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Are Fragments Islands? Landscape Context and Density-Area Relationships in Boreal Forest Birds

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ABSTRACT: We investigated the role of matrix type as a determinant of change in bird densities with forest patch area (patch area effect) in two different Fennoscandian landscape types: mature forest fragments surrounded by cut-over or regenerating forest and true forested islands surrounded by water. Since the matrix of forested archipelagoes offers no resources to and impedes movement of forest birds, we predict that patch area effects on bird densities should be stronger on forested islands than in forest patches fragmented by forestry. We compiled correlation estimates of the bird density–patch area relationship from the literature and analyzed the data using meta-analysis. Combined correlation coefficients were significantly positive on islands but were not significantly different from 0 in fragments. Within-species comparisons also showed that correlations were consistently more positive on islands than in fragments. On islands but not in fragments, the densities of forest specialist species were more sensitive to area than were the densities of forest generalists, suggesting that specialists are more sensitive to changes in matrix quality. Migration status was only weakly associated with bird responses to island or fragment area. Thus, forest fragments do not function as true islands. We interpret this as the result of compensatory effects of the surrounding matrix in terms of availability of resources and enhanced connectivity (matrix quality hypothesis). A purely patch-centered approach seems an unrealistic framework to analyze population processes occurring in complex landscapes. The characteristics of the habitat matrix should therefore be explicitly incorporated into the assessment of species' responses to habitat fragmentation.

Keywords: archipelagoes, habitat fragmentation, forest birds, meta-analysis, matrix quality, patch area effect.

Factors determining animal distribution in habitat patches have been the subject of intense ecological study and debate over the past 2 decades (Connor and McCoy 1979; Gilpin and Hanski 1991). The discussion on the mechanisms explaining animal distribution in isolated habitat patches was first brought to the forefront by the equilibrium theory of island biogeography (ETIB; MacArthur and Wilson 1967) and, later on, by metapopulation theory (Gilpin and Hanski 1991). This discussion has been further stimulated by the impact of habitat loss and fragmentation on natural systems (Andrén 1994). Fragmentation decreases the availability of a focal habitat, the remnants of which are often arranged across the landscape as island-like habitat fragments.

The ETIB essentially focused on presence/absence of species in relation to area. It assumed that the number of individuals within a taxon increased linearly with the area of an island (MacArthur and Wilson 1967) but that the number of individuals per unit area remained constant. Population density should then not change with increasing area (table 1). Several studies have since investigated area-related variation in species densities (patch area effect [PAE] or patch size effect sensu Connor and McCoy 1979; Haila 1983; Bender et al. 1998; Connor et al. 2000) to better understand the determinants of species distribution in patchy landscapes. For Connor and McCoy (1979) or Haila (1983), the number of individuals per species in each patch was consistent with the random sampling hypothesis, which states that species distributions in small patches are random samples of their distribution in larger patches. As in the ETIB, densities of individual species are not varying with area. Two other hypotheses that have been proposed to explain relationships between animal density and area are the resource concentration hypothesis (Root 1973) and the density compensation hypothesis (MacArthur et al. 1972; table 1). For Root (1973), the density of individual species should increase with patch area as a result of greater concentration of critical resources in larger

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Table 1: Summary of the main hypotheses relevant to this study and their underlying subhypotheses

	Predicted PAE[a]	Predicts differences in PAE according to matrix type	Main references
Equilibrium theory of island biogeography/ random sampling hypothesis	No effect	No	MacArthur and Wilson 1967; Connor and McCoy 1979
Resource concentration hypothesis (habitat diversity hypothesis, enemies hypothesis, movement hypothesis)[b]	Positive	No	Root 1973
Density compensation hypothesis	Negative	No	MacArthur et al. 1972
Matrix quality hypothesis (dispersal hypothesis, habitat compensation hypothesis, habitat supplementation hypothesis)[b]	…	Yes[c]	Dunning et al. 1992; Norton et al. 2000; Vandermeer and Carvajal 2001

Note: The equilibrium theory, random sampling hypothesis, density compensation hypothesis, and resource concentration hypothesis all focus on mechanisms that are internal to the islands or fragments to explain variation, or lack of variation, in animal densities with island or fragment area. The matrix quality hypothesis is specific to fragments and focuses on mechanisms external to the habitat patches (quality of the matrix) to explain variation, or lack of variation, in animal densities with patch area. For each type of hypothesis, their predictions in relation to patch area effects (PAE) are summarized.

[a] Patch area effect, relationship between patch area and animal density.

[b] See the introduction to this article for more information on the underlying subhypotheses.

[c] Predicts larger PAEs in landscapes with low-quality matrices regardless which of the previous hypotheses holds within a specific landscape.

habitat patches (resource concentration hypothesis). These critical resources may be of different kinds, such as habitat heterogeneity (habitat diversity hypothesis; Root 1973; Ambuel and Temple 1993) or safety from predators (enemies hypothesis; Root 1973; Askins et al. 1987; table 1). As an alternative mechanism underlying the resource concentration hypothesis (table 1), Root (1973) considered that the higher densities of animals in larger patches might be solely a consequence of increased attraction of larger patches to moving individuals (movement hypothesis; Connor et al. 2000; but see Bowman et al. 2002). In contrast to the resource concentration hypothesis, the density compensation hypothesis of MacArthur et al. (1972) stated that individual species present in both large and small patches should have higher densities on smaller patches as a consequence of lower species richness there, resulting in reduced interspecific competition. Consequently, the density compensation hypothesis predicts a negative PAE on density. These hypotheses (table 1) cover the reported range of relations between density and area. No theory has been proposed that predicts a unimodal pattern where patches of intermediate size have the highest or the lowest animal densities (Connor et al. 2000).

Even though habitat patches may be surrounded by matrix of varying quality, all the hypotheses previously mentioned take for granted that the patches of a given habitat are embedded in a matrix that has no particular value for the species considered (Fahrig 1997). This certainly applies to true islands but is not necessarily applicable to terrestrial habitat fragments (Wiens 1994). Several authors have hypothesized that matrix quality probably affects processes that control the density of individual species in fragments (matrix quality hypothesis; Fahrig 2001; Ricketts 2001; Vandermeer and Carvajal 2001) and that matrix quality should affect PAE whatever the validity of the patch-centered hypothesis previously mentioned. Two mechanisms have been suggested for matrix quality to affect PAE. First, matrix quality can affect movement and dispersal of individuals (dispersal hypothesis; Moilanen and Hanski 1998; Pither and Taylor 1998; table 1) and the colonization-extinction dynamics of the system. This can lead to differences in densities between patches of similar characteristics but imbedded in different matrices (Gustafson and Gardner 1996; Vandermeer and Carvajal 2001). For example, movement and dispersal should be more difficult between islands than between habitat fragments (Martin and Lepart 1989; Gilpin and Hanski 1991). This may result in small islands being more difficult to recolonize after extinction and, therefore, they are more likely to host, on average, smaller densities than fragments. Second, matrices may differ in their ability to provide alternative habitats for some species (habitat compensation hypothesis; Norton et al. 2000) or to provide specific resources to the individuals occupying a fragment (habitat supplementation hypothesis; Dunning et al. 1992; table 1). In both cases, a matrix of high quality is expected to increase densities of individual species, especially in small habitat patches (Estades 2001). There is empirical evidence that resources from matrix habitats are commonly used, at least by some species associated with forest fragments (Hanski and Haila 1988; Loman and von Schantz 1991; Machtans et al. 1996). When food resources can be obtained from the matrix, the density of some species could, theoretically, be even larger in smaller patches than in larger ones (Loman and von Schantz 1991; Estades 2001).

The effect of matrix quality on the relationship between density and patch area has not been explicitly tested across different species. The objective of this article is to propose such a test. The manipulation of landscape characteristics is complex, and studies involving replicates of landscape treatments are scarce (Schmiegelow et al. 1997). Because replication is often infeasible in studies at the landscape level, Oksanen (2001) recommended combining studies via a meta-analytical approach (see also Bender et al. 1998). Even if the manipulation of matrix type and quality across different landscapes is, in most cases, not an option, we can find natural situations in which these factors can be used in a quasi-experimental design. In northern Europe, forestry has, as elsewhere, created heavily fragmented forest landscapes in which patches of mature forest are surrounded by a matrix of younger forests, clear-cuts, and, to a lesser extent, agriculture (Esseen et al. 1997). Fennoscandia is also characterized by numerous archipelagoes, both in the Baltic Sea and in lakes, in which forest patches are surrounded by water while remaining close to the mainland (Haila et al. 1983; Martin and Lepart 1989). This allows a comparison of the density-area relationship in two different landscape contexts. In the first, the matrix surrounding the forest patches can contain food resources usable by some of the bird species living in the patches (Hanski and Haila 1988; Loman and von Schantz 1991). In the second, forest patches are surrounded by water, a challenging barrier to dispersal (Matthysen et al. 1995; Bélisle and St. Clair 2001) and devoid of resources available to forest birds.

We used studies that provided information on the relationships between forest bird densities and forest patch area in these two types of Fennoscandian boreal forest landscapes to test the influence of matrix type (water vs. terrestrial habitat) on species density. First, we tested whether the overall PAE estimated across different species supported the predictions from the ETIB, the resource concentration hypothesis, and the density compensation hypotheses in the landscapes with a low-quality matrix (i.e., islands) as well as in the landscapes with a higher-quality matrix (i.e., forest fragments). Second, we studied whether PAEs depended on species biology in each of the two landscapes. Given that different species are unlikely to react in similar ways to the matrix that surrounds a forest patch, we predicted that PAE would be dependent not only on matrix type but also on how a species perceived matrix quality. For example, species that are habitat generalists should be more flexible in their use of different forest types and, thus, more capable of using resources available in the matrix habitats. For such species, we expect larger PAEs on islands than in fragments. Mature forests specialists are, by definition, more restricted to the patches of mature forests (Väisänen et al. 1998), and we thus expect this group of birds to show less variation in PAE when islands are compared with fragments. However, even if both groups are equally capable of exploiting resources in the terrestrial matrix, their relative perception of the permeability of the matrix that surrounds islands (i.e., suitability for moving across; dispersal hypothesis) could still influence individual distributions with PAE being larger in islands if water poses difficulties to individual movement. Similarly, earlier studies have shown that movements of resident birds are more constrained by habitat type than those of migrant birds (Desrochers et al. 1999), also suggesting possible differences in effects of matrix quality on PAE (Bender et al. 1998).

Methods

Data Compilation

We reviewed the studies that directly or indirectly tested for the effect of patch area on the density of forest birds in islands and forest fragments. We paid special attention to control as much as possible for habitat characteristics in the forest patches. To do so, we restricted the analysis to a single biogeographical area and to one habitat type, the boreal forest of Fennoscandia. In this region, numerous studies have been conducted on how fragmentation caused by forestry affects forest bird populations (Haila et al. 1987; Berg 1997; Edenius and Sjöberg 1997; Mönkkönen et al. 2000). Another set of studies has focused on the forest bird communities inhabiting archipelagoes either situated along the Baltic coast or in lakes (Haila 1983; Haila et al. 1983; Martin and Lepart 1989).

We defined fragments as patches dominated by mature forest habitats embedded in a matrix that consisted of a dynamic mosaic of forest stands of different ages, created by forestry, together with a variety of peat lands and, to a much lesser extent, cultivated areas (Esseen et al. 1997). Intensive forestry with clear-cutting started in the late 1940s, and most of the areas were already heavily fragmented by 1970 (Mönkkönen 1999). In the archipelagoes, the islands were covered mainly by mature forests. The archipelagoes in the Baltic Sea and in the lakes of Fennoscandia consist of islands that are close to each other and close to their mainland. Their spatial arrangement and shapes closely resemble those observed for the forest patches. However, we paid further attention to potential differences in the two major landscape variables likely to influence PAEs: patch isolation and cover of focal habitat in the landscape (Andrén 1994). Patch isolation was defined as the distance to the nearest patch (fragment or island), and maximum and minimum values for this variable were estimated in each data set (table 2). We compared these minimum and maximum values between the two landscape categories. These extreme values did not differ between landscape categories even when the study of Rolstad and Wegge (1987) was excluded to avoid giving too much weight to a data set that had information on only one species (t-test $= 0.42–1.08$, df $= 6–7$, $P \geq .32$). The only noticeable pattern was a nonsignificant trend for higher maximum values in the studies on fragments. This resulted mainly from larger study areas in the Rajasärkka data set (table 2). In theory, a bias toward higher isolation in fragments would increase PAEs there, and, therefore, such a bias would make our results more conservative.

Because of a long history of intensive forestry in the region, larger stretches of old-growth forests are missing on the mainland. The proportion of mature forest cover ranged between 12% and 30% in the data sets and did not differ between the islands and fragments (t-test $= 0.61–1.07$, df $= 6–7$, $P > .32$), suggesting that focal habitat cover should have no measurable effect on PAE differences between our two landscape categories. This assumption was reinforced by the lack of effect of focal habitat cover on PAE found by Bender et al. (1998) even though focal habitat cover varied in this case from a few percent to 80% between data sets.

The terrestrial matrices in the fragment system consisted of mosaics of secondary forests of varying age. Differences in matrix composition and configuration between different terrestrial landscapes consisted of minor (<20%) differences in the proportion of agriculture and peat land. We considered the differences in matrix quality between the fragment studies to be minimal when compared with the water "matrix" characteristic of the island studies.

The effect of matrix type on density-area relationship may be confounded if habitat structure co-varies with fragment area (Martin et al. 1995). To limit this potential bias, we selected individual studies that used explicit criteria in their selection of the islands and fragments of mature forests to minimize overall habitat differences between patches (Haila 1983; Martin and Lepart 1989). Forest patches and islands consisted of mature forests dominated by the same conifer species irrespective of their area. We used only data on species that breed in forest habitats, excluding the few observations of species that typically breed in agricultural or other nonforested habitats.

Estimation of Bird Population Density

Data on bird densities were collected using two methods: point counts and transect counts performed during the breeding season. In the studies using transect counts, bird

Table 2: Summary of studies included in this study

Study	Matrix type	Number of bird species	Range of patch areas (ha)	Number of islands/ fragments	Landscape habitat cover (%)	Isolation (m)	Study area extent (km)
Haila et al. 1987	Fragments	45	.4–56	34	15[a]	100–1,000[b]	20 × 20
Rolstad and Wegge 1987	Fragments	1	.45–155	12	30[b]	<500[b,c]	20 × 15
Berg 1997	Fragments	21	2–1,000	24	18[c]	450[b,d]	80 × 80
A. Rajasärkkä, N. Finland, unpublished data	Fragments	52	12.5–995	39	20[c]	230–14,000[a]	240 × 240
A. Rajasärkkä, S. Finland, unpublished data	Fragments	50	8.5–887	56	12[c]	200–11,000[a]	300 × 300
Edenius and Sjöberg 1997	Fragments	8	2–17.8	18	26[b]	50–600[b]	18 × 18
Haila et al. 1983	Islands	64	.5–582	44	29[a]	<100–1,000[b,e]	12 × 12
Haila 1983	Islands	41	.5–885	41	27[a]	<100–1,000[b,e]	20 × 15
Martin and Lepart 1989	Islands	34	1–347	13	12[a]	<200–1,500[b,e]	20 × 15

Note: Studies listed assessed the relationship between population density of individual species and patch area. For each study, figures for overall landscape habitat cover (proportion of old forest within the study area), isolation (minimum interpatch distance in meters), and extent of the study area (km) are described. Habitat was conifer-dominated forests in all patch types.

[a] Measured on map.

[b] Given in the cited article.

[c] Obtained from regional forestry statistics.

[d] Only mean values given in the cited article.

[e] No absolute minimum values available.

densities were calculated by dividing the number of individuals observed by the area covered by each transect. In studies using point counts, we used the number of individuals per species contacted per point count as the density estimate. When this number was not available (Martin and Lepart 1989), we used the frequency of occurrence of a species in a sample of point counts as estimator of species density (Bibby et al. 1992). For both point and transect counts, we assumed that species detectability was independent of patch area (Lynch and Whigham 1984). We tested for possible sampling biases in point count studies including islands with areas smaller than the sampling unit (Martin and Lepart 1989), but we did not find weaker PAEs when excluding such subsets of small islands. This indicates that sampling biases are unlikely to induce an increase of PAEs within island landscapes.

In order to detect true relationships between density and patch area for the rare species that typically inhabit large patches, and as suggested by Connor et al. (2000), we included zero patches (patches in which a given species was not detected) in the calculation of specific density-area relationships. However, to test for the specific predictions of the density compensation hypothesis in islands or fragments, we analyzed PAEs of species that occurred in both large and small patches, the latter being defined as species present in at least one patch within the lower-area quartile.

Following Raivio and Haila (1990), we classified species as specialists (found primarily in older forests, i.e., detected at very low frequencies in mosaics created by forestry) and generalists (regularly detected outside older forests in the mosaics created by forestry). We used other published accounts (Helle 1985; Jokimäki and Huhta 1996) to assign species not listed by Raivio and Haila (1990) as either specialists or generalists. We also classified species as migrants (which undergo long-distance movements from their breeding sites) and residents (which remain close to their breeding site during the nonbreeding season) based on information from the Finnish breeding bird atlas (Väisänen et al. 1998).

Our literature survey yielded nine studies with the desired characteristics: three studied archipelagoes of forested islands and six studied sets of forest fragments (table 2). We obtained data on the relationship between bird population density and area for 60 species on islands (102 individual estimates) and 63 species in fragments (a total of 175 individual estimates; see appendix). For 52 of these species, we were able to obtain at least one estimate of the density-area relationship in the set of island studies and one estimate from fragments (subset 1; see appendix). For 30 species, we obtained two estimates or more per matrix type (subset 2; see appendix).

Analytical Approach

The availability of research conducted on single landscapes allows combining of independent studies that view each of them as replicates or observations in subsequent statistical analysis. Meta-analysis is a powerful quantitative method for summarizing and analyzing such data sets (Gurevitch and Hedges 1993; Cooper and Hedges 1994) in order to determine whether different studies share a common statistical relationship and whether this relationship is related to one or several predictor variables.

Effect size in a meta-analysis is defined as the level of statistical relationship between two variables of interest (e.g., patch area and population density for a particular species; Hedges and Olkin 1985). We have opted for the Pearson product-moment correlation coefficient, r, as a measure of the PAE. This value not only describes the strength and direction of the linear relationship between patch area and density but can also be used as a measure of the intensity of the PAE on density. Highly positive or negative correlations indicate a strong association between patch area and population density (Bender et al. 1998), whereas weak correlations near 0 indicate that population density is not related to patch area. Correlation coefficients are widely used in meta-analytic procedures for the calculation and combination of effect sizes (Hedges 1994; Raudenbush 1994). Many studies of the relationship between the density of animal populations and area do provide r, which makes it a convenient effect size. For studies that did not report r or that did not provide the data necessary to calculate r, we applied the procedure outlined in Cooper and Hedges (1994) to estimate r from other test statistics such as Student's t and the treatment means to determine the sign of r (see Connor et al. 2000 for a similar approach).

For each species within a study, we calculated independent estimates of the relationship between population density and area. In other words, following previous approaches in the study of PAE across species (Bender et al. 1998; Connor et al. 2000), we assumed within each study that species responded independently of each other to variation in patch area. We then used a single estimate of r for each species per matrix type. For some of the species included in the analyses, we were able to obtain more than one estimate of the PAE, and for these species, we calculated a mean estimate of PAE. Effect sizes based on correlation coefficients are dependent on the size of the sample from which they have been estimated (Hunter 1982). To obtain species mean estimates of PAE from the correlations provided by different studies, we calculated a weighted average of the available estimates per species and matrix type. This weighted average ($\bar{r}$) takes into account the number of patches from which the correlation has been estimated and therefore controls for sample size and gives more weight to estimates obtained from larger samples (Hunter 1982):

$$\bar{r} = \frac{\sum (N_i r_i)}{\sum N_i},$$

where r_i is the correlation for study i and N_i is its sample size. We also calculated the variance (s_r^2) of each weighted mean estimate using the formula suggested by Hunter (1982):

$$s_r^2 = \frac{\sum [N_i(r_i - \bar{r})^2]}{\sum N_i}.$$

Correlation coefficients (r and $\bar{r}$) were normalized using Fisher's transformation of r, Z_r (Sokal and Rohlf 1995).

For species that had both island and fragment PAEs (at least two per matrix type), we calculated an additional effect size, Hedges's d, a modification of Hedges's g, which accounts for small sample sizes (Hedges and Olkin 1985). Within a given species, Hedges's d estimates the standardized mean difference of PAEs between islands and fragments. The method used is analogous to the analysis of data sets in which different studies involving control versus treatment are compared to detect overall treatment effects (Hedges and Olkin 1985). In our case, we use island versus fragment estimates for each species as analogous to control versus treatment data for a particular study in a large data set involving different studies. All meta-analytic procedures were performed using MetaWin software (Rosenberg et al. 1997).

Testing for Differences in PAE between Islands and Fragments

If patch area influences bird densities, we expect to find significant departures from 0 in correlation coefficients between patch area and density (PAE; Connor et al. 2000). Therefore, we first tested whether combined correlation coefficients for the species included in each matrix type were significant. The ratio of the overall mean Z_r to its standard error is distributed as $N(0, 1)$, so if the absolute value of the ratio exceeds 1.96, one would reject the null hypothesis at the $P = .05$ level (Cooper and Hedges 1994).

To analyze the relationship between population density and patch area within each matrix type using individual species estimates, we combined transformed correlation coefficients (Z_r) obtained for individual species using the procedures outlined in Cooper and Hedges (1994), Hedges (1994), and Raudenbush (1994) for random effects models. We fitted random effects models for all hypothesis tests. In this way, we consider the correlation coefficient estimated for each species to be drawn from an underlying distribution of correlations rather than considering each species as providing an estimate of a single common value (Connor et al. 2000). The random effects meta-analysis is equivalent to mixed-effects linear model, with fixed effects as covariates and the random effects being the deviation of the true effect size of a study from the value predicted by the model (Raudenbush 1994). Weighted averages of effect sizes within species categories (e.g., specialists/generalists, sedentary/migratory) were obtained by weighting Z_r values by the reciprocal of the sum of their conditional variance ($1/[N - 3]$), where N is the sample size of the effect size estimate) and the random effects variance (Raudenbush 1994). Random effects variance was estimated using the iterative maximum likelihood procedure presented by Raudenbush (1994). Given that the effect size estimates were weighted by their variances, model fitting involved weighted least squares regression (Hedges 1994).

To determine whether differences in average correlation within each matrix type were related to the habitat preference or the migration status of the species, we then fitted a one-factor random effect model separately for each landscape.

The effect of matrix quality on the density-area relationship could decrease as minimum patch area increases. This might be so because as patch area increases, the relative amount of edge habitat decreases nonlinearly, which can possibly reduce the role of the matrix as an alternative habitat. If this were the case, studies not including small patches may show correlations between density and patch area closer to 0 than studies with smaller minimum patch sizes. We tested whether this effect was present in our data by fitting random effects weighted least squares regression models to our data by using mean minimum patch area as predictor variable of species-specific PAE.

We used two different methods to test our prediction of consistent within-species lower PAE in landscapes with a matrix of lower quality. The first one involved fitting a standard repeated-measures ANOVA (Sokal and Rohlf 1995) to the estimates of the PAE per species using matrix type (island vs. fragment) as a within-subject factor. To determine whether within-species differences between matrix types were related to species ecology, we assessed the interaction among habitat preferences, migration status, and the within-subject factor matrix type. Repeated-measures ANOVA is a convenient procedure for our particular purpose because it does not estimate group differences using mean averages across species. Rather, it assesses whether paired comparisons (within-subject factor) of multiple estimates per species have a significant directional component (Sokal and Rohlf 1995). While this approach allowed us to use species for which we had only one estimate per matrix type (subsets 1 and 2), it did not account for the variability due to differences in sample size (number of patches) used to estimate the correlation coefficients for each species within each study. To overcome this problem, we tested whether overall Hedges's d estimates between island and fragment differed from 0 for species with two or more PAE estimates within each matrix type (restricted to subset 2). Hedges's d estimates that differ from 0 would be expected if PAE estimates for each species on the islands were different from their estimates in the fragments. We also fitted a one-factor random effect model to assess the effect of species habitat preference and migratory status on differences in Hedges's d between islands and fragments.

Results

Overall PAE Variation in Relation to Matrix Type and Species Groups

Combined correlation coefficients estimating overall PAE on islands were significantly positive, whereas correlation coefficients estimated from fragments did not significantly differ from 0 (table 3). Patch area had an overall significant positive effect on bird density on islands but not in fragments. The PAEs were also positive in the subset of species present in both large and small islands (mean ± SE, all data, $n = 29$, 0.13 ± 0.022, $P < .0001$; subset 1, $n = 25$, 0.17 ± 0.027, $P < .0001$) and did not differ significantly from 0 in fragments (mean ± SE, all data, $n = 33$, -0.05 ± 0.025, NS; subset 1, $n = 28$, 0.03 ± 0.023, NS). When we calculated estimates separately according to species habitat preference or migration status, correlations were also significantly larger than 0 on islands and not different from 0 in fragments (table 3). When we restricted our analyses to sets of species (subset 1, $n = 52$, and subset 2, $n = 30$) for which we had estimates both from islands and fragments, overall combined estimates were still significantly larger than 0 on islands but not in fragments (table 3).

Species habitat preference (specialists vs. generalists) was an important moderator variable in the variation in PAE among species on islands except in the smaller of the subsets (subset 2; table 4). For subset 1 species, a significant amount of variation in correlation coefficients observed on the islands was also attributable to the migration status (table 4). In fragments, neither migratory status nor habitat preference significantly affected overall PAE in any of the subsets analyzed (table 4).

The PAEs for individual species were independent of minimum patch area both on islands (P ranging from .19 to .21) and in fragments (P ranging from .23 to .72). This suggests that the area of the smallest patches did not influence the results.

Within-Species Differences in PAE and Matrix Type

For species detected in both matrix types, repeated-measures ANOVA showed a consistent trend for stronger PAE estimates on islands than in fragments (table 5). The same approach indicated that species habitat preference or migratory status did not affect the trend for stronger positive correlations on islands than in fragments (table 5).

The meta-analysis of standardized mean differences in PAE between matrix types for each species (Hedges's d effect size) also indicated that PAE of individual species was stronger on islands than in fragments (table 6). When taking species habitat preference and migration status into account, we still found a consistent trend of larger PAE on islands. However, using this method, we found that specialist species showed significantly larger difference in Hedges's d between the two matrix types than generalists (table 6). Specific differences in PAE between matrix types were larger but only marginally significant ($P < .10$) for migrants than for resident species (table 6).

Discussion

Why Are Fragments Not Islands?

Our findings support the matrix quality hypothesis by showing that bird densities in fragments of mature forest in landscapes fragmented by forestry differ from those observed on forested islands embedded in a matrix of water unsuitable to forest birds (Simberloff and Martin 1991; Wiens 1994; Estades 2001). In the same boreal setting, Schmiegelow and Mönkkönen (2002) have shown that the effects of fragmentation in a landscape dominated by forestry differ from those observed in a landscape dominated by agriculture. They emphasized not only the importance of the patches and their configuration but also the quality of the matrix (Moilanen and Hanski 1998; Vandermeer and Carvajal 2001).

On islands, the significant positive PAEs that we observed for bird densities suggest that larger islands have a better intrinsic value for breeding forest birds. These results support the predictions of the resource concentration hypotheses (Root 1973). Reviewing actual density and area relationships in different groups of animals, Connor et al. (2000) also came to the conclusion that densities of animal populations are, overall, positively correlated to area, a conclusion that supports the general validity of the resource concentration hypothesis. Several studies on islands (Simberloff and Martin 1991; Martin et al. 1995) as well as in fragments (Sjöberg and Ericson 1997; Brotons et al.

Table 3: Combined transformed correlation coefficients (Z_r) between area and individual densities derived from random factor meta-analytic models on species inhabiting islands and fragments

	Overall		Migrants		Residents		Specialists		Generalists	
	Z_r (n)	P	Z_r (n)	P	Z_r (n)	P	Z_r (n)	P	Z_r (n)	P
All forest species:										
Islands	.24 ± .039* (60)	<.0001	.21 ± .05* (36)	<.0001	.31 ± .06* (24)	<.0001	.40 ± .05* (18)	<.0001	.17 ± .03* (42)	<.0001
Fragments	.005 ± .03 (63)	.43	.004 ± .03 (39)	.45	.009 ± .05 (24)	.43	.01 ± .04 (23)	.40	.01 ± .05 (40)	.48
Subset 1:										
Islands	.25 ± .04* (52)	<.0001	.17 ± .05* (32)	<.0001	.38 ± .07* (20)	<.0001	.43 ± .08* (18)	<.0001	.16 ± .05* (34)	<.001
Fragments	−.004 ± .02 (52)	.42	.01 ± .02 (32)	.31	−.03 ± .03 (20)	.16	.02 ± .04 (18)	.31	−.01 ± .02 (34)	.31
Subset 2:										
Islands	.20 ± .04* (30)	<.0001	.25 ± .07* (20)	<.001	.13 ± .10 (10)	.11	.29 ± .08* (8)	<.001	.17 ± .04* (22)	<.0002
Fragments	−.02 ± .03 (30)	.25	−.01 ± .03 (20)	<.37	−.03 ± .06 (10)	.31	−.03 ± .06 (8)	<.32	−.01 ± .03 (22)	.039

Note: Values are weighted means ± SE; group sample sizes are given in parentheses. See appendix for species included in different data subsets.

* Estimates differed significantly from 0 at $P < .05$ when using reference P values obtained using the Dunn-Sidak method (with reference $P < .002$).

Table 4: Results of random effect meta-analytic models assessing the role of habitat preference (habitat: specialist vs. generalists) and migration status (migration: migrants vs. residents) on density-area relationship on islands and fragments

	Islands			Fragments		
Source of variation	df	*Q*	*P*	df	*Q*	*P*
All forest species:						
Habitat	1	12.64	.0002***	1	.27	.59
Migration	1	1.63	.20	1	.01	.92
Subset 1:						
Habitat	1	9.87	.002**	1	.73	.39
Migration	1	6.16	.013*	1	1.17	.28
Subset 2:						
Habitat	1	2.31	.29	1	.04	.85
Migration	1	1.05	.30	1	.01	.76

Note: Sources of variation were assessed separately in random, single-factor models. See appendix for species included in different data sets. The variable Q is total heterogeneity used to judge significance (P values) according to the degrees of freedom (df) of the test.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

2003) have identified different mechanisms that underlie this hypothesis (table 1). They include the positive effects of area on the quality of the microhabitat and its heterogeneity (habitat diversity hypothesis), an important determinant of bird density in forest environments (Wiens 1989). Matthysen et al. (1995) and Connor et al. (2000) have argued that area does also correlate positively with social facilitation, higher probability of finding mates, higher overwintering survival rate, or enhanced annual recolonization (movement hypothesis). Finally, Ambuel and Temple (1983), Askins et al. (1987), and Rolstad and Wedgge (1987) have shown that area correlates negatively with predation risk (enemies hypothesis), also resulting in lower species densities on small islands.

Conversely, our results offered no support for the ETIB or the random sampling hypothesis developed for island bird communities (Haila 1983; Haila et al. 1983) or the hypothesis of density compensation on the smaller islands as a result of the lower number of competitors (MacArthur et al. 1972). Haila et al. (1983) and Martin and Lepart (1989) came to the same conclusion on density compensation. Only for two forest generalist species, the chaffinch and the willow warbler, did they find higher densities on smaller islands than on larger ones or the mainland. The negative overall PAE value we observed for the chaffinch in the analysis at the species level is consistent with these results (appendix). The positive overall PAE we found for the willow warbler is not.

The lack of significant PAEs in forest fragments is consistent with the expectations from the ETIB and the random placement hypothesis in these landscapes. This suggests that mechanisms that explain positive PAEs on islands are compensated for by the higher quality of the matrix in fragments. The highly dynamic matrix created by forestry in this boreal setting, even if it is of lower quality for most forest birds than mature forest (Esseen et al. 1997), can, indeed, as suggested by Estade's model (2001), provide resources to the species present in the forest fragments (habitat supplementation hypothesis). Berg (1997) actually observed that several species were able to use the surrounding landscape by increasing the area available to individuals for retrieving resources (Loman and von Schantz 1991). Their results support both the habitat compensation (Norton et al. 2000) and the habitat supplementation (Dunning et al. 1992) hypotheses as explanations for the lower PAEs in fragmented forest landscapes.

Other processes linked to matrix characteristics could partially account for the differences in the density-area relationships that we detected between islands and fragments. In particular, since some forest birds are known to avoid crossing even small forest gaps (Desrochers et al. 1999), water could pose more problems to individual movement and dispersal of forest birds than does a terrestrial environment containing some kind of vegetation (e.g., Machtans et al. 1996). The recolonization of small islands may, therefore, be more difficult than in terrestrial fragments, all other things being equal (dispersal hypothesis; Matthysen et al. 1995). Since small islands may be more subject to stochastic population events, lower connectivity provided by the matrix around islands may induce stronger PAEs compared with terrestrial landscapes. In fragments, small patches may also be better buffered against stochasticity by better connectivity at a landscape

Table 5: Results of standard repeated-measures ANOVA assessing the species-specific differences in the density-area relationship between matrix types (islands vs. fragments)

Source of variation (within-subject effects)	Subset 1			Subset 2		
	df	*F*	*P*	df	*F*	*P*
Matrix type	1	33.23	.001***	1	13.88	.001***
Matrix type × habitat	1	1.89	.18	1	1.18	.29
Matrix type × migration	1	1.09	.30	1	.85	.37
Matrix type × migration × habitat	1	.09	.76	1	.00	.97
Error	48			26		

Note: Matrix type = islands versus fragments; habitat = species main habitat preference (specialists vs. generalists); migration = species migration status (migrant vs. resident). See appendix for species included in different species subsets.

*** $P < .001$.

scale (e.g., rescue effect; Brown and Kodric-Brown 1977) or less sensitive to negative abiotic edge effects (Murcia 1995) associated with a more open matrix (water). In contrast, some negative edge effects, such as increased predation risk, have been specifically associated with small fragments (Saunders et al. 1991; Andrén 1994) on the premise that the matrix could be suitable to potential enemies of forest birds. This would result in predation pressure being higher in small fragments than on small islands. Because we failed to see any PAE in fragment systems, our results, together with those from other studies in boreal landscapes fragmented by forestry (Schmiegelow and Mönkkönen 2002), do not support such negative effects of the matrix on the bird communities.

PAE and Species Biology

Overall differences in PAE between matrix types does not necessarily preclude among-species variation in their density-area responses within a given matrix type. Estades (2001) suggests that variation in species' ability to use resources in the matrix will affect their response to area. Bender et al. (1998) have shown that while forest interior species had decreasing densities with decreasing area, edge species, to the contrary, had increasing densities with decreasing area. In our study, forest specialists, a categorization being analogous to the interior forest species used by Bender et al. (1998), had larger PAEs on islands than did generalists. This suggests that given a low-quality matrix, the densities of forest specialists on the habitat patches may be more affected by area-mediated variation in resource availability and in habitat quality than the densities of forest generalists (Sjöberg and Ericson 1997). The larger declines in PAE from islands to fragments detected for specialists indeed suggest that a decrease in matrix quality is more likely to have a negative effect on the densities of specialists than generalists.

In fragments, we expected generalists to benefit more than specialists from food found in the matrix (Wiens 1989), but fragment area had no consistent overall effect on either group. This suggests that there was little difference between specialists and generalists in their ability to use the resources from the matrix mosaic generated by forestry. This mosaic could be quite similar to the one resulting from natural disturbance in boreal forests with its mixture of stands of different ages (Esseen et al. 1997). Bird species in boreal forests may be well adapted to use or move across heterogeneous landscapes provided that the quality of the matrix is sufficient (Imbeau et al. 2001; Schmiegelow and Mönkkönen 2002). A better understanding of the role of flexibility in resource use or of exploratory behavior (Lefevbre et al. 1996) in the response of a species to matrix structure and quality could bring important insights on the mechanisms behind the bird's response to landscape structure.

Since migrant species are faced with the need for different habitat types during their yearly cycle (Mönkkönen and Welsh 1994; Imbeau et al. 2001), we also expected this group of species to be less sensitive to changes in landscape context than resident species. Our results on this issue proved inconclusive. Although on islands we found residents that had significantly stronger PAEs than migrants, which supports findings by Bender et al. (1998), this association disappeared in the subset of species with more than two estimates per matrix type (table 4). This suggests that the subset of these resident forest species is not a random sample from the total species pool and might not include the most sensitive resident species. The lack of significant PAE differences between matrix types for both migrant and resident birds (tables 5, 6) also suggests that, overall, and at least for the species studied here, matrix effects are perceived in the same way irrespective of migratory habit. Nonsignificant PAEs for both migratory types in fragments are not consistent with the prediction that fragmentation by forestry should affect residents more than migrants (Mönkkönen and Welsh 1994).

Table 6: Results of meta-analysis of standardized mean differences (Hedges's *d*) in species-specific patch area effects (PAE) between matrix types in species subset 2 ($n = 30$)

			Random factor model	
Islands vs. fragments	Hedges's *d* (*n*)	*P*	*Q* (df)	*P*
Overall	.92 ± .24* (30)	<.0001		
Habitat:				
Specialists	1.61 ± .05* (8)	<.00001	3.38 (1)	.05*
Generalists	.67 ± .28 (22)	<.02		
Migration status:				
Migrants	1.21 ± .31* (20)	<.001	2.95 (1)	.079
Residents	.31 ± .44 (10)	.49		

Note: Values are Hedges's $d \pm$ SE; group sample sizes are given in parentheses. One-factor random meta-analytic models were used to assess the role of species habitat preference and species migration status. A positive Hedges's *d* means that for a given species, PAE is stronger on island landscapes than in fragments.

* Estimates differed significantly from 0 at $P < .05$ when using reference *P* values obtained using the Dunn-Sidak method (with reference $P < .01$).

Habitat Loss versus Fragmentation

Habitat fragmentation results first and above all in a drastic reduction of population caused by habitat destruction (Saunders et al. 1991; Andrén 1994). Our results from the islands suggest that area reduction can further negatively affect populations via decreases in individual densities (pure fragmentation effects; sensu Schmiegelow and Mönkkönen 2002). However, our results from fragments suggest that this negative effect of area can be mitigated by the quality of the matrix. Overall, our study supports the contention that the effects of fragmentation are dependent on the landscape context and on how species life histories fit in this context (Mönkkönen and Reunanen 1999); this is consistent with the view that habitat loss, not fragmentation per se, may be the most critical factor for forest bird population in landscapes fragmented by forestry (Schmiegelow and Mönkkönen 2002). In such landscapes, the strong positive PAEs that would be expected if matrix quality were nil (see islands) seems to be compensated by the higher quality of the intervening matrix (Åberg et al. 1995; Norton et al. 2000). That species responses to specific habitat characteristic do vary with landscape and geographic context is not a novel observation (e.g., Villard 1998). However, it emphasizes the need to understand how individual species responses to habitat characteristics are influenced by the landscape context in order to predict the effects of habitat fragmentation on population persistence.

Extending the findings of earlier studies on PAE (e.g., Bender et al. 1998; Connor et al. 2000), we caution against generalization of results on PAE estimates obtained in different landscape contexts because species responses may strongly differ in landscapes with different matrix qualities. Therefore, the patch-oriented approach stemming from the island biogeography theory and continued by the metapopulation theory may fail to capture how species use heterogeneous landscapes and may prevent us from correctly predicting species distributions (Ricketts 2001; Vandermeer and Carvajal 2001). Patch-centred approaches should be based on good knowledge of the habitat use of the focal species (Moilanen and Hanski 1998). In the absence of such information or when species are suspected to be influenced by the quality of the matrix, this factor should be explicitly incorporated into the assessment of population responses to landscape configuration and habitat fragmentation (Gustafson and Gardner 1996; Renjifo 2001).

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APPENDIX

Table A1: Species used in the study

Species	Island PAE	*n*	Fragment PAE	*n*	Habitat preference	Migratory status
Accipiter gentilis[a]	.09	1	.69	1	GEN	MIG
Accipiter nisus[a]	.07	1	.10	1	GEN	MIG
Aegolius funereus		…	.69	1	GEN	RES
Anthus trivialis[a,b]	.39	2	−.02	4	GEN	MIG
Bombycilla garrulus[a]	.4	1	.07	1	SPE	MIG
Bonasia bonasa		…	.00	3	SPE	RES
Carduelis chloris[a]	.13	2	−.64	1	GEN	RES
Carduelis flammea[a]	−.05	1	.22	2	GEN	MIG
Carduelis spinus[a,b]	.24	3	.11	5	GEN	MIG
Certhia familiaris [a,b]	.04	2	.06	4	SPE	RES
Columba palumbus[a,b]	.74	2	−.15	4	GEN	MIG
Corvus corax[a,b]	−.06	2	−.03	3	GEN	RES
Corvus corone[a,b]	−.15	3	.13	2	GEN	RES
Cuculus canorus[a,b]	.47	3	.17	3	GEN	MIG
Dendrocopos major[a]	.74	1	.03	4	SPE	RES
Dryocopus martius[a,b]	.27	2	.14	3	SPE	RES
Emberiza citrinella[a]	.01	1	−.33	2	GEN	RES
Emberiza rustica		…	.09	3	GEN	MIG
Erithacus rubecula[a,b]	.47	2	−.02	4	GEN	MIG
Falco columbarius	.55	1		…	GEN	MIG
Ficedula hypoleuca[a,b]	.17	3	−.13	4	SPE	MIG
Ficedula parva		…	−.15	2	SPE	MIG
Fringilla coelebs[a]	−.11	1	−.06	4	GEN	MIG
Fringilla montifringilla[a]	.03	1	−.08	4	GEN	MIG
Garrulus glandarius[a]	.79	1	−.04	3	GEN	RES
Jynx torquilla[a,b]	.44	2	.15	3	GEN	MIG
Lagopus lagopus	−.08	1		…	GEN	RES
Loxia curvirostra[a,b]	.23	3	.04	3	GEN	MIG
Loxia leucopteris		…	.12	1	GEN	MIG
Loxia pytyopsittacus		…	.14	2	GEN	RES
Luscinia luscinia	.29	1		…	GEN	MIG
Muscicapa striata[a,b]	.25	3	.07	4	SPE	MIG
Oriolus oriolus		…	−.12	1	GEN	MIG
Parus ater[a]	.28	1	−.16	3	GEN	RES
Parus caeruleus[a,b]	.03	2	−.33	2	GEN	RES
Parus cinctus[a]	.76	2	.24	1	SPE	RES
Parus cristatus[a,b]	.36	2	.04	4	SPE	RES
Parus major[a,b]	.09	2	−.05	4	GEN	RES
Parus montanus[a,b]	.28	2	.03	3	GEN	RES
Perisoreus infaustus[a]	.46	1	.30	2	SPE	RES
Phoenicurus phoenicurus[a,b]	.46	2	−.01	4	SPE	MIG
Phylloscopus collybita[a]	−.20	1	−.16	3	SPE	MIG
Phylloscopus sibilatrix[a,b]	.20	2	−.16	3	SPE	MIG
Phylloscopus trochiloides[a]	.43	1	.09	2	SPE	MIG
Phylloscopus trochilus[a,b]	.21	3	−.07	5	GEN	MIG
Pica pica	.38	1		…	GEN	RES
Picoides tridactylus[a]	.41	1	.03	3	SPE	RES
Picus canus	.34	1		…	GEN	RES
Pinicola enucleator[a]	.39	1	.00	1	SPE	MIG
Prunella modularis[a,b]	.21	2	.03	4	GEN	MIG
Pyrrhula pyrrhula[a]	.55	1	−.09	3	SPE	RES

Table A1 (*Continued*)

Species	Island PAE	*n*	Fragment PAE	*n*	Habitat preference	Migratory status
Regulus regulus[a,b]	.32	2	.08	5	SPE	RES
Scolopax rusticola[a,b]	0	2	.09	3	GEN	MIG
Sitta europaea		…	−.14	1	GEN	MIG
Strix uralensis		…	.12	1	SPE	RES
Sylvia atricapilla[a]	.53	2	−.15	1	GEN	MIG
Sylvia borin[a,b]	.25	2	.00	3	GEN	MIG
Sylvia communis	−.14	2		…	GEN	MIG
Sylvia curruca[a,b]	−.31	2	.09	3	GEN	MIG
Sylvia nisoria	.11	1		…	GEN	MIG
Tarsiger cyanurus		…	.09	1	SPE	MIG
Tetrao tetrix[a,b]	−.09	2	−.05	3	GEN	RES
Tetrao urogallus[a]	.22	1	.05	4	SPE	RES
Tringa ochropus[a]	−.08	1	.03	3	GEN	MIG
Troglodytes troglodytes[a]	.32	1	−.14	2	GEN	MIG
Turdus iliacus[a,b]	.02	2	.05	4	GEN	MIG
Turdus merula[a,b]	−.09	2	−.27	2	GEN	MIG
Turdus philomelos[a,b]	.26	2	−.03	5	GEN	MIG
Turdus pilaris[a,b]	−.03	2	−.02	2	GEN	MIG
Turdus viscivorus	…	…	.02	3	SPE	MIG

Note: Includes information on weighted mean patch area effect (PAE) estimates per matrix type (island vs. fragments) and the number of studies per matrix type in which the species was available. For species in which only one PAE estimate (*r*) was available, the original estimate is shown. Species were also categorized according to habitat preference (specialists [SPE] vs. generalists [GEN]) and migratory status (migrants [MIG] vs. residents [RES]).

[a] Species included in subset 1 (for which there was at least one PAE estimate for both matrix types; $n = 52$).

[b] Species included in subset 2 (for which there were two or more than two PAE estimates per matrix type; $n = 30$).

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