Research

Species' response patterns to habitat fragmentation: do trees support the extinction threshold hypothesis?

Daniel Montoya, Fabio S. Alburquerque, Marta Rueda and Miguel A. Rodríguez

D. Montoya (daniel.montoya@alu.uah.es), F. S. Alburquerque, M. Rueda and M. A. Rodríguez, Depto de Ecología, Univ. de Alcalá, ES–28871 Alcalá de Henares, Madrid, Spain.

In fragmented landscapes the relationship between the probability of occurrence of single species and the amount of suitable habitat is usually not proportional, with a threshold habitat level below which the population becomes extinct. Ecological theory predicts that, although the reduction in species' occurrence probabilities (and eventually the extinction threshold) is a direct consequence of habitat loss, habitat fragmentation might reduce species' occurrence probabilities and affect the location of this threshold by reducing its predicted occurrence to lower levels of habitat amount. However, little is known about the validity of this extinction threshold hypothesis. Here, we performed analyses on the relationships between the probability of occurrence of eight tree species and the availability of forest habitat for two different empirical scenarios of low and moderate to high fragmentation. We partitioned the effects of habitat amount versus fragmentation by using two metrics: (1) the percentage of forest cover, and (2) the proportion of this percentage occurring in the largest forest patch. We find that, although decreasing forest cover had negative effects on the occurrence of tree species irrespective of fragmentation levels, forest fragmentation significantly modified the response pattern in six tree species, although only one species confirmed the extinction threshold hypothesis, which we interpret as a consequence of high degree of forest specialism and low dispersal ability. For most species, fragmentation either had positive effects or did not affect significantly the species' probability of occurrence. This indicates that the effects of habitat fragmentation on tree species are weak relative to the effects of habitat amount, which is the main determinant of the reduction in species' occurrence probabilities, and eventually species extinction, in fragmented landscapes.

The current, massive anthropogenic alteration of natural habitats is one main threat to terrestrial biodiversity (Baille et al. 2004). Recent changes in habitat availability have been observed to affect species richness patterns (Bascompte and Rodríguez 2001, Montoya et al. 2008), population abundance and distributions (Lande 1987, Venier and Fahrig 1996, Donovan and Flather 2002), species range sizes (Purvis et al. 2000), population growth rates (Bascompte et al. 2002), trophic chain lengths (Komonen et al. 2000), species interactions (Fortuna and Bacompte 2006), animal body sizes (McKinney 1997, Cardillo and Bromham 2001), and genetic diversity (Gibbs 2001). These studies and many others (Fahrig 2003) demonstrate that the modification of habitat areas where species grow and interact may significantly alter the ecological structure and dynamics of ecosystems, as well as drive individual species to extinction.

Human-impacted habitats typically appear fragmented – i.e. broken into more or less isolated patches – for which the expression habitat fragmentation has been commonly used as a general term encapsulating the variety of patterns and processes that accompany landscape change (Lindenmayer and Fischer 2006). Fragmented landscapes usually comprise a subset of populations inhabiting different habitat fragments, whose dynamics constitute the focus of the metapopulation theory (Hanski 1999). However, as noted by Fahrig (2003), a clear distinction between the per se consequences of habitat loss and habitat fragmentation (i.e. of the rupture of habitat after controlling for habitat loss) is needed to understand how this whole phenomenon operates. From the comprehensive review of empirical studies made by Fahrig (2003), it seems that whereas habitat loss per se effects on biodiversity are strong and consistently negative, those of habitat fragmentation per se are much weaker and at least as likely to be positive as negative. This contradicts the findings of several theoretical studies indicating that fragmentation per se aggravates the effects of habitat loss (Bascompte and Solé 1996, Boswell et al. 1998, Hill and Caswell 1999, Solé and Bascompte 2007). The conclusions of these theoretical studies are summarized in percolation theory (Solé and Bascompte 2007) by the extinction threshold hypothesis (reviewed by Fahrig 2002), which predicts that fragmentation causes (1) an accelerated decrease of population sizes across the gradient of shrinking habitat, and (2) a sooner appearance in this gradient of the so called extinction threshold (i.e. the amount of habitat below which the population cannot sustain itself and goes extinct [species' occurrence probability = 0]). However, there have been very few empirical investigations addressing this hypothesis

(Jansson and Angelstam 1999) and the validity of these predictions begs for empirical tests.

An important issue for any habitat-related study is the definition of habitat. According to Hall et al. (1997) and Lindenmayer and Fischer (2006), the precise meaning of 'habitat' refers to the resources and conditions present in an area that produce occupancy for a particular species. Because of the species-specific nature of this definition, habitat loss and fragmentation are also species-specific entities (Lindenmayer and Fischer 2006) and should be treated as such by any strict analysis of species–habitat relationships. This habitat definition is the one implicitly assumed in theoretical studies (and, hence, in the extinction threshold hypothesis), as modeled species and habitats posses the attributes that the researcher has assigned to them. However, for empirical studies, particularly for those involving several species, using a precise definition is not possible in many instances, as it requires an in depth information of the key habitat needs of every species, which is unlikely to be available in advance in many instances. This explains why a common, operational practice is to focus not on habitats, but on vegetation types (e.g. forest) or land uses, and on species that are believed to be strongly linked to them (e.g. forest species) (Lindenmayer and Fischer 2006). Investigating species reactions to changes in these habitat proxies has the inherent, practical interest that vegetation and land use types are common references for decision making in conservation. Further, although theory-derived predictions of species–habitat relationships cannot be expected to apply fully when using these habitat proxies, to what extent they do also merits evaluation. Indeed, for the particular case of the extinction threshold hypothesis, if it was observed that many species fitted its predictions, then this would send a clear applied message: that fragmentation of the focal vegetation (or land use) type does generally limit species' persistence and, hence, should be taken into account in multispecies conservation plans.

In the present study we built on the findings of a previous broad-scale investigation that involved ~90 000 survey sites distributed across peninsular Spain, 34 tree species that are native (28) or introduced (6) to this region, and that used forest as habitat proxy for these species (Montoya et al. 2008). These authors analyzed how the occurrence of each tree species was determined by local forest amount in the neighbourhood. They found that while some species exhibit null (4) or positive responses (6) to decreasing local forest cover, most species (24) have negative responses. These results support the use of forest as habitat proxy for most tree species (the latter ones) and, hence, that conservation plans aimed at protecting or increasing local forest cover are likely to have positive impacts on the persistence of these trees, at least in peninsular Spain. However, Montoya et al. (2008) did not quantify forest fragmentation, for which the question of whether forest spatial configuration is also important for tree species occurrence remains open.

Here, we address the effects of habitat loss vs habitat fragmentation for a subset of eight tree species (*Fagus sylvatica*, *Ilex aquifolium*, *Pinus nigra*, *P. sylvestris*, *Quercus faginea*, *Q. petraea*, *Q. robur* and *Q. suber*), which we selected because they meet the following three characteristics: to be negatively associated with decreasing forest amount (as indicated by Montoya's et al. 2008 results), to be native for peninsular Spain (exotics were excluded because of their frequent use as plantations in the study area, which might underestimate the effects of habitat cover and fragmentation; Costa et al. 2001), and to have a broad native range distribution within this region (i.e. >121 200 km², or ≥25% of the study area), to facilitate building robust statistical models. In order to test the predictions of the extinction threshold hypothesis directly, we used an approach similar to that of theoretical studies. That is, we investigated the effects of forest amount and fragmentation at the landscape level (sensu McGarigal and Cushman 2002), with each landscape consisting on a 10 × 10 km cell, and the set of studied cells covering the whole study area. Therefore, each of our analysis units (cells) consisted in a constellation of forest patches, not in an individual patch. Approaches using individual patches (instead of constellations of patches in predefined areas) as analysis units are more common in the literature, but as discussed by Fahrig (2003), they are less appropriate to investigate theoretical propositions such as the extinction threshold hypothesis.

There are at least 40 fragmentation measures used in metapopulation studies (McGarigal et al. 2002), many of which have strong relationships with each other and with the amount of habitat (Fahrig 2003). This makes the question of how to differentiate between more and less fragmented sites a difficult issue. We adopted a strategy based on quantifying, for each cell, both its percentage of forest cover (hereafter PFC), and the proportion of this percentage occurring in the largest forest patch (hereafter, relative largest patch size [rLPS]; Bascompte and Solé 1996, Solé and Bascompte 2007). By combining these two metrics we were able to differentiate among empirical scenarios reflecting low and moderate to high fragmentation (Fahrig 2002). Our rationale is as follows: for any given PFC value, scarcely fragmented cells are those having most of its forest cover concentrated into a single patch (i.e. with high rLPS), as it is obvious that the remaining forest will be too limited as to constitute many additional fragments. Conversely, for the same PFC value, cells with a reduced largest patch (i.e. with lower rLPS) should be more fragmented, as the rest of their patches will be even smaller, and often more numerous than in the former case since patch areas ought to sum up to give the same amount of PFC. This approach allowed us estimating species' occurrence probabilities along the forest cover gradient for different levels of fragmentation, as well as testing directly the extinction threshold hypothesis. We specifically addressed two questions: (1) how do probabilities of occurrence of individual tree species change with forest cover reduction in situations with low and higher fragmentation? (2) To what extent the extinction threshold hypothesis can be generalized across tree species?

Material and methods

Dataset

We analysed data from an extensive field survey carried out in peninsular Spain (492 173 km²). This region spans from 36°N to 43.5°N and 9°W to 3°E, housing a large

altitudinal gradient (sea level – 3500 m); it comprises a mosaic of different climates (from semiarid climates to Mediterranean and humid Atlantic climates), and a number of different landscapes. The Second Spanish Forest Inventory (Inventario Forestal Nacional 1986–1996, ICONA 1995) surveyed this area according to a 1 km resolution grid, yielding ~90 000 circular survey sites of 25 m radius each distributed across the woody surface of this region. Each site was sampled for many attributes, including presence/absence of several species of trees; stem diameter and height; altitude and slope.

For the purpose of this study, the original presence/absence data for the eight selected tree species (species' selection criteria were described in the Introduction) were re-scaled from their original resolution to a grid comprising 6757 cells of 10 × 10 km each, in which each single cell contained 0–100 original survey sites (0–100 presences of any given tree species). We focused on relationships occurring within the native range distribution of each species in Peninsular Spain, for which we crossed our grid with published species' range maps (Montoya et al. 2007) and excluded, for each species, all cells that lied outside of its native range. Exotic species were thus excluded because most of them have been traditionally used in our study region as plantations (Costa et al. 2001), which might underestimate the effects of habitat loss and fragmentation. This procedure rendered different numbers of analysis cells for each species, being *Quercus robur* the one with a lower representation in our dataset (a total of 1212 cells in which the species was present or absent; see Table 2 for the numbers of cells of the rest of the species). Note that the tree species selected were all widely distributed within the study region, and that their occurrences have been previously documented to be positively related with the amount of forest cover in the local neighbourhood, so that reductions in this cover result in reductions of the likelihood of finding the species in all cases (Montoya et al. 2008). A previous study conducted in the same region and using the same dataset explored the relationships between the occurrence probabilities of several tree species and the proportion of habitat amount (Montoya et al. 2008), demonstrating that, at the scale of peninsular Spain, forest amount varies independently of climate, topography, soil and major perturbation events; the effects on the species' probability of occurrence can thus be interpreted as a consequence of habitat loss and fragmentation.

Forest cover and fragmentation were quantified by processing the CORINE Land Cover database 2000 (CLC2000), a satellite imagery-based land cover classification with a 100-m pixel resolution. CLC2000 provides consistent information on land cover across Europe and is divided into 44 classes (<http://natlan.eea.europa.eu/dataservice/metadetails.asp?id=822>). We focused on three of these classes describing the distribution of broadleaved, coniferous and mixed forests, and classified each pixel as forest habitat, depending on whether they were included or not in any of these three categories. After that we generated two forest layers namely broadleaved (broadleaved plus mixed forests classes), and coniferous (coniferous plus mixed forests classes). Next, we superimposed the 10 × 10 km grid to the obtained forest layers and we calculated the proportion of forest cover (PFC) as the percent area of each grid cell covered by forest pixels. Also, we generated one variable related to the forest
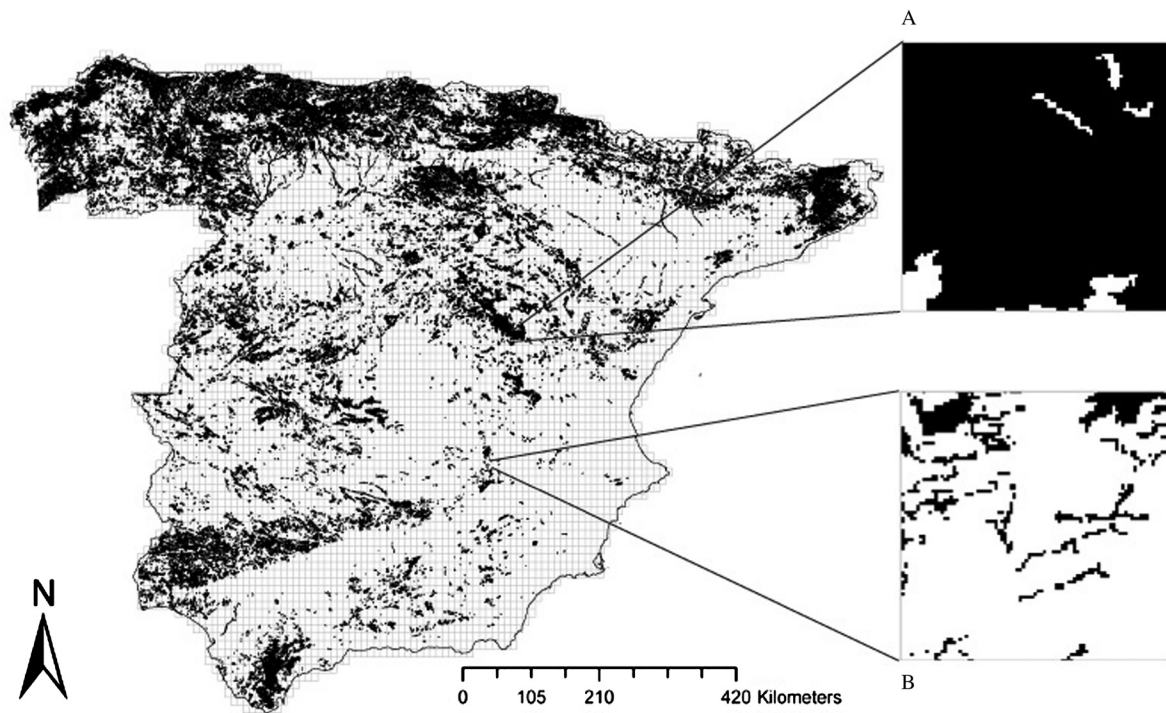

Figure 1. Distribution of survey sites in peninsular Spain. IFN2 consisted of ~90 000 circular sampling sites (radius = 25 m) distributed across peninsular Spain. The effects of forest amount and fragmentation were investigated at the landscape level by generating 10 × 10 km cells covering the whole study area. Every cell consisted on a constellation of forest patches and showed different fragmentation levels. Black areas correspond to forest cover; white areas correspond to forest loss. (A) Cell with high forest cover and low fragmentation. (B) Cell with low forest cover and high fragmentation.

vegetation spatial structure namely the largest forest patch (rLPS), which represents the proportion of PFC occurring in the largest forest patch (see Introduction). These analyses were done separately for broadleaved and coniferous forest classes (Fig. 1).

Analytical protocols

Given that our analysis cells contain 0–100 original survey sites, we used Poisson models to explore species responses to forest amount and fragmentation. The Poisson distribution describes the probability to find a certain number of events (observed number of presences of a given species [0–100]) in a given amount of time or space (i.e. the cells' PFC values, in our case).

$$P(\rho_j, PFC_q) = \frac{\lambda^{\rho_j} \times e^{-\lambda}}{\rho_j!} \qquad (1)$$

$$\lambda(j, PFC_q) = M_j + (C_j \cdot PFC_q) \qquad (2)$$

where ρ_j is the density of occupancy of species j in cell q ($0 \leq \rho_j \leq 100$); PFC_q represents the proportion of forest cover in cell q; λ is the rate parameter of the Poisson distribution, which here represents the expected value of the density of occupancy of species j along the PFC gradient; e is the base of the natural logarithm; and M_j and C_j are species-specific parameters for species j and with respect to PFC_q.

Given the structure of this model, the probability of presence of species j is zero when

$$P(\rho_j = 0, PFC_q) = e^{-\lambda} \qquad (3)$$

To explore how forest cover affects the probability of presence of species j, we can transform Eq. 3 as

$$P(\rho_j > 0, PFC_q) = 1 - e^{-\lambda} \qquad (4)$$

Equation 4 thus gives the probability of finding a given species j along the PFC gradient (Hilborn and Mangel 1997) irrespective of the number of presences in cell q. This allowed us to explore the relationships between PFC and species probability of occurrence.

To investigate how forest fragmentation influences the probability of occurrence of tree species, we divided the cells corresponding to each species (i.e. those laying within its native range distribution in Peninsular Spain) into two separate groups according to the proportion of PFC represented by rLPS. As explained above, forest fragmentation levels increase as rLPS values decrease. Thus, we defined the two fragmentation groups as: (1) cells where rLPS $\geq$ 90% of PFC (very low fragmentation), and (2) cells where rLPS $\leq$ 50% of PFC (moderate to high fragmentation). In order to test if this selection criterion might affect the results, we also performed the analyses using a different break-point criteria (rLPS $\geq$ 90%, < 90% of PFC). Note that using rLPS $\geq$ 90%, <90% of PFC is very conservative, since a break-point criterion of 90% implies that the cells below the break-point (rLPS < 90% of PFC) comprise a high variation

in terms of rLPS, and are thus underestimating the effects of habitat fragmentation. The selection of different break-point criteria, however, did not change our main results (Table 2, Fig. 3).

We used likelihood ratio tests (LRT) to evaluate the goodness of fit between null models (intercept model) and models with PFC_q as predictor of species' probability of occurrence. LRT is a statistical test to compare hierarchically nested models that approximately follows a χ^2 distribution (Huelsenbeck and Crandall 1997, Huelsenbeck and Rannala 1997). LRT assigns likelihood scores to models and determines whether the difference in likelihood scores between two models is statistically significant by considering the degrees of freedom, which, in the LRT, are equal to the number of additional parameters in the more complex model. This information is then used to determine the critical value of the test statistic from standard statistical tables. Here, we compare models that differ in one parameter (PFC_q), so the expected difference between null models and PFC_q models at $p < 0.05$ must be ≥ 1.92 (or ≥ 19.51 at $p < 0.00001$). In all cases, likelihood ratio tests selected the more complex models containing PFC_q as a predictor of species' probability of occurrence (Table 1, 2).

The regression models treated the data as independent, and so did not include the potential effects of spatial autocorrelation, i.e. a tendency for plots close to each other to have similar PFC_q, and/or λ (j, PFC_q), values. This autocorrelation reduces the effective sample size of the regression (Diniz-Filho et al. 2003), compared to that carried out here, by a fraction that is currently unknown; however, the effects of this are unlikely to be substantial here because the (uncorrected) sample size is so large (756–4150 for each species) compared to the number of parameters to be estimated (two for each species). Moreover, we used different break-point criteria to estimate the effects of forest fragmentation on the probability of presence of tree species, one of them being highly conservative: this method is likely to have increased the confidence intervals of C_j and M_j by a larger fraction that would the inclusion of the effects of spatial autocorrelation.

Results

Probabilities of occurrence significantly decreased along with the reduction of forest cover for all eight tree species, both in cells with low fragmentation (with rLPS $\geq$ 90%), and in those with moderate-to-high fragmentation (rLPS $\leq$ 50%) (Fig. 2). However, there were clear differences in how species reacted to forest cover reduction in each fragmentation scenario. Superposition of species-forest cover relationships in different fragmentation scenarios showed that habitat fragmentation significantly modified species' probability of occurrence along the habitat cover gradient in six tree species (Fig. 2, 3), although these changes usually occur after a certain level of habitat destruction has been reached. Percolation theory suggests a threshold level in the relationship between largest patch size and habitat destruction, and thus the effects of habitat fragmentation that we observe are stronger once a critical destruction value has been reached (Bascompte and Solé 1996, Solé and Bascompte 2007).

Table 1. Parameter estimates (MLE) of the Poisson models (M_j, C_j) and their lower and upper 95% CI obtained for each tree species for cells with very low (rLPS ≥ 90% of PFC) and moderate-to-high (rLPS <50% of PFC) forest fragmentation. Species are listed in rank order of total number of analyzed cells (n). Likelihood ratio χ^2 tests of model fit and their p-values are also provided.

Fragmentation level and tree species	n	M_j (lower; upper)	C_j (lower; upper)	Model fit (L.ratio χ^2 test)	
				L.ratio χ^2	p
Low fragmentation (rLPS ≥ 90% PFC)					
Quercus faginea	1073	0.628 (0.580; 0.676)	0.025 (0.024; 0.026)	1646.56	<0.001
Quercus petraea	393	−1.348 (−1.542; −1.154)	0.049 (0.046; 0.051)	1419.08	<0.001
Quercus suber	442	0.026 (−0.070; 0.122)	0.036 (0.034; 0.037)	1453.76	<0.001
Ilex aquifolium	331	−0.070 (−0.208; 0.069)	0.030 (0.027; 0.032)	710.96	<0.001
Pinus nigra	381	−0.178 (−0.293; -0.063)	0.042 (0.041; 0.044)	2647.26	<0.001
Pinus sylvestris	365	0.058 (−0.046; 0.162)	0.047 (0.045; 0.049)	3281.76	<0.001
Fagus sylvatica	275	0.486 (0.380; 0.60)	0.036 (0.034; 0.037)	1904.25	<0.001
Quercus robur	275	1.549 (1.459; 1.639)	0.012 (0.010; 0.013)	190.56	<0.001
Moderate-to-high fragmentation (rLPS < 50% PFC)					
Quercus faginea	1358	1.130 (1.089; 1.171)	0.013 (0.010; 0.015)	85.22	<0.001
Quercus petraea	592	−0.432 (−0.568; −0.296)	0.038 (0.033; 0.044)	183.54	<0.001
Quercus suber	565	0.401 (0.321; 0.482)	0.049 (0.045; 0.053)	518.47	<0.001
Ilex aquifolium	601	−0.110 (−0.217; −0.003)	0.054 (0.050; 0.058)	734.33	<0.001
Pinus nigra	487	0.232 (0.140; 0.323)	0.054 (0.051; 0.056)	1326.24	<0.001
Pinus sylvestris	480	0.329 (0.242; 0.417)	0.053 (0.050; 0.055)	1478.87	<0.001
Fagus sylvatica	499	−0.251 (−0.372; −0.129)	0.057 (0.053; 0.061)	675.62	<0.001
Quercus robur	481	1.554 (1.488; 1.620)	0.018 (0.015; 0.020)	152.78	<0.001

The mismatches between species' probability of occurrence between fragmentation scenarios showed that most tree species were benefited by moderate to high levels of fragmentation.

The only species that matched the predictions of the extinction threshold hypothesis is *Fagus sylvatica* (Fig. 2a, 3a). That is, while in the moderate-to-high fragmentation scenarios the occurrence probability of this species showed an accelerated decrease with forest cover reduction and a clear extinction threshold (i.e. there was a point in which its occurrence probability fell to 0), in the low fragmentation scenario the probability of occurrence declined more gently and no extinction point was found.

The rest of tree species were not negatively affected by habitat fragmentation and rejected the extinction threshold hypothesis. Some of them showed an extinction threshold (occurrence probability = 0) caused by quantitative habitat loss; others responded positively to fragmentation by

Table 2. Parameter estimates (MLE) of the Poisson models (M_j, C_j) and their lower and upper 95% CI obtained for each tree species for cells with very low (rLPS ≥ 90% of PFC) and higher (rLPS <90% of PFC) forest fragmentation. Species are listed in rank order of total number of analyzed cells (n). Likelihood ratio χ^2 tests of model fit and their p-values are also provided.

| Fragmentation level and tree species	n	M_j (lower; upper)	C_j (lower; upper)	Model fit (L.ratio χ^2 test)	
				L.ratio χ^2	p
Low fragmentation (rLPS ≥ 90% PFC)					
Quercus faginea	1073	0.628 (0.580; 0.676)	0.025 (0.024; 0.026)	1646.56	<0.001
Quercus petraea	393	−1.348 (−1.542; −1.154)	0.049 (0.046; 0.051)	1419.08	<0.001
Quercus suber	442	0.026 (−0.070; 0.122)	0.036 (0.034; 0.037)	1453.76	<0.001
Ilex aquifolium	331	−0.070 (−0.208; 0.069)	0.030 (0.027; 0.032)	710.96	<0.001
Pinus nigra	381	−0.178 (−0.293; −0.063)	0.042 (0.041; 0.044)	2647.26	<0.001
Pinus sylvestris	365	0.058 (−0.046; 0.162)	0.047 (0.045; 0.049)	3281.76	<0.001
Fagus sylvatica	275	0.486 (0.380; 0.60)	0.036 (0.034; 0.037)	1904.25	<0.001
Quercus robur	275	1.549 (1.459; 1.639)	0.012 (0.010; 0.013)	190.56	<0.001
Higher fragmentation (rLPS < 90% PFC)					
Quercus faginea	3077	0.90 (0.87; 0.93)	0.024 (0.023; 0.026)	1212.95	<0.001
Quercus petraea	1350	−0.496 (−0.583; −0.409)	0.035 (0.033; 0.038)	608.37	<0.001
Quercus suber	1295	0.219 (0.163; 0.274)	0.046 (0.044; 0.048)	1376.43	<0.001
Ilex aquifolium	1247	−0.094 (−0.164; −0.023)	0.043 (0.040; 0.045)	1505.42	<0.001
Pinus nigra	1194	0.247 (0.191; 0.304)	0.047 (0.045; 0.048)	3891.21	<0.001
Pinus sylvestris	1179	0.496 (0.445; 0.546)	0.046 (0.045; 0.047)	4748.64	<0.001
Fagus sylvatica	1036	−0.122 (−0.195; −0.049)	0.050 (0.048; 0.052)	2381.48	<0.001
Quercus robur	937	1.460 (1.413; 1.506)	0.019 (0.018; 0.021)	601.70	<0.001
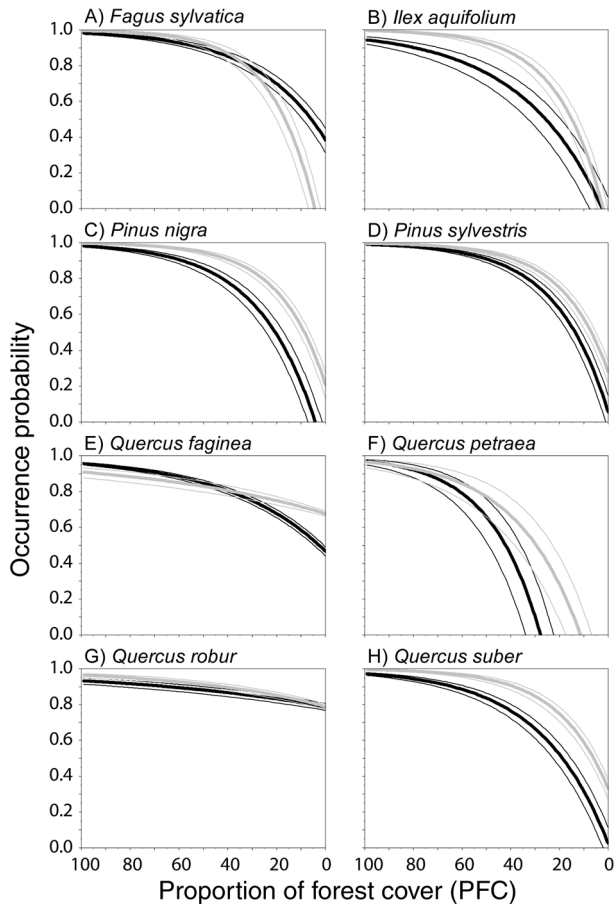
Figure 2. Variation of tree species' occurrence probabilities across the gradient of decreasing forest cover (note that PFC decreases to the right) in scenarios with very low (black curves) and moderate-to-high (grey curves) forest fragmentation (i.e. with rLPS ≥ 90% of PFC, and rLPS <50% of PFC, respectively). Thin lines represent 95% CI for each curve.
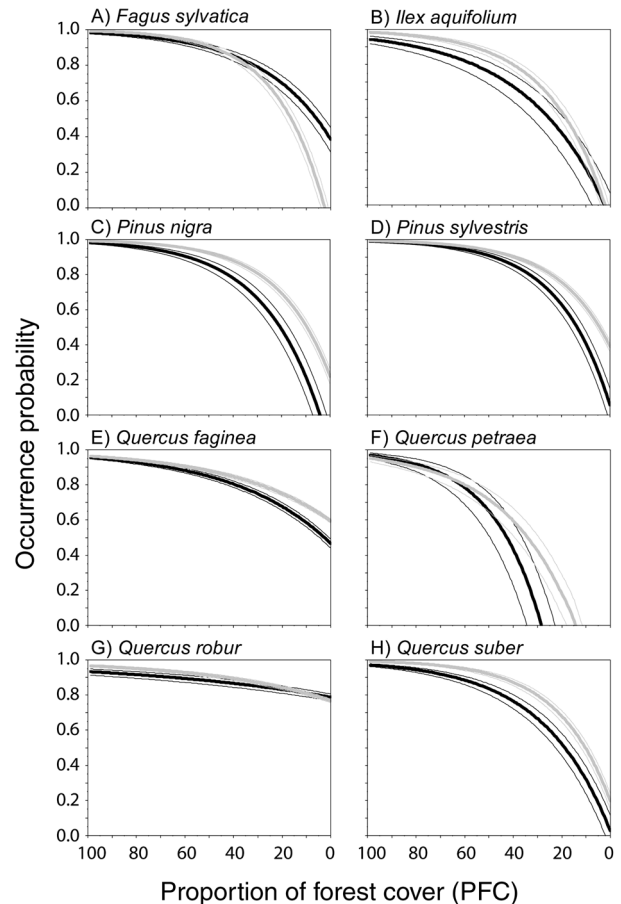
Figure 3. Variation of tree species' occurrence probabilities across the gradient of decreasing forest cover (note that PFC decreases to the right) in scenarios with very low (black curves) and larger (grey curves) forest fragmentation (i.e. with rLPS ≥ 90% of PFC, and rLPS <90% of PFC, respectively). Thin lines represent 95% CI for each curve.

showing increased occurrence probabilities in fragmented landscapes. These results indicate that fragmentation can affect the occurrence probability of certain tree species beyond the effects of habitat loss, but that only a few species show an extinction threshold.

Ilex aquifolium and *Quercus robur* neither confirmed nor rejected the extinction threshold hypothesis (they showed similar occurrence probabilities in different fragmentation scenarios). For *Ilex aquifolium*, occurrence probabilities were higher for the case of moderate-to-high fragmentation when PFC was above ~20% (Fig. 2b). This suggests that, as long as forest cover does not drop to very low levels, *I. aquifolium* might in fact be benefited by fragmentation. Probability of occurrence of *Quercus robur*, on the other hand, did not significantly change between fragmentation scenarios (Fig. 2g).

Five out of eight species rejected the extinction threshold hypothesis (*Quercus faginea, Q. petraea, Q. suber, Pinus nigra, P. sylvestris*), irrespective of the break point criterion used to discriminate between different fragmentation scenarios (Fig. 2, 3). These species showed higher occurrence probabilities in fragmented areas, and thus positive effects of fragmentation were the norm for these species.

Discussion

This is to our knowledge the first broad-scale study exploring the effects of forest amount and fragmentation on the presence probability of different tree species. Given that each point in the forest cover gradient was related to different levels of fragmentation, relationships of species' occurrence probabilities with forest cover could be compared between different fragmentation scenarios across the species' native ranges in our study region (Peninsular Spain), which in turn allowed investigating predictions of the extinction threshold hypothesis for each species (Fahrig 2002). A first conclusion that can be derived from our results is that, irrespective of the level of forest fragmentation, the occurrence probability of all tree species tends to decrease along with diminishing forest cover. This was expected, as it is consistent with the responses of the same and additional tree species to forest cover variation found in the same region at a fined-grained scale (Montoya et al. 2008), and with the reactions generally reported in the literature for many other animals and plants in other areas (Andrén 1994, Boutin and Hebert 2002, Fahrig 2002, 2003).

Beyond this common trend, our data also show that only one species (*Fagus sylvatica*) supports the predictions of the extinction threshold hypothesis. When forest fragmentation was moderate to high, the occurrence probability of *F. sylvatica* declined more sharply with the reduction of forest cover, and an extinction threshold (the amount of forest cover at which the species' occurrence probability becomes zero) was reached, whereas no such threshold was found when fragmentation was low (Fig. 2a, 3a). Conversely, the other species showed a range of responses that included null and even positive reactions to increased fragmentation; some species reached the extinction threshold (occurrence probability = 0) as a direct consequence of habitat loss (*P. nigra, Q. petraea*). Taken together, these results can be interpreted in line with the general conclusions reached by Fahrig (2003); i.e. that the occurrences of most species are commonly more limited by habitat amount than by habitat fragmentation, which may even have positive effects on persistence (Andrén 1994, Boutin and Hebert 2002), and that the extinction threshold hypothesis is not generally supported by empirical data. Further, habitat loss by itself can drive some tree species to extinction in areas where fragmentation is not important.

Why tree species behave differently under different forest fragmentation scenarios?

According to Kunstler et al. (2005), *F. sylvatica* is a late successional tree with a large tolerance to low light conditions (Pacala et al. 1994, Lin et al. 2002), and clearly specialized to live in dense forest plots, where it shows higher recruitment rates. This is consistent with Montoya's et al. (2008) observation that *F. sylvatica* is the most vulnerable tree of our species group to decreasing forest cover levels measured at fine-grained scale, and may, at least in part, explain why this species supported the extinction threshold hypothesis. Conversely, even though the occurrence of the other species we studied was also positively related with forest cover (Montoya et al. 2008), previous evidence suggests that they are not so closely associated with forest interior conditions as *F. sylvatica* does, which may explain their different responses to fragmentation (Fahrig 2002). For instance, Arrieta and Suarez (2005) investigated the seedling emergence and survival rates of *Ilex aquifolium* in landscapes of our study region, and found that both characteristics were higher in forest edges. This suggests that forest edges constitute a good habitat for *I. aquifolium*. Similarly, a common characteristic among European oaks (*Q. robur*) is that they require high solar irradiances, especially at the seedling stage (Barry-Langer and Nebout 1993). Moreover, *Quercus* species with sclerophyllous leaves show intermediate to high tolerance to solar radiation (e.g. *Q. suber*; Valladares 2005, Valladares and Niinemets 2008), which again indicates good survival opportunities for *Quercus* species at the edge of forest patches. Moreover, this might also be true for *Pinus* species given their reported tolerance to high light conditions (Debain et al. 2003, Kunstler et al. 2006). The relative amount of forest edge is expected to be larger in fragmented forests compared with non-fragmented ones for the same level of forest cover, and this increased edge amount may in fact lead to more opportunities for establishment and survival of edge

tolerant/loving species (Fahrig 2002). This in turn might explain both the positive or null reactions to forest fragmentation of *Ilex*, *Quercus*, and *Pinus* species, as well as their lack of support to the extinction threshold hypothesis.

Complementary explanations for our findings can be provided by the different dispersal capabilities of the studied species. For instance, Kunstler et al. (2007) found that distance to the nearest adult population (a fragmentation variable) was the main explanatory variable of beech populations' recruitment rates and survival in fragmented landscapes, which these authors related with the limited dispersal abilities shown by this species. Thus, larger difficulties of *F. sylvatica* to colonizing remaining forest patches may have limited its persistence where fragmentation was higher, which constitutes an additional reason for the support given by *F. sylvatica* to the extinction threshold hypothesis (Fahrig 2002). Conversely, our observation that the occurrence probabilities of *P. nigra* and *P. sylvestris* were higher when fragmentation was moderate to high (Fig. 2, 3), may be related with the good colonizing abilities that have been reported for *Pinus* species (Debain et al. 2003, Kunstler et al. 2006). Indeed, this characteristic is likely to have favoured the survival and recruitment rates of individuals of these species in cells with greater fragmentation. Likewise, in the case of *Quercus* species, observed positive (*Q. faginea*, *Q. petraea* and *Q. suber*) and null (*Q. robur*) effects of forest fragmentation on occurrence probabilities can be accounted for by the fact that *Quercus* species are mainly dispersed by birds and mammals (e.g. the European jay *Garrulus glandarius*, Gómez 2003). This interpretation is consistent with that, unlike wind, animals actively deliver seeds toward suitable habitat remnants (directed dispersal) and may increase average dispersal distances (Johst et al. 2002, Purves and Dushoff 2005, Montoya et al. 2008), as well as with the prediction of recent theoretical models based on metapopulation theory (Hanski 1999) that animal-mediated seed dispersal confers increased species robustness to habitat loss (Purves et al. 2007). All in all, these evidences coupled with our results suggest that life-history traits and, especially, dispersal capabilities, play a key role in determining the response of each species to forest fragmentation, as well as its potential conformity with the extinction threshold hypothesis (Fahrig 2002). This is in agreement with early theoretical predictions where spatially implicit models were compared to their spatially explicit counterparts (Bascompte and Solé 1996): these models showed that a difference in the location of the extinction threshold certainly requires short-range dispersal.

Another aspect to consider when interpreting our results is how we differentiated between more and less fragmented cells. Habitat fragmentation is a complex process that may alter habitat configuration in many ways, affecting, among other aspects, the number, size, shape and physical connectivity of the remaining patches, the inter-patch distances, the area-weighted average patch size (Jaeger et al. 2007) and the ratio of edge-to-interior habitat in the landscape. The consequences of these changes for populations and communities are not mutually independent; they feed back on each other and with habitat amount in ways that can amplify their individual effects, complicating the selection of variables to differentiate between high and low fragmented areas to a large extent (McGarigal et al. 2002, Fahrig 2003). Here, we used

the proportion of the cell's forest cover that is concentrated into the largest patch (rLPS) as an indicative variable of forest fragmentation. When most of the existing forest cover appears concentrated into one, relatively large patch of continuous forest (e.g. with rLPS $\geq$ 90% of PFC), we can be reasonably certain that the level of fragmentation is very low. Conversely, a high proportion of forest cover concentrated outside the largest forest patch (e.g. with rLPS < 50% of PFC) indicates that all existing patches are relatively small (i.e. no large portions of continuous forest exist), and that fragmentation is higher (Fahrig 2002). This is indeed a simple and crude way of characterizing fragmentation levels, as it is clear that cells showing similar forest cover and rLPS values may, to some unknown extent, differ in terms of the above-mentioned characteristics that define the spatial configuration of habitats. Although our characterization of less and more fragmented cells could be viewed as conservative, as it did not capture all the spatial subtleties that might affect species' occurrences in fragmented habitats, we believe that it was sufficient to uncover any strong signal left by forest fragmentation on the distribution of the studied species. Moreover, given that we found qualitatively similar results for different rLPS cut-off levels (i.e. Fig. 2: $\geq$ 90% and < 50%; and Fig. 3: $\geq$ 90% and < 90%), we see unlikely that a finer characterization of forest fragmentation levels could render radically different results. Our approach, however, does not prevent from using alternative fragmentation variables.

We want to note that even though introduced species have been excluded from the current analysis, our subset of species has been also subject to human influences in some parts of continental Spain (e.g. *Q. suber*, *P. sylvestris*; Blondel and Aronson 1999). Although this may be affecting the observed response patterns of tree species, the effects of habitat amount and habitat fragmentation would be underestimated in plantations, and therefore, the observed relationships between species' probability of occurrence and habitat amount and fragmentation might be even more pronounced for these tree species.

To summarize, by using a large database that reflects the current distribution of eight tree species across Peninsular Spain, we have investigated how each species' occurrence probabilities vary with forest cover in different scenarios of forest fragmentation, and to what extent the observed patterns lend support to the extinction threshold hypothesis. Even though the probability of occurrence decreased with forest cover in all cases, only one species (*F. sylvatica*) agreed with the predictions of the hypothesis, which we attributed to a larger linkage with forest interior conditions and more limited dispersal abilities of beech populations. In opposition, larger tolerance to (or preference for) solar radiation (i.e. forest edge situations) and better dispersal capabilities can explain why the hypothesis was not sustained by the other species. So, although our study only lent support to the extinction threshold hypothesis for one out of the eight species analyzed, it also permitted us conjecturing which characteristics may lead species vulnerability to habitat fragmentation. In particular, to posses a limited dispersal and a low tolerance to insolation typical of habitat edge environments. This is indeed a simple message, but still one worthy of further attention. Specially because, if it was confirmed by future studies, then biodiversity conservation in fragmented landscapes would benefit from having a simple rule to differentiate among species that may suffer or benefit from fragmentation.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–364.

Arrieta, S. and Suarez, F. 2005. Spatial pattern of seedling emergence and survival as a critical phase in holly (*Ilex aquifolium* L.) woodland recruitment in central Spain. – For. Ecol. Manage. 205: 267–282.

Bascompte, J. and Solé, R. V. 1996. Habitat fragmentation and extinction thresholds in spatially explicit models. – J. Anim. Ecol. 65: 465–473.

Bascompte, J. and Rodriguez, M. A. 2001. Habitat patchiness and plant species richness. – Ecol. Lett. 4: 147–420.

Bascompte, J. et al. 2002. Patchy populations in stochastic environments: critical number of patches for persistence. – Am. Nat. 159: 128–137.

Baille, J. et al. 2004. 2004 IUCN red list of threatened species: a global assessment. – International Union for Conservation of Nature, Cambridge, UK.

Barry-Langer, A. and Nebout, J. P. 1993. Les chênes pédonculés et sessile en France et en Belgique. – Editions du Perron, Alleur-Liège.

Blondel, J. and Aronson, J. C. 1999. Biology and wildlife of the Mediterranean region. – Oxford Univ. Press.

Boswell, G. P. et al. 1998. Habitat fragmentation, percolation theory and the conservation of a keystone species. – Proc. R. Soc. Lond. B 265: 1921–1925.

Boutin, S. and Hebert, D. 2002. Landscape ecology and forest management: developing an effective partnership. – Ecology 12: 390–397.

Cardillo, M. and Bromham, L. 2001. Body size and risk of extinction in Australian mammals. – Conserv. Biol. 15: 1435–1440.

Costa, M. et al. 2001. Los bosques ibéricos. Una interpretación geobotánica. – Planeta, Barcelona.

Debain, S. et al. 2003. Reproductive variability in *Pinus sylvestris* in southern France: implications for invasion. – J. Veg. Sci. 14: 509–516.

Diniz-Filho, J. A. F. et al. 2003. Spatial autocorrelation and red herrings in geographical ecology. – Global Ecol. Biogeogr. 12: 53–64.

Donovan, T. M. and Flather, C. H. 2002. Relationships among North American songbird trends, habitat fragmentation, and landscape occupancy. – Ecol. Appl. 12: 364–374.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. – Ecol. Appl. 12: 346–353.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Syst. 34: 487–515.

Fortuna, M. A. and Bascompte, J. 2006. Habitat loss and the structure of plant–animal mutualistic netwoks. – Ecol. Lett. 9: 281–286.

Gibbs, J. P. 2001. Demography versus habitat fragmentation as determinants of genetic variation in wild populations. – Biol. Conserv. 100: 15–20.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. – Ecography 26: 573–584.

Hall, L. S. et al. 1997. The habitat concept and a plea for standard terminology. – Wildlife Soc. B 25: 173–182.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Hilborn, R. and Mangel, M. 1997. The ecological detective. Confronting models with data. – Princeton Univ. Press.

Hill, M. F and Caswell, H. 1999. Habitat fragmentation and extinction thresholds on fractal landscapes. – Ecol. Lett. 2: 121–127.

Huelsenbeck, J. P. and Crandall, K. A. 1997. Phylogeny estimation and hypothesis testing using maximum likelihood. – Annu. Rev. Ecol. Syst. 28: 437–466.

Huelsenbeck, J. P. and Rannala, B. 1997. Phylogenetic methods come of age: testing hypotheses in an evolutionary context. – Science 276: 227–232.

Inventario Forestal Nacional 1995. Segundo inventario forestal nacional. – Ministerio de Agricultura, Pesca y Alimentación, Madrid, Spain.

Jaegger, J. A. G. et al. 2007. Time series of landscape fragmentation caused by transportation infrastructure and urban development. – Ecol. Soc. 12: 22.

Jansson, G. and Angelstam, P. 1999. Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. – Landscape Ecol. 14: 283–290.

Johst, K. et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. – Oikos 98: 263–270.

Komonen A. et al. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. – Oikos 90: 119–126.

Kunstler, G. et al. 2005. Growth, mortality, and morphological response of European beech and downy oak along a light gradient in sub-Mediterranean forest. – Can. J. For. Res. 35: 1657–1668.

Kunstler, G. et al. 2006. Indirect facilitation and competition in tree species colonization of sub-Mediterranean grasslands. – J. Veg. Sci. 17: 379–388.

Kunstler, G. et al. 2007. *Fagus sylvatica* L. recruitment across fragmented Mediterranean Landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. – Div. Dist. 13: 799–807.

Lande R. 1987. Extinction thresholds in demographic models of territorial populations. – Am. Nat. 130: 624–635.

Lin, J. et al. 2002. Sapling growth and survivorship as a function of light in a mesic forest of southeast Texas, USA. – Oecologia 132: 428–435.

Lindenmayer, D. B. and Fischer, J. 2006. Habitat fragmentation and landscape change. – Island Press.

McGarigal, K. and Cushman, S. A. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. – Ecol. Appl. 12: 335–345.

McGarigal, K. et al. 2002. FRAGSTATS: Spatial pattern analysis program for categorical maps. – Comp. software prog. Univ. Mass., Amherst. www.umass.edu/landeco/research/fragstats/fragstats.html

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. – Annu. Rev. Ecol. Syst. 28: 495–516.

Montoya, D. et al. 2007. Contemporary richness of Holarctic trees and the historical pattern of glacial retreta. – Ecography 30: 173–182.

Montoya, D. et al. 2008. Animal vs wind dispersal and the robustness of tree species to deforestation. – Science 320: 1502–1504.

Pacala, S. et al. 1994. Sapling growths as a function of resources in a north temperate forest. – Can. J. For. Res. 24: 2175–2183.

Purves, D. W. and Dushoff, J. 2005. Directed seed dispersal and metapopulation response to habitat loss and disturbance: application to *Eichhornia paniculata*. – J. Ecol. 93: 658–669.

Purves, D. W. et al. 2007. Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. – Ecol. Monogr. 77: 77–97.

Purvis, A. et al. 2000. Predicting extinction risk in declining species. – Proc. R. Soc. Lond. B 267: 1947–1952.

Solé, R.V. and Bascompte, J. 2007. Self-organization in complex ecosystems. – Princeton Univ. Press.

Valladares, F. 2005. Ecología del bosque mediterráneo en un mundo cambiante. – Ministerio de Medio Ambiente, Madrid, Spain.

Valladares, F. and Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. – Annu. Rev. Ecol. Evol. Syst. 39: 237–257.

Venier, L. and Fahrig, L. 1996. Habitat availability causes the species abundance–distrubution relationship. – Oikos 76: 564–570.