

# Presence and abundance of the Eurasian nuthatch *Sitta europaea* in relation to the size, isolation and the intensity of management of chestnut woodlands in the NW Iberian Peninsula

Juan P. González-Varo · José V. López-Bao · José Guitián

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**Abstract** Throughout most of the north-west Iberian Peninsula, chestnut (*Castanea sativa*) woods are the principal deciduous woodland, reflecting historical and ongoing exploitation of indigenous forests. These are traditionally managed woodlands with a patchy distribution. Eurasian nuthatches (*Sitta europaea*) inhabit mature deciduous woods, show high site fidelity, and are almost exclusively found in chestnut woods in the study area. We studied the presence and abundance of nuthatch breeding pairs over two consecutive years, in relation to the size, degree of isolation and intensity of management of 25 chestnut woods in NW Spain. Degree of isolation was assessed in view of the presence of other woodland within a 1-km band surrounding the study wood. Wood size was the only variable that significantly predicted the presence of breeding pairs (in at least one year,  $R^2 = 0.69$ ; in both years,  $R^2 = 0.50$ ). The number of pairs was strongly predicted by wood size,

isolation and management ( $R^2 = 0.70$  in 2004;  $R^2 = 0.84$  in 2005); interestingly, more isolated woods had more breeding pairs. Breeding density was likewise significantly or near-significantly ( $P \leq 0.1$ ) higher in small isolated woods, which is possibly attributable to lower juvenile dispersal in lightly forested areas and/or to lower predator density in smaller and more isolated patches. Breeding density was higher (though not significantly so) in more heavily managed woods, possibly due to the presence of larger chestnut crops and larger trees (with higher nuthatch prey abundance). Our findings highlight the complexity of the relationships between the patch properties and the three studied levels (presence, number and density of pairs), and also the importance of traditionally managed woodlands for the conservation of forest birds.

**Keywords** Habitat fragmentation · *Sitta europaea* · Forest birds · Traditional management · *Castanea sativa* · Presence · Number of pairs · Breeding density · Habitat quality

J. P. González-Varo (✉)  
Dep. Biología Vegetal y Ecología, Universidad de Sevilla,  
C/ Profesor García González n 2, 41012 Sevilla, Spain  
e-mail: juanpe@us.es

J. V. López-Bao  
Estación Biológica de Doñana, CSIC, Avenida de Maria  
Luisa s/n, Pabellón del Perú, 41013 Sevilla, Spain

J. Guitián  
Dep. Bioloxía Celular y Ecoloxía, Universidade de  
Santiago, Facultade de Bioloxía s/n, Campus Sur, 15782  
Santiago de Compostela, Spain

## Introduction

Many bird species are highly selective as regards habitat type and vegetation structure at various scale-levels (Ambuel and Temple 1983; Cody 1985). This implies that landscape-scale vegetation can predict bird species distributions at the regional level

(Seoane et al. 2004). Over the last two decades, various studies have addressed the influence of anthropic forest fragmentation on bird diversity and abundance (Ambuel and Temple 1983; Howe 1984; Haila et al. 1993; Hinsley et al. 1995; Trzcinski et al. 1999; Villard et al. 1999; Bellamy et al. 2000; Santos et al. 2002; Ferraz et al. 2007). Some of these studies have shown the importance of wood size and quantity of woodland in the landscape for determining the presence of forest bird species. However, the effect of degree of isolation is controversial: unless isolation is very pronounced, it does not seem to have uniform effects on bird diversity and abundance (reviewed in Fahrig 2003). Recently, besides size and isolation, habitat quality (i.e., species-specific key resources; sensu Morrison 2001) has started to be included in models of populations in fragmented landscapes, as an important determinant of the persistence of some species in habitat patches (see, e.g., Verboom et al. 1991; Zanette 2001; Franken and Hik 2004; Alderman et al. 2005).

Throughout most of the north-west Iberian Peninsula, indigenous mature forests (e.g., *Quercus robur*, *Fagus sylvatica*, etc.) have been intensively exploited and are currently very scarce. Traditionally, these habitats have been replaced with meadows and farmland, and more recently with dense plantations of conifers and *Eucalyptus* species. A traditional formation in this region is the chestnut (*Castanea sativa*) grove, surrounding small villages and managed for sweet chestnuts and timber. These woodlands are typically comprised of large chestnut trees, many of them well over 200 years old. This is the most important remaining deciduous woodland type (by age, area and conservation) in this region, and for centuries has in many respects acted as a substitute for the indigenous deciduous forests throughout most of NW Spain. These woods provide habitat for a diverse community of forest birds, some of them almost exclusively found in this habitat (Gutián et al. 2004).

Eurasian nuthatches (*Sitta europaea*) are small resident birds of mature broadleaved woodlands. They live in territories of 1–3 ha that they maintain in pairs throughout the year for feeding and breeding (Cramp and Perrins 1993). They nest in natural holes in large trees or in holes previously used by woodpeckers (Picidae). Only young birds disperse, and dispersal distances range from 1 km in

continuous forest to more than 3 km in highly fragmented landscapes (<2% of forest cover) (see Matthysen and Schmidt 1987; Matthysen et al. 1995; van Langevelde 2000). Due to its strict forest dependence, the response of the nuthatch to forest fragmentation has been assessed in a number of studies in Central and Northern Europe (Verboom et al. 1991; Matthysen et al. 1995; Opdam et al. 1995; Matthysen and Currie 1996; Bellamy et al. 1998; Matthysen 1999; van Langevelde 2000; Alderman et al. 2005). These studies have generally been performed in highly deforested lowlands, and have shown the negative effects of forest fragmentation on nuthatches, including the species' presence restricted to isolated woods, scarce presence of breeding in small woods ( $\leq 10$  ha), lower abundance in small woods than in continuous forest, and the limitation of highly fragmented landscapes for supporting viable populations without external immigration.

In the present study, we investigated the presence and abundance of breeding pairs of nuthatches in traditionally managed chestnut woods in a mountainous area of NW Spain, over two consecutive years. We used two measures of isolation, the first considering only high-quality woodlands, the second considering all woodland habitats in the surrounding landscape. Low-habitat-quality areas can be seen as “grey zones”, increasing habitat heterogeneity and possibly very important for the connectivity of high-quality habitats (Haila 1993; Debinski 2006).

The study considers three principal hypotheses:

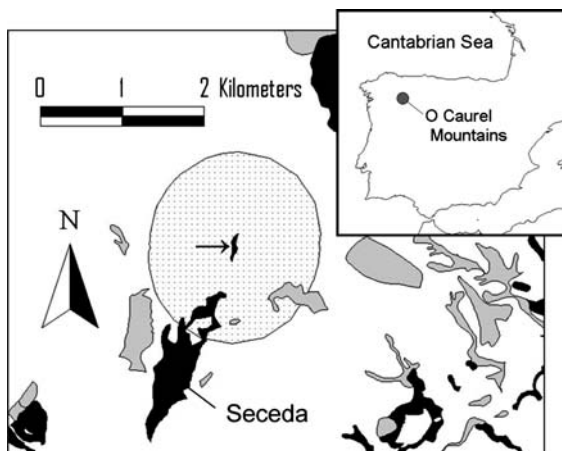
- (1) Breeding nuthatches have a higher probability of presence in larger and less isolated woods than in smaller and more isolated ones.
- (2) Wood size, habitat quality and degree of isolation determine both number and density of breeding pairs, the first two factors with positive effects and the third with negative effects.
- (3) The degree of isolation from woodland habitats in general (i.e., both high and low quality) is more important in determining the presence of breeding pairs, while the degree of isolation from high-quality habitats is more important in determining the *abundance* of breeding pairs (absolute number and density).

## Methods

### Study area

The study was carried out in the O Caurel Mountains, a montane area located in the province of Lugo in NW Spain (Fig. 1), extending over about 400 km<sup>2</sup>. Most of the territory ranges between 800 and 1,300 m a.s.l., and slopes are very pronounced. Currently, about 20% of the area is covered by woodland, the rest by agricultural fields and heathland. The most common woodland types are chestnut wood and patches of oak wood dominated by young *Quercus pyrenaica*; these two types make up most of the woodland cover, with very similar proportions (each occupying about 8% of the territory). Mature deciduous forest (*Fagus sylvatica*, *Quercus petraea* and *Q. robur*) and conifer plantations are also present, in similar proportions (3 and 2% of the territory, respectively) (coverages obtained from A. Larrinaga, I. Pulgar and M. Maceira, unpublished digital map).

There is usually little or no understorey in the chestnut woods, although some bilberry (*Vaccinium myrtillus*), bramble (*Rubus caesius*), hazel (*Corylus avellana*), rowan (*Sorbus aucuparia*) and other shrubs can be found in less managed areas. The chestnut woods showed considerable variation in size, location



**Fig. 1** Geographical location of the O Caurel Mountains, and map illustrating definition of a 1-km buffer area around a chestnut (*Castanea sativa*) wood (→). Mature woods of high habitat quality for the breeding of Eurasian nuthatches (*Sitta europaea*) (chestnut woods and deciduous mixed forest) are shown in black. Low-quality woods (young oak patches and pine plantations) are shown in grey. Non-forested habitat is in white

and degree of isolation, giving rise to an “archipelago” of forest fragments throughout the study area.

### Selection and characterization of woods

Of the 85 chestnut woods currently present in the study area, we have chosen 25 sample woods that differed in size and degree of isolation. Based on a very detailed vegetation map of the study area (A.L., I.P. and M.M., unpublished digital map), we obtained (using the GIS package ArcView 3.2; ESRI 1999) the following data on the selected woods: wood size (Area), perimeter–area ratio (P/A), a shape complexity index (Decirc; Turner et al. 2001) which gives values equal to 1 when wood shape is similar to a circle and larger values with more irregular shapes, and two indices of “buffering” (the degree to which the wood is surrounded by other woodland habitats, i.e., the inverse of isolation) (Bender et al. 2003). The indices of buffering were obtained on the basis of the known dispersal distances of the nuthatch (see Introduction), taking into account buffer bands (1 km width) from the edge of each wood, and calculating (1) the area within the buffer band occupied by chestnut woods and mature mixed forest (high-quality woodland buffer,  $B_{HQ}$ ), and (2) the area within the buffer band occupied by any woodland type (total woodland buffer,  $B_{Total}$ ). For calculation of these indices, woodland quality was evaluated in line with the classification proposed by B. Enoksson and A.G.M. Schotman (unpublished), on the basis of tree size, species composition and food availability (nuts, acorns, etc.) (cited in Bellamy et al. 1998). Specifically, chestnut woods fall into the “excellent” category (5) that is the maximum habitat quality for the breeding nuthatch. The young oak patches would be in the lower categories (2 or 3), mainly in view of the small size of the trees (DBH < 20 cm, personal observation), while the dense conifer plantations would be in the lowest categories (0 or 1), representing poor or very poor breeding habitat (Bellamy et al. 1998). Thus, our index  $B_{HQ}$  basically considers only woodland suitable for breeding, while  $B_{Total}$  is a wider index of all woodland habitats, and thus of connectivity. Note that  $B_{HQ}$  and  $B_{Total}$  are inverse to the degree of isolation: in other words, the more forest area within the buffer band, the less isolated is the wood (see Fig. 1).

Chestnut tree morphology in the study area is strongly dependent on anthropic management: pruning generates very large trunks with several pollards and broad crowns, while non-pruned trees have thinner trunks and narrower crowns. In each wood, we measured the diameter at breast height (DBH) and pruning height (Height) of 30 randomly selected adult trees with DBH > 20 cm (or of all trees in those woods comprising fewer than 30 trees), and average DBH and Height values were thus obtained for each wood. Based on morphology, we also calculated the percentage of managed trees (%MT) among the 30 trees measured.

#### Nuthatch census

Each wood was visited twice during the period 15 April–10 May 2004 and 2005 (two visits per year), except for one wood, which was visited only in 2005. All visits were by the same observer. The censuses consisted of estimation of the number of breeding pairs by means of 10-min point counts separated by about 200 m, throughout the whole area (Gibbons et al. 1996). The number of points ranged from 1 to 30, depending on the size of the wood, with the aim of obtaining proportionally similar sampling effort. Additionally, the observer walked routes between the census points to establish and differentiate the territories of the located pairs. The birds were detected by call or by direct observation. A pair was counted when it was directly observed, when a nest was found, or when a single bird was observed carrying food or nesting material in the bill. If, after the census, the species had not been detected, playback of the male call was used to confirm absence. Because nuthatches are conspicuous and vocal, with loud and very distinctive calls and male song, and because the absence of leaves on the trees allowed good visibility, we think there is a very low probability that pairs were missed in our censuses. Using this procedure, for each wood we estimated the number of breeding pairs ( $N_p$ ) and breeding density (Bd, i.e.,  $N_p/\text{Area}$ ).

#### Statistical analyses

The statistical significance of between-year differences in number of pairs and in breeding density was assessed by Wilcoxon matched pair tests.

Relationships between presence/absence of breeding pairs and wood size and degree of isolation were analyzed by simple logistic regressions, with presence of pairs in at least one year or in both years as the dependent variable, and wood size (Area) and the two buffering indices ( $B_{\text{HQ}}$  and  $B_{\text{Total}}$ ) as predictor variables. To evaluate the explanatory power of the logistic models we calculated an analogue of standard  $R^2$ , which can be interpreted in a similar way as in standard regressions  $R^2$  (Christensen 1990; see, e.g., Desrochers and Hannon 1997).

Relationships between the number of breeding pairs and wood characteristics were analyzed using generalized linear models (GLM), with the number of pairs (in 2004 or 2005) as the response variable, and wood characteristics as predictor variables. Model selection was based on the Akaike information criterion (AIC), which estimates the improvement in fit with addition of variables (Quinn and Keough 2002). Given the AIC of the different models, we obtained the AIC difference ( $\Delta\text{AIC}$ ) for each model, calculated as the difference between the AIC value of that model and the minimum AIC value obtained.  $\Delta\text{AIC}$  values of 2 or less indicate models well fitted to the data (Burnham and Anderson 2002). Correlation matrices were first constructed for the wood characteristics variables, to avoid inclusion of highly correlated variables (Pearson's  $r > 0.55$ ) in the analyses.

Relationships between breeding density and characteristics of those woods where the nuthatch was breeding were assessed by Spearman rank correlation analysis. We did not use GLM to analyse these relationships due to the small sample size when only considering occupied woods.

All analyses were performed with the software STATISTICA v.6 (StatSoft 2001).

## Results

### Wood characteristics

Table 1 shows descriptive statistics for the variables measured in the 25 woods studied. Area ranged from 0.5 to 70 ha and was strongly correlated with the two shape indices, P/A ( $r = -0.79$ ,  $P < 0.001$ ) and Decirc ( $r = 0.73$ ,  $P < 0.001$ ). Thus, the smaller the wood, the higher the P/A ratio and the rounder the shape.

**Table 1** Descriptive statistics of the 25 chestnut (*Castanea sativa*) tree woods in O Caurel, NW Spain

Variables	Mean (±SD)	Minimum	Maximum
Area (ha)	19.6 (±21.2)	0.5	70.8
P/A	281 (±142.6)	93.8	556.3
Decirc	2.07 (±0.73)	1.09	4.24
$B_{HQ}$ (ha)	30.8 (±28.2)	0	102.6
$B_{Total}$ (ha)	93.3 (±72.8)	10	284.2
DBH (cm)	90.6 (±18.2)	52.2	132.6
Height (cm)	278.9 (±56.7)	180	405
%MT	63.7 (±20.4)	10	100

Area, wood size; P/A, Perimeter/area ratio; Decirc, shape complexity index;  $B_{HQ}$  and  $B_{Total}$ , buffering indices; DBH, diameter at breast height; Height, pruning height; %MT percentage of managed trees

Area was not correlated with either of the buffering indices,  $B_{HQ}$  or  $B_{Total}$  ( $r = 0.26$  and  $r = 0.29$ ,  $P > 0.1$  in both cases). The two buffering indices were correlated ( $r = 0.62$ ,  $P = 0.001$ ), as expected given that  $B_{Total}$  includes all woodland included in  $B_{HQ}$ . Percent MT was only significantly correlated with Area ( $r = 0.49$ ,  $P < 0.05$ ). DBH and Height were correlated with each other ( $r = 0.54$ ,  $P < 0.001$ ), but not with any other variable ( $P > 0.05$ ).

P/A and Decirc were excluded from all subsequent analyses to avoid collinearity with Area. Due to the high correlation between the two buffering indices,

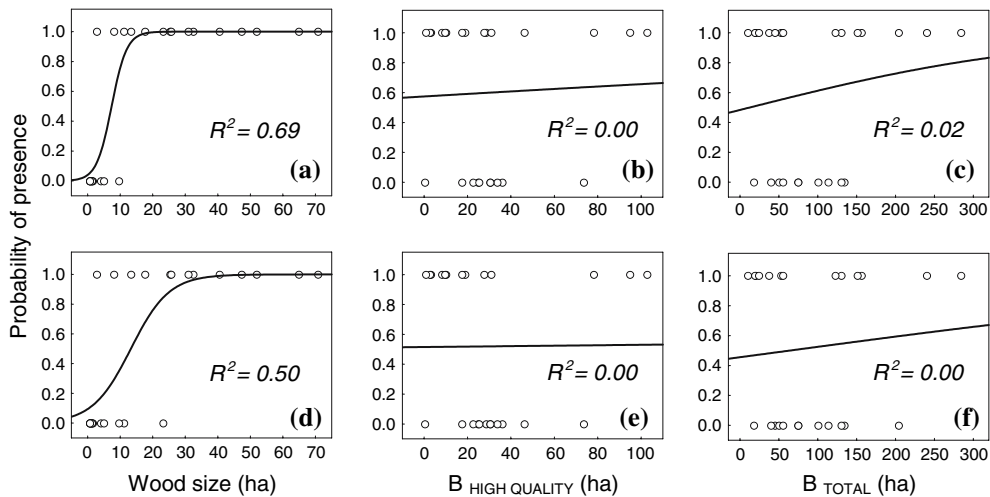
we performed a first regression with both and then excluded the worst predictor of the two from the GLM analysis of number of pairs.

Occupancy of woods

During the spring of 2004, 13 of the 24 studied woods were occupied by nuthatches, versus 15 of 25 in 2005. We recorded two colonization events (i.e., presence in woods not occupied the previous year) and no local extinctions (i.e., absence in a wood previously occupied) in 2005 with respect to 2004. The 17% of woods with area below 10 ha were occupied by nuthatches in both years ( $n = 12$ ); among the woods with area over 10 ha ( $n = 13$ ), 85% were occupied in 2004 and 100% in 2005. Area was the best predictor of the presence of breeding pairs in at least one year ( $R^2 = 0.69$ ) and in both years ( $R^2 = 0.50$ ; Fig. 2), with a high level of significance in both cases ( $P \ll 0.001$ ). However, neither of the buffering indices significantly predicted the presence of breeding pairs (Table 2, Fig. 2).

Number of pairs

Overall, 43 pairs were recorded in the 24 woods visited in 2004, and 45 pairs in the 25 woods visited



**Fig. 2** Logistic regressions showing relationships between wood size and the two measures of buffering (high-quality buffer  $B_{HQ}$  and total buffer  $B_{Total}$ ) and the probability of

continuous presence of breeding pairs of nuthatches in at least one year (a, b, c) and in both years (d, e, f) of the study

**Table 2** Chi-square values in logistic regressions for prediction of presence of breeding pairs of Eurasian nuthatches (*Sitta europaea*) (in at least one or in both years) from size (*Area*) and degree of isolation ( $B_{\text{HQ}}$  and  $B_{\text{Total}}$ ) of chestnut woods

Variable	One year	$R^2$	Both years	$R^2$
Area	23.47 ***	0.69	17.43 ***	0.50
$B_{\text{HQ}}$	0.054 ns	0.00	0.001 ns	0.00
$B_{\text{Total}}$	0.75 ns	0.02	0.24 ns	0.00

$n_{\text{one}} = 25$ ,  $n_{\text{both}} = 24$ ;  $\text{df} = 1$

\*\*\* $P < 0.001$

ns,  $P > 0.05$

in 2005. All birds were apparently paired, except for a single male observed only once in a wood without recorded breeding in either year. The number of breeding pairs ( $N_p$ ) in the woods was very similar in 2004 and 2005 ( $r = 0.96$ ,  $P \ll 0.001$ ), with no differences between the two years ( $Z = 0.533$ ,  $P > 0.1$ ). All the models selected based on  $\Delta\text{AIC}$  included Area and high-quality buffer  $B_{\text{HQ}}$  as the best predictors, with very similar results for 2004 and 2005. Moreover, %MT was included in 2 of the 5 models for 2004, and in all models for 2005 with  $\Delta\text{AIC} \leq 2$  (Table 3). The models explained a substantial proportion of the variance in  $N_p$  ( $R^2 = 0.68$ – $0.84$ ), with a high level of significance ( $P \ll 0.001$ ).

Area was the best predictor of  $N_p$  in both years (Table 3, Fig. 3).  $B_{\text{HQ}}$  was the second-best predictor in both years, but this variable appears to be

negatively related with number of pairs (i.e., higher  $N_p$  when there is less chestnut and other high-quality woodland in the surrounding landscape). When we used  $B_{\text{Total}}$  instead of  $B_{\text{HQ}}$  for model building,  $B_{\text{Total}}$  was again included as the second-best predictor, although with a lower significance level than  $B_{\text{HQ}}$ . %MT was positively associated with  $N_p$ , although this relationship was not statistically significant in 2004 ( $P > 0.05$ ).

### Breeding density

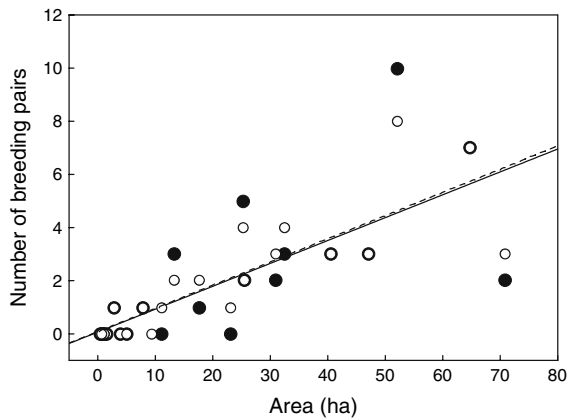
Breeding density (Bd) of nuthatches in the studied woods ranged between 0.3 and 3.4 pairs/10 ha. Bd values were very similar in 2004 and 2005 ( $r = 0.94$ ,  $P \ll 0.001$ ), so there were no differences between years ( $Z = 0.652$ ,  $P > 0.1$ ). Bd showed a negative relationship with Area and with the two buffering indices ( $B_{\text{HQ}}$  and  $B_{\text{Total}}$ ) (Table 4): in other words, Bd was higher in smaller and more isolated woods (Fig. 4). The correlation with Area was only marginally significant in both years ( $0.05 < P \leq 0.1$ ), while the correlation with the buffering indices was nonsignificant ( $B_{\text{HQ}}$ ) or marginally significant ( $B_{\text{Total}}$ ) in 2004, but in both cases significant in 2005 ( $P < 0.05$ ) (Table 4). Moreover, Bd showed apparently positive relationships with DBH and %MT, although none of these correlations were statistically significant (Table 4).

**Table 3** Generalized linear models of factors affecting number of pairs of nuthatches in 2004 and 2005. Models were ranked in each case by AIC from best- to worst-fitting model, and only

Year	Predictors in model						$R^2$
	Area (ha)	$B_{\text{HQ}}$	%MT	DBH	Height	$\Delta\text{AIC}$	
2004	0.836	-0.399				0	0.68
	0.746	-0.367	0.170			0.3	0.70
	0.792	-0.390			0.091	1.5	0.69
	0.822	-0.392		0.043		1.8	0.69
	0.717	-0.362	0.161		0.071	2.0	0.71
2005	0.812	-0.282	0.217			0	0.84
	0.819	-0.287	0.217	-0.032		1.8	0.84
	0.810	-0.282	0.217		0.003	2.0	0.84

Area, wood size;  $B_{\text{HQ}}$ , area of high-quality woodland within 1 km; %MT, percentage of managed trees; DBH, diameter at breast height; Height, pruning height

$n_{2004} = 24$  and  $n_{2005} = 25$



**Fig. 3** Relationship between wood size and the number of breeding pairs of nuthatches. *Filled circles and solid line* represent 2004 data; *open circles and dashed line* 2005 data

**Discussion**

**Occupancy of woods**

Wood size was the only variable that predicted the occupancy of woods by breeding nuthatches (i.e., presence/absence). Opdam et al. (1995), in a study in the Netherlands, found that even with optimal habitat, nuthatches were breeding in only a subset of woods smaller than 10 ha, while all woods larger than 10 ha

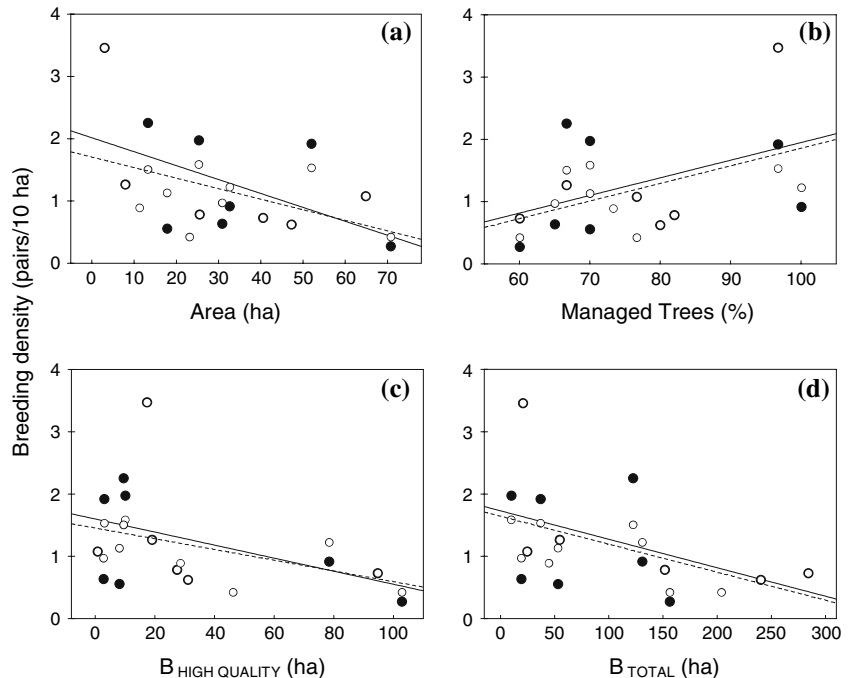
**Table 4** Values and significance level of the Spearman rank correlation between breeding density of nuthatches (Bd) and the wood characteristics where the species were present

Variable	Bd <sub>2004</sub>		Bd <sub>2005</sub>	
	<i>R<sub>s</sub></i>	<i>P</i>	<i>R<sub>s</sub></i>	<i>P</i>
Area (ha)	-0.51	0.074	-0.43	0.101
<i>B<sub>HQ</sub></i>	-0.33	0.271	-0.58	0.023
<i>B<sub>Total</sub></i>	-0.50	0.081	-0.71	0.003
%MT	0.38	0.195	0.31	0.266
DBH	0.34	0.231	0.16	0.576
Height	0.02	0.943	<0.01	0.989

*n*<sub>2004</sub> = 13 and *n*<sub>2005</sub> = 15

had breeding pairs. Our results are rather similar in spite of the very different geographic location, woodland type and topography. These findings suggest that this species’ breeding presence in woods is basically determined by its territorial requirements alone, but this is only expected to be the case when the degree of isolation does not limit re-occupation of empty woods after a local extinction (Hanski 1998). The low carrying capacity of woods smaller than 10 ha, usually sufficient only for a single pair, suggests that these are likely to have a higher local extinction risk and higher frequency of colonization/

**Fig. 4** Relationships between wood size (a), percentage of managed trees (b) and the two measures of buffering (*B<sub>HQ</sub>*, c, and *B<sub>Total</sub>*, d; see Methods), and the breeding density of nuthatches. For descriptive purposes only, least squares regression lines are shown. *Filled circles and solid line* represent 2004 data; *open circles and dashed line* 2005 data



extinction than larger woods (Verboom et al. 1991). In line with this, when we considered the presence of nuthatches in *both* years of the study, the probability of a given wood being occupied was lower than when we considered presence in one of the two years (Fig. 2a, d).

Habitat destruction may negatively affect the organisms in two ways: through habitat loss in terms of overall proportion of suitable habitat in the landscape, or through habitat fragmentation per se (see Fahrig 2003). In the second case, the isolation and spatial configuration of fragments are more relevant for the organism than in the case of habitat loss. In a review, Andr n (1994) shows how, with low proportions of suitable habitat (<10–30%), the degree of isolation of fragments has marked effects on the presence and abundance of many bird and mammal species, whereas with higher overall proportions the size of individual habitat patches was the main determinant (see also Trzcinski et al. 1999; Villard et al. 1999). This seems to have been the case in the present study, in which the buffering indices did not show any significant association with the presence of breeding nuthatches in woods, in disagreement with our initial hypotheses.

#### Number of pairs and breeding density

The number of pairs of breeding nuthatches was higher in larger woods (Fig. 3). The number of pairs is an absolute abundance measurement, and thus of course we expect this result (see our initial hypothesis 2). Likewise as expected, wood area was the best predictor of number of pairs in all models. Surprisingly, breeding density (i.e., a relative abundance measurement) was negatively correlated with wood area (Fig. 4a). Also surprisingly, both number of pairs and breeding density were higher in isolated woods, i.e., in woods with lower woodland cover (whether high quality or high-plus-low quality) in the surrounding landscape (Fig. 4c, d). Various studies focusing on this species have found that breeding densities are higher in large continuous woods than in small isolated ones (e.g., Verboom et al. 1991; Matthysen 1999). Bellamy et al. (2000) observed that, although of course there are generally more breeding pairs in larger woods, the densities of some bird species (blackbird *Turdus merula*, dunno

*Prunella modularis*, wren *Troglodytes troglodytes*, great tit *Parus major*, blue tit *P. caeruleus*, chaffinch *Fringilla coelebs* and robin *Erithacus rubecula*) will be higher in small woods; they attributed this to the trophic and structural resources existing at the edges of the wood, such as fruits or shrubs for nesting. However, nuthatches rarely use the understory of woodland edges and, as we have shown, do not tend to be present in smaller woods, where the edge effect would be stronger.

We suggest two possible reasons for the higher densities seen in smaller and more isolated woods in the present study. First, bird movements may be limited in relatively unforested landscapes, leading to a “crowding effect” in small and more isolated patches (Debinski and Holt 2000). Zarette (2001), in a study of forest patches in New South Wales in Australia, found that densities of resident forest birds were typically twice as high in small isolated fragments, even when these had less food than larger fragments. She suggests that this could be due to limitations on the juvenile dispersal of her study species. The probability of a forest bird crossing a gap decreases sharply with increasing distance between the forest patches (Desrochers and Hannon 1997; B lisle et al. 2001). A bird’s decision whether or not to travel is likely to be influenced by its perception of the landscape, and this is probably different in lowland landscapes (in which most previous studies have been carried out) than in more mountainous landscapes.

The second possible reason for the higher densities seen in smaller and more isolated woods is a lower abundance of predators in these woods, due to the larger home range they need, especially in fragmented landscapes (Andr n 1994). For example, Matthysen (1999) found that even though nuthatch densities were higher in larger forests, adult survival was lower than in smaller fragments. The O Caurel region supports a diverse community of forest predators, including raptors (e.g., sparrowhawks *Accipiter nisus*) and carnivorous mammals (e.g., martens *Martes martes* and *M. foina*, genets *Genetta genetta*, wild and domestic cats *Felis sylvestris* and *F. domesticus*), all with diets including small forest birds (Bas et al. 1978). G tmark & Post (1996), in a study of sparrowhawk prey in Sweden (based on the relationships between the abundance of prey species remains in sparrowhawk pellets and that species’

abundance in the environment), found that nuthatches have a high relative risk of predation by these raptors. On the other hand, in a study by Löhrl (cited in Cramp and Perrins 1993) of the breeding of nuthatches in natural cavities, 17% of nests (7 of 42) had been predated by great spotted woodpeckers (*Dendrocopos major*). Nilsson (1987) also found woodpecker predation rates of up to 14%, as well as evidence of other interferences by these birds that led to nuthatch breeding failure. In a study considering the effects of forest fragmentation on various bird species in England (Hinsley et al. 1995), the amount of woodland within 1 km of the perimeter of each woodland fragment was the variable that best predicted the presence of breeding *D. major* in that fragment, in line with the fact that this species can travel easily between nearby fragments. By contrast, in our study, this variable (here called  $B_{\text{Total}}$ ) showed a negative association with nuthatch breeding density. Note that *D. major* is likewise abundant in our study area (Gutián et al. 2004).

The findings of these previous studies point out the importance of predation in nuthatch populations: if landscape structure affects the presence and abundance of nuthatch predators, effects on the presence and abundance of nuthatch are to be expected. Zanette et al. (2003) reported a higher number of fledglings of the song sparrow (*Melospiza melodia*) in low-predation-pressure sites located on islands (which had fewer species of predators, and lower predator abundances). We think that a similar situation may occur in the small isolated woods of our study area. Different scenarios can be generated if on some habitat patches one member of an antagonist interaction is not present (Fahrig 2003; Ryall and Fahrig 2006): predators may be present regionally but require larger habitat patches than the prey species. In the present context, the nuthatch may thus be subject to lower predation pressure in smaller and more isolated woodland patches. Theoretical modelling of predator–prey relations has reported this type of prey response (i.e., higher abundances in small isolated patches) when the predators, though tolerating the matrix, do not inhabit it (Ryall and Fahrig 2006).

These two possible reasons for the higher breeding densities seen in smaller and more isolated woods are not incompatible, and both are supported by the stronger correlation between Bd and  $B_{\text{Total}}$  than between Bd and  $B_{\text{HQ}}$ . The degree of isolation of the woods studied seems to have effects on nuthatches at

an individual scale, but not at the population scale (see Haila et al. 1993). Thus, isolation may hinder the dispersal of individuals, or reduce the risk of predation, but does not seem to have affected the presence of pairs in the more isolated woods.

### Effects of woodland management

Absolute and relative abundances of nuthatches, measured as number of pairs and breeding density, respectively, showed a positive relationship with intensity of management. This is probably because intensity of management is an indirect measure of sweet chestnut crop, which is a food resource for the nuthatch (Gutián et al. 2004); indeed, one of the main reasons for pruning trees is to increase the chestnut crop. The availability of seeds of this type (nuts, acorns, etc.) is one of the most important determinants of nuthatch survival during the autumn and winter (Nilsson 1987). Enoksson (1990) found autumn increases in population density in years in which he supplied food to the nuthatches. Similarly, Matthysen (1999) attributed the higher densities of nuthatches in urban parks to the availability of anthropic food in this habitat. In addition, pruning produces trees with thicker trunks and more branches, leading to a higher abundance of arthropods (the main food source for nuthatches for most of the year; Cramp and Perrins 1993) in the bark. Moreover, large trunks typically have holes suitable for use by nuthatches as nest sites.

### Conclusions

Our results, as expected, show the importance of the size of chestnut woods for the presence and number of nuthatch breeding pairs. Interestingly, our results also indicate positive effects of the degree of isolation of the wood on both number of pairs and breeding density; to our knowledge, this is the only study to date that has reported positive effects of isolation on the abundance of the Eurasian nuthatch. Finally, increased habitat quality derived from traditional management of woods seems to have positive effects on breeding pair abundance. Thus, habitat, food availability and the configuration of the landscape can interact to influence the pattern of distribution and abundance of nuthatches, but also probably the pattern of interactions with other species. Possible

interspecific interactions are not often considered when unexpected results arise in studies of habitat fragmentation (see Fahrig 2003). However, interspecific effects on bird abundance can operate in synergy with habitat quality (see Zanette et al. 2003). Certainly, the view of patchy landscapes as “islands” surrounded by ecological desert greatly oversimplifies the natural processes linking different types of habitat (Haila 2002). Species-specific key resources (food, shelter and space) and processes (predation and competition) can expand or contract the niche limits of species which might not perceive the landscape as a binomial structure of “habitat” and “non habitat” (continuum theory; Fischer and Lindenmayer 2006).

In rural landscapes, the existence of traditional broadleaved woodlands, like the chestnut woods (or like the *dehesas* of southern Spain), has been a key factor in the conservation of many forest bird species, allowing their persistence on a regional scale in highly managed areas. As mentioned, in most of the north-west Iberian Peninsula chestnut woods have for hundreds of years largely substituted for the oak-dominated indigenous mature deciduous woodland. The highly anthropic nature of these woods, their patchy distribution, the role they play in the landscape as climax woodland and recent changes in the rural way of life (notably depopulation) make these habitats living laboratories that may perhaps help us to understand how ecosystems respond to anthropic transformations.

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