Composition of an avian guild in spatially structured habitats supports a competition–colonization trade-off

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Assuming better colonization abilities of inferior competitors, the competition–colonization trade-off (CCTO) is one of the hypotheses that explains spatial variation of species composition in fragmented habitats. Whereas this mechanism may structure some plant and insect communities, ecologists have failed to document its operation in other natural systems, and its generality has been questioned. We combined fieldwork and published data to study the composition of a guild of passerines (*Parus cristatus*, *Parus montanus*, *Parus ater* and *Regulus regulus*) inhabiting 10 landscapes that differed in the amount of forest habitat. The species were ordered in a stable, well-defined competitive hierarchy, and the dispersal ability of each species was inversely correlated with its position in this hierarchy. In functionally continuous landscapes, superior competitors occupied most fragments and all guild members commonly occurred. The relative incidences of superior and inferior competitors were reversed, and differences amplified, in landscapes where patches were physically (distance) or functionally (matrix hardness) isolated. We found little support for two competing hypotheses, namely reduced habitat quality in isolated patches and lower abundance of a keystone predator (*Glaucidium passerinum*) in fragmented landscapes. We concluded that the CCTO offered the most probable explanation for variation in the composition of the *Parus* guild across landscapes.

Keywords: community structure; habitat fragmentation; isolation thresholds; keystone predator; landscape processes

1. INTRODUCTION

The effects of local interactions and landscape processes on community structure are highly interrelated (Chesson 2000). One prominent manifestation of this synergy is the existence of trade-offs between life-history traits of a species (Kneitel & Chase 2004). In particular, the competition–colonization trade-off (CCTO) states that relative ability of a species to compete in a habitat patch is inversely related to its ability to colonize empty patches. The CCTO predicts that, above some isolation threshold, habitat patches will contain inferior, but not superior, competitors. While this trade-off has been documented in some plant and insect communities (Amarasekare 2003; Turnbull *et al.* 2005), many other studies on plants and animals have failed to support it empirically (e.g. McCarthy *et al.* 1997; Jakobsson & Eriksson 2003). Yet, investigations on the generality of the trade-off, by detecting its operation in natural systems, have been encouraged (Amarasekare 2003).

Predation is a competing hypothesis to explain reduced species richness in isolated habitat patches. If the colonization ability of a keystone predator (KP) is lower than that of the superior competitor among its prey species, then a fraction of patches without a predator may not contain some of the competitively inferior prey species (Shurin & Allen 2001). A further alternative hypothesis is

that reduced habitat quality in isolated patches explains the absence of some species (Harrison & Bruna 1999).

In this paper, we examine the incidence of species within a guild of passerines in landscapes that differ in the spatial structure of their forest habitat with a twofold aim. We first show that patterns of guild composition are consistent with the operation of a CCTO. Second, we examine whether spatial variation in guild composition can be better explained by the patch quality or the KP hypotheses.

(a) Mechanisms of competition and relative mobility

In the boreal forests of the western Palaearctic, the *Parus* guild includes four species (Suhonen *et al.* 1992): crested tit (*Parus cristatus*); willow tit (*Parus montanus*); coal tit (*Parus ater*); and goldcrest (*Regulus regulus*). These species depend on mature coniferous forest (above 60 years of age) for foraging and breeding, and most populations are sedentary.

Guild members compete for food and predator-safe sites. Aviary experiments suggest that coal tits are more efficient foragers than their *Parus* congeners (Alatalo & Moreno 1987; Kothbauer-Hellmann & Winkler 1997). However, field studies have shown that interspecific dominance follows body size, with clear competitive superiority of the two larger over the two smaller species (crested tit > willow tit >> coal tit > goldcrest; Alatalo *et al.* 1986). Small species are excluded from predator-safe sites at the microhabitat level through interference. The dominance hierarchy

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remains stable in a variety of conditions (Alerstam *et al.* 1974; Hogstad 1978; Alatalo *et al.* 1986), i.e. each species experiences a spatially homogeneous competitive environment (Amarasekare 2003).

The two superior competitors show high site tenacity and intraspecific territoriality all year around (Ekman 1979a). This trait is accompanied by relatively short dispersal distances. At the end of the dispersal period, Ekman (1979a) found 87 and 58% first-year willow tits and crested tits, respectively, within 3 km of their natal site. For willow tits, 89% of natal dispersal events across continuous forest were within 0.8 km (Ekman 1979b). Mean dispersal distances for two different populations of willow tit were 0.8 (Haftorn 1997) and 1.7 km (Orell *et al.* 1999). By contrast, only 10% of young coal tits recruited within a radius of 1 km (Dietrich *et al.* 2003). The occasional migratory habits of the two subordinate species also suggest higher mobility (Alerstam *et al.* 1974; Hildén 1982). Furthermore, in a study of gap crossing between stands of mature forest, the dominant tit species did not venture into open habitats, whereas 12% of coal tits spontaneously crossed clearcuts and agricultural land (Rodríguez *et al.* 2001). Therefore, the separation of mature forest stands by open areas may enlarge the differences in isolation by distance between superior and inferior competitors within the guild.

(b) Predictions

Within landscapes, the CCTO hypothesis predicts that distant habitat patches will be occupied only by poor competitors. Patch isolation has a physical component (between-patch distances exceed modal or maximum dispersal distances) and a qualitative component (behavioural reluctance to enter inhospitable matrix). Matrix permeability varies across landscapes, and the CCTO hypothesis predicts lower incidence of superior competitors as matrix hardness increases. Landscapes containing lower proportions of forest feature greater separation between forest remnants (Gustafson & Parker 1992; Andrén 1994). The CCTO hypothesis predicts that the incidence of superior competitors, but not that of inferior competitors, will decrease in fragmented landscapes where little mature forest is left.

Kullberg & Ekman (2000) have explicitly proposed the KP mechanism for the tit species of the *Parus* guild in the following terms. The coal tit is assumed to be the superior competitor owing to its higher foraging efficiency and its higher potential for population growth (larger clutch sizes and double broods). Coexistence with other tit species occurs only when coal tit density is depressed, primarily by selective predation by pygmy owls (*Glaucidium passerinum*). In the absence, or under low levels of pygmy owl predation, and despite its inferiority in the interference component of competition, coal tits build large populations, deplete food and outcompete larger tits. Since the outcome of competition depends upon predation intensity, tit species experience a spatially heterogeneous competitive environment (Amarasekare 2003). The KP hypothesis predicts that (i) coal tit density and pygmy owl density should be negatively correlated, (ii) in the absence of pygmy owl, coal tit density should be higher than where the owl occurs, and (iii) in the absence of pygmy owl, the coal tit should be the only tit species, or at least its density should be higher than the density of the other tit species.

2. MATERIAL AND METHODS

(a) Field study

We determined the incidence of birds in forest fragments in two landscapes of south-central Sweden. The forest landscape (450 km²; 59°40' N, 15°30' E) contained about 90% managed forest, distributed in even-age stands of up to 500 ha. In the agricultural landscape (2000 km²; 59°30' N, 15°20' E), forest covered 60% of the area, interspersed with farmland. Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominated the forest in both landscapes. Given the age distribution of forests (Ståhl 2004), the proportions of mature forest in the agricultural and forest landscapes were 20 and 30%, respectively.

We wanted to detect differences in species mobility while minimizing the possible effect of landscape attributes on the settlement component of colonization. Therefore, we selected forest patches that varied in isolation, but fulfilled the minimum requirements of size and quality for the birds (composition and density of tree species). Mean territory size for the guild members varies between 9 and 24 ha of coniferous forest (Ekman 1979a; Hildén 1982; Suhonen *et al.* 1992). We selected 35 patches of mature forest larger than 20 ha in the agricultural landscape and 20 patches of mature forest in the forest landscape. Using maps and aerial photographs, we measured patch size and the distance to the nearest continuous forest block (agricultural landscape) or to the closest stand older than 35 years and larger than the focal patch (forest landscape). In each patch, we measured tree species composition and the number of stems at six sampling plots with a relascope, and calculated the percentage of each tree species (Sillerström & Forshed 1985). At these plots, we also estimated the per cent cover in the shrub layer (0–1 m) within a 5 m radius, an attribute that enhances habitat quality for insectivorous birds (Jokimäki & Huhta 1996). In 1993, we recorded the occurrence of each bird species in forest patches by walking slowly along 3–4 line transects 100 m apart between 06.00 and 10.00 in April when birds' singing activity was at its peak. Sampling effort was proportional to patch size. We used logistic regression to assess the effects of distance, landscape type, the interaction between distance and landscape type, patch size and predictors of patch quality on the probability of occurrence of the four species.

(b) Species mobility

We examined the pattern of ringed bird recoveries in Sweden for the four species. Ringing recovery distances result from different processes, from local movements through natal dispersal to large-scale migration, but could provide at least a coarse representation of interspecific differences in general mobility. Species with lower mobility were expected to show higher recapture rates in the same or close ringing stations and shorter recovery distances than more mobile species.

(c) Literature review

We searched the Zoological Record and ISI Web of Science databases (Institute for Scientific Information, Thomson, Philadelphia, PA) for papers describing bird distribution in the coniferous forests of Fennoscandia and the Baltic region. We examined 131 articles and selected those reporting the occurrence of two or more species of the *Parus* guild in sets of forest fragments or islands. When original data were provided, we recalculated the incidence of each species in a subset of the largest patches (larger than 8 ha; larger than 20 ha if five or more patches above this size were surveyed).

Table 1. Incidence of species belonging to the *Parus* guild in different systems of forest patches. (The original results of this study (systems 1 and 2) and results reported in the literature (systems 3–10) are shown. Patch attributes are type (F, forest fragment; I, island) and size (range of patch sizes). Landscape attributes include %forest (the percentage of mature coniferous forest in the landscape), matrix (matrix type; Y, forest less than 60 years of age and clearcuts; F, farmland; S, seawater), distance (range of distances to the nearest permanently occupied source), gap (maximum gap width between contiguous pairs of islands separating the focal archipelago from the nearest source), and *n* (number of patches; for published studies, number of patches larger than 8 ha for which incidence was recalculated).)

system	patch attributes		landscape attributes					incidence				source
	type	size (ha)	%forest	matrix	distance (km)	gap (km)	<i>n</i>	crested tit	willow tit	coal tit	goldcrest	
1	F	5–42	30	Y	0.05–0.6	1.0	20	0.95	0.90	0.80	0.95	this study, forest
2	F	21–61	20	F	0.2–1.3	1.3	35	0.31	0.71	1.00	1.00	this study, agricultural
3	F	8–101	42	Y	<1.0	1.0	10	1.00	1.00		1.00	Haila <i>et al.</i> (1987)
4	I	38–582	35	S	10.0–17.3	1.2	5	1.00	1.00	0.60	1.00	Haila (1981)
5	I	29–582	35	S	10.0–15.0	1.2	14	0.46	0.98	0.47	0.71	Haila <i>et al.</i> (1983)
6	F	8 ^a	20	F	0.5 ^a	1.0	24 ^b	0.63	0.33	0.92	1.00	Berg (1997)
7	I	11–233	16	S	4.2–10.9	1.3	9	0.11	0.11		0.89	Martin (1983)
8.1 ^c	I	20–347	29	S	0.1–2.5	0.1	24	0.13	0.13		0.58	Martin & Lepart (1989)
8.2 ^c	I	20–233	20	S	2.5–8.0	1.3	33	0.09	0.09		0.45	Martin & Lepart (1989)
8.3 ^c	I	20–105	9	S	8.0–11.3	1.3	24	0.00	0.12		0.67	Martin & Lepart (1989)
9	I	22–1241	—	S	0.2–44.0	44.0	16	0.38		1.00	1.00	Wiggins & Møller (1997)
10 ^d	I	220–314000	—	S	4.0–85.0	85.0	9	0.44	0.44	1.00		Kullberg & Ekman (2000)

^a Mean value.

^b Data for 12 forest fragments and 12 sampling plots of similar size in continuous forest could not be separated.

^c Archipelago divided into inner (less than 2.5 km to the mainland; system 8.1), middle (2.5–8 km; system 8.2) and outer sections (more than 8 km; system 8.3).

^d Eight isolated islands or archipelagoes in the Baltic region.

The proportion of mature coniferous forest in the landscape or archipelago, the matrix type and the distance of forest patches to the nearest continuous forest block or to the continent (assumed to hold permanent populations of the species recorded in the focal landscape) were taken from the papers. If not reported, we used a geographical information system and digital land cover maps (CORINE Land Cover and Global Land Cover) to measure these variables in landscape samples (more than 50 km²) encompassing the area surveyed (Hansen *et al.* 2000). When there were additional islands between the focal archipelago and the mainland, we measured the gap between each pair of adjacent islands on satellite images (Google Earth, <http://earth.google.com>). When possible, we also reanalysed the relationship between bird occurrence and landscape attributes for our subsets of large patches using generalized linear models (GLMs) with binomial errors.

(d) Predator and prey densities

We obtained breeding density of pygmy owl and tit species in Sweden from Hagemeyer & Blair (1997). Density classes were the log₁₀, truncated to the integer, of the estimated number of breeding pairs within 50 km Universal Transverse Mercator (UTM) cells. On the Global Land Cover digital map, we measured the proportion of mature coniferous forest in circular, cell-centred landscape samples covering 40% of the cell area. As pygmy owls depend on mature forest, we added the proportion of forest as a covariate in GLMs that examined the effect of pygmy owl density on tit density.

(e) Comparison between hypotheses

We used log-linear path models to compare the relative ability of the CCTO and KP hypotheses to explain spatial variation in the occurrence of superior competitors. Log-linear path models consist of a series of logit models for a set of categorical endogenous variables (Goodman 1973), and are analogous with structural equation models in that they assume causality (expressed as conditional probabilities) and establish the relative strength of direct and indirect effects (Vermunt 1997a). Since the willow tit is widespread in Sweden, we restricted our analyses to the occurrence of the crested tit. Based on exploratory GLMs, we categorized the proportion of mature forest in a factor with three levels (less than 0.1, 0.1–0.5, greater than 0.5). Using the LEM software (Vermunt 1997b), we specified a full path model that considers the direct effect of forest cover in the landscape (CCTO prediction) and its indirect effect through the density of pygmy owls and coal tits (KP prediction; figure 3). *A priori*, we defined several submodels nested within the full path model, fitted them to the data, and chose that with the minimum AIC value as the most parsimonious (Burnham & Anderson 2002).

3. RESULTS

(a) Field study: incidence

In the forest landscape, all species were present in most fragments (table 1), and the incidence of superior competitors was higher than in the agricultural landscape, although this difference was significant only for crested tit ($\chi^2_c = 18.30$, $p < 0.001$; willow tit, $\chi^2_c = 1.62$, $p = 0.203$;

Figure 1. The probability of occurrence in forest patches of individual species (thin lines), and of co-occurrence of the complete guild (thick line), as a function of the distance to (a) the nearest patch of larger size in a forest landscape or to (b) a continuous forest block in an agricultural landscape.

table 1). Conversely, in the forest landscape, the incidence of inferior competitors was lower than in the agricultural landscape, although the effect was significant only for coal tit ($\chi^2 = 4.92$, $p = 0.027$; goldcrest, $\chi^2 = 0.09$, $p = 0.764$; table 1). In the forest landscape, all four species coexisted in 70% of fragments, whereas the entire guild occurred only in 23% of fragments in the agricultural landscape ($\chi^2 = 9.94$, $p = 0.002$).

(b) Field study: response to isolation

For crested tits, patch occupancy almost did not vary with distance to the nearest larger fragment in the forest landscape, but decreased markedly with the distance to continuous forest in the agricultural landscape (figure 1; effect of the interaction landscape type $\times$ distance, $G = 29.14$, $p < 0.001$). The response of willow tit to isolation was qualitatively similar to that of crested tit, but of lower intensity (figure 1; interaction landscape type $\times$ distance, $G = 5.61$, $p = 0.061$). The response of inferior competitors to isolation was quite different. The effect of distance to the nearest larger forest stand or continuous forest block did not affect their occurrence (coal tit, $G = 0.36$, $p = 0.549$; goldcrest, $G = 0.05$, $p = 0.823$). Moreover, the interaction landscape type $\times$ distance did not explain any additional deviance relative to a model containing only the main effects.

The probability of finding the four species in the same patch decreased with the distance to the nearest larger forest stand or continuous forest block, and this effect was more marked in the agricultural landscape than in the forest landscape (figure 1). The effects of distance

Table 2. Rates of recapture and recovery distances of the *Parus* guild members in Sweden during an 11-year period. (Data after Bird Ringing Centre annual reports, 1978–97; Swedish Museum of Natural History, Stockholm.)

species	ringed birds	recaptures (per 1000 birds)	recovery distance (km)	
			mean	maximum
crested tit	1490	4.03	<10	<10
willow tit	16 135	1.67	63	438
coal tit	36 146	1.30	91	850
goldcrest	364 335	0.99	490	2322

($G = 12.23$, $p < 0.001$) and of the interaction landscape type $\times$ distance ($G = 6.46$, $p = 0.011$) on the probability of co-occurrence of all species were significant, but the effect of landscape type alone was not ($G = 1.50$, $p = 0.221$).

(c) Field study: effect of other variables

The fact that goldcrest (in both landscapes) and coal tit (in the agricultural landscape) were found in all, or nearly all, forest fragments indicates that they did not respond to variation in either patch size or patch quality. For other species–landscape combinations, and for all models including landscape type and distance, the effects of patch size, tree composition, tree density and cover of the shrub layer did not significantly explain additional deviance in the incidence of any bird species (logistic regression, $p > 0.1$). Patch size was independent of distance to the nearest larger forest stand or continuous forest block ($r = 0.060$; power of the correlation: $1 - \beta = 0.936$). The proportion of conifers, a measure of available protective cover, did not significantly decrease with that distance either ($r = -0.247$, d.f. = 53, $p = 0.153$; $1 - \beta = 0.999$).

(d) Species mobility

Crested tit and willow tit showed higher recapture rates and shorter recovery distances than coal tit and goldcrest (table 2). Recapture rates and recovery distances showed a perfect inverse correlation across species (table 2).

(e) Patterns of incidence in different landscapes

We found 14 papers reporting the distribution of species of the *Parus* guild in patches of mature coniferous forest. Half of the studies were undertaken in forest fragments, the other half on islands. We excluded six of these sources because the frequency of occupancy could not be calculated, all patches were less than 20 ha, or only one bird species occurred regularly. From the remaining eight studies, we selected 168 fragments or islands (86% of them larger than 20 ha) where bird occurrence was reported. Island systems predominated in the final sample (table 1). We also included the two landscapes presented in this study.

We identified two distinct patterns of bird occupancy. In four systems, the incidence of the dominant bird species was similar to the incidence of subordinates (an ‘even’ distribution pattern), and occupancy rates were 0.46 or more for all species (systems 1 and 3–5 in table 1). In the other systems, the occupancy rates of dominant species were consistently lower than those of subordinate species (an ‘uneven’ distribution pattern), and the incidence of dominants was typically less than 0.4 (systems 2 and 6–9

Figure 2. The observed (symbols) and predicted (lines) incidence of (a) superior and (b) inferior competitors in landscapes with different proportions of mature forest.

in table 1). Interestingly, we found no study reporting high occupancy rates only for dominant bird species.

The mean ($\pm$ s.d.) proportion of forest in the landscape for systems showing an even distribution pattern (0.36 ± 0.05) was significantly higher than the mean for samples with an uneven distribution pattern (0.19 ± 0.07 ; Mann-Whitney $U=0$, $n_1=4$, $n_2=6$, $p<0.001$). The distance to the nearest permanent source of colonists greatly varied across systems (table 1). However, the distance to the source did not discriminate between the two patterns of relative bird occupancy ($U=9$, $n_1=4$, $n_2=6$, $p=0.522$).

The incidence of crested tit and willow tit increased significantly with the proportion of mature forest in the landscape (logistic regression; Wald's test, $Z=4.11$, $p=0.003$; and $Z=4.35$, $p=0.002$, respectively, figure 2). Conversely, the incidence of coal tit decreased significantly with the proportion of mature forest in the landscape ($Z=3.75$, $p=0.030$), whereas there was no significant effect on goldcrests ($Z=0.96$, $p=0.370$, figure 2).

Considering only the terrestrial systems, patch dispersion in a matrix of young forests (systems 1 and 3, table 1) produced an even pattern of bird distribution, whereas we found an uneven pattern in landscapes with forest fragments embedded in a harder farmland matrix (systems 2 and 6). The subdivision of the Sipoo archipelago (system 8, table 1) into three subsets of islands at increasing distances from the mainland, accompanied with increasing dispersion of the remaining forested habitat, allowed a comparison of species response to isolation keeping constant regional density. The incidence of the inferior competitor (goldcrest) was high in all the three subsets, while the incidence of the best

competitor (crested tit) decreased from 0.13 in the inner islands to zero in the outer islands (table 1).

Among the 53 islands considered by Wiggins & Møller (1997), 16 were larger than 20 ha (table 1). All of them were occupied by coal tit and goldcrest irrespective of their distance to the mainland. The incidence of crested tit decreased with the distance to the mainland (log-transformed; logistic regression, $G=6.65$, $p=0.010$), the number of gaps between potential stepping stones ($G=6.01$, $p=0.014$) and the width of the largest gap between contiguous stepping stones (log-transformed; $G=3.89$, $p=0.048$). These three predictors of isolation were correlated. The model including distance predicts a decreasing probability of crested tit occurrence from 0.86 to 0.20 for islands 0.2 and 6.0 km away from the mainland, respectively.

Kullberg & Ekman (2000) reported the distribution of the three tit species in nine large islands of the Baltic region. All species coexisted in four islands, whereas the coal tit was the only species on the remaining islands (table 1). The authors found that neither island area nor distance to the mainland discriminated between islands occupied only by the coal tit and the other islands. However, we observed that the islands where the dominant tit species occurred were connected to the mainland with stepping stones, and the islands occupied only by the coal tit were not. In the first group of islands, we counted at most five gaps wider than 1 km between contiguous stepping stones, and the largest gap was 4.52 km wide. Maximum gap width had a significant positive effect on the probability that the coal tit occurred alone in the focal island (logistic regression; $G=5.23$, $p=0.022$). For superior competitors, the model predicted a decreasing probability of occurrence from 0.92 to 0.09 in islands whose maximum gap width increased from 3.0 to 6.0 km, respectively.

(f) Density of pygmy owl and tits

Pygmy owls were absent from 25 out of the 200 cells that cover Sweden. The coal tit was seldom the only tit species in the absence of pygmy owl (three out of 25 cells, or 12%). Contrary to the prediction of the KP hypothesis, the probability of the coal tit occurring as the only tit species was higher in cells containing the pygmy owl than in those without the pygmy owl regardless of whether the proportion of mature forest was included ($G=8.58$, $p=0.003$) or not ($G=12.80$, $p<0.001$) as a covariate in the logistic regression model. On the other hand, the probability that coal tit occurred as the only tit species was inversely related to the proportion of mature forest in the landscape sample (logistic regression; $G=5.49$, $p=0.019$), supporting the CCTO hypothesis. The willow tit showed a widespread distribution in Sweden (98.5% of cells) irrespective of the occurrence of competitors or the predator. Hence, we examined whether coal tits were able to exclude only crested tits in the absence of pygmy owls. Within the coal tit range in Sweden, the KP hypothesis predicted that crested tit should always occur in the presence of pygmy owl, but it was absent in 16% of 159 cells occupied by the predator. Likewise, crested tit should not occur in the absence of pygmy owl, but it was present in 44% of nine cells without the predator (goodness of fit $\chi^2=639$, d.f.=3, $p<0.001$).

Table 3. Parsimony of path models of crested tit occurrence in 50 km UTM cells over Sweden ($n=200$). (Causal relationships are expressed as conditional probabilities. Δ_{AIC} : difference between AIC values of the fitted model and the most parsimonious model (whose $\Delta_{AIC}=0$). Acronyms: occurrence of crested tit (cr_o), and pygmy owl (py_o); abundance of coal tit (co_a) and pygmy owl (py_a); proportion of mature coniferous forest in the landscape (for).)

model	hypothesis	Δ_{AIC}
<i>(a) occurrence of pygmy owl included in the full model</i>		
1. $for, cr_o for$	CCTO	0.0
2. $py_o, co_a py_o, cr_o co_a$	KP	17.5 ^a
3. $for, py_o for, co_a py_o, co_a for, cr_o co_a, cr_o for$	CCTO + KP	345.6
4. $for, py_o for, co_a py_o, cr_o co_a, cr_o for$	CCTO + KP	346.6
<i>(b) abundance of pygmy owl included in the full model</i>		
1. $for, cr_o for$	CCTO	0.0
2. $py_a, co_a py_a, cr_o co_a$	KP	151.6 ^a
3. $for, py_a for, co_a py_a, co_a for, cr_o co_a, cr_o for$	CCTO + KP	464.1
4. $for, py_a for, co_a py_a, cr_o co_a, cr_o for$	CCTO + KP	465.0

^a Effect opposed to KP prediction.

Mean density of coal tit ($\pm$ s.d.) in cells with the pygmy owl (4.59 ± 0.88 , $n=159$) was not significantly higher than that in cells without the pygmy owl (4.89 ± 1.17 , $n=9$; $U=594$, $p=0.359$). In sympatry, pygmy owl density had a positive effect on coal tit density either when the proportion of mature forest was included as a covariate (multiple regression; $r=0.573$, $F_{2,156}=38.03$, $p<0.001$; $1-\beta=0.999$) or when it was not ($r=0.568$, $F_{1,157}=74.57$, $p<0.001$; $1-\beta=0.999$). Pygmy owl density was positively correlated with forest cover ($r=0.293$, $p<0.001$; $1-\beta=0.977$), but coal tit density was not ($r=0.094$, $p=0.239$; $1-\beta=0.777$).

The indirect positive effect of pygmy owl occurrence or abundance on the presence of crested tit through depression of coal tit abundance, as predicted by the KP hypothesis, was not supported by path models (figure 3). Models including indirect effects showed a poorer fit than those including only direct effects (table 3). The sign and significance of the relationships were consistent in the full model (figure 3) and any of the submodels presented in table 3. The most parsimonious models of crested tit occurrence were those specifying a direct effect of mature forest cover (table 3).

4. DISCUSSION

The quantitative and qualitative components of patch isolation influenced the structure of the *Parus* guild. We argue that this effect was consistent with the operation of a CCTO for three reasons. First, the incidence of superior competitors decreased with decreasing cover of mature forest, with increasing separation between forest patches and with increasing hardness of the intervening matrix. Second, the incidence of inferior competitors was insensitive to habitat dispersion in landscapes with inhospitable matrix, at least within the range of values in the studied landscapes. Third, in isolated patches, apparently beyond the reach of superior competitors, inferior competitors tended to occupy all available

Figure 3. Full path model of crested tit occurrence in cells of a 50 km UTM grid over Sweden ($n=200$). Signs after 'exp' denote whether the expected relationships were positive or negative according to the CCTO hypothesis, the KP hypothesis or the assumption that pygmy owl is a poor disperser (PD; Kullberg & Ekman 2000). Signs after 'obs' indicate significant relationships found in logistic regression and log-linear path analysis.

patches, whereas their incidence was lower in landscapes widely populated by superior competitors.

(a) Incidence of superior competitors

Physical isolation strongly affected the incidence of superior competitors in fragmented landscapes. First, incidence drops nonlinearly with decreasing forest cover, as does proximity to the nearest habitat patch (Gustafson & Parker 1992). This is the expected response to habitat fragmentation of habitat specialists with poor colonization abilities, and the threshold we found in the proportion of remaining habitat (20–30%, figure 2) is quantitatively similar to those reported for several birds and mammals (Andrén 1994). Second, within landscapes, we found a negative effect of distance to the nearest source of colonists on the probability of patch occupancy. Relying on a weak effect of distance to the mainland, Kullberg & Ekman (2000) discarded interspecific differences in colonization ability among tits as an explanation for the absence of superior competitors in some islands. Our reanalysis showed that the occurrence of these poor colonists was restricted to islands connected to the mainland by smaller islands that could act as stepping stones, and that functional isolation might be better described by the maximum gap between contiguous islands. Third, distance thresholds in landscapes with a hard matrix were strikingly similar to maximum dispersal distances reported in the literature. In the two published datasets we could model, a sea gap of 6 km indicated the position of a threshold above which the occurrence of superior competitors was unlikely. For the crested tit, Lens & Wauters (1996) reported a maximum natal dispersal distance of 5 km across open land, whereas for the crested tit and willow tit, Ekman (1979a) reported 6.5 km across forest land. Martin & Lepart (1989) found that the density of crested tit and willow tit in the mainland adjacent to the Sipoo archipelago (systems 7 and 8; table 1) was very low, which may explain the low incidence of these species in a set of seemingly accessible islands.

Superior competitors occupied a large fraction of patches in the forest landscapes we examined. These and other landscapes subjected to forestry are characterized by a homogenization of stand sizes, with mean values well below 25 ha, and by a stable distribution of stands ages, with mature stands covering one-third of the forest land (Esseen *et al.* 1997; Ståhl 2004). With this distribution of stand age and size, most pairs of contiguous mature stands

lie within 1 km. Younger stages of forest succession cover the gaps and function as a permeable matrix for crested tit and willow tit (Rodríguez *et al.* 2001). Therefore, mature patches are probably accessible to a large fraction of dispersing individuals. In other words, superior competitors might perceive managed forests as functionally continuous landscapes.

For a given separation of mature stands, the incidence of the crested tit decreased significantly when farmland matrix replaced young forests. Matrix hardness may amplify the negative effect of distance, as has been documented in other taxa (Åberg *et al.* 1995; Ricketts 2001). This is consistent with the remarkable reluctance of the crested tit (and willow tit) to fly across clearcuts or farmland gaps just a few hundred metres wide (Rodríguez *et al.* 2001). For the crested tit, we found a discrepancy between the isolation thresholds in agricultural landscapes (approx. 0.5 km) and some archipelagos (less than 1.2 km; Haila 1981; Wiggins & Møller 1997). Differences in predation risk between matrix types might explain such discrepancy. Reluctance to enter open habitats with high predation risk by small raptors is one important mechanism explaining the avoidance of open land by tits (Rodríguez *et al.* 2001). Sea gaps free of raptors might be a more permeable matrix than equally narrow farmland gaps.

The crested tit ranks highest in the competitive dominance hierarchy and was the most sensitive species to the spatial dispersion of mature forest. Accordingly, the crested tit seems to be the least mobile species in the guild, judging from the ringing recovery data. The willow tit exhibited a response qualitatively similar to that of the crested tit, yet attenuated (systems 2, 5 and 8; table 1), in agreement with its lower rank in the dominance hierarchy and its slightly better colonization capabilities.

At least two alternative hypotheses could explain the absence of superior competitors in highly isolated patches of mature forest. First, habitat might lose quality if isolated (Harrison & Bruna 1999), and bird absence could be attributed to difficulties in settling in an unsuitable habitat rather than to restricted mobility. Internal patch quality may decrease due to edge effects and/or distance effects via lower colonization rate of arthropod prey. However, the absence of the crested tit and willow tit we found in isolated patches was unlikely to have been due to a potential reduction in habitat quality because: (i) patch size was independent of isolation, and the minimum patch size was often larger than the mean home range size of a multispecies flock (14.7 ha; Suhonen *et al.* 1992); by restricting the analysis to patches larger than 20 ha, we actually removed the positive effects of area on the occurrence of some species (Wiggins & Møller 1997), (ii) no variable of internal quality entered the incidence models, (iii) protective cover within patches did not decrease with isolation, (iv) arthropod density may vary little for fragments larger than 1 ha (Ozanne *et al.* 2000), (v) arthropod species from the adjacent agricultural matrix may also invade the forest patch (Gurdebeke *et al.* 2003), and (vi) forest fragmentation may not alter the foraging niches of species in the *Parus* guild (Nour *et al.* 1997).

The second alternative was the KP hypothesis (Kullberg & Ekman 2000). Predictions derived from this hypothesis received little support. The presence of the pygmy owl, even in high numbers, was not associated with a reduced density, or absence of the coal tit. Rather, the

densities of predator and prey were positively correlated. Therefore, we did not observe the population depression of the coal tit predicted by the KP hypothesis. Moreover, we found no evidence of a deterministic exclusion of the crested tit by the coal tit in the absence of the pygmy owl. Not surprisingly, path models of crested tit occurrence that considered the explicit mechanism of the KP hypothesis were less parsimonious than models representing the predictions of the CCTO hypothesis.

(b) Incidence of inferior competitors

Beyond some isolation threshold, forest patches were occupied only by inferior competitors. Coal tit and goldcrest were able to inhabit large but distant islands (Alerstam *et al.* 1974; Martin & Lepart 1989; Wiggins & Møller 1997; Kullberg & Ekman 2000) that superior competitors conceivably could not reach. Inferior competitors were also widespread in forest patches embedded in a hard agricultural matrix. Their incidence was affected little by the distance of forest fragments to the nearest source of colonists. Indeed, inferior competitors may colonize very small relict forest fragments in open farmland (Loman & von Schantz 1991). The general pattern is congruent with the hypothesis of higher dispersal capabilities in these species.

(c) Guild composition

Within trees, interference produces spatial segregation of species in the *Parus* guild (Suhonen 1993). At larger spatial scales, complete deterministic competitive exclusion does not apply to this guild. The rule in continuous coniferous forest is local coexistence of dominant and subordinate species (Hogstad 1978; Alatalo *et al.* 1986; Suhonen *et al.* 1992). Competition, however, entails a cost for subordinate species. Ekman (1986) suggested that mortality of subordinate species may be consistently higher in the presence of dominant species due to restricted access to predator-safe sites, which may translate into negative growth rates and eventual extinction (Kullberg & Ekman 2000). Thus, in patches with dominant species, local populations of coal tit and goldcrest might persist as sinks. Effective competitive exclusion could be regarded as a stochastic process, i.e. one of the possible outcomes of the suboptimal conditions experienced by inferior competitors. Consistently, coal tits were absent from some patches in our forest landscape, where the incidence of dominant species was high. Subordinate species did not occupy every fragment in other landscapes where apparently mature coniferous forest was functionally continuous for dominants (cf. Haila 1981; Haila *et al.* 1983). Indeed, the incidence of the coal tit decreased with the proportion of mature forest in the landscape and the concurrent increasing incidence of superior competitors. Recently, Amarasekare & Nisbet (2001) have proposed a theoretical framework whose predictions resemble our empirical findings: inferior competitors may occur as sink populations coexisting locally with superior competitors.

In landscapes with many isolated patches, the guild was locally unsaturated, often because one of the two superior competitors was lacking. Inferior competitors spread in these landscapes free of dominants. Among others, Amarasekare (2003) has advocated the search of natural systems that consider the CCTO as a mechanism explaining

variation in community composition in spatially structured habitats. The *Parus* guild may conform to such a system. We reviewed studies highly heterogeneous in scope, none of which was specifically directed to test the operation of the CCTO. Our field study constitutes an exception that provides associative indirect evidence. However, an explicit experimental approach to demonstrate the existence of the trade-off in the *Parus* guild remains to be undertaken.

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REFERENCES

- Åberg, J., Jansson, G., Swenson, J. E. & Angelstam, P. 1995 The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia* **103**, 265–269. (doi:10.1007/BF00328613)
- Alatalo, R. V. & Moreno, J. 1987 Body size, interspecific interactions, and use of foraging sites in tits (*Paridae*). *Ecology* **68**, 1773–1777. (doi:10.2307/1939868)
- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1986 Interspecific competition and niche changes in tits (*Parus* spp.): evaluation of nonexperimental data. *Am. Nat.* **127**, 819–834. (doi:10.1086/284527)
- Alerstam, T., Nilsson, S. G. & Ulfstrand, S. 1974 Niche differentiation during winter in woodland birds in southern Sweden and island of Gotland. *Oikos* **25**, 321–330. (doi:10.2307/3543950)
- Amarasekare, P. 2003 Competitive coexistence in spatially structured environments: a synthesis. *Ecol. Lett.* **6**, 1109–1122. (doi:10.1046/j.1461-0248.2003.00530.x)
- Amarasekare, P. & Nisbet, R. M. 2001 Spatial heterogeneity, source–sink dynamics, and the local coexistence of competing species. *Am. Nat.* **158**, 572–584. (doi:10.1086/323586)
- Andrén, H. 1994 Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**, 355–366.
- Berg, Å. 1997 Diversity and abundance of birds in relation to forest fragmentation, habitat quality and heterogeneity. *Bird Study* **44**, 355–366.
- Burnham, K. P. & Anderson, D. R. 2002 *Model selection and multimodel inference*, 2nd edn. New York, NY: Springer.
- Chesson, P. 2000 Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–366. (doi:10.1146/annurev.ecolsys.31.1.343)
- Dietrich, V. C. J., Schmoll, T., Winkel, W. & Lubjuhn, T. 2003 Survival to first breeding is not sex-specific in the coal tit (*Parus ater*). *J. Ornithol.* **144**, 148–156. (doi:10.1046/j.1439-0361.2003.02062.x)
- Ekman, J. 1979a Coherence, composition and territories of winter social groups of the willow tit *Parus montanus* and the crested tit *P. cristatus*. *Ornis Scand.* **10**, 56–68. (doi:10.2307/3676345)
- Ekman, J. 1979b Non-territorial willow tits *Parus montanus* in late summer and early autumn. *Ornis Scand.* **10**, 262–267. (doi:10.2307/3676070)
- Ekman, J. 1986 Tree use and predator vulnerability of wintering passerines. *Ornis Scand.* **17**, 261–267. (doi:10.2307/3676836)
- Esseen, P. A., Ehnström, B., Ericson, L. & Sjöberg, K. 1997 Boreal forests. *Ecol. Bull.* **46**, 16–47.
- Goodman, L. A. 1973 The analysis of multidimensional contingency tables when some variables are posterior to others: a modified path analysis approach. *Biometrika* **60**, 179–192. (doi:10.1093/biomet/60.1.179)
- Gurdebeke, S., de Bakker, D., Vanlanduyt, N. & Malfait, J. P. 2003 Plans for a large regional forest in eastern Flanders (Belgium): assessment of spider diversity and community structure in the current forest remnants. *Biodivers. Conserv.* **12**, 1883–1900. (doi:10.1023/A:1024162910018)
- Gustafson, E. J. & Parker, G. R. 1992 Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecol.* **7**, 101–110. (doi:10.1007/BF02418941)
- Haftorn, S. 1997 Natal dispersal and winter flock formation in the willow tit, *Parus montanus*. *Fauna Norv. Ser. C* **20**, 17–35.
- Hagemeijer, W. J. M. & Blair, M. J. (eds) 1997 *The EBCC atlas of European breeding birds: their distribution and abundance*. London, UK: T & AD Poyser.
- Haila, Y. 1981 Winter bird communities in the Åland archipelago: an island biogeographic point of view. *Holarctic Ecol.* **4**, 174–183. (doi:10.1111/j.1600-0587.1981.tb00995.x)
- Haila, Y., Järvinen, O. & Kuusela, S. 1983 Colonization of islands by land birds: prevalence functions in a Finnish archipelago. *J. Biogeogr.* **10**, 499–531. (doi:10.2307/2844607)
- Haila, Y., Hanski, I. K. & Raivio, S. 1987 Breeding bird distribution in fragmented coniferous taiga in southern Finland. *Ornis Fennica* **64**, 90–106.
- Hansen, M., de Fries, R., Townshend, J. R. G. & Sohlberg, R. 2000 Global land cover classification at 1 km resolution using a decision tree classifier. *Int. J. Remote Sens.* **21**, 1331–1365. (doi:10.1080/014311600210209)
- Harrison, S. & Bruna, E. 1999 Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* **22**, 225–232. (doi:10.1111/j.1600-0587.1999.tb00496.x)
- Hildén, O. 1982 Winter ecology and partial migration of the goldcrest *Regulus regulus* in Finland. *Ornis Fennica* **59**, 99–122.
- Hogstad, O. 1978 Differentiation of foraging niche among tits, *Parus* spp., in Norway during winter. *Ibis* **120**, 139–146.
- Jakobsson, A. & Eriksson, O. 2003 Trade-offs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. *Evol. Ecol.* **17**, 233–246. (doi:10.1023/A:1025526903281)
- Jokimäki, J. & Huhta, E. 1996 Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. *Ornis Fennica* **73**, 97–113.
- Kneitel, J. M. & Chase, J. M. 2004 Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.* **7**, 69–80. (doi:10.1046/j.1461-0248.2003.00551.x)
- Kothbauer-Hellmann, R. & Winkler, H. 1997 Prey detection in two tit species, *Parus ater* and *P. cristatus*. *Ethology* **103**, 339–349.
- Kullberg, C. & Ekman, J. 2000 Does predation maintain tit community diversity? *Oikos* **89**, 41–45. (doi:10.1034/j.1600-0706.2000.890105.x)
- Lens, L. & Wauters, L. A. 1996 Effects of population growth on crested tit *Parus cristatus* post-fledging settlement. *Ibis* **138**, 545–551.

- Loman, J. & von Schantz, T. 1991 Birds in a farmland: more species in small than in large habitat island. *Conserv. Biol.* **5**, 176–188. (doi:10.1111/j.1523-1739.1991.tb00122.x)
- Martin, J. L. 1983 Impoverishment of island bird communities in a Finnish archipelago. *Ornis Scand.* **14**, 66–77. (doi:10.2307/3676255)
- Martin, J. L. & Lepart, J. 1989 Impoverishment in the bird community of a Finnish archipelago: the role of island size, isolation and vegetation structure. *J. Biogeogr.* **16**, 159–172. (doi:10.2307/2845090)
- McCarthy, M. A., Lindenmayer, D. B. & Drechsler, M. 1997 Extinction debts and risks faced by abundant species. *Conserv. Biol.* **11**, 221–226. (doi:10.1046/j.1523-1739.1997.95381.x)
- Nour, N., Matthysen, E. & Dhondt, A. A. 1997 Effects of habitat fragmentation on foraging behaviour of tits and related species: does niche space vary in relation to size and degree of isolation of forest fragments? *Ecography* **20**, 281–286. (doi:10.1111/j.1600-0587.1997.tb00372.x)
- Orell, M., Lahti, K., Koivula, K., Rytönen, S. & Welling, P. 1999 Immigration and gene flow in a northern willow tit (*Parus montanus*) population. *J. Evol. Biol.* **12**, 283–295. (doi:10.1046/j.1420-9101.1999.00030.x)
- Ozanne, C. M. P., Speight, M. R., Hambler, C. & Evans, H. F. 2000 Isolated trees and forest patches: patterns in canopy arthropod abundance and diversity in *Pinus sylvestris* (Scots Pine). *Forest Ecol. Manage.* **137**, 53–63. (doi:10.1016/S0378-1127(99)00317-5)
- Ricketts, T. H. 2001 The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* **158**, 87–99. (doi:10.1086/320863)
- Rodríguez, A., Andrén, H. & Jansson, G. 2001 Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* **95**, 383–396. (doi:10.1034/j.1600-0706.2001.950303.x)
- Shurin, J. B. & Allen, E. G. 2001 Effects of competition, predation, and dispersal on species richness at local and regional scales. *Am. Nat.* **158**, 624–637. (doi:10.1086/323589)
- Sillerström, E. & Forshed, N. 1985 *Grundbok för skogsbrukarens*. Falköping, Sweden: Skogsstyrelsen.
- Ståhl, G. (ed.) 2004 *Skogsdata 2004. Sveriges officiella statistik*. Umeå, Sweden: Institutionen för Skoglig Resurshushållning och Geomatik, SLU.
- Suhonen, J. 1993 Predation risk influences the use of foraging sites by tits. *Ecology* **74**, 1197–1203. (doi:10.2307/1940490)
- Suhonen, J., Alatalo, R. V., Carlson, A. & Höglund, J. 1992 Food resource distribution and the organization of the *Parus* guild in a spruce forest. *Ornis Scand.* **23**, 467–474. (doi:10.2307/3676678)
- Turnbull, L. A., Manley, L. & Rees, M. 2005 Niches, rather than neutrality, structure a grassland pioneer guild. *Proc. R. Soc. B* **272**, 1357–1364. (doi:10.1098/rspb.2006.3585)
- Vermunt, J. K. 1997a *Log-linear models for event histories*. Thousand Oaks, CA: Sage Publications.
- Vermunt, J. K. 1997b *LEM: a general program for the analysis of categorical data*. Tillburg, The Netherlands: Department of Methodology and Statistics, Tillburg University.
- Wiggins, D. A. & Möller, A. P. 1997 Island size, isolation, or interspecific competition? The breeding distribution of the *Parus* guild in the Danish archipelago. *Oecologia* **111**, 255–260. (doi:10.1007/s004420050233)