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# Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds

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## ABSTRACT

**Aim** Theory predicts that fragmentation aggravates habitat loss, increasing the extinction threshold of habitat specialists. However, contradictory empirical results have fuelled claims that fragmentation has been overemphasized, and more attention should be given to habitat loss for preserving species. We assess variation in species sensitivity to forest amount and fragmentation and evaluate if fragmentation is related to extinction thresholds in seven forest bird species.

**Location** Europe.

**Methods** We use the percentage of forest cover and the proportion of cover occurring in the largest patch to partition effects of forest amount versus fragmentation, and apply logistic regression to model the presence–absence of 17 forest bird species. For seven species showing robust models, we define two fragmentation scenarios, low and maximum, across the forest cover gradient and quantify species' sensitivity to forest contraction with no fragmentation, and to fragmentation under constant forest cover. Finally, we develop two tests of the extinction threshold hypothesis by comparing the occurrence probability of each species under the two fragmentation scenarios at different forest covers.

**Results** As expected, forest contraction had negative impacts on the occurrence probability of all seven species modelled, but – in line with theory – fragmentation also led to a higher extinction threshold for three (Western capercaillie, Hazel grouse and Eurasian pygmy-owl). One species (Black woodpecker) exhibited the opposite pattern indicating that it probably benefits from fragmentation. Differences among species responses may reflect dispersal abilities, specializations in resources/habitat characteristics and/or sensitivity to potential modifications of interspecific interactions.

**Main conclusions** Although forest amount is of primary importance for the persistence of forest specialist birds, fragmentation is also relevant for some, and neglecting forest fragmentation would be a mistake for these species. Species-specific traits can be helpful for interpreting species' reactions to fragmentation, and it should not be assumed that it always, or never, matters.

## Keywords

**Extinction threshold hypothesis, forest amount, forest bird species, forest fragmentation, fragmentation theory, species-specific traits.**

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## INTRODUCTION

Habitat destruction is the dominant threat affecting biodiversity in terrestrial ecosystems (Sala *et al.*, 2000). Two key issues con-

cerning conservation are the amount of habitat needed to achieve conservation goals and the importance of habitat fragmentation (Fahrig, 2001, 2002). Habitat 'fragmentation' is an element of the pattern of habitat that differs from how much

habitat there is (e.g. Haila, 2002). Nonetheless, the term has been used in many ways, commonly to illustrate human practices that destroy habitat, even though habitat might be removed without increasing fragmentation (e.g. Fischer & Lindenmayer, 2007). This loose use of the term has generated confusion, complicating understanding of the impacts of habitat amount and fragmentation on biodiversity. Haila (2002) and Fahrig (2003), among others, have argued for discrimination between habitat loss per se and habitat fragmentation per se, but the debate remains open, and although many studies have implicitly assumed independent effects of habitat loss and fragmentation, there is increasing awareness of their interdependence, recognizing that fragmentation is often a consequence of habitat loss (see Didham *et al.*, 2012).

Theoretical results from both stochastic and deterministic models indicate that fragmentation *sensu strictu* aggravates the impacts of habitat loss on populations (Fahrig, 2002). Moreover, the models converge to predict that the greater the fragmentation, the earlier the appearance of the extinction threshold in the habitat loss gradient (*sensu* Fahrig, 2003); that is, of the minimum amount of habitat below which either the long-term population persistence probability is  $< 1$  in stochastic models, or the equilibrium population size (or proportion of the landscape occupied) is 0 in deterministic models (Fahrig, 2002; see also Lande, 1987; Bascompte & Solé, 1996). Hereafter we refer to this as the *extinction threshold hypothesis*; although there are several explanations for relationships between critical thresholds and habitat amount, most focus on habitat fragmentation (Swift & Hannon, 2010).

Contrary to theory, the observed effects of fragmentation are generally weaker than those of habitat amount and can be negative, neutral or positive (e.g. Fahrig, 2003; Bennett *et al.*, 2006), which led Fahrig (2002) to suggest that models are missing important processes. Indeed, since Levins (1966), it is accepted that generality, precision and realism cannot be maximized simultaneously in a model, and it may be that the extinction threshold hypothesis emerged from a lack of realism in the models that led to it (as suggested by Fahrig, 2002). However, Levins (1966) also claimed that a robust theoretical outcome is one that appears across a range of models, which is the case for the extinction threshold hypothesis. So, might problems lie in the structure of the empirical studies themselves or in the interpretation of their results? Two lines of argument suggest that both could be influencing empirical evaluations of the importance of fragmentation.

Firstly, species can differ in their responses to the loss and fragmentation of habitats due to their specific characteristics and habitat needs. For example, highly dispersive species should be less likely to suffer from fragmentation than less dispersive species (e.g. Bascompte & Solé, 1996). Therefore, empirically observed differences in responses to habitat fragmentation among species that differ in their dispersal capabilities (e.g. Montoya *et al.*, 2010) cannot be construed as discrediting the extinction threshold hypothesis. On the contrary, these differences are key for the interpretation of results. Moreover, in contrast to claims that species' responses to the alteration of habitats

should be viewed in an individualistic fashion (e.g. Fischer & Lindenmayer, 2006), Didham *et al.* (2012) argued for the existence of sets of traits generating 'interdependent' responses among them, generating common responses to fragmentation for species with similar resource or habitat requirements, dispersal capabilities, or sensitivity to fragmentation-driven altered interspecific interactions (see Angelstam, 1992; Andrén, 1995; Hanski, 1995). This opens a venue for investigation: to what extent are species' responses to fragmentation (including extinction thresholds) related to traits?

Secondly, empirical studies must cope with difficulties in measuring habitat characteristics. The habitat concept is species specific, with its precise meaning referring to the resources and conditions that permit occupancy for a particular species (Lindenmayer & Fischer, 2006). As theoretical studies model species and habitats with characteristics that researchers assign to them, a species-specific habitat definition is implicit. However, in empirical analyses, quantifying the conditions limiting the occurrence of every species might be impossible. Consequently, the common practice is to use human-perceived habitats, often based on vegetation type or land use, and assign these habitat proxies to groups of species as if all of them had identical needs (Fischer & Lindenmayer, 2007). Thus, it is not surprising that empirical analyses have found varying responses to habitat fragmentation and, hence, limited support for the extinction threshold hypothesis or other theoretical propositions (see Fahrig, 2002, 2003; but see Montoya *et al.*, 2010).

Even if theory-derived predictions of species-habitat relationships do not always apply when using habitat proxies as defined above (e.g. types of vegetation or land use), investigating species reactions to changes in such proxies has the practical importance in that vegetation and land use types are commonly used for decision making in conservation (see also Fischer & Lindenmayer, 2007). Thus, if there were species for which fragmentation of the vegetation (or land use) type is found to worsen effects of habitat loss, conservation plans and initiatives involving these species should consider fragmentation. Moreover, if fragmentation is found to worsen effects of habitat loss in studies involving broad regions (see Montoya *et al.*, 2010 for an example) or continents, specific policies could be devised for the conservation of fragmentation-sensitive species across these areas.

Here we present a broad-scale, grid-based analysis of the relationships between occurrences of forest bird species and forest amount and fragmentation across Europe. Because more than two-thirds of this region should be forested under present climatic conditions (Huntley & Birks, 1983), forest birds represent an important set of species to address our objectives. We concentrated on species that are associated with mature forest. Further, because long-term persistence of forest birds in landscapes depends on maintaining breeding populations, our analyses are based on the occurrence of breeding populations. Thus, for each species we used breeding bird atlas data covering Europe (Hagemeyer & Blair, 1997), which map the occurrence of at least one breeding pair at each site. Two key questions underpin this study: (1) How (positively or negatively) and to

what extent is each species sensitive to forest loss and fragmentation, and (2) is fragmentation related to extinction thresholds? A third question is, if species respond differently to fragmentation, to what extent might this be due to differences in dispersal capabilities and/or habitat needs among them? While responses to the first two questions are directly derived from the analysis of our database, the third can be surmised based on the biology and behaviour of the species.

## METHODS

### Bird data

The spatial distribution of birds and their nesting and foraging habits were taken from Hagemeyer & Blair (1997), which integrates 25 years of effort by volunteer ornithologists and specialists and describes the occurrence of species' breeding pairs in the 50 km × 50 km Universal Transverse Mercator grid system. Our analysis units comprised 1341 cells after excluding areas with insufficient bird or forest cover sampling, all islands except Great Britain, and all coastal cells containing < 50% of the landmass of inland cells (see Appendix S1 in Supporting Information). We focused on forest-specialists, which were defined as species primarily associated with forest habitat for nesting and feeding. According to descriptions provided by Hagemeyer & Blair (1997), 35 forest specialists exist in the study area (see Appendix S2), of which we excluded those with breeding pairs present in < 15% or > 70% of the cells, as statistical models and evaluations are less credible for them (Jiménez-Valverde *et al.*, 2008). This resulted in 17 species for modelling (see Appendix S2).

We generated a 'potential distribution map' for each species that approximates the area in which it occurs or has likely occurred throughout the mid-20<sup>th</sup> century. This was done by superimposing the atlas maps and range maps provided by Petterson *et al.* (1957, 1967, 1982), Jonsson (1993) and Mullarney *et al.* (1999) to attain a synthetic map for each species that we considered its study area (i.e. the subset of cells for which we recorded the presence/absence of breeding pairs). All other cells were excluded; i.e. each species was analysed using a unique set of cells.

### Forest variables

We used the CORINE Land Cover CLC2000 and CLC90-Switzerland databases to quantify forest amount and fragmentation. CORINE Land Cover is a remotely sensed land cover classification covering Europe (except Norway and Serbia), of which we utilized the 250-m pixel resolution series (data available at <http://www.eea.europa.eu/data-and-maps/>; accessed November 2010). Of the 44 land cover classes, we identified all pixels belonging to broadleaved, coniferous or mixed forests. Forest amount and fragmentation for each cell was quantified as the percentage of cell's area covered by forest (percentage forest cover [*PFC*]) and the percentage of forest cover that corresponds to the largest patch (relative largest patch size [*rLPS*]). The latter has been used in theoretical (see Bascompte & Solé, 1996) and

empirical studies (Montoya *et al.*, 2010) and serves to distinguish between scenarios reflecting low and high fragmentation. For example, when *PFC* = 40%, weakly fragmented cells are those with most forest clumped in a single patch (e.g. with *rLPS* > 90%), as remaining forest is too small to represent additional fragments. Conversely, strongly fragmented cells would have very small *rLPS* (e.g. < 10%), as this indicates that all remaining forest is scattered in small, numerous patches (see Montoya *et al.*, 2010 for discussion and utilization of *rLPS*).

### Data analysis

#### Species distribution modelling

We used logistic regression with binomial errors to model presence/absence of breeding pairs of each species as a function of *PFC* and *rLPS*:

$$P(j, PFC_q, rLPS_q) = \frac{e^{k(j, PFC_q, rLPS_q)}}{1 + e^{k(j, PFC_q, rLPS_q)}} \quad (1)$$

$$k(j, PFC_q, rLPS_q) = M_j + C_j(PFC_q) + CC_j(rLPS_q) \quad (2)$$

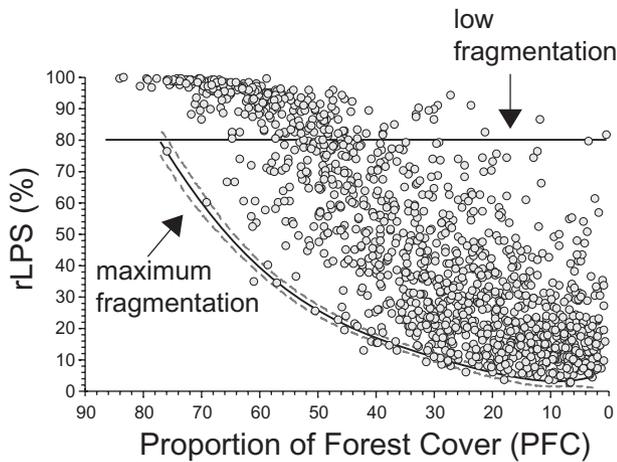
where  $P(j, PFC_q, rLPS_q)$  is the probability of finding species *j* in cell *q* with forest cover *PFC<sub>q</sub>* and relative largest patch size *rLPS<sub>q</sub>*, and *M<sub>j</sub>*, *C<sub>j</sub>* and *CC<sub>j</sub>* are species-specific parameters of the regression model for species *j* with respect to *PFC<sub>q</sub>* and *rLPS<sub>q</sub>*.

To ensure that interpretations were based on robust models, the 17 species were subjected to a second selection process based on the *P*-value of each model's chi-square and two additional model performance indexes, the area under the receiver operating characteristic curve (AUC) and McFadden's rho-squared ( $\rho^2$ ). AUC ranges from 0.5 to 1 with values < 0.7 indicating poor capacity of the model to predict presences and absences (Pearce & Ferrier, 2000). We thus discarded species whose models rated below this level. McFadden's rho-squared ( $\rho^2$ ) approximates an ordinary least squares coefficient of determination ( $r^2$ ) (McFadden, 1979). However,  $\rho^2$  tends to be much lower than  $r^2$ , and  $\rho^2$  values from 0.2 to 0.4 represent excellent fits (McFadden, 1979). We thus also excluded species with  $\rho^2 < 0.2$ .

Finally, the presence of spatial autocorrelation in model residuals can violate the assumption of independently distributed errors in regression models, so we also assessed spatial autocorrelation levels in model residuals with Moran's *I* coefficients (Diniz-Filho *et al.*, 2003) computed using SAM 4.0 (Rangel *et al.*, 2010). Logistic regression modelling was done in Matlab (version 7.0, MathWorks Inc., Natick, MA, USA), and AUC values were calculated with the 'PresenceAbsence' package (Freeman & Moisen, 2008) implemented in R Development Core Team (2008).

#### Sensitivity analysis to forest amount and fragmentation

To facilitate comparison among species, parameterized logistic models were used to generate scalar metrics of species' sensitivity



**Figure 1** Forest fragmentation (measured as the percentage of forest occurring in the largest patch, *rLPS*) as a function of the proportion of forested area (*PFC*) in  $\approx 50 \text{ km} \times 50 \text{ km}$  cells in the study area. The upper solid line delimitates cells with low fragmentation (*rLPS* = 80%). The lower solid and discontinuous lines (95% CIs) correspond to a polynomial regression on 32 cells located at the lower edge of the cloud of points. We used this line to quantify maximum fragmentation in terms of *rLPS* at varying levels of *PFC* (see text). Note that *PFC* decreases to the right.

ties to changes in both forest cover at a constant fragmentation level ( $\Omega_{j,cover}$ ), and fragmentation at a constant forest cover ( $\Omega_{j,fragm}$ ). For the constant fragmentation scenario we fixed *rLPS* at 80%, a low fragmentation level found at most forest cover levels (see Fig. 1), and then computed the proportional reduction in occurrence due to a reduction in forest cover from a high value (*PFC* = 75%) to a low one (5%):

$$\Omega_{j,cover} = \ln \left[ \frac{P(j, PFC_q = 5, rLPS_q = 80)}{P(j, PFC_q = 75, rLPS_q = 80)} \right] \quad (3)$$

where a positive or negative  $\Omega_{j,cover}$  indicates that the species *j* responds positively or negatively to forest contraction.

For the scenario of constant forest cover, we took into account that whereas cells with low fragmentation (e.g. with *rLPS* = 80%) can occur throughout the forest cover gradient, differences between minimum and maximum fragmentation (indicated by higher and lower *rLPS* values, respectively) increase as forest cover decreases (Fig. 1). Based on these relationships, we focused on a moderately low forest amount (*PFC* = 25%) and computed the proportional reduction in occurrence due to an increase from low to high fragmentation at this forest cover (i.e. for the *rLPS* values of 80 and 9%, respectively):

$$\Omega_{j,fragm} = \ln \left[ \frac{P(j, PFC_q = 25, rLPS_q = 9)}{P(j, PFC_q = 25, rLPS_q = 80)} \right] \quad (4)$$

where a negative  $\Omega_{j,fragm}$  indicates a negative response of species *j* to increased fragmentation, whereas a positive  $\Omega_{j,fragm}$  indicates that fragmentation favours occurrence of the species.

It should be noted that the logarithmic scale generates a non-linear relationship of  $\Omega_{j,cover}$  and  $\Omega_{j,fragm}$  with proportional reduction in occurrence; for example,  $\Omega_{j,\bullet} = -3$  represents a 95% reduction;  $\Omega_{j,\bullet} = -1$  a 63% reduction;  $\Omega_{j,\bullet} = -0.5$ , a 39% reduction, and  $\Omega_{j,\bullet} = +1$  represents a 170% increase.

We generated 95% confidence intervals (CI) for  $\Omega_{j,cover}$  and  $\Omega_{j,fragm}$  using a bootstrap procedure implemented in Matlab (version 7.0, MathWorks Inc.). We produced 1000 samples for each species by resampling with replacement triads of *PFC*<sub>q</sub>, *rLPS*<sub>q</sub> and species occurrence (1 or 0) values from each original sample. Each bootstrap sample comprised the same number of cells as the original sample and was used to parameterize the logistic model (equations 1 and 2) and to compute  $\Omega_{j,cover}$  and  $\Omega_{j,fragm}$  as in equations 3 and 4, respectively. We generated 1000 ranked values per scalar metric, of which the values at the 25th and 976th positions corresponded to the lower and upper 95% CI.

We also computed  $\Omega_{j,cover}$  and  $\Omega_{j,fragm}$  substituting the *rLPS* values of 80% in equations 3 and 4 by 100%, assuming that fragmentation could be zero at any level of forest cover. We did this because although there were no cells with zero fragmentation (i.e. with *rLPS* = 100%) when *PFC* falls below  $\approx 60\%$  (see Fig. 1), this was found when we used a different source of forest data (DeFries *et al.*, 2000; see details and patterns in Appendix S3). However, we obtained qualitatively similar results using either 80% or 100% *rLPS*, so we only report those for *rLPS* = 80%.

#### Testing the extinction threshold hypothesis

Formally, the extinction threshold is defined as the amount of habitat below which the probability of long-term population persistence is  $< 1$  (see Fahrig, 2002). However, a shift from a probability of 1 to  $< 1$  is of no value when utilizing logistic models, as probabilities of 1 (and 0) are approached asymptotically but never reached. Consequently, we tested the extinction threshold hypothesis following two alternative procedures.

First, we adopted a criterion analogous to the LD<sub>50</sub> of a drug, the dose that kills half of a group of experimental subjects (see Woodroffe & Ginsberg, 1998 for a similar approach focused on carnivore extinction). We defined the extinction threshold of a species as the amount of habitat at which its logistic probability of occurrence falls to 0.5, so the prediction of the extinction threshold hypothesis of fragmentation theory is that this probability is reached at a higher habitat amount when the habitat loss occurs with fragmentation.

This was tested using the logistic model parameterized for each species to estimate  $P(j, PFC, rLPS)$  at nine levels of forest cover (*PFC* values of 85, 75, 65, 55, 45, 35, 25, 15 and 5%) for two fragmentation situations (low and maximum). The definition of the fragmentation scenarios was based on the empirical relationships between forest fragmentation and forest amount (Fig. 1). That is, we assumed low fragmentation to be the same at all instances (*rLPS* = 80%) and computed  $P(j, PFC, rLPS)$  for each of the resulting nine pairs of *PFC* and *rLPS*; (85,80), (75,80), (65,80), . . . , (5,80). For maximum fragmentation, we

examined the cloud of points and selected 32 cells that delimited it from below (i.e. cells representative of higher fragmentation at different levels of forest cover). Then we generated a fourth-order polynomial regression of  $rLPS$  on  $PFC$  with these cells and computed the maximum empirical fragmentation for each of the selected forest cover values. This provided  $rLPS$  values of 80, 75, 52, 34, 22, 14, 9, 4 and 3%, so that  $P(j, PFC, rLPS)$  was computed for the  $PFC$  and  $rLPS$  pairs of (85,80), (75,75), (65,52) ... (5,3). To obtain a 95% CI for each  $P(j, PFC, rLPS)$ , we repeated all calculations for the 1000 bootstrap samples generated for each species.

As for the case of the sensitivity analyses, we repeated this test of the extinction threshold hypothesis using the same maximum fragmentation scenario (i.e. with the same paired levels of  $PFC$  and  $rLPS$ ) but no fragmentation (i.e.  $rLPS = 100%$ ) at all levels of  $PFC$ . Again, the results did not differ and are not shown to reduce redundancy.

Our second test defined the extinction threshold as the location in the  $PFC$  gradient of the lower inflection point of the logistic curve (i.e. the  $PFC$  value at which the second derivative is greatest). Specifically, for each species and fragmentation scenario – i.e. low (with  $rLPS = 80%$ ) and maximum ( $rLPS$  values generated with the polynomial regression described above) – we computed the second derivative of the logistic curve at decreasing 0.1% intervals between the  $PFC$  levels of 85 and 5%, identified the maximum value and retained that  $PFC$  point. Statistical differences between the extinction thresholds found for each fragmentation scenario were again established based on bootstrapped 95% CIs. If a species' occurrence was negatively affected by fragmentation, its extinction threshold should occur at significantly higher levels of  $PFC$  for the maximum fragmentation scenario. We also computed the 95% CIs for the probability of occurrence at which each extinction threshold was found. A lack of significant differences between fragmentation scenarios would support the robustness of our definition of the extinction threshold for this test. Still, a potential limitation of this method is that the inflection point could occur outside of the range of  $PFC$  values included in the analysis, in which case the test would be uninformative. Second derivative values of the logistic curve were generated with the 'e1071' package for R.

## RESULTS

Of the 17 bird species selected initially for modelling, we obtained robust models for seven (Table 1), which were used for further analyses. The two-factor habitat models reduced the spatial autocorrelation at all distance classes (see Appendix S4). The largest amount of residual positive spatial autocorrelation remained in the shortest distance class, but with Moran's  $I$ -values lower than 0.2 in all cases. Thus, despite the simplicity of the models, they described effectively the occurrence patterns of all seven species.

### Sensitivity to forest amount and fragmentation

As expected for forest specialists, all species responded negatively to decreased forest cover under low fragmentation (a

negative  $\Omega_{j,cover}$  with 95% CIs not including zero), with  $\Omega_{j,cover}$  values ranging from  $-1.18$  for Black woodpecker to  $-4.50$  for Ural owl (Fig. 2a). This meant that, under the modelled scenario of decreasing forest cover from 75% to 5%, the proportional reduction in the occurrence probability ranged between 72% and 98% across all species.

In contrast, for the scenario of high fragmentation (i.e. from  $rLPS_q = 80%$  to 9%) at a constant forest cover ( $PFC_q = 25%$ ) three species showed significantly negative  $\Omega_{j,fragm}$  values (Fig. 2b), the two grouse (Western capercaillie and Hazel grouse) and the Eurasian pygmy-owl, although the owl had a weaker negative response to fragmentation as indicated by the closer proximity of its upper 95% CI to zero (see Fig. 2b). One species, the Black woodpecker, responded positively and, hence, is more likely to be found in more fragmented cells, and the occurrence of three species was not significantly affected by fragmentation (Tengmalm's owl, Ural owl and Three-toed woodpecker).

### Fragmentation and extinction thresholds

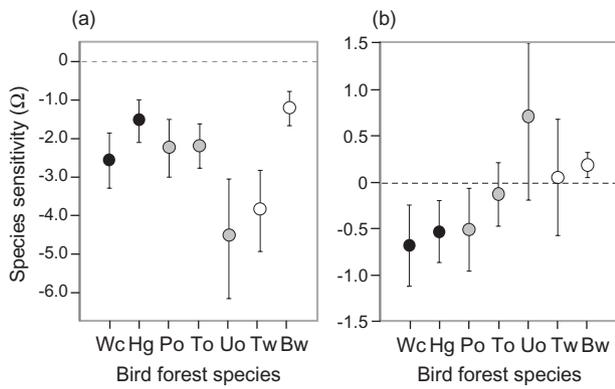
Relationships between occurrence probabilities and forest cover are shown in Fig. 3 for the low and maximum scenarios of forest fragmentation. Our first test of the extinction threshold hypothesis focused on where in the gradient of decreasing forest amount occurred the first overlap between an occurrence probability (or its 95% CI) and the critical probability of 0.5 (i.e. at which the presence or absence of the species become equally likely), as we took this level as indicating an elevated chance of extinction. Thus, if this occurred at a higher forest cover for the scenario of maximum fragmentation, then fragmentation leads to a higher extinction threshold, as predicted by the hypothesis. This was the case for the three species negatively affected by fragmentation. For both Western capercaillie and Eurasian pygmy-owl, the first overlap with the critical probability of 0.5 occurred at a forest cover of 45% under maximum fragmentation, and at 35% under minimum fragmentation (see Fig. 3a & c), whereas, for Hazel grouse, the 0.5 probability was first found at a forest cover of 35% and 25% for maximum and minimum fragmentation, respectively (Fig. 3b). Additionally, if we compare both fragmentation scenarios, the distance between the confidence intervals of their corresponding curves is generally higher for the two grouse (see Fig. 3a & b) than for Eurasian pygmy-owl, in which intervals overlapped at all instances, and only in two occasions the overlap did not include the mean occurrence probability values (i.e. at  $PFC$  levels of 45% and 35%, see Fig. 3c). This indicates that significant differences only occurred at these forest cover levels for this species. Overall, these results indicate that although the extinction threshold hypothesis was supported for three species, support was stronger for the two grouse than for Eurasian pygmy-owl, consistent with the weaker negative sensitivity to fragmentation detected for the latter.

The results for the remaining species were also consistent with the sensitivity analysis. Tengmalm's owl, Ural owl and Three-toed woodpecker had no significantly different occurrence

**Table 1** Sample sizes ( $N$ ) and goodness-of-fit statistics for the logistic regressions (the area under the ROC curve [AUC], and McFadden's rho-squared [ $\rho^2$ ]) of 17 forest specialist bird species in Europe.

Common name	Scientific name	$N$	AUC	$\rho^2$	$M_j$ (lower; upper)	$C_j$ (lower; upper)	$CC_j$ (lower; upper)
Western capercaillie	<i>Tetrao urogallus</i> (Linnaeus, 1758)	793	<b>0.87</b>	<b>0.35</b>	-3.913 (-4.456;-3.346)	0.084 (0.064;0.102)	0.012 (0.003;0.022)
Three-toed woodpecker	<i>Picooides tridactylus</i> (Linnaeus, 1758)	517	<b>0.87</b>	<b>0.35</b>	-4.281 (-4.991;-3.468)	0.103 (0.077;0.130)	-0.0002 (-0.013;0.013)
Hazel grouse	<i>Tetrastes bonasia</i> (Linnaeus, 1758)	798	<b>0.83</b>	<b>0.28</b>	-2.647 (-3.097;-2.174)	0.068 (0.050;0.085)	0.012 (0.003;0.022)
Eurasian pygmy-owl	<i>Glaucidium passerinum</i> (Linnaeus, 1758)	648	<b>0.83</b>	<b>0.27</b>	-3.255 (-3.819;-2.691)	0.068 (0.048;0.089)	0.009 (-0.0009;0.020)
Tengmalm's owl	<i>Aegolius funereus</i> (Linnaeus, 1758)	858	<b>0.83</b>	<b>0.27</b>	-2.694 (-3.130;-2.257)	0.079 (0.062;0.096)	0.002 (-0.005;0.011)
Black woodpecker	<i>Dryocopus martius</i> (Linnaeus, 1758)	1063	<b>0.81</b>	<b>0.21</b>	-0.110 (-0.478;0.256)	0.094 (0.075;0.113)	-0.014 (-0.025;-0.003)
Ural owl	<i>Strix uralensis</i> (Pallas, 1771)	345	<b>0.74</b>	<b>0.26</b>	-4.160 (-5.089;-3.061)	0.103 (0.066;0.140)	-0.010 (-0.028;0.008)
Red crossbill	<i>Loxia curvirostra</i> (Linnaeus, 1758)	1217	0.81	0.13	-0.991 (-1.346;-0.636)	0.048 (0.033;0.064)	0.004 (-0.003;0.012)
Willow tit	<i>Parus montanus</i> (Conrad, 1827)	858	0.70	0.08	1.000 (0.640;1.359)	0.062 (0.044;0.081)	-0.021 (-0.033;-0.010)
Eurasian treecreeper	<i>Certhia familiaris</i> (Linnaeus, 1758)	1124	0.69	0.08	0.154 (-0.119;0.427)	0.053 (0.040;0.067)	-0.014 (-0.022;-0.005)
Firecrest	<i>Regulus ignicapilla</i> (Temminck, 1820)	1022	0.69	0.07	0.204 (-0.098;0.508)	0.052 (0.037;0.067)	-0.004 (-0.013;0.004)
European pied flycatcher	<i>Ficedula hypoleuca</i> (Pallas, 1764)	1182	0.68	0.07	-0.175 (-0.415;0.065)	0.056 (0.044;0.069)	-0.020 (-0.028;-0.012)
Grey-faced woodpecker	<i>Picus canus</i> (Gmelin, 1788)	803	0.66	0.02	0.251 (-0.068;0.571)	0.033 (0.019;0.047)	-0.013 (-0.022;-0.004)
Middle spotted woodpecker	<i>Dendrocopos medius</i> (Linnaeus, 1758)	860	0.64	0.04	0.771 (0.466;1.076)	0.035 (0.022;0.049)	-0.028 (-0.036;-0.020)
Collared flycatcher	<i>Ficedula albicollis</i> (Temminck, 1815)	504	0.62	0.04	-0.663 (-1.084;-0.241)	0.043 (0.026;0.060)	-0.021 (-0.031;-0.011)
Spotted nutcracker	<i>Nucifraga caryocatactes</i> (Linnaeus, 1758)	620	0.62	0.03	-0.317 (-0.723;0.087)	0.030 (0.014;0.046)	-0.004 (-0.014;0.004)
Red-breasted flycatcher	<i>Ficedula parva</i> (Bechstein, 1792)	503	0.61	0.06	-0.356 (-0.783;0.069)	0.038 (0.018;0.058)	-0.001 (-0.013;0.010)

All models were significant at chi-squared  $P$ -value  $< 0.0001$ . The models of the first seven species (in bold) met all three quality criteria described in the Methods (i.e. significant  $P$ -value,  $AUC \geq 0.7$  and McFadden's  $\rho^2 \geq 0.2$ ) and were selected for further analysis. Parameter estimates (and their 95% CIs) of the logistic models  $M_j$ ,  $C_j$ ,  $CC_j$  are provided.  $M_j$ ,  $C_j$ ,  $CC_j$  result from the regression model for species  $j$  with respect to forest amount (PFC) and forest fragmentation ( $rLPS$ ), and are the parameters used in further analyses testing the sensitivity to forest loss and fragmentation and the extinction threshold hypothesis for the first seven species.



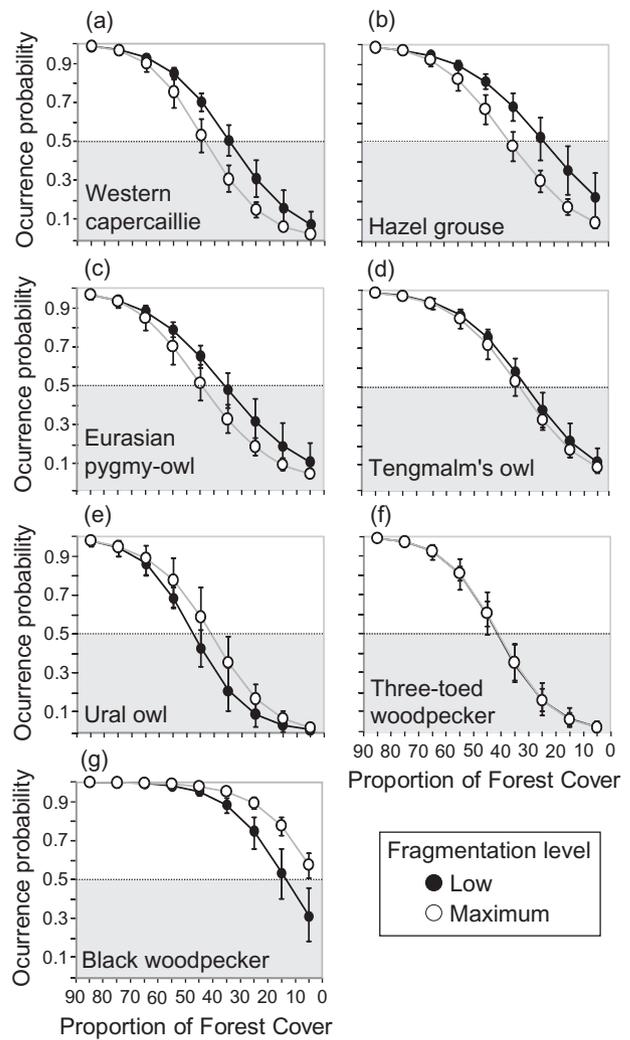
**Figure 2** Sensitivity ( $\Omega_j$ ) ( $\pm$  95% CIs) of seven forest-specialist birds to forest cover reduction (a) and forest fragmentation (b). Colours of the circles represent the family to which species belong: black (Phasianidae), grey (Strigidae) and white (Picidae). Wc, Western capercaillie; Hg, Hazel grouse; Po, Eurasian pygmy-owl; To, Tengmalm's owl; Uo, Ural owl; Tw, Three-toed woodpecker; Bw, Black woodpecker.

probabilities between the scenarios of maximum and minimum fragmentation at any forest cover level (Fig. 3d–f), consistent with their neutral sensitivity to fragmentation. For the Black woodpecker, we found the converse response to that predicted by the hypothesis (Fig. 3g). Again, Black woodpecker probably benefits from fragmentation, particularly where the amount of forest habitat is moderate to low.

Our second test compared both fragmentation scenarios looking for the *PFC* value at which the lower inflection point of the logistic curve is reached, which was assumed to correspond with the extinction threshold. Consistent with the previous results, this threshold was significantly higher for maximum fragmentation for the two grouse and Eurasian pygmy-owl (Fig. 4a–c), whereas no differences were found for Tengmalm's owl, Ural owl and Three-toed woodpecker (Fig. 4d–f). For Black woodpecker the test was uninformative, as the lower inflection point of its logistic curves was below meaningful *PFC* values (i.e. < 0%). With the exception of this species, occurrence probabilities at the extinction threshold did not differ across species and scenarios,  $P(j, PFC, rLPS) \sim 0.2$  in all cases (see Fig. 4), indicating that the results are not artefacts generated by the method.

**DISCUSSION**

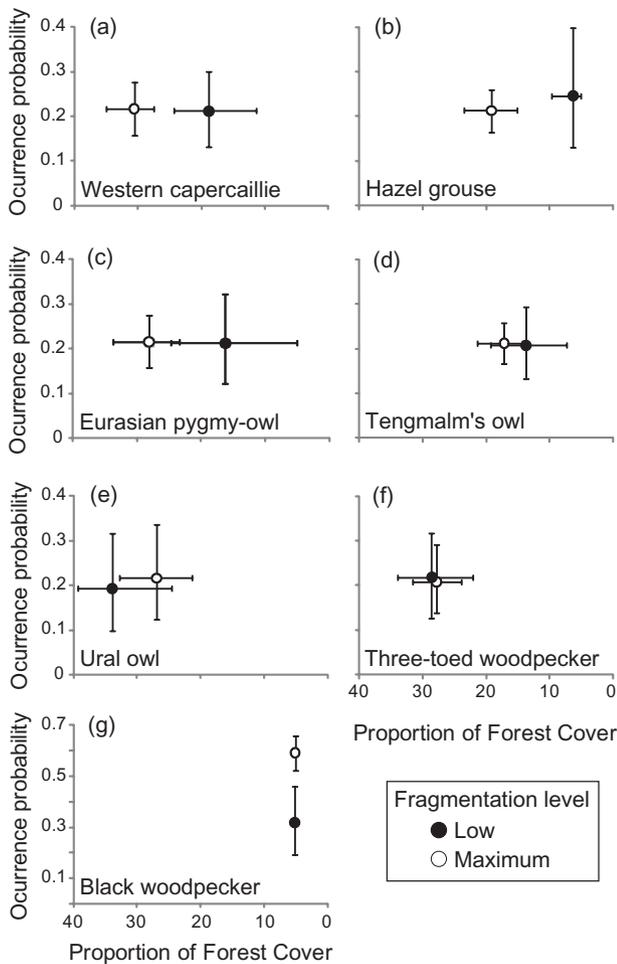
A long-standing tenet of fragmentation theory is that extinction thresholds occur earlier in the habitat loss gradient if habitat contraction takes place in concert with its fragmentation. This has received much attention due to its implications for biodiversity conservation. But debate about the validity of this hypothesis continues, fuelled by empirical results that have been interpreted as discrediting it. For the seven bird species that can be categorized as forest specialists, we found, as expected, that forest contraction has negative effects on the occurrence probability of all of them. However, we also found that responses to fragmentation vary across species. This might reflect to some



**Figure 3** Occurrence probabilities of the seven forest-specialist birds (a–g) averaged over nine values of forest cover (from 5% to 85%) under the two scenarios of forest fragmentation, low (in black) and maximum (in white) (see Methods). Bars represent 95% confidence intervals. Note that proportion of forest cover decreases to the right.

extent that, instead of defining and measuring habitat characteristics taking into account the specific needs of each species (a difficult task, particularly in broad scale studies), we used a general definition of habitat for all species (forests), which is common practice in fragmentation studies. Irrespective, we cannot conclude that the lack of conformity with the extinction threshold hypothesis of each species means that the hypothesis is incorrect. Rather, we can ask what aspects of the species' biology influence the outcomes under the study constraints.

Two forest-specialist herbivores, Western capercaillie, the world's largest grouse, and Hazel grouse, were negatively affected by fragmentation and supported the extinction threshold (see Figs 3 & 4). Both species are widely accepted as being severely impacted by forest fragmentation (Storch, 1991; Saari *et al.*, 1998), which can be directly related with several species-specific traits that predispose them to be vulnerable in frag-



**Figure 4** PFC extinction thresholds for the seven forest-specialist birds (a–g) under low (black) and maximum (white) fragmentation scenarios. Each extinction threshold reflects the PFC value coinciding with the lower inflection point of its corresponding logistic curve (i.e. that at which the second derivative of the curve is maximal). Bars are for 95% confidence intervals for extinction thresholds (horizontal) and occurrence probabilities at each threshold (vertical). Significantly different extinction thresholds between both fragmentation scenarios are indicated by lack of overlap in the horizontal direction, whereas similar extinction probabilities in both cases are indicated by overlaps in the vertical direction. Note that because no lower inflection point was found for any of the logistic curves of the Black woodpecker within the range of meaningful PFC values ( $\geq 0\%$ ), points in panel (g) do not reflect extinction thresholds, but occurrence probabilities at 5% PFC.

mented habitats; they are sedentary, territorial habitat specialists that require extensive home ranges and have low dispersal ability (Åberg *et al.*, 2000; Pakkala *et al.*, 2003).

For the three owls, negative effects of forest fragmentation and support for the extinction threshold hypothesis were found for Eurasian pygmy-owl but not for Tengmalm's owl and Ural owl (see Figs 2–4). In this case, neither low dispersal ability nor habitat specialization seem to be behind the Eurasian

pygmy-owl's sensitivity to fragmentation; females and juveniles of this species (and also Tengmalm's owl) can migrate up to 600 km – a behaviour not observed in Ural owls (Lehikoinen *et al.*, 2011) – and the Eurasian pygmy-owl can be classified as a generalist forager (Kullberg, 1995). A more likely explanation relates to indirect effects of fragmentation through alteration of inter-specific interactions. Due to its smaller size (c. 60 g), Eurasian pygmy-owls are preyed upon by a number of larger predators, including the other two owls (Mikkola, 1983). This has been thought to explain the affinity of this species for mature forests, as cleared and fragmented forests increase its exposure to predators (Strøm & Sonerud, 2001), and in turn could explain the support we found in Eurasian pygmy-owl to the extinction threshold hypothesis.

Positive effects of forest fragmentation were detected for the Black woodpecker, whereas the Three-toed woodpecker had a neutral response (see Figs 2–4). Although both are found in mature forests (Cramp, 1985), the more specialized Three-toed woodpecker is limited by the availability of conifer bark beetles (Fayt, 2006), and can suffer from intensive forest management (Angelstam & Mikusiński, 1994). In contrast, the weakly territorial Black woodpecker has high dispersal capability, a broader diet and may use a wide spectrum of forest habitats, which makes this species more of a forest generalist (Mikusiński, 1995). Moreover, lower predation pressure on this species in cutover and open forests compared with old forest stands (Rolstad *et al.*, 2000), and an increase of the density and diversity of invertebrates in forest edges (Peltonen & Heliövaara, 1998) can influence the persistence of Black woodpecker in fragmented forests (Tjernberg *et al.*, 1993). This may also explain why forest fragmentation only increased the occurrence probability of Black woodpecker at relatively low forest cover levels ( $\leq 35\%$ ; see Figure 3g).

Thus, species' biology coupled with our results suggest that dispersal ability, degree of specialization (in resource and/or habitat use) and sensitivity to interspecific interactions may be key determinants of species' reactions to fragmentation (see Angelstam, 1992; Andrén, 1995; Hanski, 1995). The importance of these traits also suggests that, even though habitat needs are expected to differ across species (Lindenmayer & Fischer, 2006), there exist common 'themes' (*sensu* Lawton, 1992, 337) or 'interdependences' (*sensu* Didham *et al.*, 2012) in species' responses to fragmentation, which can be used to identify potentially sensitive species in conservation.

Didham *et al.* (2012) also proposed a type of interdependency, to refer to the entanglement of habitat loss and fragmentation and emphasizing that fragmentation is most often a consequence of habitat reduction. Although following Fahrig's (2003) suggestions, we devised a technique to measure species sensitivities to one process separately from the other (see Fig. 2), finding that fragmentation effects that only occur within particular forest cover ranges (see Fig. 3) are consistent with Didham *et al.*'s (2012) propositions. This can be explained by the observation that not all fragmentation levels are possible for any amount of forest cover, with greater cover allowing only low to moderate fragmentation (see Fig. 1). This should be taken

into account in future tests of the extinction threshold hypothesis, and more generally in studies examining fragmentation effects.

Our study has potential limitations that may have led to underestimating forest amount and, specially, fragmentation effects. Firstly, our database comprised species presence/absence data, and potential effects on population density could not be investigated. Secondly, the coarse resolution of our species occurrence data (~50 km) precluded matching spatially each species' presence with a particular type of forest (i.e. broadleaf, conifer or mixed forests) and, hence, we could not conduct separate tests for different forest types, which might have obscured the signals found in some cases (e.g. for the Three-toed woodpecker, as this occurs primarily in coniferous forests). And thirdly, although we were able to differentiate between less and more fragmented cells by using a single fragmentation metric (*rLPS*), this could not capture all spatial subtleties of the configuration of habitat patches (e.g. number, size, physical connectivity or inter-patch distances) that might affect species' occurrences (see Montoya *et al.*, 2010). Thus, our analysis should be viewed as a conservative test of fragmentation effects. These limitations may also account for the fact that we obtained robust models for only 7 out of 17 bird species initially investigated, and leave open the possibility that future, finer datasets will detect stronger reactions to fragmentation, even for those species that appeared to be insensitive to it in the present analysis.

To conclude, although we followed common practice when dealing with real world conservation issues and have used a habitat proxy, we detected broad-scale, fragmentation-driven, increased extinction thresholds in three out of seven European forest specialist birds, much in line with what has been proposed by theory. Although our results have emphasized the primary importance of habitat amount per se effects on species persistence, they also highlight that there is a risk in neglecting fragmentation, at least for some species. Sensitive species are likely characterized by low dispersal ability, specialization in resources/habitat characteristics and/or elevated sensitivity to interspecific interactions. This is an important message for future tests of fragmentation theory.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Appendix S1** Map of the survey area showing the 1341 grid cells used as our analysis units

**Appendix S2** List of the 35 European bird species that nest and feed primarily within forest habitats

**Appendix S3** Forest fragmentation (*rLPS*) as a function of the proportion of forested area (*PFC*) in  $\approx 50 \text{ km} \times 50 \text{ km}$  cells in all Europe.

**Appendix S4** Spatial correlograms for the seven species selected for modelling.

## BIOSKETCH

**Marta Rueda** is a post-doctoral fellow interested in biogeography and global ecological and evolutionary patterns. Her current research interest also includes fragmentation theory and community phylogenetics at broad scales.

Author contributions: M.R. and M.Á.R. designed the study and wrote a first version of the manuscript together with B.A.H.; R.M.V. digitized the bird species maps and assisted M.R. and I.M.-C. in generating the variables; M.R., I.M.-C and M.F. performed the statistical analyses. All authors provided and discussed ideas at all stages of the investigation and contributed to the final draft.

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