Qualitative geographical variation in interspecific interactions

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We explore geographical variation in the density relationship between potential competitor forest bird groups, resident *Parus* spp. and migrant *Fringilla* spp., across Europe using published bird census results. In addition, we summarized results from three experimental studies from northern Europe on their density associations. Based on anticipated changes in the relative intensity of positive and competitive interactions we predicted a unimodal density association between *Parus* and *Fringilla*: at low and intermediate densities the two groups are positively associated (positive interaction), whereas high densities promote interspecific competition. In central Europe where densities are high, densities were unimodally related to each other. In northern and southern Europe linear and positive associations appeared. Experimental studies provided consistent support for positive interspecific interactions in the north. The results suggest that species interactions may indeed vary in relation to the density of potential competitor and switch from positive to negative along environmental gradients.

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The basic question in ecology is to explain the variation of species' abundances in natural communities. A wide array of different biotic and abiotic factors have been detected (see e.g., Menge and Sutherland 1987, Huston 1994, Rosenzweig 1995) but ever since Clements (1916), the role of biotic interactions in structuring communities has been of utmost interest to ecologists. Direct and indirect trophic (predation, parasitism, disease, apparent competition) and non-trophic (competition, mutualism) interactions among organisms have been shown to either limit or enhance species' abundances in communities (Menge and Sutherland 1987, Huston 1994, Rosenzweig 1995).

For logistical and inferential reasons, species interactions are usually studied on a local scale. This obviously has resulted in a commonly held view that these interactions are somewhat fixed and do not show much spatial or temporal variability. According to the niche concept, relationships with heterospecific individuals depend on the overlap in niche dimensions in relation to the available resources. Resource levels, however, may vary in space or time (e.g., Wiens 1977). There is a growing body of evidence suggesting that variation in abiotic conditions, such as climate and physical stress, can switch interactions from competition to facilitation in plant and animal communities (e.g. Callaway et al. 2002, Bruno et al. 2003). Change in species interactions may also be linked to large-scale variation in conditions. Leonard (2000) showed that a switch in intertidal species interactions was due to a latitudinal variation in thermal stress and predation. Therefore, variation in environmental conditions is potentially an important factor affecting the outcome of interspecific interactions (see also Dunson and Travis 1991).

Temperate and boreal breeding bird communities occur under a wide range of abiotic conditions that may affect community structure. A well-known geographic pattern in breeding bird communities is the increase in the proportion of migrant birds of the total species and pair numbers with increasing seasonality

(MacArthur 1959, Herrera 1978, Morse 1989). According to Herrera (1978) such a pattern is because the carrying capacity of the environment during the severe season (winter) regulates the size of resident species populations below the levels of summer time carrying capacity, which in turn affects the number of migrants that may enter the habitats. In other words, due to the diffuse competition between residents, migrants fit in the breeding assemblages in high numbers only where resident populations are regulated to a low level (see also Morse 1989). According to this explanation, competition between resident and migrant birds is a driving force in habitat selection of migrants resulting in inverse numeric relationships.

This hypothesis does not take into account the possibility that species interactions may qualitatively change along environmental or geographical gradients. In central Europe, where the proportion of residents of the numbers of breeding birds is high, some studies have found competition between residents and migrants (Reed 1982, Gustafsson 1987, Sasvári et al. 1987). By contrast, in northern Europe, where the proportion of residents is low, the presence of residents has been shown to increase the species' number and abundance of migrants in local communities (Mönkkönen et al. 1990, Timonen et al. 1994, Forsman et al. 1998, Thomson et al. 2003, see also Elmberg et al. 1997). This pattern in the north has been suggested to stem from heterospecific attraction, a concept coined by Mönkkönen et al. (1990) to describe the habitat selection process where individuals prefer selecting habitat patches already occupied by individuals of another species. It was hypothesized that particularly migrant birds may use earlier established residents as cues to profitable breeding sites in conditions where direct and accurate assessing of the quality of available patches is difficult, therefore resulting in a positive association. Thus, there seems to be qualitative variation in species interactions along a geographical gradient.

Variation in environmental conditions is one potential reason causing geographical variation in interspecific interactions. Forsman and Mönkkönen (2002) showed that both the density of residents and migrants decreased with increasing latitude in Europe but that the resident density declined much more steeply, suggesting that changing factors (e.g., winter climate) limit resident populations to a low level. This would in turn leave more room in communities in the north for migrants and make heterospecific attraction a profitable habitat selection strategy. The density and proportion of residents in communities (Forsman and Mönkkönen 2002) increases southwards, which may decrease the benefits of heterospecific attraction and make competitive interactions more likely, until the point is reached when competitive interactions prevail and the density association between residents and migrants turns negative. In other words,

during habitat selection, migrants may start to avoid habitat patches with high resident densities. This suggests that there might be a geographical north-to-south gradient of interactions between residents and migrants. More generally, we expect to see a unimodal relationship between resident and migrant densities along increasing density of residents, where positive interactions prevail at low densities and negative interactions at high densities relative to resources.

We tested the prediction of the non-linear association between the densities of potential competitors at three different spatial scales. First, we examined how densities of *Fringilla* spp., the chaffinch *Fringilla coelebs* L. and the brambling *F. montifringilla* L., vary on the scale of whole Europe relative to the density of resident titmice (*Parus* spp.) based on analyses of published bird census data. Second, these data were split into three geographic regions according to the major forest biomes to see if patterns differed between the Mediterranean, central and northern Europe. Third, we summarized information from three published experimental studies, carried out in Finland, where titmice densities have been manipulated and the numerical response of *Fringilla* spp. to this variation monitored (Mönkkönen et al. 1990, Forsman et al. 1998, Thomson et al. 2003) to support the conclusion that the density associations in the census data were at least partly due to interspecific interactions.

Material and methods

Fringilla species were selected as the focal species for a number of reasons. Firstly, they can be considered as a single species (for our purposes) as they are ecologically very similar in their habitats and behaviour (Mikkonen 1985, Khlebosolov and Zakharov 1997) with bramblings replacing chaffinches in northern boreal forests across an overlap zone in central Fennoscandia (Järvinen and Väisänen 1979). Chaffinch is a widespread species and very numerous all over Europe from the Mediterranean to central Fennoscandia (Mönkkönen 1994) making a geographical scale analysis feasible. Even though the chaffinch is not strictly a migratory bird in the southwestern parts of its range, it colonises breeding habitats about one week later than *Parus* spp. e.g., in southern England in the first week of May (Newton 1964) as opposed to late April in titmice species (Dunn 1976). In winter, chaffinches largely desert the breeding habitats and frequent different kinds of semi-open habitats.

Secondly, *Fringilla* species are habitat generalists, and therefore less constrained by the structural and floristic composition of the habitat than habitat specialists. Third, they are ecologically very similar to titmice, and particularly to the great tit (*Parus major*), with respect to habitat requirements, foraging behaviour and diet (Reed 1982, Mönkkönen et al. 1996). Indeed, in certain

environmental conditions, the chaffinch and the great tit have been shown to compete by inhabiting mutually exclusive territories and responding aggressively to each other's calls (Reed 1982) while in other conditions occurring in territories overlapping more than expected by chance alone (Reed 1982, Timonen et al. 1994).

We collected published (and one unpublished) bird census data originating from censuses carried out in mature forests i.e. excluded data from early successional forests and open habitats. We used tree height (>20 m) and/or tree age (average >100 yr) as criteria. From each data set we extracted the total density (pairs 10 ha^{-1}) of titmice and the *Fringilla* spp. Censuses covered Europe from Great Britain to west Russia and from the Mediterranean basin to Finnish Lapland. Censuses were made using four different census methods: mapping (Enemar 1959), line transect (Järvinen and Väisänen 1983), point count (Blondel et al. 1970) and single visit study plot (Palmgren 1930) methods. Different census methods have been shown to provide consistent density estimates (Helle and Fuller 1988, Forsman and Mönkkönen 2002, Mönkkönen and Forsman 2003) and we therefore pooled censuses over methods.

Trend surface analysis is one of the most powerful and easiest tools of spatial pattern analysis (Legendre and Legendre 1998). Here we first modeled *Fringilla* spp. density as a nonlinear function of the geographic coordinates of the study sites using second order polynomial regression, i.e. we included latitude, longitude, their squared terms and interaction into the model. Secondly, titmice density with its squared term was entered into the model to test for the predicted unimodal relationship between *Fringilla* spp. and titmice densities. In multiple regression, parameters are estimated controlling for the effects of other variables in the model, and thus allowing us to test if titmice density has any independent explanatory power after controlling for geographical patterns in *Fringilla* spp. abundance (see Freckleton 2002). To end up with as simple model as possible we used backward elimination of terms as recommended by Legendre and Legendre (1998).

These census data were also divided into three latitudinal groups corresponding to major forest biomes in Europe. The southernmost data (below 45°N) all come from the Mediterranean area, where winter climate is benign and titmice densities are high but variable. Central European data (46–59°N) represent the temperate deciduous forest zone with mild winters and high titmice and chaffinch densities. Data from northern Europe (60°N or above) represent the boreal biome with harsh winters and low titmice densities (Table 1). For each region separately we reran the regression modeling described above.

Three independent experimental studies (Mönkkönen et al. 1990, Forsman et al. 1998, Thomson et al. 2003, in south-central, northern and central Finland, respec-

Table 1. The number of census data (N) used in this study as well as averages (Standard Deviation) of titmice and *Fringilla* spp. densities (pairs 10 ha^{-1}) for the whole Europe data and for each region separately.

	N	Titmice (SD)	*Fringilla* (SD)
Europe	107	8.56 (8.59)	8.10 (5.47)
Mediterranean	13	13.05 (11.45)	5.97 (4.46)
Central Europe	56	12.14 (7.99)	10.12 (5.56)
Northern Europe	39	2.02 (2.12)	5.96 (4.59)

tively) have been carried out to test for numerical response of *Fringilla* spp. to manipulated titmice densities during breeding season. Unfortunately, no comparable experiment on these species groups has been done further south in Europe (see Discussion for experiments on other species). The studies of Mönkkönen et al. (1990) and Forsman et al. (1998) involved a pair-wise reciprocal treatment where titmice where either completely removed or their densities were augmented. Thomson et al. (2003) created a continuum of titmice densities and regressed *Fringilla* spp. densities against it. We summarized the results of these experiments by combining the probabilities from tests of significance (see Sokal and Rohlf 1995). The test statistics, $-2\Sigma \ln p_i$, where p_i stands for probability of accepting H_0 in the original test, follows χ^2-distribution with 2k degrees of freedom (k is the number of separate tests).

Results

We found that at the scale of the whole of Europe, *Fringilla* densities were unimodally related to latitude and longitude, as well as to titmice densities as predicted (Table 2, Fig. 1). The highest density of *Fringilla* spp. occurs at mid-latitude (ca 55°N), at mid-longitude (31°E) and at intermediate titmice density (28 pairs 10 ha^{-1}; Fig. 1). The coefficient of determination of the model (0.30) is a very high value considering all the possible factors affecting *Fringilla* densities (year-to-year variation, forest type, etc.).

The patterns, when analyzing the three regions separately, differed as expected from each other. In northern Europe, a positive linear relationship with titmice density (Fig. 1) but a convex latitudinal pattern emerged (Table 2). It is notable that in northern Europe, the model explained a major part of variation in *Fringilla* densities ($r^2 = 0.66$). In central Europe, where the sum of titmice and *Fringilla* densities was the highest (Table 1), there was a significant unimodal relationship between titmice and *Fringilla* (the chaffinch in that area) densities (Fig. 1), and also an increase in *Fringilla* density towards east (Table 2). In central Europe, *Fringilla* densities were positively related to titmice densities below titmice density of 21 pairs 10 ha^{-1}, and above it negatively. In the Mediterranean region, a

Table 2. Final regression models for *Fringilla* density against titmice density (TD) and geographic variables (LATI = latitude; LONGI = longitude). Parameters and coefficients are only given for the final model after the backward elimination of terms. r^2 represents adjusted coefficient of determination of the final model.

	B	t	p
Whole Europe: $F_{6,100} = 8.55$, $p < 0.001$, $r^2 = 0.30$			
Constant	−78.35	3.14	0.002
TD	0.599	3.18	0.002
TD^2	−0.011	2.25	0.026
LATI	3.00	3.18	0.002
$LATI^2$	−0.027	3.13	0.002
LONGI	0.200	2.14	0.035
$LONGI^2$	−0.003	2.09	0.040
Northern Europe: $F_{3,35} = 26.02$, $p < 0.001$, $r^2 = 0.66$			
Constant	645.1	2.10	0.043
TD	1.341	4.09	< 0.001
LATI	−19.79	2.08	0.045
$LATI^2$	0.152	2.07	0.046
Central Europe: $F_{3,51} = 4.68$, $p = 0.006$, $r^2 = 0.17$			
Constant	0.692	0.261	0.796
TD	0.888	2.97	0.005
TD^2	−0.021	2.48	0.016
LONGI	0.262	3.02	0.004
Mediterranean, $F_{1,11} = 5.70$, $p = 0.036$, $r^2 = 0.28$			
Constant	2.999	1.85	0.092
TD	0.227	2.39	0.036

positive linear relationship between titmice and *Fringilla* densities emerged (Fig. 1) with no geographic trends (Table 2).

Of the three experiments, two showed a statistically significant positive response by *Fringilla* spp. to augmented titmice density (Mönkkönen et al. 1990, Thomson et al. 2003) and in the third the trend was the same (Forsman et al. 1998). Combining probabilities yielded a value of test statistics of 20.4, which is significant at p < 0.01 with 6 degrees of freedom. This suggests that the results of the three experiments are consistently providing support for the hypothesis that increased titmice densities result in increased *Fringilla* spp. densities.

Discussion

Our results provide support for the predicted unimodal density relationship along a gradient of densities of putative competing species groups. At low density the two species groups varied in parallel but at high density they showed negative association. Particularly strong support for the predicted non-linearity between titmice and *Fringilla* densities was found in central European forest bird data where both titmice and chaffinches may reach substantially high densities. Because geographic variation was controlled for, this quadratic relationship does not stem from spatial patterns in densities. The summary of local experiments from northern Europe also fell in line with the prediction that positive associations should prevail in the north where densities are invariably low (see Table 1).

The predicted gradient in interspecific interactions, i.e. competitive interactions at high and positive interactions at low density, is one potential mechanism for the non-linear density pattern we observed. This could take place during the breeding habitat selection of *Fringilla* spp. The results of the local experiments indicate that, at low tit densities, experimentally increased titmice density result in parallel increase in *Fringilla* spp. density. A negative density association at high tit densities can result from the avoidance, during habitat selection by the chaffinch, of habitat patches with high densities of potential competitors. Perception of potential competitors and aggression and avoidance has indeed been shown to occur (Martin and Martin 2001).

We cannot rule out the possibility that the unimodal pattern results from partially different habitat requirements between the *Fringilla* and titmice (parallel preferences in some part of the environmental gradient but contrasting preference in some other), but this seems implausible because both the *Fringilla* and the most common titmice species are forest habitat generalists. However, the experiments indicate that the positive density association cannot be solely explained by parallel habitat requirements. Another alternative mechanism could be nest predation (Martin 1988). Assuming that tit density correlates positively with productivity of the habitats, and therefore total density of birds, increasing bird densities can result in proportionally high nest predation rates among the most abundant species. From the point of view of the chaffinch, it would be beneficial to avoid such high nest predation risk areas, which in turn would lead to decreasing densities. However, our focal species do not share the same nesting sites titmice being hole-nesters and *Fringilla* open cup-nesters, and nest predators are likely to be different as well.

The unimodal curve for central Europe (and also for all European data) attains to its maximum at a titmice density of 21 pairs 10 ha^{-1} above which negative density relationships prevailed. In central and southern Europe such high densities are still quite common (see Fig. 1). Thomson et al. (2003) created a continuum of titmice densities to explicitly test the prediction of non-linear density relationship between resident (titmice) and migrant birds, but found a strong linear positive relationship. They concluded that titmice densities should have been much higher (well above 10 pairs 10 ha^{-1}) than they were in their study areas (max. 5.6 pairs 10 ha^{-1}) for a non-linear relationship to emerge between titmice and chaffinch densities. Titmice densities > 10 pairs 10 ha^{-1} did not exist in our census data (Fig. 1) and are likely to be rare in northern European forests. Therefore, we may conclude that competitive interactions between titmice and *Fringilla* are unlikely in boreal environments. The regional scale results of the present study considering northern Europe further support this conclusion, as we found no indication of negative relationship between
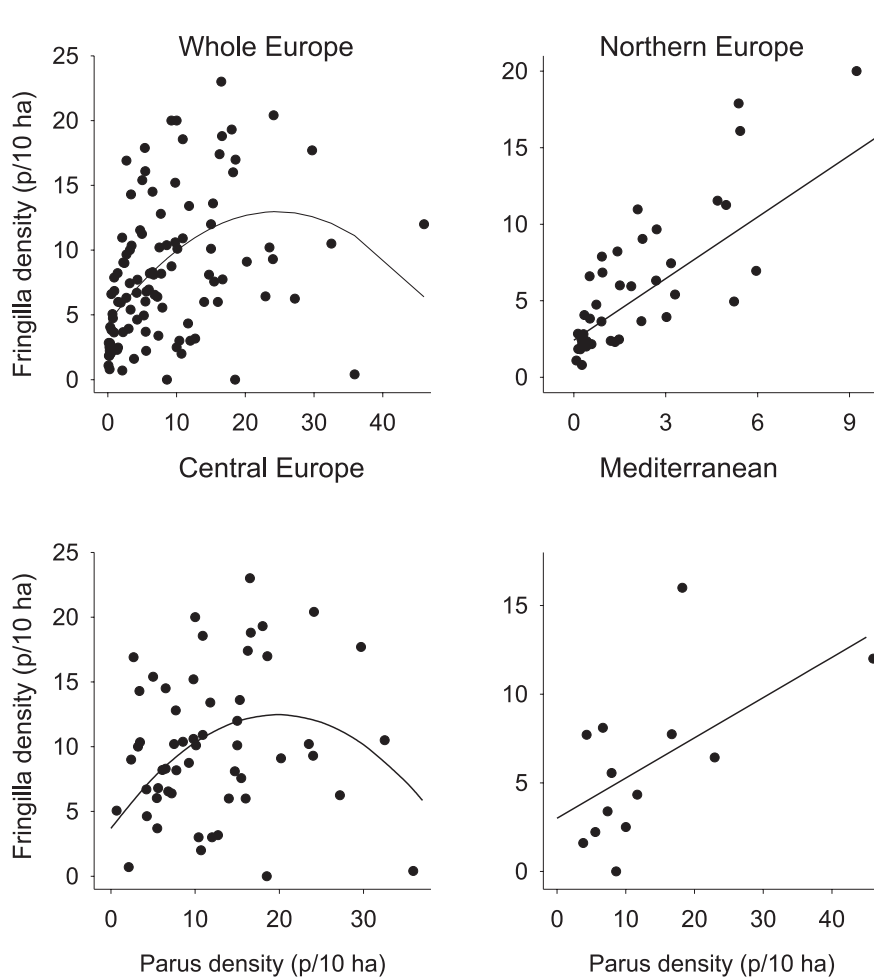
Fig. 1. *Fringilla* spp. density in relation to titmice density for the whole European data, and separately for Mediterranean, central European and northern European data. Lines are fitted using parameters in Table 2.

titmice and *Fringilla* densities. It further seems that both locally ($r^2 = 0.64$ in Thomson et al. 2003) and regionally (Table 2) titmice density is a major determinant of *Fringilla* densities in northern forests.

Unfortunately there is only very little local scale evidence outside Fennoscandia to support either positive or negative interactions between titmice and chaffinches. Reed (1982) showed that competition between chaffinches and great tits affects their spatial distribution on Scottish islands where the two species occupy non-overlapping territories. When chaffinches were experimentally removed great tit expanded their territories to areas formerly occupied by chaffinches. On mainland Scotland, however, the two species territories overlapped more than expected by chance alone possibly indicating positive interactions.

Some studies have focused on the effects of titmice on the collared flycatcher *Ficedula albicollis* in central European temperate forests. In Sasvári et al. (1987) data, the annual fluctuation in density of the collared flycatcher tended to correlate negatively with the com-

bined density of the great and blue tit ($r = -0.45$, $p = 0.059$). In this non-experimental study, titmice density was on average about 19 pairs 10 ha^{-1}, and highest densities were up to 27 pairs 10 ha^{-1}. This negative density relationship may be because of competition over nest-boxes but Sasvári et al. (1987) also observed a negative effect of titmice on flycatchers' breeding performance. Likewise, Gustafsson (1987) observed that experimentally increased titmice densities had a negative impact to collared flycatcher fitness parameters, and in his study areas titmice densities were up to 27 pairs 10 ha^{-1}. It is worth stressing that studies suggesting competitive interactions in temperate forests have dealt with nest-box breeding populations and that in such cases resident densities may be unnaturally high compared to natural densities (e.g. Wesolowski et al. 1987). Nevertheless, these studies indicate that competitive interactions between resident titmice and migrants are possible. Our correlative approach suggests the same applies between titmice and the *Fringilla*, but only at high densities of titmice.

By and large, both experimental and empirical results were according to the predicted unimodal pattern. A non-linear response to variability in competitor's density can be understood as an interspecific Allee-effect. The Allee-effect (Allee et al. 1949) for single species populations predicts that population growth or individual fitness reaches its peak at intermediate population density. This is because at low density, mating success or communal protection against predators, for example, is drastically reduced while at high density intraspecific competition intensifies, both resulting in lowered fitness (Stephens and Sutherland 1999, Courchamp et al. 1999). The Allee-effect can be extended to interspecific interactions, in which case individual fitness or population growth rate is a non-linear, unimodal function of the density of putative competitors. With increasing density of the competitor the benefits from social aggregations (see e.g., Morse 1977, Pulliam and Millikan 1982) become gradually outweighed by the negative effects of interspecific competition. This scenario was suggested by our experiment (Forsman et al. 2002) in which experimentally augmented titmice densities resulted in fitness benefits in the pied flycatcher *Ficedula hypoleuca* in terms of earlier nesting and larger broods compared to that of areas devoid of titmice. Moreover, flycatchers seemed to actively choose the company of titmice and it was shown that those flycatcher pairs that selected to nest in close vicinity to titmice nests were able to raise better quality fledglings (higher mass, longer wings) than pairs nesting further away.

It is important to realize that the outcomes of interspecific interactions are highly variable. We do not want to give an impression that positive interactions, such as heterospecific attraction and the fitness benefits from such aggregations, would always be important and intensive. Such interactions are more likely among habitat generalist species, such as titmice and *Fringilla* that are not intimately dependent on specific structural or floristic components of their habitat.

Our understanding of how animals are distributed in their environment is largely built on the concept that the most important factor affecting the suitability of any particular site in the environment is the presence of competitors (Tregenza 1995). The basis for much of this work has been the ideal free distribution theory, which is based on the assumed biological realism that fitness related characters are always negatively affected by the increasing density of putative competitors in a patch (see e.g. Parker and Sutherland 1986). We emphasize the need to widen the view so that the whole spectrum of potential interactions will become incorporated into this work. For any progress in our understanding of distribution of populations and community organization, it is important to acknowledge that species interactions may also qualitatively vary and switch from positive to negative along environmental gradients.

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