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Forest birds in forest fragments: are fragmentation effects independent of season?

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The aim of this study was to examine whether effects of habitat fragmentation on forest birds persist across seasons We noted the presence or absence of 18 bird species in 16 wood plots on 12 occasions (six in winter and six in spring) Woodland area ranged between 0.5 and 200 ha. All patches consisted of mature deciduous woodland Degree of fragmentation for each woodland patch was indexed by the factor scores on the first two axes resulting from a principal component analysis, performed on a number of area and isolation variables. Both in winter and in spring, species richness correlated negatively with degree of fragmentation. The number of species observed was higher in winter than in spring for most patches, but the difference was unrelated to the degree of fragmentation On a species level, little evidence was found for an effect of interaction between season and degree of fragmentation on the frequency of occurrence. The effects of fragmentation seem to depend on season in the Great Spotted Woodpecker Dendrocopos major *and the Treecreeper* Certhia brachydactyla, *but not in the other species considered Fragmentation has a negative effect on the frequency of occurrence of the Nuthatch* Sitta europaea, *Goldcrest* Regulus regulus, *Treecreeper, Great Spotted Woodpecker and the Starling* Sturnus vulgaris, *and a positive effect for the Chaffinch* Fringilla coelebs *and, possibly, the Lesser Spotted Woodpecker* Dendrocopos minor. *Seasonal changes in frequency of occurrence were noted in four of the species considered*

Over the last two decades, many studies have discussed the impact of forest fragmentation on woodland bird communities.[1–18] It is generally agreed that reduction in patch size and increasing isolation of habitat patches negatively affect populations of woodland-associated birds, although the relative importance of different aspects of fragmentation may vary among species. For instance, while the presence of specialist woodland birds such as the Jay *Garrulus glandarius* and the Marsh Tit *Parus palustris* is primarily determined by the area of the wood itself, the presence of edge species such as the Blackbird *Turdus merula* and the Starling *Sturnus vulgaris* may depend more on the perimeter of woodland, or on characteristics of the surrounding landscape.[16]

In the vast majority of studies, bird censuses have been restricted to the breeding season. As a consequence, our knowledge of the effects of habitat fragmentation on bird communities outside the breeding season is limited.[7] Conclusions from studies on the effect of fragmentation in the breeding season may not apply to other seasons. For instance, while Galli *et al.*[19] noted a negative effect of forest fragmentation on Downy Woodpeckers *Picoides pubescens* and Blue Jays *Cyanocitta cristata*, Yahner[7] found that the same bird species benefited from habitat clear-cutting in winter. This led him to suggest that wintering bird communities may

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be less sensitive to forest fragmentation than breeding bird communities.[7,13] Data from Telleria and Santos on resident insectivorous passerines in central Spain[18] seem to support this hypothesis. In eight out of nine of these birds, the number of occupied forest fragments during winter was higher than that occupied in spring. McIntyre, studying a bird community in northeastern Georgia forests, found significant interactions between season and patch size for number of species and diversity.[17]

In this paper, we investigate whether the relationship between bird occurrence and forest fragmentation holds in different seasons (winter and spring). The impact of habitat fragmentation on woodland birds may vary between seasons because the relative suitability of the habitat remnants may change with season. For instance, bad weather conditions in winter may exert a more profound influence on birds in small fragments than in large ones. If so, smaller and more isolated remnants that tend to support few birds in spring, will contain even fewer birds in winter. On the other hand, many woodland birds relax territorial defence in winter, when food availability is low, and join flocks.[20–22] Such flocks may make use of wood fragments that have areas below the critical breeding home range size of a given species. If so, small fragments are expected to hold higher numbers of birds in winter than spring.

METHODS

Selection of forest fragments

We performed bird censuses in 16 study plots of mature woodland in the vicinity of Antwerp, Belgium. The plots are dispersed in a landscape that is a mosaic of small-scale agricultural activity and fast-growing residential and industrial areas. Agricultural activities include market gardening, cattle breeding and maize cultivation. Many roads with ribbon development cross the area. Most houses are typical suburban, single-family dwellings with gardens. Some poplar *Populus* spp. and pine *Pinus* spp. plantations are present in the area, but were not visited during this study.

One study site consists of a large (>200 ha) forest, another site is a medium-sized wood of 30 ha, three sites are fragments between 8 and 10 ha, and the remaining sites have areas between 0.5 and 4 ha. Individual patches were chosen to represent the size range of woodlands in the region.

All study sites are covered with mature deciduous woodland, dominated by Common Oak *Quercus robur* (70–90%), with 10–30% being trees of other species, including Beech *Fagus sylvatica*, Larch *Larix decidua*, birches *Betula* spp. and Sycamore *Acer pseudoplatanus*. The understorey consists of Bird Cherry *Prunus padus*, Alder *Alnus glutinosa*, Hazel *Coryllus avellana* and Rhododendron *Rhododendron ponticum*. Bracken *Pteridium aquilinum* and brambles *Rubus* spp. form most of the herb layer.

Bird census

Fieldwork was carried out from December 1992 to June 1993. Birds were censused using point counts of ten minutes' duration.[23] The intention of the study was not to estimate the exact abundance of bird populations in the woods, but to determine seasonal effects on the frequency of occurrence. Therefore we did not count the number of individuals that were observed, but merely noted the presence or absence of each species considered (see Table 2 for a full list). Only birds within a distance of around 100 m were scored, to avoid the same individuals being counted at different points within a site. Birds flying over the canopy were ignored.

Each plot was visited twice a month, with an approximate interval of 15 days (depending on the weather: no counts were conducted during heavy rain or high winds). This resulted in a total of six counts for winter (December, January, February) and six for spring (April, May, June).

The number of count points per plot varied with the area of the plot. We censused birds at only one point in each of the smallest fragments (0.5–4 ha), at three points in the small fragments (8–10 ha) and at four points in the medium-sized forest (30 ha). In the large (>200 ha) wood, we performed counts at ten points. Whereas our observations covered most of the total area of the smaller (<11 ha) sites, this was not the case in the larger woods. This may result in an underestimation of the effect of fragmentation; while we are confident of our estimates of occurrence in the small fragments, we may have missed an occasional species in the larger forest. However, as the same procedure was followed during both winter and spring, this problem should not affect the interpretation of the major aim of this study (investigating seasonality of fragmentation effects).

Fragmentation parameters

Previous studies have demonstrated that both patch size and degree of isolation may affect the bird species richness of a forest. Owing to the limited number of plots in this study, we decided not to try to dissect both components of fragmentation. Rather, we opted to quantify the degree of fragmentation of the plots by combining a number of fragmentation parameters, including measures of both area and distance to nearby forests.

This was achieved by performing a principal component analysis on the following variables: (1) the area of the plot, (2–4) the total area of wood within a radius of 500, 1000 and 2000 m from the centre of the plot, (5, 6) the shortest distance between the plot and the nearest forest patch of at least 10 and 25 ha respectively, and (7–9) the number of woodland patches with a minimum area of 1 ha within a radius of 500, 1000 and 2000 m respectively from the centre of the plot. Areas and distances were $\log_{10}$ transformed and counts were square-root transformed to improve normality.

The first two principal components accounted for 75.8% (46.3 and 29.5% respectively) of the total variation. Subsequent axes had eigenvalues smaller than 1 and were not considered further. The first principal component (PC1) had high positive loadings for the area of the plot (0.86), for the total amounts of forested area within a radius of 1000 m (0.90) and within 2000 m (0.77). It had high negative loadings for the distances to the nearest forest of >10 ha (–0.80) and of >25 ha (–0.82). Plots that score low on this first axis can be said to have a high degree of fragmentation. The second principal component (PC2) was positively correlated with the number of forest patches within a distance of 500 m (0.89), 1000 m (0.88) and 2000 m (0.84). Study plots that score high on this axis can be said to have a large number of forest patches in the immediate surroundings. We used the factor scores of individual study plots on the first two principal components as indices for the degree of fragmentation (Table 1).

Analyses

We performed analyses at the community level (species richness) and at the species level (frequency of occurrence). Species richness was determined for each study plot and for both seasons by simply counting the species present. A species was considered 'present' in a plot during a given season when it was seen at least once during one of the six visits. To assess the interaction between season and fragmentation, we subtracted species richness in spring from that in winter for each individual plot and correlated the difference with the fragmentation indices.

At a species level, we determined the frequency of occurrence for each bird species separately. The frequency of occurrence for a

Table 1. Factor loadings for the first two principal components (PC1 and PC2).

	PC1	PC2
Area of the plot	0.863	–0.036
Distance to nearest forest of ≥10 ha	–0.789	0.103
Distance to nearest forest of ≥25 ha	–0.824	0.334
Number of forests of ≥1 ha within a radius of 500 m	0.262	0.889
Surface of wooded area within a radius of 500 m	0.701	0.490
Number of forests of ≥1 ha within a radius of 1000 m	0.057	0.876
Surface of wooded area within a radius of 1000 m	0.898	0.160
Number of forests of ≥1 ha within a radius of 2000 m	–0.329	0.844
Surface of wooded area within a radius of 2000 m	0.767	0.242
Cumulative proportion of variation explained (%)	46.33	75.86

given bird species in a given plot and season was defined as the number of times that the species was seen divided by the number of visits paid to that plot in that season. The difference in the frequency of occurrence in winter and spring was calculated per plot and correlated with the fragmentation indices to assess the seasonality of fragmentation effects. This analysis takes account of the repeated structure of our data.

RESULTS

Species richness

The percentage of bird species observed per plot and per season ranged between 44% and 100%. In both seasons, the number of bird species observed in a plot was positively correlated with the factor scores for that plot on the first principal component (winter: partial correlation coefficient r = 0.52, P = 0.046; spring: r = 0.70, P = 0.004), suggesting that numbers drop with increasing degree of fragmentation (Fig. 1). The partial correlations with the factor scores on the second principal component were not significant (both $P > 0.3$).

Most plots considered contained more bird species in winter than in spring (paired t-test, t_{15} = 2.91, P = 0.01). The difference in the number of species per plot varied from –2 (two species more in spring than in winter) to +6 (six species more in winter). We found no relation between the gain or loss in the number of species in a plot and the two measures of fragmentation (partial correlation with PC1: r = –0.42, P = 0.11; with PC2: r = –0.115, P = 0.68). This suggests that the effect of fragmentation on species richness is similar in spring and winter.

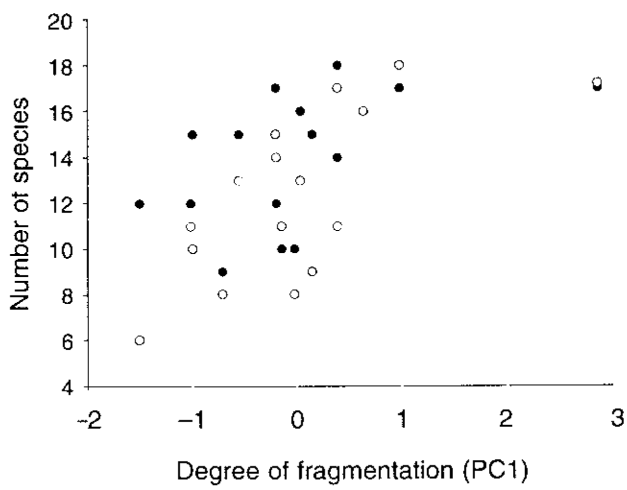

Figure 1. Number of bird species observed in plots of different degrees of fragmentation in winter (●) and spring (○). The degree of fragmentation displayed is a linear combination of several isolation and area parameters, obtained via principal component analysis (see Methods). Note that plots to the right are *less* fragmented than plots to the left.

Frequency of occurrence of individual species

The frequency of occurrence differed strongly among species (Fig. 2). Great Tit *Parus major* and Blue Tit *Parus caeruleus* were most often present (seen in 90% and 84% respectively of all visits), followed by the Wren *Troglodytes troglodytes* (75%), Robin *Erithacus rubecula* (66%) and Blackbird (64%). Green Woodpecker *Picus viridis* (11%), Willow Tit *Parus montanus* (9%) and Lesser Spotted Woodpecker *Dendrocopos minor* (2%) were seen most rarely. Species that were most seldom observed in winter were also rarely observed in spring and vice versa. That is, overall frequency of occurrence in winter and spring were correlated (r_s = 0.86, n = 18, $P < 0.0001$). Goldcrests *Regulus regulus* deviated most from this rule: they were seen considerably more in winter (39%) than in spring (6%).

Within plots, seven of the 18 species (Song Thrush *Turdus philomelos*, Green Woodpecker, Robin, Long-tailed Tit *Aegithalos caudatus*, Blackbird, Starling and Willow Tit) were seen more often in spring than in winter. However, the difference was only significant for the Green Woodpecker (z = 2.54, P = 0.011). The other 11 species were more frequently seen in winter, and the difference was significant in the case of the Lesser Spotted Woodpecker (z = 2.03, P = 0.04), the Great Tit (z = 1.95, P = 0.05) and the Goldcrest (z = 3.52, P = 0.00044).

Evidence for effects of fragmentation on the frequency of occurrence was found in five out of the 18 species. In the Nuthatch *Sitta europaea*, the frequency of occurrence in the respective plots was positively correlated with the scores of these plots on PC1, and this both in winter (r_s = 0.55, P = 0.03) and in spring (r_s = 0.62, P = 0.01). This attests to the preference of the Nuthatch for larger, less isolated woods. Significant positive correlations between frequency of occurrence and the scores on PC1

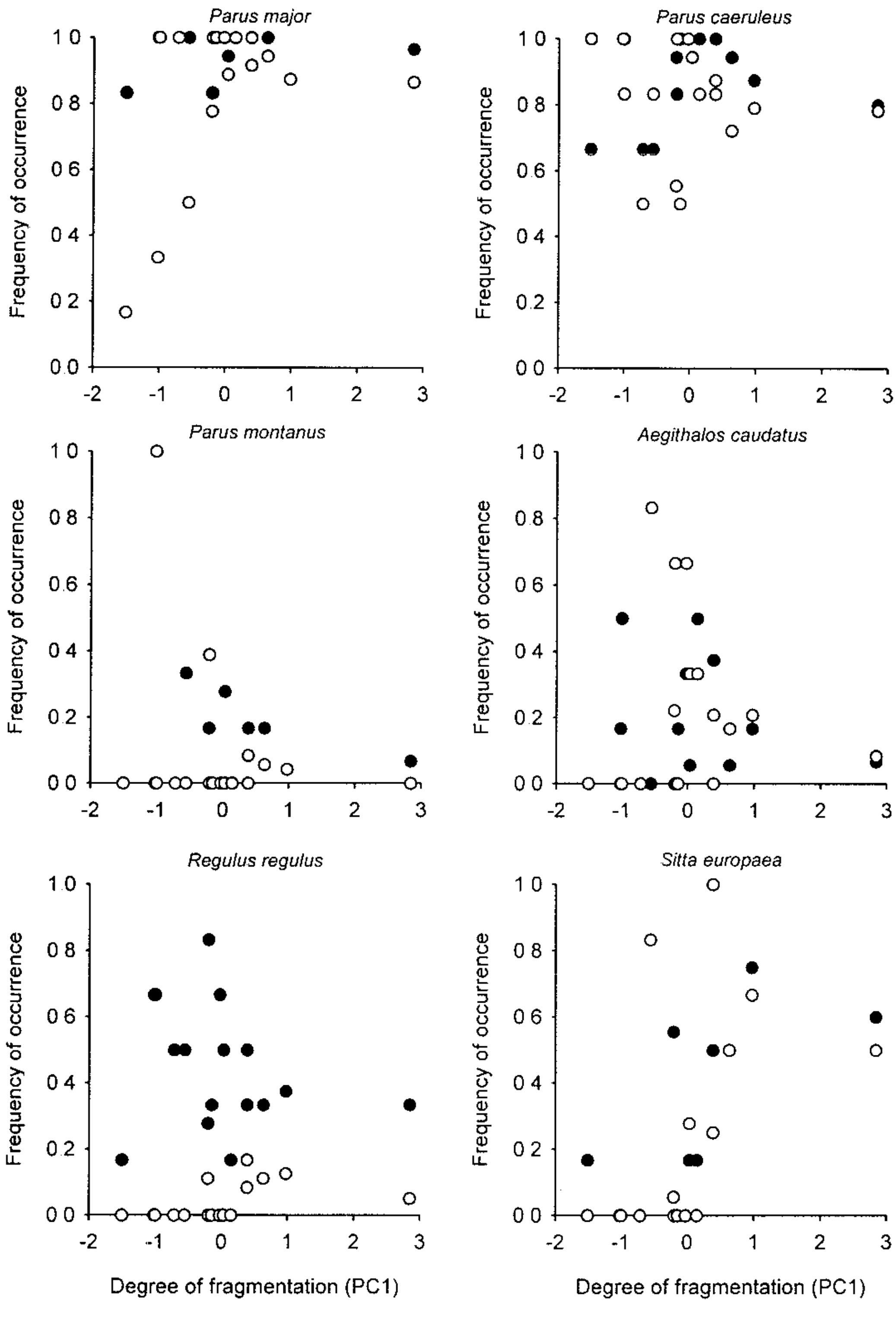

Figure 2. Frequency of occurrence of 18 bird species in 16 plots of different degrees of fragmentation, in winter (●) and spring (○). As in Fig 1, plots to the right are *less* fragmented than plots to the left. *continued*

were also found for the Goldcrest (in spring, r_s = 0.67, P = 0.005), for the Treecreeper *Certhia brachydactyla* (in winter: r_s = 0.48, P = 0.058), for the Great Spotted Woodpecker *Dendrocopus major* (in spring: r_s = 0.49, P = 0.052) and for the Starling (in spring: r_s = 0.64, P = 0.008). This suggests that at least in one season, these birds were affected negatively by forest fragmentation. Significant negative relationships between the frequency of occurrence and the scores on

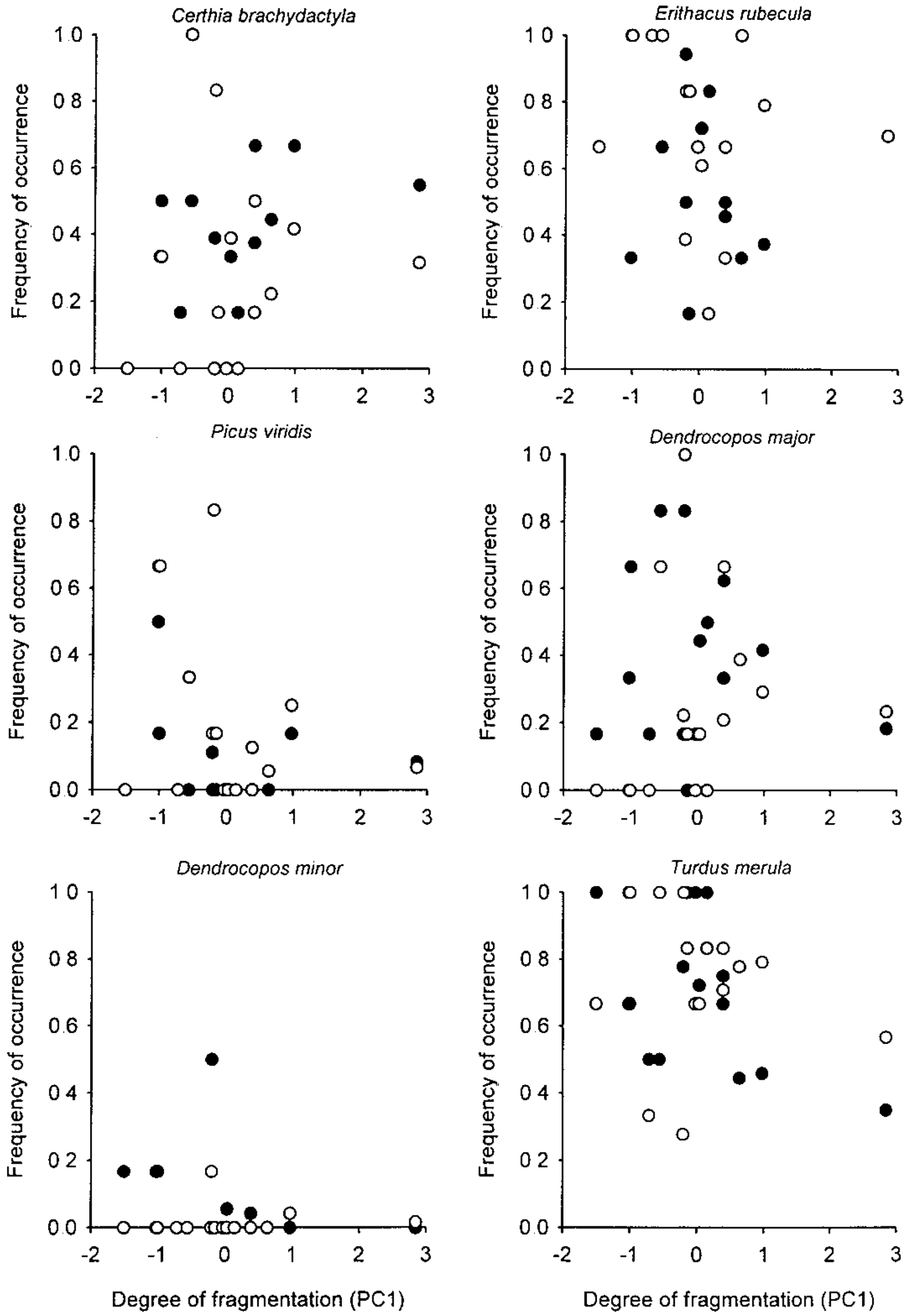

Figure 2 continued.

PC1 were found in the Chaffinch *Fringilla coelebs* (in spring: $r_s = -0.59$, $P = 0.017$) and in the Lesser Spotted Woodpecker (in winter: $r_s = -0.52$, $P = 0.040$). The negative correlations would suggest that these bird species are more often observed in smaller, more isolated woods.

In most species, seasonal differences in frequency of occurrence were unrelated to the degree of fragmentation (Table 2). A significant relation was found in only two species. In the Lesser Spotted Woodpecker, the difference in frequency of occurrence between seasons

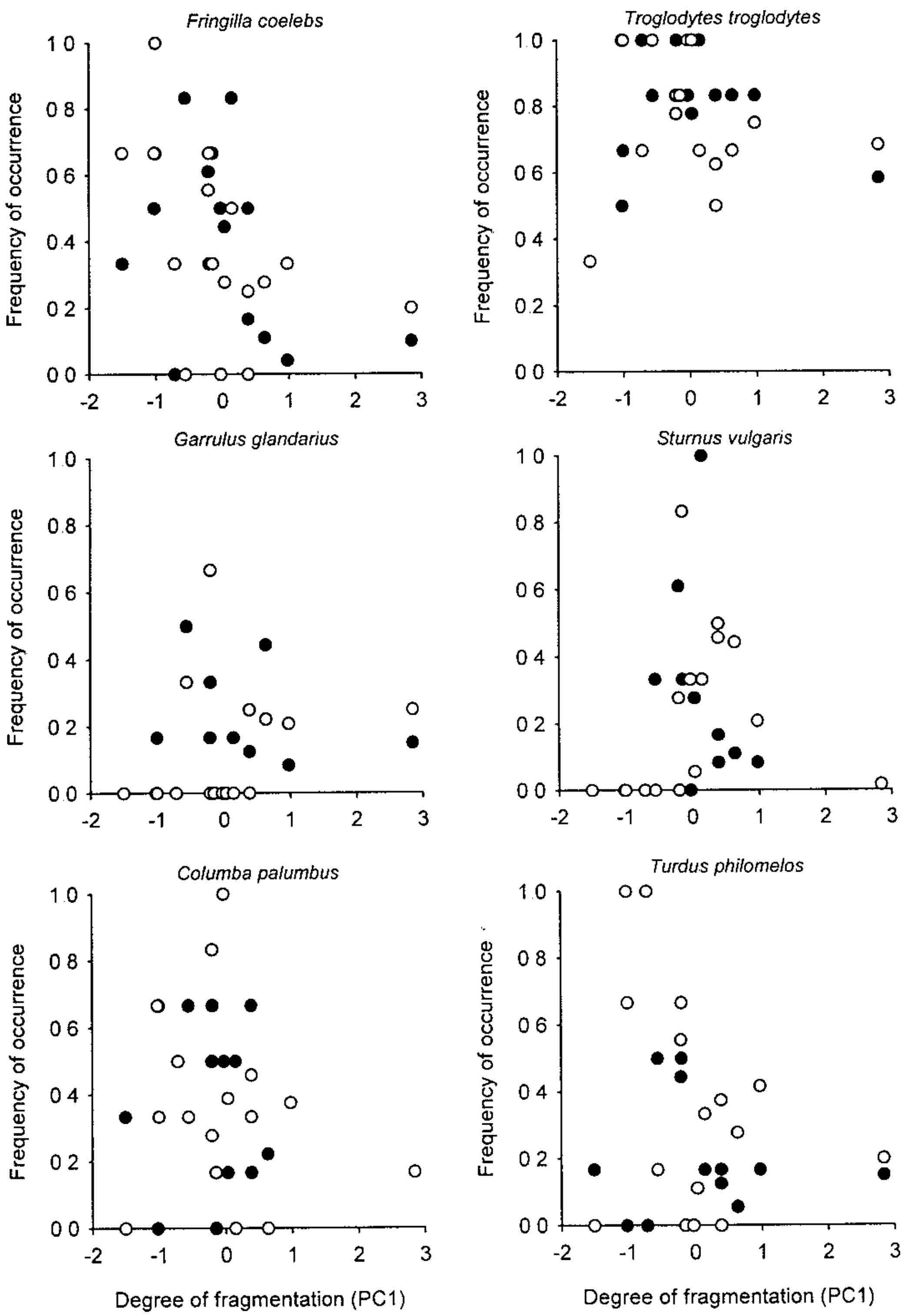

Figure 2 continued

decreased with increasing scores for the plot on PC1. Figure 2 shows that the probability of observing a Lesser Spotted Woodpecker is small and unaffected by season in the least fragmented forests, while in the most fragmented ones, the chances are also low in spring, but relatively high in winter. In the Treecreeper, fragmentation (PC1) seems to have a negative effect on the frequency of occurrence in winter, but not in spring. None of the correlations with PC2 was significant (all $P > 0.2$).

Table 2. Frequency of occurrence (%) per species in winter and spring and summary of statistical analyses.

	Frequency of occurrence		*Correlation with degree of fragmentation*					
	Winter	*Spring*	r_{winter}	P	r_{spring}	P	r_{diff}	P
Blue Tit *Parus caeruleus*	0.89	0.80	0.15	0.55	–0.28	0.29	0.27	0.31
Great Tit *Parus major*	0.95	0.86	0.03	0.91	0.20	0.46	–0.20	0.45
Willow Tit *Parus montanus*	0.09	0.08	0.42	0.11	0.06	0.81	0.43	0.09
Long-tailed Tit *Aegithalos caudatus*	0.15	0.19	0.13	0.64	0.22	0.41	–0.23	0.39
Treecreeper *Certhia brachydactyla*	0.42	0.28	**0.48**	**0.06**	0.17	0.52	**0.49**	**0.05**
Nuthatch *Sitta europaea*	0.45	0.35	**0.55**	**0.03**	**0.62**	**0.01**	0.13	0.64
Goldcrest *Regulus regulus*	0.39	0.06	–0.24	0.37	**0.67**	**0.01**	–0.32	0.23
Great Spotted Woodpecker *Dendrocopos major*	0.35	0.25	0.10	0.72	0.49	0.05	–0.31	0.24
Lesser Spotted Woodpecker *Dendrocopos minor*	0.04	0.01	**–0.52**	**0.04**	0.39	0.13	**–0.65**	**0.01**
Green Woodpecker *Picus viridis*	0.08	0.15	–0.03	0.92	–0.23	0.38	0.41	0.11
Blackbird *Turdus merula*	0.60	0.68	–0.36	0.17	–0.19	0.48	–0.19	0.48
Song Thrush *Turdus philomelos*	0.18	0.32	–0.11	0.69	–0.27	0.31	–0.14	0.62
Robin *Erithacus rubecula*	0.61	0.71	–0.27	0.31	–0.35	0.19	0.03	0.91
Wren *Troglodytes troglodytes*	0.75	0.74	0.21	0.43	–0.30	0.27	0.38	0.14
Starling *Sturnus vulgaris*	0.15	0.19	0.37	0.16	**0.64**	**0.01**	–0.34	0.20
Chaffinch *Fringilla coelebs*	0.31	0.32	–0.36	0.17	**–0.59**	**0.02**	0.30	0.27
Wood Pigeon *Columba palumbus*	0.30	0.30	–0.17	0.53	–0.18	0.52	–0.04	0.87
Jay *Garrulus glandarius*	0.14	0.16	0.15	0.59	0.37	0.15	–0.25	0.36

The Spearman rank correlation coefficients are shown for the relationship between the frequency of occurrence of a species in the 16 plots and the degree of fragmentation of these plots (estimated by the score on the first principal component). Positive values indicate a negative effect of fragmentation on the frequency of occurrence. r_{winter} and r_{spring} describe the relationship in winter and in spring respectively. r_{diff} links the difference in frequency of occurrence between seasons to degree of fragmentation, and thus is an estimator for the interaction between season and fragmentation effects. Significant correlations are emboldened.

DISCUSSION

The general lack of significant interactions between season and fragmentation effects suggests that the latter persist across seasons. In our study, fragmentation reduced species richness of the woodland bird community to a similar extent in summer and winter. In most plots, species richness was lower in spring than in winter, but the difference in the number of species between seasons was unrelated to the degree of fragmentation.

Of the 18 species considered, only two (the Lesser Spotted Woodpecker and the Treecreeper) showed a significant season × fragmentation interaction. The case of the Lesser Spotted Woodpecker is dubious. Our results suggest that this species would increase its use of fragmented areas in winter compared with the breeding season, a pattern reported in other species.[15,18] However, the Lesser Spotted Woodpecker is a rare species in our area and it is also quite secretive. This explains the low frequency of occurrence in both seasons and throughout the range of fragments. Differences in detectability between larger and smaller forest patches, and pure chance effects, may have contributed to the presumed interaction between season and fragmentation in this species. Treecreepers seem to prefer less fragmented woodlands in winter, but not in spring. Willow Tits show the same tendency, but the relationship between difference in occurrence and fragmentation is not statistically significant in this species. The pattern is opposite to that described in some species, such as the Blackbird and Chaffinch. The latter species are reported to withdraw partially from forests in winter, because they are attracted by a greater variety and abundance of food available at forest edges.[24] We do not know why Treecreepers and Willow Tits are associated with large forests more in winter than in spring.

One explanation might be that larger forests offer better microclimatic conditions in winter. Other potentially important factors are seasonal variation in food abundance, levels of inter- and intraspecific competition, predation intensity and availability of refuges. It is not clear, however, why any of these factors would be of importance to Treecreepers and Willow Tits, and not to the rest of the species studied. Obviously, more detailed knowledge on the mechanisms of fragmentation is needed to understand the interspecific differences in response to habitat reduction and isolation.

Apart from the trends in the Treecreeper and Willow Tit, we found little evidence to corroborate our hypothesis of an interaction between season and fragmentation effects. Small patch size and high degree of isolation seem to have the same effects in winter and spring. This may imply that the same factors (e.g. predation rate, food availability, climate conditions) determine the suitability of patches in both seasons, or that a seasonal change in one factor is compensated by an opposite change in another factor. Alternatively, the relative suitability of the plots may change over seasons, but site fidelity keeps the birds from switching to more suitable patches.

Our results indicate that the 18 species studied differ markedly in their tolerance to habitat fragmentation, as has been shown in earlier studies.[1,4,10,12,16,18] The exact origin of this variation remains unclear. Edge species in general seem to cope better with forest fragmentation than specialist forest interior species, but why this is the case remains largely unexplored. The particular importance of fragmentation for the Nuthatch[14,25] is confirmed by this study.

Frequency of occurrence (regardless of degree of fragmentation) was found to decrease from winter to spring in the Lesser Spotted Woodpecker, the Great Tit and the Goldcrest. This may reflect a behavioural shift in these birds. Great Tits and Goldcrests are territorial and sedentary during the breeding season, but join mixed-species flocks during winter. Both their mobility and detectability may be higher in winter. The pattern may also originate from seasonal patterns in mortality. Green Woodpeckers were observed more often in spring than in winter, possibly because the presence of these birds is often revealed by their territorial advertisement.

In conclusion, we found no convincing evidence to reject our null hypothesis that there is no effect of season on effects of habitat fragmentation. At least in our study area, and for the birds considered, fragmentation effects seem independent of season.

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