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# Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain)

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**Abstract**

We analysed the composition and configuration patterns of the forested landscape in the Cantabrian range (NW Spain) determining how different forest communities are currently affected by long-term fragmentation process. We also evaluated the regional reserve network in relation to forest fragmentation and forest heterogeneity at the landscape level. The current landscape scenario is characterised by low forest habitat cover (22%) and a fragment size distribution strongly skewed towards small values (<10 ha). Forest classes differ strongly in fragment size, internal heterogeneity, shape, dispersion and isolation. Beech forests were less fragmented than other types, being the dominant class in terms of surface and fragment occurrence. Fragmentation was heavier in forests occurring in agriculture-suitable areas (i.e. valley bottoms, southern exposures), such as ash-maple and oak forests, as well as in second-growth forests developed after tree-line deforestation for pastures (i.e. holly and rowan forests). The current reserve network in the Asturias region covers preferentially bigger and less isolated forest fragments. This was a consequence of protection biased towards beech forests, to the detriment of an adequate representativeness of most other forest types, some of them with high ecological value. Future expansion of the reserve network should be based on landscape information, to promote both the protection of well-conserved, less-fragmented forests as well as the inclusion of under-represented target forest types.


*Keywords:* Fragmentation; Landscape; Montane forest; NW Spain; Reserve network adequacy

## 1. Introduction

The negative consequences of habitat loss and the concomitant fragmentation are evident in both recently and historically managed forests of temperate regions (Whitcomb et al., 1981; Harris, 1984; Wilcove et al., 1986; Santos et al., 1999, 2002; Lindenmayer and Franklin, 2002). Among processes driven by fragmentation, the population declines of forest species, the alteration of species interactions (e.g. predation, pollination), and the disruption of key ecological functions are major causes of forest

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biodiversity change (Harrison and Bruna, 1999; Davies et al., 2001; Lindenmayer and Franklin, 2002). In this context, a growing theoretical and empirical framework links these processes with the landscape configuration and composition of fragmented forests (Noss, 1990; Fahrig and Merriam, 1994; Harrison and Bruna, 1999). In fact, it is known that landscape properties such as the proportion of forest habitat in the landscape (Andrén, 1994; Cooper and Walters, 2002; Fahrig, 2002), the size distribution of fragments (Wilcove et al., 1986; Andrén, 1994; Laurance et al., 2002), the fragment shape (Andrén, 1995; Murcia, 1995; Hill and Caswell, 1999) and the degree of fragment isolation (Verboom et al., 1991; Andrén, 1994; Laurance et al., 2002) underpin the impoverishment of forest biodiversity.

The explicit relationship between fragmentation and biodiversity makes essential the analysis of landscape patterns for forest conservation and management purposes (Turner et al., 2001; Gutzwiller, 2002; and references therein). For example, forest reserve design has frequently taken into account fragmentation patterns to preserve larger and less isolated forest fragments (Harris, 1984; Ranta et al., 1998; Lambeck and Hobbs, 2002), and to establish priorities for the protection of species sensitive to fragmentation by preserving their habitats (Arnold, 1995; Rebane et al., 1997; and references therein). More recently, the inclusion of small fragments in protection networks has been emphasized, since these small reserves might represent high-quality remnants, especially in chronically fragmented landscapes where large reserves include higher proportion of degraded land (Schwartz, 1999; Götmark and Thorell, 2003). Complementary to these fragmentation concerns, the study of landscape composition might be applied to conservation goals such as the protection of rare landscape elements and the establishment of reserve networks efficiently representing forest heterogeneity, and thus biological diversity, at regional scale (Caicco et al., 1995; Scott et al., 2001; Lambeck and Hobbs, 2002). The degree of biodiversity representativeness achieved by a reserve network will depend on its comprehensiveness, i.e. its ability to contain the full range of forest habitat types, but also on its adequacy, that is, the amount of each habitat type represented (Pressey et al., 1993; Lambeck and Hobbs, 2002). In this sense, international commissions have called for the near-protection of a target percentage ($\geq$10%) of the total land area of each ecosystem or habitat type, to maintain ecological processes and biological phenomena at the regional scale (Soulé and Sanjayan, 1998; and references therein). Despite that this target coverage is considered far from adequate (Soulé and Sanjayan, 1998), it can still be a useful tool for documenting a serious lack of representativeness in reserve networks (e.g. Caicco et al., 1995; Scott et al., 2001; Reyers et al., 2001).

The overall goal of the present study is to evaluate the fragmentation patterns and the protection status of the historically managed montane forest in the Cantabrian range (NW Spain). This mountain range contains the largest portion of the remnant Atlantic deciduous forests on the Iberian peninsula. It represents the southernmost boundary of this system in Western Europe and is still sheltering high plant and animal species richness, because it is an ecotonal zone between the Eurosiberian and the Mediterranean regions in Europe (Polunin and Walters, 1985; Díaz and Fernández, 1987; Rebane et al., 1997). Our specific goals are: (1) to describe the composition and configuration of fragmented forest communities, by considering different forest types as particular components of the regional landscape; and (2) to evaluate the ability of the current reserve network to cope with fragmentation as well as to represent the heterogeneity of the Cantabrian forests at the landscape level.

## 2. Methods

### 2.1. Study area

This study considers the montane area of the Cantabrian range in the Asturias region (NW Spain), i.e. roughly covering the northern exposure of the range. The study area spans 42.8–43.5° N, and 4.5–7.1° W (Fig. 1). The landscape of study was arbitrarily established as the area above 700 m a.s.l. up to the highest peak at 2648 m a.s.l., comprising 416,491 ha. We considered the potential forest area as the surface comprised between 700 and

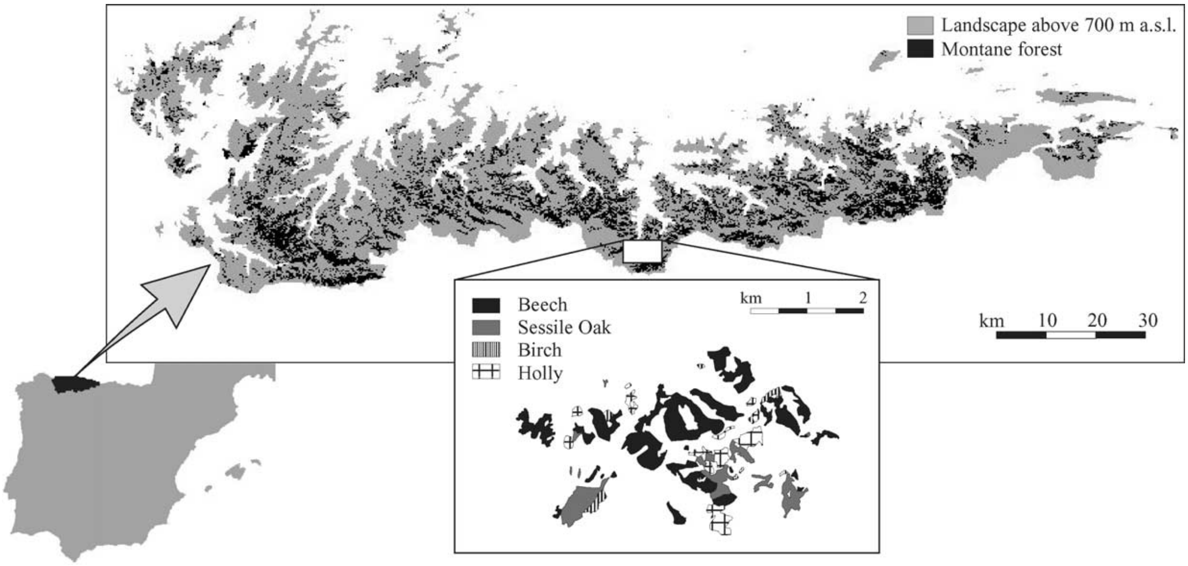


Fig. 1. Map of the study area representing the geographical location, the sampled landscape in the Cantabrian range and the composition of forest fragments.

1700 m a.s.l. (montane lower limit and tree-line, respectively, Díaz and Fernández, 1987), accounting then for 389, 379 ha. We considered this potential forest area to approximately fit to the surface of original, once unfragmented forests. The climate of the region is Atlantic, with precipitation distributed throughout the year. Annual average temperature is ca. 8.2 °C and total precipitation is ca. 1250 mm. Originally covered by Atlantic deciduous forests, the Cantabrian range has a long history of deforestation by human causes. Indeed, Holocene pollen analysis reveals major decreases in forest cover associated to anthropogenic activity by 3000 BP (Muñoz-Sobrino et al., 1997). Historically, traditional cattle ranging and selective logging transformed large patches of natural forests to pasturelands. More recently, other factors such as road construction, surface mining, increased fire frequency by human-induced causes, and timber exploitation in plantations have accounted for additional losses of natural forest habitat. Most of the forests in this area might be considered as mature forest with some degree of management, but some second-growth forests have developed during the last century after pasture abandonment. Thus, the current regional landscape contains remnant forest fragments standing out from a non-forest matrix mainly composed of pastures, heathlands in abandoned meadows and areas of shallow soil, and scattered small villages.

### 2.2. The GIS database

Vegetation and topographic information was derived from the geographic information system (GIS) of the regional environmental agency (Consejería de Medio Ambiente, Principado de Asturias), which represents the actual (not potential) vegetation cover and was generated in 1994. To obtain the vegetation layer, we merged together 37 single 1:25,000-scale sheets, each covering ca. 126 km$^2$. The available vegetation data of forest vegetation, in the form of vectorial polygons, was classified into eight main different types, depending on dominant canopy species: (1) beech, *Fagus sylvatica* L. (Fagaceae); (2) Pyrenean oak, *Quercus pyrenaica* Willd. (Fagaceae); (3) sessile oak, *Quecurs petraea* Liebl. (Fagaceae); (4) ash-maple, *Fraxinus excelsior* L. (Oleaceae), *Acer pseudoplanatus* L., *Acer platanoides* L. (Aceraceae); (5) white birch, *Betula alba* L. (Betulaceae); (6) holly, *Ilex aquifolium* L. (Aquifoliaceae); (7) rowan, *Sorbus aucuparia* L. (Rosaceae); and (8) conifer plantations [mainly aforestations of

*Pinus sylvestris* L. and *Pinus radiata* D. Don (Pinaceae)].

We considered a monospecific forest patch, in the aforementioned terms, as a forest fragment, whenever isolated in a non-forest matrix. Sometimes, forest classes appeared in patches adjacent to each other (Fig. 1). In such cases, we considered that the adjacent forest classes formed a unique forest fragment surrounded by non-forest habitats. Then we calculated the area of the whole fragment, and the area occupied by each habitat type, and assigned each fragment to one of the eight forest classes outlined above, depending on the identity of the dominant class (in terms of coverage) among the patches within the fragment. The digital map of forests resulting from the aforementioned procedure was rasterized to a cell size of 15 m, a patch being defined as any collection of pixels that touch either at sides or corners, i.e. eight-neighbour clumping method. However, we retained the vectorial vegetation map in order to perform several database-related calculations.

## 2.3. Topographic data

To form the topographic base of the vegetation information, we built a digital elevation model (DEM) with a cell size of 100 m from 1:200,000 digital elevation contours (50 m elevation interval). We used the DEM raster file to derive slope and aspect information for each 100 m cell. Subsequently, we assigned elevation, slope and aspect to forest fragments. Each fragment was assigned its average elevation and slope values. Original aspect data (0–360°) were reclassified into four quadrants according to the exposure to cold weather: northern, 316–45°; eastern, 46–135°; southern, 136–225°; and western, 226–315°. Then we assigned to each fragment its most frequent aspect, i.e. the mode aspect of the DEM cells within the fragment.

## 2.4. Fragmentation patterns

### 2.4.1. Landscape level metrics

We used FRAGSTATS (McGarigal et al., 2002) on the raster data to calculate the coverage for all montane forest and for each forest class within the landscape, and the forest class occurrence in terms of percentage of fragments belonging to each class.

### 2.4.2. Within fragment heterogeneity

We obtained the number and coverage of the different patches included in each fragment, calculating a Simpson's index of within-fragment diversity as $\mathrm{SI} = 1/\sum p_i^2$ (where $p_i$ = coverage of the forest class $i$).

### 2.4.3. Fragment size, shape and isolation indexes

We used FRAGSTATS to obtain the following characteristics of fragments: fragment size, fragment shape via fractal dimension, and isolation via Euclidean nearest neighbour distance (NND) and proximity index. Fractal dimension ($D$) characterises the degree of shape complexity of a polygonal fragment, such that the perimeter ($P$) is related to the area ($A$) by $P = \sqrt{A^D}$ (i.e. $\log P = 1/2D \log A$). For simple Euclidean shapes $P = \sqrt{A}$ and $D = 1$, whereas for increasingly complex shapes, the perimeter becomes plane-filling and $P = A$ with $D = 2$ (Mladenoff et al., 1993; Pan et al., 2001; McGarigal et al., 2002). Proximity index accounts for the number, the size and proximity of neighbouring fragments within a specific search radius from a focal fragment, higher index values indicating lower isolation (Gustafson and Parker, 1992). That is, isolation decreases for fragments surrounded by a higher number of fragments, bigger fragments or/and nearer fragments. Since the choice of a search radius is arbitrary, we firstly checked for differences in the behaviour of the proximity index at different search radii, from $d = 30$ m (the minimum nearest neighbour distance found in the database) to increasing distances in a log scale ($d = 300$, 3000 and 30,000 m). We found that proximity values asymptotied at $d_{300}$ for all forest classes, maintaining the ranking of differences among classes at the higher scales (based on ANOVAR considering the scale of distance as a repeated measure term). Thus, all subsequent analyses involving proximity index were performed at $d_{300}$. Isolation indexes for each fragment were calculated separately for neighbours of the same class and for neighbours of any class. Additionally, an index of dispersion at the landscape scale was calculated for each forest class as $R_c = 2d_c(\lambda/\pi)$, where $d_c$ = mean of the same-class NND and $\lambda$ = density of fragments ($R_c > 1$ indicates patches are regularly distributed, $R_c = 1$ patches are randomly distributed and $R_c < 1$ patches are aggregated; Forman, 1995).

### 2.5. Fragmentation and protection status

A fragment was considered under protection when its surface was total or partially included within the territory of an established protected area. We derived this information from the GIS database. The regional reserve network included in the studied landscape is currently composed of four areas under legal protection: the regional reserve and ''Man and the Biosphere'' reserve ''Reserva Natural Integral de Muniellos'', the regional parks and MAB reserves ''Parque Natural de Somiedo'' and ''Parque Natural de Redes'', and the national park ''Parque Nacional de Picos de Europa'' (Anon., 1994). These reserves have been established in the last 20 years, excepting the Picos de Europa National Park, which was established in 1918. Reserves do not exclude traditional land uses such as cattle grazing (excepting in the Muniellos Reserve) but imposse legal restrictions on new land uses such as road construction, mining and timber deforestation.

### 2.6. Statistical analyses

Elevation, slope, fragment size and perimeter were compared among forest classes using ANOVA. We performed ANCOVA with fragment size as a covariable to check for fragment size effects on the differences among classes on heterogeneity. The same procedure was used to compare fractal dimension among forest classes. For that analysis, we included only fragments between 0.56 and 10 ha, to achieve a range of sizes adequately represented in all forest classes, and to avoid biases resulting from the inclusion of smaller fragments (see also Turner et al., 2001). Aspect and size distributions were compared among forest classes by chi-square and median test, respectively. ANOVAR was performed to compare proximity index among forest classes, considering the neighbour type (same-class or any-class neighbours) as repeated measures.

Our analysis of fragmentation in relation to protection level had two steps. First, we checked for the efficiency of the current reserve network to cope with future fragmentation. For that, we compared, between protected and unprotected fragments, fragmentation surrogate variables (fragment size, shape and isolation indexes), and altitude and slope by ANOVA, whereas aspect was compared by chi-square. Second, we evaluated whether the current reserve network was representing the availability of the different forest classes in the landscape, or conversely, that some forest classes were under-represented relative to others (gap analysis; Caicco et al., 1995; Scott et al., 2001). For that, we compared via chi-square the actual distribution of protected fragments among different forest classes with a theoretical distribution of protected fragments depending on the relative class-availability in the landscape.

Data corresponding to rowan forest were excluded from most analyses, due to the small sample size in relation to remaining forest classes (see Table 1). Type III sum of squares was chosen since the design of the database was unbalanced (Shaw and Mitchell-Olds, 1993). When necessary, variables were transformed for normality, homocedasticity and linearity, using the arcsine transformation for data expressed as frequencies, and the log-transformation for the remaining ones (Zar, 1996). All analyses were performed with JMP statistical package (SAS Institute Inc., 2001).

## 3. Results

### 3.1. Fragmentation patterns

#### 3.1.1. Landscape level metrics

Current forests covered 90,336 ha, accounting for 21.7% of the studied landscape and 23.2% of the potential forest area within this landscape, and occurring in 12,228 forest patches that aggregated in 8978 forest fragments. Beech forest was the dominant class, both in terms of number of fragments and coverage in the landscape (Table 1). Oak and birch forests showed intermediate values of these variables, whereas the remaining classes represented together less than 21% of fragments and 9% of total forest area.

#### 3.1.2. Within-fragment heterogeneity

Most of the fragments contained only a single patch type (80–95% of fragments for all forest classes, Table 1) although the maximum number of patches per fragment was as high as 186. The number of patches per fragment and the diversity of patches (Simpson's index) were significantly higher for beech forests than

Table 1
Characteristics of forest fragments of different classes related to their occurrence in the landscape and the forested surface, the within-fragment heterogeneity, topography and physiognomy[a]

| | Beech | Pyrenean oak | Sessile oak | Ash-maple | Birch | Holly | Rowan | Conifers | All classes |
|---|---|---|---|---|---|---|---|---|---|
| Number of fragments (%) | 2417 (26.92) | 1442 (16.02) | 1593 (17.74) | 456 (5.08) | 1663 (18.52) | 456 (5.08) | 56 (0.63) | 895 (9.97) | 8978 |
| Landscape surface (%) | 13.77 | 1.25 | 3.69 | 0.25 | 1.14 | 0.20 | 0.03 | 1.36 | 21.73 |
| Forest surface (%) | 63.45 | 5.78 | 17.02 | 1.13 | 5.26 | 0.94 | 0.14 | 6.27 | – |
| Single-patch fragments (%) | 83.06 | 91.18 | 90.19 | 91.31 | 90.64 | 94.54 | 80.00 | 91.55 | 88.82 |
| Number patches per fragment | 1.89 ± 0.14 a | 1.17 ± 0.03 b | 1.35 ± 0.07 b | 1.16 ± 0.04 b | 1.18 ± 0.02 b | 1.09 ± 0.03 b | 1.22 ± 0.06 | 1.26 ± 0.06 b | 1.07 ± 0.00 |
| Simpson's index | 1.10 ± 0.01 a | 1.06 ± 0.01 b | 1.06 ± 0.01 b | 1.07 ± 0.01 ab | 1.06 ± 0.00 b | 1.04 ± 0.01 b | 1.13 ± 0.04 | 1.05 ± 0.01 b | 968.2 ± 2.5 |
| Altitude (m a.s.l.) | 1043.8 ± 4.8 a | 886.1 ± 3.7 b | 978.9 ± 5.1 c | 846.9 ± 6.1 d | 983.0 ± 7.9 c | 1129.3 ± 11.2 e | 1444.2 ± 21.5 | 799.5 ± 3.6 f | 654.0–1747.1 |
| Aspect (mode, %) | N 40.49 | S 39.61 | S 32.54 | E 34.07 | N 36.07 | W 32.50 | N 48.21 | E 27.96 | – |
| Slope (%) | 20.53 ± 0.19 a | 18.12 ± 0.20 b | 21.51 ± 0.19 c | 17.49 ± 0.41 be | 14.88 ± 0.23 d | 16.83 ± 0.40 e | 19.62 ± 0.89 | 10.03 ± 0.27 f | 17.88 ± 0.09 |
| Area (ha) average | 23.72 ± 4.43 a | 3.63 ± 0.34 b | 9.65 ± 2.87 b | 2.25 ± 0.38 cd | 2.86 ± 0.34 c | 1.85 ± 0.39 d | 2.33 ± 0.50 | 6.33 ± 1.15 c | 10.06 ± 1.31 |
| Area (ha) median | 1.19 a | 0.87 b | 0.87 b | 0.63 cd | 0.70 c | 0.54 d | 0.89 | 0.61 cd | 0.83 |
| Perimeter (km) | 3.99 ± 0.55 a | 1.30 ± 0.07 b | 2.02 ± 0.29 b | 0.96 ± 0.08 cd | 1.03 ± 0.06 c | 0.79 ± 0.08 d | 1.01 ± 0.14 | 1.27 ± 0.12 cd | 2.06 ± 0.16 |

[a] Mean (± S.E.) values followed by different superscript letters are different at $P < 0.05$ after Bonferroni-Dunn test (means) or partial chi-square (medians). The modal aspect and the percentage of fragments showing this aspect are indicated.

for the remaining classes (Table 1). However, both the number of patches by fragment and the diversity of patches were positively related to fragment size, leading to significant interaction terms in the ANCOVAs considering the forest class as main effect and fragment size as a covariable (number of patches: $F_{6,8660} = 54.14$, $P < 0.0001$; Simpson's index: $F_{6,8660} = 7.92$, $P < 0.0001$).

### 3.1.3. Topography

Forest classes were distributed differentially in altitude, with pine plantations and ash-maple forests occurring at lowest altitudes on average, oaks, birch and beech at middle altitudes, and holly and rowan above 1100 m a.s.l. ($F_{6,8914} = 245.20$, $P < 0.0001$, one-way ANOVA; Table 1). Aspect differed significantly among forest classes (chi-square = 992.42, $P < 0.0001$, d.f. = 21, Table 1), beech and birch appearing mostly northwards, oaks southwards, pines and ash-maple eastwards, and holly westwards. Steepness was lowest at pine plantations and highest for sessile oak and beech ($F_{6,8914} = 269.22$, $P < 0.0001$; Table 1).

### 3.1.4. Fragment size (area)

The distribution of fragment size was strongly biased towards small values, with 55.4% of the fragments smaller than 1 ha. Only 1.4% of fragments were > 100 ha and 0.1% were > 1000 ha. All forest classes showed distributions skewed towards small sizes (Fig. 2), but differed significantly in average fragment size ($F_{6,8915} = 58.81$, $P < 0.0001$, one-way ANOVA), perimeter ($F_{6,8915} = 54.71$, $P < 0.0001$), and the size distribution (chi-square = 195.56, $P < 0.0001$, d.f. = 6, Median test). Beech fragments were larger than the other classes, whereas holly and ash-maple forests were, on average, the smallest fragments (Fig. 2, Table 1).

### 3.1.5. Shape (fractal dimension)

Fragment shape differed among forest classes ($F_{6,4753} = 12.42$, $P < 0.0001$, ANCOVA), with pine plantations having the lowest average fractal dimension (Fig. 3). Among natural forests, holly and beech were the classes with the most regular shape. Fractal dimension increased proportionally to fragment size for all classes ($F_{1,4753} = 430.90$, $P < 0.0001$) while differences in fractal dimension among classes were

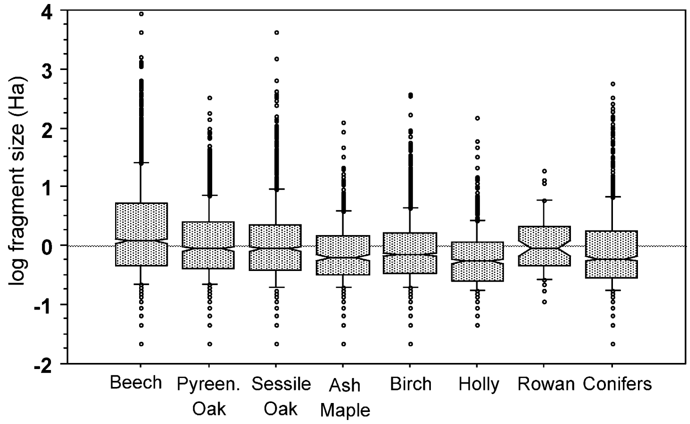


Fig. 2. Box plots representing the size distribution of fragments belonging to different forest classes.

independent from fragment area (Interaction forest class-area: $F_{6,4753} = 1.36$, $P = 0.23$, Fig. 3).

### 3.1.6. Isolation

Dispersion indexes indicated aggregated distributions for all forest classes (Fig. 4). Birch forest had a comparatively higher $R_c$ value, despite having a density value lower than beech and similar to oaks (Table 1). The dispersion index was minimal for rowan, holly and ash-maple forests, also characterized by larger NND. Averaging all fragments, NND was significantly larger when considered to the same class

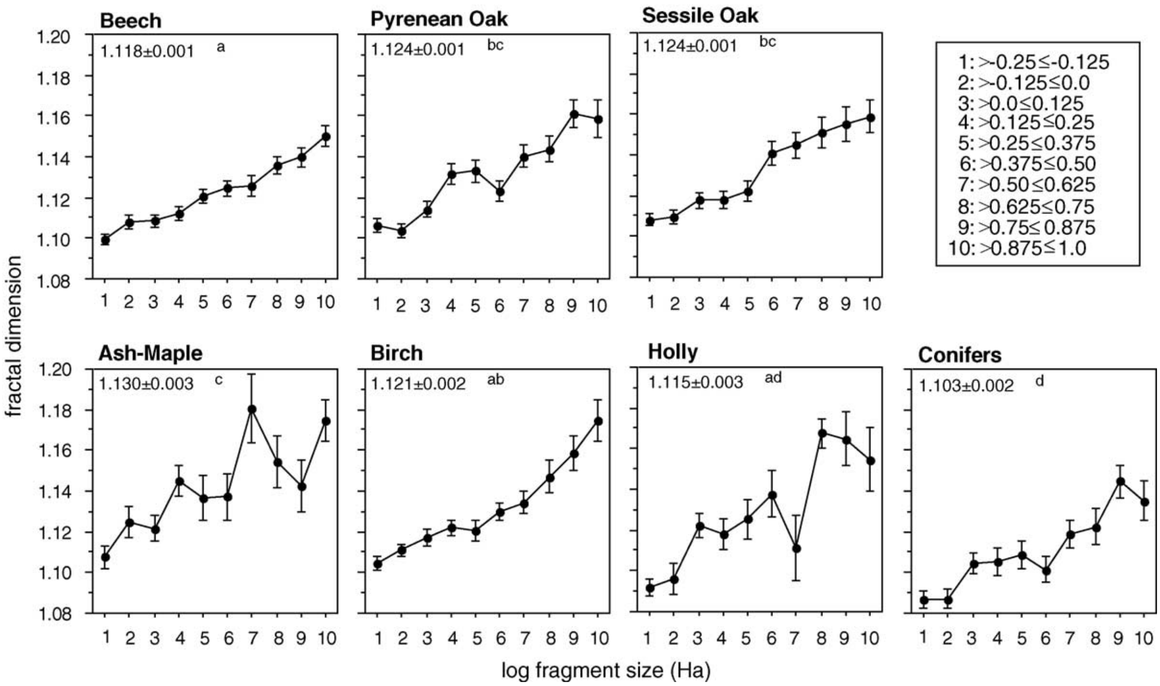


Fig. 3. Fractal dimension (mean ± S.E.) of different forest classes in relation to fragment size (categorized in 10 progressive intervals for representation). The mean value (±S.E.) for all fragments within each forest class is also shown (values followed by different letters are different at $P < 0.05$ after Bonferroni–Dunn test).

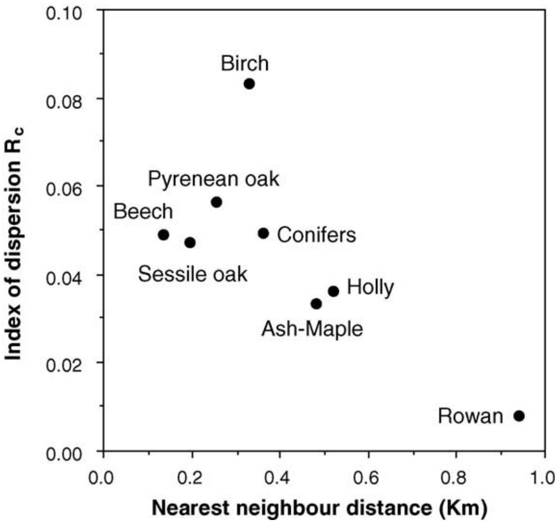


Fig. 4. Values of the dispersion index $R_c$ plotted against the average same-class nearest neighbour distance, for different forest types.

neighbour (265.01 ± 7.86 S.E.) than to neighbour of any-class (103.52 ± 52 S.E.; $t = 45.37$, $P < 0.0001$); this difference being consistent for all forest classes ($t > 14.0$, $P < 0.0001$, for all cases). Proximity index differed among forest classes for both types of neighbour ($F_{6,8915} = 276.22$, $P < 0.0001$, ANOVAR, Fig. 5), differences being stronger when considering the same-class neighbours (Interaction forest class-neighbour type $P < 0.0001$). Beech forests were less isolated than the other forests, considering both same-class and any-class neighbours. Ash-maple and holly forest showed the highest isolation, when considering the distance to the same-class fragments (Fig. 5).

### 3.2. Fragmentation and protection status

Protected fragments were significantly larger and showed higher values of the proximity indexes than unprotected ones (Table 2). However, fractal dimension and nearest neighbour distances were independent of the protection status of the fragments. Protected fragments were located at higher altitudes and steeper slopes (Table 2). Most protected fragments were oriented northwards, whereas the modal aspect for unprotected fragments was eastwards (Table 2).

The percentage of forest area under current protection was 27.6%, which included 18.15% of

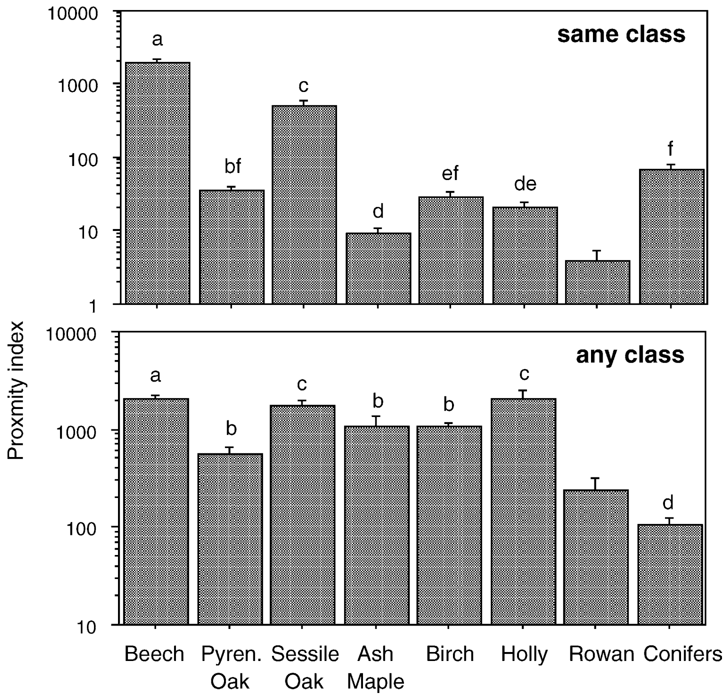


Fig. 5. Proximity index (mean + S.E.) for different forest classes, both considering neighbours of the same class and neighbours of any class.

Table 2
Fragmentation and topographical variables (mean ± S.E.) for forest fragments under the coverage or not of a protected reserve of the Asturian Cantabrian range[a]

| | Protected | Unprotected | $F$ | $P$ |
|---|---|---|---|---|
| Fragment area (ha) | 27.41 ± 3.33 | 6.91 ± 1.42 | 110.71 | <0.0001 |
| Fractal dimesion | 1.11 ± 0.00 | 1.11 ± 0.00 | 2.27 | 0.131 |
| NND to same class (m) | 264.3 ± 20.1 | 265.1 ± 8.6 | 1.45 | 0.229 |
| NND to any class (m) | 88.4 ± 5.5 | 106.3 ± 2.3 | 3.12 | 0.077 |
| Proximity index to same class | 1798.4 ± 130.6 | 444.7 ± 55.7 | 125.58 | <0.0001 |
| Proximity index to any class | 2975.8 ± 185.9 | 1016.5 ± 79.2 | 127.66 | <0.0001 |
| Altitude (m) | 1042.2 ± 6.4 | 954.7 ± 2.7 | 169.23 | <0.0001 |
| Slope (°) | 20.39 ± 0.25 | 17.42 ± 0.10 | 109.23 | <0.0001 |
| Aspect | N (33.58%) | E (27.80%) | $\chi^2$ = 30.36 | <0.0001 |

[a] $F$ and $P$ values resulting from one-way ANOVAs comparing both types are also shown. The modal aspect (% of fragments) and the results of a chi-square test comparing the distribution of aspects among fragment types are also indicated.

Table 3
Results of the gap analysis evaluating the coverage of the different forest classes within the reserve network[a]

| | Within class area | | Within protected area | | |
|---|---|---|---|---|---|
| | % Of surface protected | % Of fragments protected | % Of surface | % Of fragments | $\chi^2$ |
| Beech | 34.25 | 32.89 | 78.78 | 57.65 | 272.07*** |
| Pyrenean oak | 9.83 | 10.06 | 2.06 | 10.51 | **18.31***** |
| Sessile oak | 27.81 | 11.36 | 17.15 | 13.13 | **11.41***** |
| Ash-maple | 8.16 | 19.08 | 0.34 | 6.30 | 1.96 N.S. |
| Birch | 5.53 | 6.86 | 1.05 | 8.27 | **64.37***** |
| Holly | 4.65 | 8.77 | 0.16 | 2.90 | **8.63**** |
| Rowan | 9.56 | 10.71 | 0.05 | 0.44 | 0.61 N.S. |
| Pine | 1.78 | 1.23 | 0.40 | 0.80 | **132.91***** |

The percentages of protected surface and protected fragments respecting to the total area of each forest class, as well as the percentages of surface and fragments respecting to the total protected area in the landscape are indicated.

[a] Chi-square analyses compared, for each class, the proportion of fragments within the protected area with a theoretical distribution of protected fragments following the relative class-availability in the landscape (in bold are shown classes with actual percentages significantly lower than those derived from availability, see also Table 1; N.S.: $P > 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

forest fragments. Protection coverage differed among forest classes, with many natural forest classes, specially holly and birch, showing protection coverage lower than 10% of their total area, but beech and sessile oak having more than 27% of their total area protected (Table 3). These differences also appeared when considering the percentage of fragments under protection. When considering total forest surface under protection, beech and sessile oak forest accounted for ca. 96% of this area, but this percentage was under 2% for the other forest classes. The distribution of protected fragments among forest classes was strongly biased towards beech. Most forest classes showed percentages of occurrence within the pool of protected fragments that differed significantly from their availability in the forested landscape (Tables 1 and 3). Beech fragments are actually over-protected in relation to their availability, whereas oaks, birch and holly were underprotected.

## 4. Discussion

### 4.1. How fragmented is the Cantabrian forest?

Forests currently cover ca. 23% of the potential forest area in the Cantabrian range. This value of forest occurrence is lower than those described for other temperate (30–50%, Spies et al., 1994; Rebane et al., 1997; Fuller, 2001; Pan et al., 2001) and boreal forests

(≈50%, Mladenoff et al., 1993; Rebane et al., 1997; Löfman and Kouki, 2001) but similar to heavily fragmented forests in agricultural (e. g. Ranta et al., 1998; Carbonell et al., 1998; Santos et al., 2002) or urban landscapes (Iida and Nakashizuka, 1995). Other landscape-level fragmentation measures are the size distribution of fragments and the average fragment size (Forman, 1995). In our case, fragment size distribution is strongly skewed towards small values, this kind of lognormal distributions indicating high levels of fragmentation (Wilcove et al., 1986). In addition, both the percentage of fragments $> 1$ ha and the average fragment size are much lower than depicted in other fragmented systems (e.g. Spies et al., 1994; Ranta et al., 1998; Fuller, 2001; Pan et al., 2001).

The snapshot of the Cantabrian forest taken by our landscape analysis is the result of a long-term process including natural fragmentation as well as historical deforestation by humans but, in any case, it depicts an habitat situation for forest species characterised by low habitat cover and heavy fragmentation. Even when all forest classes are considered as a single habitat type, forest cover is below the predicted critical threshold for negative effects of fragmentation on biodiversity (Andrén, 1994). The effects of low forest coverage could be buffered in some degree by the surrounding matrix, when providing somewhat-suitable habitat for forest species (i.e. when the matrix is composed by second-growth forests, Mönkkönen and Reunanen, 1999; Lindenmayer and Franklin, 2002). This is not the case of the forest fragments considered here, which include both mature and second-growth forest in different stages of development, that strongly contrasted structurally with the surrounding pasturelands or heathlands matrix. Thus, additional losses of forest habitat would probably lead to exponential increases in fragments isolation within the agricultural matrix, negatively affecting the persistence of forest species (Andrén, 1994; Mönkkönen and Reunanen, 1999; Fahrig, 2002). This situation could be particularly important for the isolated populations of endangered forest vertebrates still present at the Cantabrian range but highly sensitive to habitat degradation, such as brown bear *Ursus arctos* and capercaillie *Tetrao urogallus* (Naves et al., 2004; Obeso and Bañuelos, 2003; see also Rolstad, 1991; Kurki et al., 2000).

### 4.2. Differences among forest types

#### 4.2.1. Heterogeneity

Most of the forest fragments in our landscape contain only one forest type, making the comparative analysis among different forest classes possible. This forest landscape is, thus, composed of an ensemble of rather homogeneous forest units standing out from a deforested matrix. However, the internal heterogeneity of fragments is related to the fragment size, with the bigger fragments being more heterogeneous. This is probably due to their higher probability of containing a wider range of habitat conditions related to altitude, soil and topographical characteristics, allowing the establishment and coexistence of different tree species on contiguous patches (Iida and Nakashizuka, 1995; Honnay et al., 1999). Thus, the bigger fragments might maintain the structure of once continuous forest, characterised by a mosaic of adjacent forest patches of different composition (Mladenoff et al., 1993; Ripple et al., 1991). On the other hand, this size related effect is the main cause of differences among forest classes on internal heterogeneity: beech forests show a higher internal patchiness mainly because of their comparatively larger area.

#### 4.2.2. Landscape cover and fragment size

Our results show differences among forest classes in terms of landscape cover, size distribution and average fragment size, despite a general trend of lognormal distributions for all classes. Beech forests are the major component of Cantabrian montane landscape in terms of both surface and the number of fragments. In addition, beech fragments are bigger on average than those of the remaining classes. Several historical and proximate causes might explain this dominance. Firstly, beech colonized the Eurosiberian region of the Iberian peninsula from the early Holocene (7000 years BP) spreading westwards from the Pyrenees, and reaching its current limit at the western part of the Cantabrian range (Huntley and Birks, 1983; Peñalba, 1994; Muñoz-Sobrino et al., 1997). This species might thus be considered as a climax tree (under the current conditions of Atlantic oceanic climate) replacing early Holocene species (such as *Quercus petraea* and *Betula alba*) from mid-altitudes after long-term anthropogenic disturbances

(Peñalba, 1994; Muñoz-Sobrino et al., 1997). Secondly, proximate causes such as higher rates of human-induced disturbance or selective logging for high-quality timber may also account for differences in coverage and average fragment size. This is probably the case for ash, maple and both oaks, species naturally occurring in areas more suitable for agriculture, such as valley bottoms or southern exposures (Spies et al., 1994). Additionally, pyrenean oak forests have been strongly affected by anthropogenic fires (Luis-Calabuig et al., 2000). The small size of holly and rowan fragments might be mostly related to their character of second-growth forests developed after old-growth tree-line deforestation for high-altitude pastures (Díaz and Fernández, 1987; Rebane et al., 1997). Holly woodlands seem to persist long time during succession thanks to herbivore pressure, which allows the presence of these prickly trees but precludes the colonization of more palatable species like beech or birch (Mitchell, 1990).

#### 4.2.3. Shape

Shape complexity, measured by fractal dimension, was similar in magnitude to that found in other montane temperate forest affected by human-induced fragmentation (e.g. Fuller, 2001; Pan et al., 2001), but showed differences among forest classes. Conifer forests were the most regular in shape, as a result of the man-made structure of plantations located in flattest and lowest areas (average values of slope an altitude are minimal among forest classes). Conversely, ash-maple and oak forests were strongly irregular, probably due to the same reasons explaining their smaller size, the use of valley bottom lands and southwards oriented slopes for agriculture and pastures (Forman, 1995). The most important consequence of increased shape irregularity are negative edge effects (Lovejoy et al., 1986; Andrén, 1995; Murcia, 1995), since, in fragments with larger perimeter/area ratio, edge effects penetrate a larger proportion of the fragment and even big fragments can be entirely physically or biotically modified (Laurance, 2000; Davies et al., 2001). On the other hand, lower susceptibility to extinction thresholds are predicted for species living in habitats with lower fractal dimension (Hill and Caswell, 1999). Therefore, at similar sizes, stronger negative effects due to shape irregularity might be predicted for ash-maple and oak forests than for the remaining classes in the Cantabrian range.

Shape complexity increased proportional to fragment size for all forest classes (see Krummel et al., 1987; Mladenoff et al., 1993; Pan et al., 2001; for similar patterns in other montane temperate forest). This indicates that different factors may be influencing the shape of small and large patches. For example, small fragments located in low agricultural areas tend to be more regular shaped reflecting their man-made limits (Krummel et al., 1987). In our case, the trend of increasing size and complexity in relation to slope suggests that large patches are usually located on or near hilltops, extending along ridges and generating amoeboid, convoluted or dendritic shapes (see also Forman, 1995). In addition, the bigger the fragment, the higher is the probability to enconter with topographical and substrate heterogeneity, altitudinal limits or small-scale disturbances at the borders of the fragment, leading to higher boundary irregularity (Forman, 1995; Iida and Nakashizuka, 1995). Finally, big fragments probably suffer higher intrusive fragmentation or perforation (sensu Forman, 1995) due to the formation of gaps related to fire or human clear-cuts, decreasing the total interior habitat and increasing the boundary length.

#### 4.2.4. Isolation

When considered at the scale of the whole Cantabrian landscape, our fragment distribution may be considered as a fine-grained pattern, since it is mostly composed of numerous small fragments. However, as judged by the low values of the dispersion index, it is better depicted as an array of clusters or local aggregations of small fragments of the same class, with low NND, within a sea of low occupancy and high inter-fragment distances (hierarchical mosaic pattern, sensu Rolstad, 1991). The dispersion index varied among forest classes, probably reflecting the requirements and responses of each class in relation to soil, topography, altitude and land use (Forman, 1995; Turner et al., 2001). However, under a general trend of increased aggregation proportional to NND (Fig. 4), birch forest showed lower clumping than expected, indicating a less pronounced pattern of hierarchical mosaic than forests like beech and oak, with smaller NND but lower $R_c$ values. These configuration differences may have important biological consequences, in terms of the metapopulation dynamics of organisms living in the respective forest classes. That is, in highly hierarchical patterns, metapopulation dynamics would be probably restricted to within-cluster dynamics, whereas less hierarchical patterns would favour dynamics expanding from local clusters to larger portions of the landscape (Rolstad, 1991).

Despite a clumped distribution at the landscape level, average nearest neighbour distances in our system indicated greater isolation among fragments than depicted for other fragmented forests (e.g. Löfman and Kouki, 2001; average NND $\approx$25 m). Isolation partially encompassed the differences in other fragmentation measures like size or landscape coverage, probably as a result of the covariation in these fragmentation variables (Harris, 1984; Andrén, 1994; Forman, 1995). Thus, biggest forests, such as beech and sessile oak, showed lower isolation than small-sized birch and ash-maple forests. On the other hand, the magnitude of these differences in isolation increased when measured respecting to the fragments of the same class. In fact, for all forest classes, the distance to a fragment of any class was smaller than the distance to a fragment of the same class, indicating that an important fraction of fragments had the nearest neighbour belonging to a different forest class. Habitat structural connectivity might be strongly affected by this fact, since the nearest fragment might not necessarily fit the habitat requirements for forest specialist species (Wiens et al., 1993; Andrén, 1994; Tischendorf and Fahrig, 2000). Under this perspective, holly and ash-maple forests, heavily affected by within-class isolation, would be less suitable for the maintenance of habitat-specialist species with low dispersal ability than beech and oak forests, but more prone to be inhabited by generalist species, able to move across and survive in a broader gradient of forest habitat types (Kozakiewicz, 1995).

### 4.3. Conservation and fragmentation

Our analysis of protection status of fragmented forests shows that the current reserve network in the Asturias region should cope positively with additional fragmentation, since it covers preferentially bigger and less isolated fragments. Additionally, the protection of large fragments could lead to higher levels of biodiversity conservation, due to the positive relationship between fragment size and within-fragment heterogeneity. However, selective protection of largest forests could hinder the conservation of small, but structurally rich forest fragments which have suffered less internal degradation by some management practices as, for example, removal of dead wood and selective logging, as has been shown for other chronically fragmented landscapes (Schwartz, 1999; Götmark and Thorell, 2003).

The patterns of size-biased protection must be interpreted in relation to the selection of some forest types to the detriment of others within the reserve network. In fact, the relationship between fragmentation surrogates and protection status is probably due to the fact that beech forests, the class with bigger and less isolated fragments, was disproportionately covered by this reserve network. More importantly, this unbalanced protection indicates important gaps in the habitat representativeness. Despite being relatively comprehensive (all the seven natural forest types are protected in some degree), the current reserve network strongly failed on its adequacy for most of habitats, since less than a third of forest classes have protected $\geq$10% surface. The proportion of "well represented" habitats is even lower than reflected in gap analyses from other networks (e.g. Scott et al., 2001). Among natural types, holly forests are the least protected, despite showing high conservation values (besides holly, they contain important populations of yew *Taxus baccata*, a tree species threatened over its range in Europe, Svenning and Magard, 1999; García and Obeso, 2003). As previously explained, the maintenance of these second-growth forests seems compatible with moderate land-use like cattle grazing. However, they are not precluded from deforestation by other causes and thus, these under-represented, small habitats should be considered as protection targets for future expansion of the reserve network (see also Reyers et al., 2001; Scott et al., 2001).

The reasons for the current patterns of protection are due to the motivations for establishment of particular reserves. The conservation of mature beech forest as the habitat of threatened species (capercaillie and brown bear) is a major biological motivation (Anon., 1994). In this case, these umbrella (and flagship) species would act as surrogates of biodiversity working efficiently against fragmentation, since they would promote the protection of less fragmented forests (but see Andelman and Fagan, 2000). However, the unbalanced protection coverage suggests that reserves have been partially proclaimed in an ad hoc fashion, because they contained areas with high scenic or tourism potential and did not conflict with other forms of land use (Pressey et al., 1993; Reyers et al., 2001; Scott et al., 2001; Götmark and Thorell, 2003). The relationship among topographical characteristics of fragments and their protection status support this hypothesis, indicating that reserves have been concentrated in areas of marginal agricultural value (higher altitudes and slopes, and northern exposures; see also Scott et al., 2001). Finally, the uncertain viability of traditional mountain land-use under the current agricultural trends of the European Union, and the consequent search of alternative ways of development such as eco-tourism, are also within the motivations of the current reserve network.

### 4.4. Concluding remarks

This study depicts the current landscape patterns of the montane forest in the Cantabrian range, evidencing severe fragmentation in all forest types and biased representativeness of forest habitats in the protected landscape. Future forest management and reserve network design should take into account these patterns to preclude increasing losses of forest surface and the consequent biodiversity decay. Particularly, the expansion of the reserve network towards new areas in the region should be based in landscape information, not merely in social convenience or opportunity, seeking to protect the less-fragmented forests but also to include those misrepresented forest types with high ecological value.

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