Bird Assemblages in Naturally Fragmented Upland Forests in Pirin National Park, Bulgaria

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Abstract: The effects of habitat fragmentation on biodiversity has become a major focus of conservation biology and landscape ecology, but most of the studies have been restricted to anthropogenic impact on habitats, while little is known about the natural fragmentation. I examined the effects of the natural fragmentation of upland temperate forests on bird assemblages, by comparing community patterns in forest patches and continuous forests, and by analyzing the effects of patch area and isolation on community structure. Bird communities did not differ significantly between studied habitat types, but when the edge and the interior of continuous forests were analyzed separately, patches and the edges of continuous forest supported more species rich, diverse and abundant bird communities than the interior of continuous forest. Patch area was the major predictor for species richness, while isolation was not significant. The response to natural fragmentation was guild- and species-specific, and the key variables determining habitat use by birds were canopy closure and shrub cover. Most of the changes in bird community structure could be accounted for edge effects.

Key words: Edge effects, Habitat fragmentation, Natural disturbance, Patchiness, *Pinus peuce,* Woodland birds

Introduction

The fragmentation and loss of natural habitats are recognized as major factors causing decrease and extinction of species all over the world (TILMAN 1994). Whereas the consequences from habitat loss are clear, the effects of habitat fragmentation are much more complex (FAHRIG 1997). For this reason quantifying the impact of forest fragmentation on wildlife community structure has become a main goal of conservation biology and landscape ecology (LINDENMAYER, FISCHER 2006). Fragmentation alters the structure of the disturbed habitats and thus, changes their "hospitality" to wildlife (MURCIA 1995, FORD *et al.* 2001). This generally affects the demographic attributes of populations such as survival, reproductive success, recruitment, immigration and emigration rates, and together, these effects increase the probability of local extinctions and can dramatically change the structure of communities (BURKEY 1989, ZANETTE 2000, STEPHENS *et al.* 2003). Thus, fragmentation patterns and habitat quality have been identified as important predictors of occurrence of breeding birds (BOLGER *et al.* 1991, CROOKS *et al.* 2001, 2004; GITHIRU, LENS 2007). According to the *Habitat fragmentation hypothesis* (SAUNDERS *et al.* 1991, FAHRIG 2003), fragmentation usually has negative effects on the species inhabiting the disturbed habitat. These effects are related to the landscape patterns such as the reduced area of the original habitat, increased isolation between fragments and changes in habitat structure near the forest edges (ANDRÉN 1994, SCHMIEGELOW, MÖNKKÖNEN 2005). However, the *Habitat supplementation / complementation hy-*

pothesis (Dunning *et al.* 1992) states that the matrix habitats and their resources can mitigate the negative effects of fragmentation on species from the original habitat and that the fragmentation effect could be positive by increasing species occurrence because of the complementing matrix habitat increase (Fahrig 2003). Both hypotheses were tested by Brotons *et al.* (2004) who found that neither hypothesis could properly explain the consequences of habitat fragmentation and that different ecological mechanisms control species pools in habitat mosaics. In addition, the fragmentation effects are species-, system- and scale-dependent and relate to the local landscape history (Santos *et al.* 2002, Schmiegelow, Mönkkönen 2002, Stephens *et al.* 2003). In this respect, most of the studies on the fragmentation effects on wildlife have been restricted to anthropogenically altered landscapes (e.g. Andrén 1994, Mörtberg 2001, Crooks *et al.* 2004, Barlow *et al.* 2006, Hansbauer
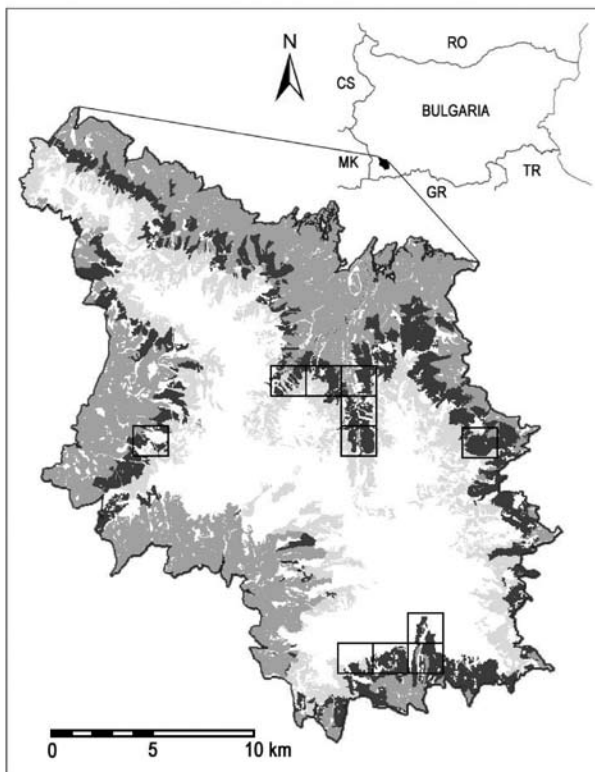

Fig. 1. Geographic location and map of the study area. Dark grey zones represent the Macedonian pine forests at the tree line zone, moderate grey represent other types of forests, pale grey represent the Dwarf pine shrubland, and white zones represent open landscapes. Boxes show the approximate distribution of the study plots (the study plots are not visible at this scale; see Material and methods for more details on the distribution of study plots within each forest type)

et al. 2008), while the landscapes where the fragmentation is a natural pattern of the dynamics remain poorly studied (Herrando, Brotons 2002, Watson 2003, Brotons *et al.* 2004, Barlow *et al.* 2006, Tubelis *et al.* 2007).

Focusing on birds, I examined effects of naturally induced upland forest patchiness on community patterns by comparing the bird communities in naturally-occurring forest patches and in continuous forests, and by analyzing the effects of patch area and isolation on the bird community structure. Further, my task was to determine the main habitat parameters accounting for the differences in the bird community structure between naturally disturbed and continuous forests. Taking into account that the patchiness created by strong winds and avalanches is a natural pattern of the upland forests studied, it could be expected that the species inhabiting there are adapted to regular disturbance and are less vulnerable to forest fragmentation. I hypothesized (i) that natural fragmentation alters habitat structure, and thus, the bird community structure; and (ii) that although the responses are likely to be species-specific, the community-level parameters (diversity, richness and abundance) would be greater in the disturbed forests and the edge of continuous forests than the interior of continuous forests.

Methods

Study area

The field work was carried out in the tree line zone in Pirin National Park, Bulgaria (41°40′ N, 23°30′ E, Fig. 1). The studied forests were native, over 60 years old, situated on the steep slopes of silicate rocks, at altitudes from 1700 to 2230 m, and are dominated by the Macedonian pine (*Pinus peuce*), with presence of up to 10% of European spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and Bosnian pine (*P. heldreichii*). Because of the inaccessibility of the area where these forests grow, they were rarely cut in the past and most of their patchiness is due to natural disturbances, such as avalanches and strong winds.

Study design

Three forest types were investigated: forest patches, the edge and interior of continuous forest. The forest patches were identified as groups of trees isolated at a distance of >20 m from other forests, with cano-

py closure >30% and area of <50 ha, on a digital map based on the geographical information systems (GIS), using ArcMap 9.0 software (ESRI 2004). The continuous forest was identified as being an unisolated part of the forest belt in the mountains. A total of 25 forest patches ranging in area from 0.72 to 17.61 ha (mean area = 5.01 ha; SD = 4.57) and with isolation from 23 to 150 m (mean isolation = 51.92 m; SD = 32.99) were selected. The studied forest patches were surrounded by a matrix of screes, grasslands and shrublands (Dwarf pine, *Pinus mugo* and Siberian Juniper, *Juniperus sibirica* communities). At least one circular study plot (with a radius of 50 m) was randomly located within each forest patch, with the constraint that the minimal distance between two adjacent study plots was 180 m (BIBBY *et al.* 1998). For each study plot in a forest patch, two controls (similar in stand age, exposure and elevation) were selected: one 50 m from the edge of the continuous forests and the second >100 m from the edge of the continuous forest. The exact location of the study plots was established in the field using a Global Positioning System (GPS) Garmin 60CS. After the first field visits, several study plots were excluded from the study because they were inaccessible. A total of 183 study plots were examined, distributed among the studied forest types as follows: 66, 59 and 58 study plots in the forest patches, edge and interior of continuous forests, respectively.

Bird sampling

The birds were sampled in June and July for three successive years (2004-2006) using the point-count technique (BIBBY *et al.* 1998). Two visits per point-count station were made each year, with a 10–40 day (on average 21) interval between the two visits. Counts were made between 0600 and 1100 h in suitable weather conditions (without fog, strong rain or wind). There was a settling down period of 2 min and the duration of a count was 5 min. All birds seen or heard were counted in two radial intervals: 0–25 m and 25–50 m. Individuals were recorded in their initial positions and those in flight were not counted.

Vegetation sampling

Within the forests, six foliage profiles were distinguished: (1) Ground level (<0.4 m high), composed of Whortleberry (*Vaccinium myrtillus*), herbs and Wild Geranium (*Geranium* spp.); (2)

Low level (0.4–1 m high), composed of Hellebore (*Veratrum* spp.), thistles and ferns; (3) Small shrubs (0.4–1 m high), composed of Siberian Juniper, Balkan Broom (*Chamaecytisus absinthioides*) and Raspberry (*Rubus* spp.); (4) Mid-level (1.6–4 m high), composed of Mountain Dwarf Pine, and saplings; (5) Sub-canopy level (4–9 m high), composed of small trees; (6) Canopy level, composed of big trees (9–30 m high). Foliage profiles, together with the canopy closure, number of dead trees and stumps (above 0.5 m high) and cover of rocks were sampled within a radius of 25 m centered in each point-count station. The diameter at breast height (DBH), tree height and tree density were calculated for the closest 10 trees (with DBH >0.2 m) to the centre of the study plot.

Data analyses

For the analyses, the point-count stations in forests with similar pattern, age elevation and exposure were grouped into 48 clusters (16 in each habitat type) (NEWTON 2007). The data on the birds and environmental variables were tested for normality using the Shapiro–Wilk's Test and the bird data were additionally *log*–transformed to meet normality assumptions for the parametric tests.

Bird data – the species richness and bird density were calculated on the basis of the maximum birds counted. The densities were computed using DISTANCE 5.0 Release 2 (THOMAS *et al.* 2006). A conventional distance sampling analysis was applied because the study was conducted in habitats with similar structure, and thus the detection probability was solely a function of the distance from the observer (BUCKLAND *et al.* 2001). For density estimates, the model of uniform key function with simple polynomial series expansion was selected on the basis of the minimum value of Akaike's Information Criterion. The diversity was described using the Shannon-Wiener diversity index, *H'* (KREBS 1999). The forest dwelling species were classified according to IANKOV (2007) and analysed as a component of the overall bird community and separately. The bird species were grouped into foraging and nesting guilds following NIKOLOV (2009) in order to determine whether the response to forest patchiness was guild-specific. The habitat preferences of birds were determined by calculation of the selection index w_i (MANLY *et al.* 1993) and further *G*-test was applied to test whether the birds had

selected studied habitats at random (KREBS 1999). To achieve reliable estimates for habitat preferences of bird species and for the relationships between birds and habitat parameters, only species with ≥15 registrations were analysed.

Bird-habitat relationships – the bird community and environmental parameters were compared among studied habitat types by ANOVA and, if a statistically significant *F*-test was obtained, the *t*-test for independent samples was used to determine which means contributed to the effect. Correlations were investigated with the Pearson product-moment correlation coefficient. The effects of the patch area and isolation on bird community parameters were tested by Multiple Regression Analysis (MRA). The relationships between the bird abundances and habitat charactersitics were determined by Redundancy analysis (RDA), applied using CANOCO 4.5 (TER BRAAK, SMILAUER 2002). The length of gradient and suitability of using linear analyses were checked by preliminary Detrended Correspondence Analysis (DCA). The significance of canonical axes was assessed by the Monte Carlo test on the basis of 499 random permutations. To test for potential bias, the effect of forest fragmentation was separated from other studied predictors by partial constrained ordinations (LEPŠ, ŠMILAUER 2003).

Spatial autocorrelation analysis – Moran's *I* statistics was used to assess whether the residuals for applied models exhibit spatial autocorrelation. The values of Moran's *I* range from −1 to +1 for negative and positive spatial autocorrelation, respectively, where the expected values in the absence of spatial autocorrelation is around zero (RANGEL *et al.* 2006). The significance of the spatial autocorrelation statistics was tested using Monte Carlo permutation test. The spatial autocorrelation analyses were computed using SAM 3.1 (RANGEL *et al.* 2006).

All statistical procedures, apart from ordination techniques and spatial autocorrelation tests, were performed using the statistical package STATISTICA 7.0 (STATSOFT 2004).

Results

Bird community structure

The detection probabilities of birds in studied habitat types were similar (<8% difference) and the bird assemblages were comparable. There were no significant differences in the bird community parameters between the naturally fragmented and continuous forests (*t*-test for independent samples, $t_{46}=0.63$, $p = 0.53$; $t_{46}=1.52$, $p = 0.13$; and $t_{46}=1.09$, $p = 0.28$ for the species richness, diversity and abundance, respectively). When the edges and interior of continuous forests were analyzed separately, the forest patches and the edges of continuous forest supported more species rich, diverse and abundant bird communities than the interior of continuous forest, but there were no such differences between the forest patches and the edges of continuous forest (Table 1, Fig. 2). The forest dwelling species did not differ among the habitat types in none of the studied community parameters (ANOVA, $F_{2,45} = 0.55$, $p = 0.58$; $F_{2,45} = 0.36$, $p = 0.7$; $F_{2,45} = 0.71$, $p = 0.5$ for the species richness, diversity and abundance, respectively).

At the guild level, the shrub-nesting, ground-nesting and ground-gleaning birds preferred the
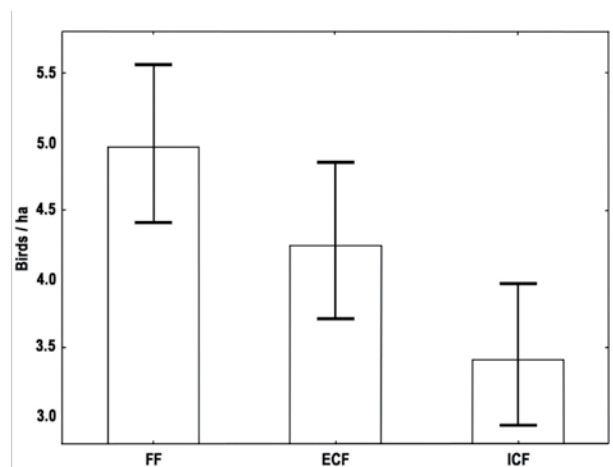

Fig. 2. Bird densities with their 95% confidence limits in the forest patches (FF), edge (ECF) and interior of continuous forests (ICF)

Table 1. Mean ± S.E. of bird species richness and diversity among the forest types[1], together with *F*-statistics and their significance[2] from ANOVAs used on the forest types (*n* = 48). [1] Within each row, the mean values that are not significantly different (*p* > 0.05, *p* - values were corrected according to the number of comparisons) are indicated by shared superscript letters. [2] **$p < 0.01$

Community parameters	Forest patches	Edge of continuous forests	Interior of continuous forests	$F_{2,45}$
Species richness	15.19 ± 0.71[a]	15.13 ± 0.51[a]	12.75 ± 0.50[b]	5.72**
Species diversity	1.05 ± 0.02[a]	1.04 ± 0.02[a]	0.98 ± 0.02[b]	5.52**

Table 2. Selection indices of the bird guilds regarding the forest patches, edge and interior of continuous Macedonian pine forests (computed by *G*-test). *n*, sample size (number of birds recorded); o_{FP}, o_{ECP}, o_{ICP}, observed proportions of birds in forest patches, edge and interior of continuous forests, respectively; p_{FP}, p_{ECP}, p_{ICP}, expected proportions of birds; w_{FP}, w_{ECP}, w_{ICP}, selection indices of bird guilds; *p < 0.5; **p < 0.01; ***p < 0.001

Bird guilds	n	Proportions			Selection indices (± S.E.)			G (d.f. = 2)
		o_{FP} (p_{FP} = 0.35)	o_{ECP} (p_{ECP} = 0.32)	o_{ICP} (p_{ICP} = 0.33)	w_{FP}	w_{ECP}	w_{ICP}	
Hollow-nesters	763	0.32	0.31	0.37	0.91 ± 0.05	0.97 ± 0.05	1.13 ± 0.05	6.59*
Canopy-nesters	1092	0.35	0.32	0.33	1.01 ± 0.04	1.00 ± 0.04	0.99 ± 0.04	0.05
Shrub-nesters	176	0.52	0.27	0.20	1.49 ± 0.09	0.85 ± 0.09	0.62 ± 0.09	28.44***
Ground-nesters	502	0.47	0.34	0.19	1.33 ± 0.06	1.08 ± 0.07	0.57 ± 0.05	54.10***
Bark-gleaners	281	0.32	0.30	0.38	0.92 ± 0.08	0.92 ± 0.09	1.16 ± 0.09	3.66
Canopy-gleaners	1635	0.36	0.32	0.32	1.04 ± 0.03	1.00 ± 0.04	0.96 ± 0.04	1.62
Shrub-gleaners	89	0.40	0.30	0.29	1.16 ± 0.15	0.95 ± 0.15	0.89 ± 0.15	1.20
Ground-gleaners	528	0.44	0.33	0.23	1.27 ± 0.06	1.03 ± 0.06	0.69 ± 0.06	31.19***

Table 3. Selection indices of the bird species regarding the forest patches, edge and interior of continuous Macedonian pine forests (computed by *G*-test). *n*, sample size (number of birds recorded); o_{FP}, o_{ECP}, o_{ICP}, observed proportions of the birds in the forest patches, edge and interior of continuous forests, respectively; p_{FP}, p_{ECP}, p_{ICP}, expected proportions of birds; w_{FP}, w_{ECP}, w_{ICP}, selection indices of bird species; *p < 0.5; **p < 0.01; ***p < 0.001

Bird species	Acronyms	n	Proportions			Selection indices (± S.E.)			G (d.f. = 2)
			o_{FP} (p_{FP} = 0.35)	o_{ECP} (p_{ECP} = 0.32)	o_{ICP} (p_{ICP} = 0.33)	w_{FP}	w_{ECP}	w_{ICP}	
Dendrocopos major	Dma	48	0.50	0.27	0.23	1.43 ± 0.21	0.85 ± 0.20	0.69 ± 0.18	4.76
Anthus trivialis	Atr	16	0.44	0.50	0.06	1.25 ± 0.35	1.56 ± 0.39	0.19 ± 0.18	6.94*
Troglodytes troglodytes	Trr	124	0.29	0.39	0.32	0.83 ± 0.12	1.21 ± 0.14	0.98 ± 0.13	3.00
Prunella modularis	Pmo	85	0.68	0.26	0.06	1.95 ± 0.14	0.81 ± 0.15	0.18 ± 0.08	50.86***
Erithacus rubecula	Eru	130	0.48	0.28	0.24	1.36 ± 0.13	0.89 ± 0.12	0.72 ± 0.11	9.55**
Phoenicurus ochruros	Poc	30	0.63	0.30	0.07	1.81 ± 0.25	0.94 ± 0.26	0.20 ± 0.14	14.98**
Turdus viscivorus	Tvi	64	0.22	0.44	0.34	0.63 ± 0.15	1.37 ± 0.19	1.04 ± 0.18	6.15*
T. torquatus	Tto	43	0.47	0.19	0.35	1.33 ± 0.22	0.58 ± 0.18	1.06 ± 0.22	4.36
Phylloscopus collybita	Pco	219	0.54	0.35	0.11	1.55 ± 0.10	1.10 ± 0.10	0.32 ± 0.06	66.53***
Regulus regulus	Rre	186	0.24	0.31	0.45	0.69 ± 0.09	0.97 ± 0.11	1.35 ± 0.11	13.86**
Poecile montana	Pmn	57	0.18	0.28	0.54	0.50 ± 0.14	0.88 ± 0.19	1.65 ± 0.20	12.97**
Periparus ater	Pat	363	0.32	0.32	0.36	0.91 ± 0.07	1.01 ± 0.08	1.09 ± 0.08	1.84
Lophophanes cristatus	Pcr	26	0.23	0.35	0.42	0.66 ± 0.24	1.08 ± 0.29	1.28 ± 0.29	1.88
Sitta europaea	Seu	121	0.28	0.33	0.39	0.80 ± 0.12	1.03 ± 0.13	1.18 ± 0.13	2.99
Certhia familiaris	Cfa	111	0.29	0.26	0.45	0.82 ± 0.12	0.82 ± 0.13	1.37 ± 0.14	6.94*
Nucifraga caryocatactes	Nca	173	0.36	0.32	0.32	1.04 ± 0.11	0.99 ± 0.11	0.96 ± 0.11	0.18
Fringilla coelebs	Fco	512	0.36	0.33	0.31	1.02 ± 0.06	1.03 ± 0.07	0.95 ± 0.06	0.72
Serinus serinus	Sse	16	0.38	0.50	0.13	1.07 ± 0.35	1.56 ± 0.39	0.38 ± 0.25	4.09
Loxia curvirostra	Lcu	83	0.55	0.24	0.20	1.58 ± 0.16	0.75 ± 0.15	0.62 ± 0.13	14.72***
Pyrrhula pyrrhula	Ppy	74	0.39	0.31	0.30	1.12 ± 0.16	0.97 ± 0.17	0.90 ± 0.16	0.62

naturally fragmented to the continuous forests, while the hollow-nesters avoided the forest patches and the edges of continuous forests, and were more abundant in the interior of continuous forests (Table 2). Of 20 analyzed species, 47% were tolerant to 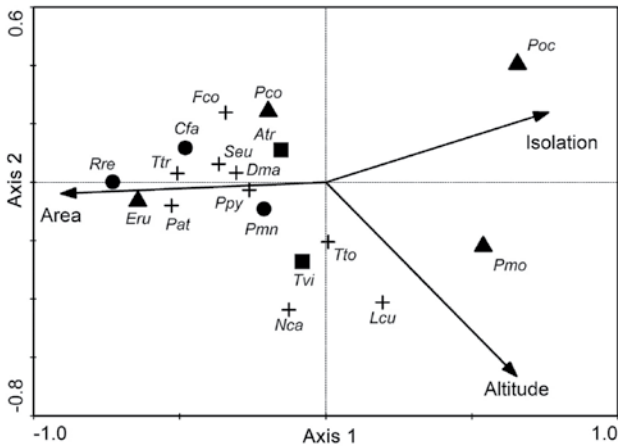forest fragmentation, 26% showed a preference for the for-est fragments (Dunnock *Prunella modularis*, Robin *Erithacus rubecula*, Black Redstart *Phoenicurus ochruros*, Chiffchaff *Phylloscopus collybita,* and Crossbill *Loxia curvirostra*), 16% preferred the interior of continuous forests (the Goldcrest *Regulus regulus*, Willow Tit *Parus montanus* and Treecreeper *Certhia familiaris*), and 11% showed preferences for the edge of continuous forests (Tree Pipit *Anthus trivialis* and Mistle Thrush *Turdus viscivorus*) (Table 3).

The area of the forest patches influenced positively the species richness (MRA, $\beta = 0.43$, $R^2 =$

Fig. 3. Ordination biplot (based on RDA) of the bird species versus the fragment parameters (area, isolation and altitude). Canonical axes were statistically significant (Monte Carlo permutation test, $F = 2.19$, $p < 0.01$). First two axes explained 21.5% of data variability (eigenvalues: 0.168 and 0.047 for the first and second axes, respectively). Environmental variables are indicated as arrows. The triangles, dots, squares and crosses represent the bird species that prefer the forest patches, edges, interior of continuous forests or those without habitat preference, respectively (see Table 4 for the acronyms)

Fig. 4. Ordination biplot (based on RDA) of clusters of the study plots according to the forest type: clusters within the forest patches, edge and interior of continuous forests are indicated as dots, squares and triangles, respectively. Grouping envelopes for the fore-mentioned clusters are indicated as solid, dashed and dotted lines, respectively

Table 4. Mean ± S.E. of habitat variables among the forest types[1], together with *F*-statistics and their significance[2] from ANOVAs used on the forest types (*n* = 48). [1] Within the rows with significant *F* - statistics, the mean values that are not significantly different ($p > 0.05$, *p* - values were corrected according to the number of comparisons) are indicated by shared superscript letters. [2] **$p < 0.01$, ***$p < 0.001$

Habitat variables	Abbreviations	Mean (± S.E.) in forest patches	Mean (± S.E.) in edge of continuous forests	Mean (± S.E.) in interior of continuous forests	$F_{2,45}$
Elevation (m a.s.l.)	ALT	2057.19 ± 14.98[a]	1998.50 ± 13.54[b]	1991.94 ± 16.31[b]	5.75**
Tree height (m)	TH	16.85 ± 0.59	18.59 ± 0.69	18.92 ± 0.66	2.93
Tree diameter at breast height (cm)	DBH	53.52 ± 2.30	52.17 ± 2.73	48.78 ± 2.65	0.91
Density of trees (trees/ha)	DT	233.29 ± 27.43	266.77 ± 29.27	294.68 ± 30.30	1.20
Number of dead trees and stumps	NDTS	4.34 ± 0.66	4.27 ± 0.42	4.71 ± 0.56	0.18
Number of foliage profiles	NFP	4.97 ± 0.15	5.32 ± 0.15	4.76 ± 0.15	3.15
Cover of ground level foliage profile (%)	GLFP	69.34 ± 2.55	75.09 ± 1.92	76.57 ± 2.80	2.42
Cover of low level foliage profile (%)	LLFP	24.01 ± 3.28	28.29 ± 2.23	29.98 ± 3.36	1.05
Cover of small shrubs (%)	SS	26.35 ± 2.88	27.79 ± 2.18	20.75 ± 3.66	1.57
Cover of mid-level foliage profile (%)	MLFP	43.46 ± 3.47[a]	28.04 ± 2.06[b]	22.32 ± 2.83[b]	16.60***
Cover of sub-canopy foliage profile (%)	SCFP	31.32 ± 2.05	30.79 ± 1.48	31.85 ± 1.79	0.09
Canopy closure (%)	CC	48.75 ± 2.13[a]	50.09 ± 2.06[a]	59.84 ± 2.55[b]	7.20**
Cover of stones and piles (%)	CRPS	19.07 ± 2.24	25.00 ± 3.38	18.23 ± 2.83	1.67

explained 41.6% of the bird data variability, with first and second RDA axes accounting for 30.2% and 11.4%, respectively. The ordination graph reveals the same environmental gradients that were found in the previous analyses. As expected from the *G*-test, the ground-gleaners were located on the left side of the first RDA axis and associated with the forest patches, while the guilds with no preferences (i.e. shrub- and canopy-gleaners) were spread across the biplot. The ground-gleaners avoided closed canopy stands and were positively associated with the availability of shrubs. Although the *G*-test showed no statistically significant habitat preferences of the bark-gleaners, their close proximity to the interior of continuous forests on the RDA biplot implies that they tend to be positively associated with this type of forest.

At the species level (Fig. 6), the first two RDA axes together explained 33.1% of the bird data vari-

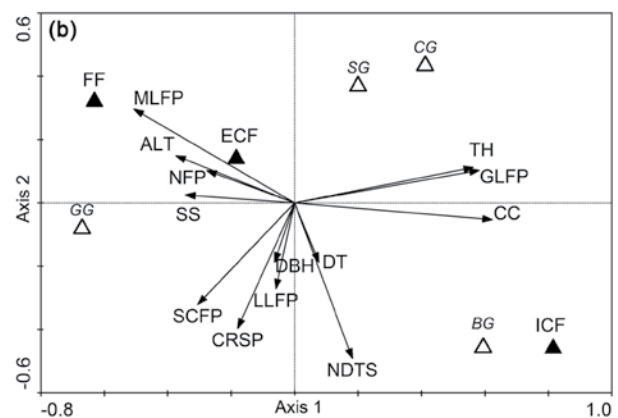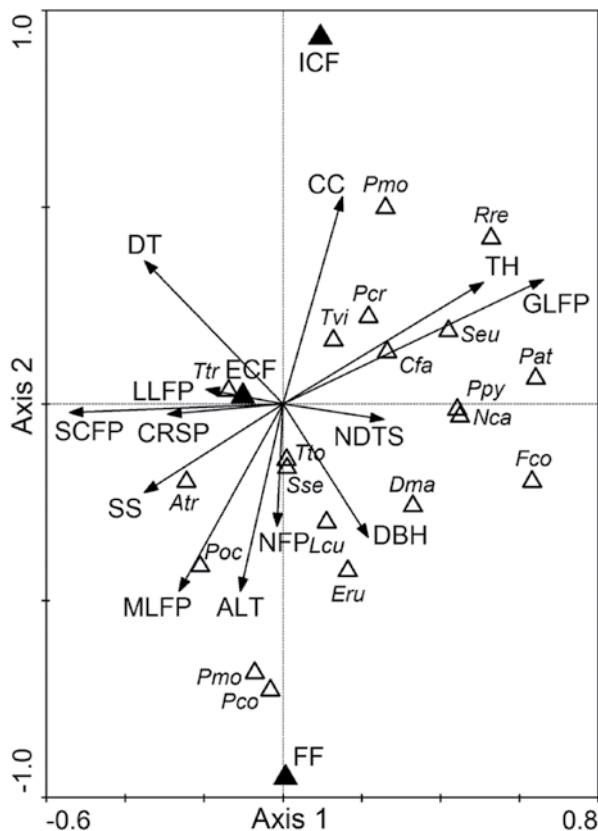**Fig. 6.** Ordination biplot (based on RDA) of bird species versus habitat characteristics. All axes were statistically significant (Monte Carlo permutation test, F = 2.01, p < 0.01). First two axes explained 33.1% of data variability (eigenvalues: 0.184 and 0.147 for first and second axes, respectively). Nominal and quantitative environmental variables are indicated as black triangles and arrows, respectively (see Table 5 for the abbreviations). Bird species are indicated as empty triangles (see Table 4 for the acronyms)

ability. The more open canopy and better developed mid-level foliage profile in forest patches favoured higher abundances of Dunnock, Chiffchaff and Black Redstart, while the closer canopy in the interior of continuous forests favoured higher abundances of Willow Tit and Goldcrest.

Potential for spatial autocorrelation

Moran's I values were very low and reach up to 0.3 over the short distances, and in most cases they were not statistically significant, which suggests that the spatial autocorrelation in residuals of the applied models is negligible.

Discussion

Bird assemblages in fragmented and continuous forests

Many studies report for negative effects of anthropogenic habitat fragmentation on bird communities (e.g. SAUNDERS *et al.* 1991, MURCIA 1995, MÖRTBERG 2001 but see CROOKS 2004; BARLOW *et al.* 2006), but this was not consistent in naturally disturbed habitats where little or no effects were observed (HERRANDO, BROTONS 2002, BROTONS *et al.* 2004). The results from the present study confirm that the natural fragmentation has little effect on the wildlife communities and this probably relates to the long history of the habitat perturbations in the ecosystem (SANTOS *et al.* 2002).

The forest characteristics could strongly affect the bird community structure (CONNER, DICKSON 1997, KIRK, HOBSON 2001, DÍAZ 2006) and the alterations in the habitat quality are key factors in determining the avian response to disturbances. As observed in other studies (GREENBERG, LANHAM 2001, ASKINS *et al.* 2007), the habitat fragmentation led to a more open canopy and better developed shrub layer within the forests. Furthermore, the fact that the fragmented forests were located at higher elevation than the continuous forests confirms that tree line ecosystems are more prone to environmental changes (CAMARERO, GUTIERREZ 2004).

In the studied upland forests, the shrub-nesting, ground-nesting and ground-gleaning birds tended to be more abundant in the forest fragments, while the hollow-nesters were positively associated with the interior of continuous forests. Similar results were observed in respect to the ground-gleaners (BOCK, LYNCH 1970) and hollow-nesters in North American

conifer woodland (Manuwal, Manuwal 2002). However, the results are not consistent over different regions and habitats. For instance, the shrub-gleaning, canopy-gleaning and bark-gleaning birds were found to be tolerant to the upland forest fragmentation in the present study, but they are sensitive to fragmentation in other forest ecosystems (Bock, Lynch 1970, Casenave et al. 1998). Conversely, the ground-nesters and scrub-nesters in the present study were found to be sensitive to the habitat fragmentation, but a similar effect was not observed in other studies (Manuwal, Manuwal 2002).

The sensitivity of bird guilds to the forest fragmentation could be explained by the habitat use of the birds at the species level. The majority of species with preference for the forest interior are hollow-nesters, while most of the species preferring fragments are ground-gleaners, scrub-nesters or ground-nesters. These results were consistent with many studies in Europe: the Dunnock and the Robin are known to prefer forest edges and fragments (Pattersson et al. 1995, Bellamy et al. 2000), while the Willow Tit (Jokimäki, Huhta 1996, Mörtberg 2001) and the Common Treecreeper (Suorsa et al. 2005) are known to be negatively affected by the forest fragmentation. Conversely, three species (Wren *Troglodytes troglodytes*, Chaffinch *Fringilla coelebs*, and Nuthatch *Sitta europaea*) were found to be sensitive to the forest fragmentation elsewhere (Opdam, Schotman 1987, Pattersson et al. 1995, González-Varo et al. 2008), but this was not observed in the present study. Many forest-edge species search for food in open habitats and their preference for forest-edges is influenced by easier access to these open habitats (Tomiałojc, Wesołowski 1990). Indeed, both species found to prefer the forest-edges in this study (Tree Pipit and Mistle Thrush) are ground-gleaners and often search for food outside of the forests. The preferences / avoidances of bird species to the studied forest types were determined mainly by their dependence on the canopy closure and shrub cover. The Chiffchaff generally avoids closed canopy forests, and the Dunnock and Robin are known to be positively related to the shrub cover (Hagemeijer, Blair 1997, Iankov 2007). The preference of the Common Crossbill for the fragmented forests may be related to the higher cone productivity along the forest edges, as observed by Pattersson et al. (1995) in upland spruce plantations in Britain. All the species negatively affected by the forest frag-

mentation were forest-dwelling species, and a significant part of the species preferring fragments was not restricted to the forest habitats (Iankov 2007). These results support the idea that species associated with the forest edges and shrubs generally show positive response to forest disturbances (Fuller 2000; Atwell et al. 2008).

Edge effects

Edge effects influence forest biodiversity by causing changes in habitat structure (Murcia 1995, Laiolo, Rolando 2005). The lack of clear difference in the bird community structure between the forest fragments and the edge of continuous forests, together with the fact that the present study was restricted to homogenous forest stands with short altitudinal and stand-age gradients, suggest that the habitat structure at the forest edges appears to be a key factor that influences the sensitivity of birds to natural forest fragmentation (Watson et al. 2004). The microclimatic conditions at the forest edges often differ from the forest interior with respect to the increased amount of sunlight, wind, and temperature variations (Schmiegelow, Mönkkönen 2005). All these factors determine a higher structural complexity of vegetation in the forest-edge zone, and together with the increased level of particular invertebrates that are an important prey item for birds, they create more ecological niches for birds (Díaz 2006). This may explain the higher species richness, diversity and density of the bird communities in the fragments and forest edges in the studied upland forests than in the interior of continuous forests. Forest edges were reported to support higher species richness and abundance of birds than forest interiors in many temperate ecosystems (Andrén 1994, Patterson et al. 1995, Tomiałojc, Wesołowski 2004), while an opposite effect was observed in the tropics (Beier et al. 2002; Watson et al. 2004). However, the history of edges may influence significantly their impact on the bird assemblages, which impact was positive in the natural edges and negative in the anthropogenic edges in the Alps (Laiolo, Rolando 2005). Further, the lack of significant differences in the vegetation structure between the fragments and the edge of continuous forests implies that the different occurrences of bird species in these two habitat types could be accounted for the higher relative cover of the habitat edge within fragments (Stephens et al. 2003).

Management implications

The result that naturally fragmented upland forests hold species rich, diverse and abundant bird communities should be interpreted with caution, as it does not provide a good reason for artificial forest fragmentation. It should be clear that the increased diversity is not universally 'good' in all cases; therefore the types of the bird species present must be evaluated (Howell *et al.* 2000). In this respect, the area-sensitive species with high conservation status (i.e., Grouses, Woodpeckers and Owls) were not considered in the study because of their rarity. Although the present study deals with common species that are not of priority from a conservation viewpoint, the studied forests hold significant densities of the Willow Tit and Common Treecreeper (both negatively affected by the forest fragmentation) not only in Bulgaria, but also at the European scale (Nikolov 2007). Therefore, these species are assumed to represent an important component of the temperate forest ecosystems and maintaining the habitat attractiveness for them by avoiding the forest fragmentation should be promoted.

However, because of the resulting economic, infrastructural and social development of the surrounding territories, there is a growing interest in enlargement of the existing ski resorts and creation of new ones on Bulgarian mountains (WWF 2008). In this context, it is almost impossible to avoid further fragmentation of the forests and a management strategy should be developed with the aim to mitigate the effects on the local biodiversity. Some appropriate management implications are: (1) to maintain a close-to-natural matrix (i.e., native grasslands, the Dwarf pine, Siberian Juniper or Balkan Broom) around the anthropogenic forest fragments because most of the forest edge-species are known to use it (Laiolo, Rolando 2005, Iankov 2007); and (2) to create forest fragments that are as large as possible, because most of the forest-interior species are area-sensitive (Dunford, Freemark 2004).

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