1.45$) on probability of colonization depended on the interpatch connectivity of the more developed maturation threshold and once this interaction was accounted for (log odds $= -2.73$), its negative effect was more important than the positive effect of the basal area of the dbh $\geq$ 7.5 cm maturation threshold (log odds $= 1.75$) (Table 3).

The spatial autocorrelation of residuals for the top most regression models (Table 3) were only significant ($p = 0.02$ for the Black Woodpecker and $p = 0.001$ for the Great Spotted Woodpecker) at the first lag distance (<15 km) which encompasses residuals of the immediate neighbours (a maximum of eight according to the atlas data).

## Discussion

Results reflected the species habitat requirements in terms of interpatch connectivity; the less developed maturation thresholds (dbh $\geq$ 7.5 cm and dbh $\geq$ 20 cm) were more relevant for the Great Spotted Woodpecker, which is the species with fewer constraints in terms of nest tree size. On the contrary, Black Woodpeckers nest in trees with dbh $\geq$ 35 cm and this was reflected in our results since the most determinant interpatch connectivity was that of the dbh $\geq$ 35 cm maturation threshold. Therefore, according to the modelling approach, the former models fairly matched the different habitat requirements of the considered woodpecker species in terms of interpatch connectivity. In addition, intrapatch connectivity (the amount of available habitat within the colonized sites) was not a priori an important factor influencing the probability of colonization. Nevertheless, it is worth noting that a surrogate of

**(a)** *Dendrocopos major*



**(b)** *Dryocopus martius*

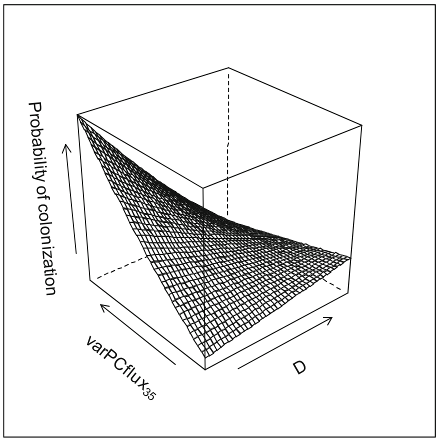


**Fig. 3** Response surface of probability of colonization to the interaction terms for the second top regression models according to the AICc framework ($2 < \Delta\text{AICc} < 4$, see Table 3). Probability of colonization was calculated using the mean values of the rest of explanatory variables. The interquartile range of the explanatory variables was shown (see Table 1). *D* distance to the colonization source; $G_i$ basal area; varPCflux$_i$ interpatch connectivity in terms of area-weighted dispersal flux; *i* forest maturation thresholds (7.5: dbh $\geq$ 7.5 cm; 20: dbh $\geq$ 20 cm and 35: dbh $\geq$ 35 cm)

intrapatch connectivity is the basal area, so the models obtained elucidated the importance of both intra- and interpatch connectivity for colonization events, especially the latter, which is in accordance with our study hypothesis.

The probability of colonization of the Great Spotted Woodpecker was better predicted by the finer spatial grain considered (2 × 2 km), while for the Black Woodpecker this was not so determinant, since it is the species with the greater dispersal capacity. Previous research has modelled range changes as a function of a more simplified approach that averaged forest structure variables on neighbouring localities at different spatial scales without considering species dispersal capacities and spatial grain issues (Gil-Tena et al. 2010). Scale issues concerning spatial grain impact on connectivity analysis have not often been considered in previous studies (but see Pascual-Hortal and Saura 2007), although landscape connectivity results from the interaction between species dispersal behaviour and landscape grain (Baguette and Dyck 2007). When dispersal abilities are high enough to perceive the entire habitat as wholly connected it would be possible to disperse directly among every pair of patches in the landscape and the existing stepping stones would play a less relevant role for upholding habitat connectivity and availability (Saura and Rubio 2010). Results concerning the spatial grain relevance according to the species dispersal capabilities agree with a previous study that showed that at large hypothetical dispersal distances, connectivity metrics based on the habitat availability (reachability) concept were less sensitive to the spatial grain size of analysis (Pascual-Hortal and Saura 2007). Nevertheless, we acknowledge that the approach followed to consider the influence of analytical spatial grain of connectivity analysis is constrained by the coarse spatial resolution of the bird atlas data (10 × 10 km). Variation coefficients of interpatch connectivity measures at 5 × 5 km for the Black Woodpecker are extremely high (Table 1), particularly if they are compared to those at 2 × 2 km. For this species, the smaller spatial extent considered (see Fig. 1) would also favour data variability at 5 × 5 km.

Significant spatial autocorrelation in model residuals was still detected in the immediate neighbourhood, particularly for the Great Spotted Woodpecker. This could be indicating that other non-considered (non-available) variables at the scale of study influence woodpecker colonization. This could be the case of detailed biotic information such as population density in the colonization sources or other data reflecting endogenous processes besides those considered through the distance to the colonization source in 1980 (Edman et al. 2011; Vallecillo et al. 2010) or limiting factors for woodpeckers such as the amount of dead trees and trophic resources (Estrada et al. 2004; Camprodon et al. 2007). In fact, foraging substrates could be very limiting to the woodpecker's distributions. Whereas the Black Woodpecker is an insectivore and above all an ant-eater (in some areas ants may comprise 97 % of its diet in summer), the Great Spotted Woodpecker is an omnivore, although insects (both wood-dwelling and surface-living) are the main food sources in all seasons (Gorman 2004). Carpenter ants do not seem to limit the distribution of the Black Woodpecker since the species does not feed exclusively on carpenter ants (Gorman 2011), although for both species the winter diet focuses on invertebrates taken from dead wood (Gorman 2004, 2011; Herrando et al. 2011). Therefore, we cannot exclude the possibility that foraging substrates are more limiting than nesting ones in our study area. Nevertheless, our modelling approach allowed us to grasp the importance per se of forest maturation and its connectivity, which can be considered an indicator of foraging resources for woodpecker colonization. Accounting for matrix characteristics could also be important for improving the modelling of Great Spotted Woodpecker colonization due to its lower dependence on forest habitats (Gil-Tena et al. 2007) and poorer dispersal capacities (Saura et al. 2011), although network connectivity analysis accounting for matrix effects is controversial and has been criticised (Rayfield et al. 2010). Alternatively, adding an autocovariate reflecting the number of occupied neighbouring atlas squares (e.g. Melles et al. 2011) or computing conditional autoregressive models would contribute to improve model performance. Yet, this modelling solution would not contribute to disentangle the role of connectivity in woodpecker colonization, which has been confirmed due to the robustness of the top regression models according to the set of models evaluated in the AIC framework (see Table 4 in Appendix 1).

### Disentangling the relative effects of different factors affecting woodpecker colonization

The approach followed here allowed us to depict how woodpeckers have expanded to those localities near the colonization source and with a high reachability of potential nest trees according to their dispersal capabilities. Previous studies in the region focusing on the colonization of open-habitat species after fires have shown that the distance to the colonization source is crucial for explaining their expansion independently from post-disturbance habitat availability, hypothesizing the key role of short-distance dispersal near the colonization source (Brotons et al. 2005, 2008). Higher natal dispersal capabilities have also been shown to boost population trends of breeding birds facing global change (Jiguet et al. 2007). In this study, the potential effect of dispersal influence on colonization of new habitats has been highlighted by means of the good prediction capability of interpatch connectivity. Forest maturation in Catalonia has been described as a regional process, representing an increment of 27 % in terms of basal area from the 10-year period between NFIs (1989–2001; Gil-Tena et al. 2009). On one hand, this maturation has certainly increased the basal area and habitat availability during the period elapsed between atlases (20 years) and probably prevented major constraints regarding short-distance dispersal according to the species requirements. On the other hand, increased habitat maturation could also represent an increasing source of feeding, nesting or foraging substrates as has been hypothesised for other birds after successful expansion thanks to large-scale favourable changes in vegetation structure due to increasing disturbance occurrence (Brotons et al. 2008). When habitat conditions are favourable populations are healthy and, therefore, could produce a surplus of dispersing individuals which will compete for the closest available territories and eventually move far away because of lack of non-occupied habitat or other endogenous factors such as inbreeding avoidance (Tittler et al. 2009).

If distance to the colonization source is not a major constraint, future range expansion rates such as those observed from 1980 to 2000 will mainly depend on habitat availability and lack of dispersal constraints. Nevertheless, as shown for the Black Woodpecker, a high probability of colonization at further distances from the colonization source is mainly related to a high basal area, indicating that an expansion is still possible but the colonization rates may not be maintained due to a smaller interpatch connectivity. It is in the range periphery where the limiting factor for species distributions is the paucity of suitable habitat embedded in an increasing hostile matrix and, therefore, dispersal limitations play a key role in shaping species distributions (Vallecillo et al. 2010; Barbet-Massin et al. 2012). In a patchy-poor connected environment, the most likely way to arrive at suitable habitat patches is stochastic, long dispersal (Brotons et al. 2005). Nevertheless, not only ecological processes but also evolutionary processes could mediate species range expansion (Thomas et al. 2001; Holt 2003). For instance, the Black Woodpecker has significantly expanded its range during the twentieth century in Europe, occupying a wide range of new regions with contrasted habitats (Cuisin 1985). In France, until 1950 the Black Woodpecker was confined to the mountainous areas and since then it has reached the western part of France. Therefore, we cannot discard an ongoing expansion of woodpeckers if evolutionary processes also mediate range expansion. Ongoing monitoring programs such as breeding bird atlases and continuous forest inventories will provide more clues regarding this issue.

### Landscape forest management implications in a global change context

Our results underline the need to explicitly consider landscape connectivity criteria as well as a multifunctional perspective when managing Mediterranean forests. There are two specific management guidelines arising from this study and they agree with other management guidelines aimed at enhancing woodpecker conservation in Catalonia (Camprodon et al. 2007). The first one entails forest management reconciliation with landscape connectivity criteria and forest structure development, allowing for a high interpatch connectivity of the most mature stands (dbh $\geq$ 35 cm) in order to preserve current range and population viability of the Black Woodpecker. This guideline goes against one of the most applied management practices in the region, high-grading. High-grading is often applied by private owners in Catalonia, who own about 80 % of the total forest area, with an average ownership size of 20 ha (Terradas et al. 2004). In fact, large-diameter trees (dbh $\geq$ 50 cm) have been shown to increase less in private than in public forests when comparing NFIs (Torras et al. 2012). In a less profitable wood market that competes with foreign markets, landscape forest management and planning by means of promoting ownership associations could be a solution not only for the forestry sector but also for biodiversity conservation. As pointed out by Camprodon et al. (2007), favouring forest structures with well-developed trees will also prevent wind and snow damage through more stable forest structures. These damage events are increasingly more prone to occur in the region and depleted forest structures are under higher risk (Martín-Alcón et al. 2010).

The second management guideline emphasizes the increasing need to consider and solve the conflicts among management practices to prevent wildfires and biodiversity conservation in the most fire-prone regions of Catalonia (Camprodon and Brotons 2006). It is based on the models for the Great Spotted Woodpecker regarding the species requirements in terms of minimum nest tree size (dbh $\geq$ 14–16.5 cm) and the influence on its colonization of connectivity of the less developed forest patches (dbh $<$ 35 cm). Connectivity needs to be enhanced to promote forest species persistence but at the same time it should be controlled for other processes such as when facing the risk of forest fires spread over large areas. Forest management has a potential role to play in mitigating the effects of climate change in the Mediterranean through modifying wildfire behaviour (De Dios et al. 2007). Some of the applied silvicultural treatments aimed at fire prevention consist in decreasing the density of forest with a large amount of small trees and increasing landscape heterogeneity through different stand age interspersions. Improvement treatments such as cleaning, thinning, and pruning may be compatible with forest development while decreasing fire hazard; this would be particularly true in dense forests when thinning treatments are applied (Torras et al. 2012). Fires are not of major concern for this woodpecker species (Estrada et al. 2004; Gil-Tena et al. 2010), so at least distance to colonization sources should be minimized according to short-distance dispersal when applying silvicultural treatments focused on fire prevention in order to guarantee potential dispersers (e.g. Brotons et al. 2005, 2008).

## Conclusions

Overall, the selection of different forest maturation thresholds and the analytical spatial grains according to data availability and species dispersal capabilities highlighted the importance to consider species habitat requirements to assess the role of forest connectivity from a functional point of view. Woodpecker colonizations in Catalonia correlated with distance to the colonization source and habitat availability (reachability). Under favourable conditions, woodpecker colonization can be envisaged as a diffusion process from the colonization source with fewer dispersal constraints due to high inter-patch connectivity fairly matching habitat requirements in terms of size of nest trees. From these results some management guidelines were provided, focusing on the need to consider a multifunctional and landscape perspective in terms of connectivity patterns in order to preserve forest biodiversity while facing the manifold challenges of global change processes impacting Mediterranean forests.

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## Appendix 1

See Table 4.

## Appendix 2

See Fig. 3.

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