ORIGINAL ARTICLE

Patterns of density, diversity, and the distribution of migratory strategies in the Russian boreal forest avifauna

Russell Greenberg*, Anna Kozlenko†, Matthew Etterson‡ and Thomas Dietsch§

Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC, USA

ABSTRACT

Aim Comparisons of the biotas in the Palaearctic and Nearctic have focused on limited portions of the two regions. The purpose of this study was to assess the geographic pattern in the abundance, species richness, and importance of different migration patterns of the avifauna boreal forest of Eurasia from Europe to East Asia as well as their relationship to climate and forest productivity. We further examine data from two widely separated sites in the New World to see how these conform to the patterns found in the Eurasian system.

Location Boreal forest sites in Russia and Canada.

Methods Point counts were conducted in two to four boreal forest habitats at each of 14 sites in the Russian boreal forest from near to the Finnish border to the Far East, as well as at two sites in boreal Canada. We examined the abundance and species richness of all birds, and specific migratory classes, against four gradients (climate, primary productivity, latitude, and longitude). We tested for spatial autocorrelation in both dependent and independent variables using Moran's I to develop spatial correlograms. For each migratory class we used maximum likelihood to fit models, first assuming uncorrelated residuals and then assuming spatially autocorrelated residuals. For models assuming unstructured residuals we again generated correlograms on model residuals to determine whether model fitting removed spatial autocorrelation. Models were compared using Akaike's information criterion, adjusted for small sample size.

Results Overall abundance was highest at the eastern and western extremes of the survey region and lowest at the continent centre, whereas the abundance of tropical and short-distance migrants displayed an east–west gradient, with tropical migrants increasing in abundance in the east (and south), and short-distance migrants in the west. Although overall species richness showed no geographic pattern, richness within migratory classes showed patterns weaker than, but similar to, their abundance patterns described above. Overall abundance was correlated with climate variables that relate to continentality. The abundances of birds within different migration strategies were correlated with a second climatic gradient – increasing precipitation from west to east. Models using descriptors of location generally had greater explanatory value for the abundance and species-richness response variables than did those based on climate data and the normalized difference vegetation index (NDVI).

Main conclusions The distribution patterns for migrant types were related to both climatic and locational variables, and thus the patterns could be explained by either climatic regime or the accessibility of winter habitats, both historically and currently. Non-boreal wintering habitat is more accessible from both the western and eastern ends than from the centre of the boreal forest belt, but the

*Correspondence: Russell Greenberg, Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC 20008, USA.
E-mail: greenbergr@nzp.si.edu
†Present address: 3760 Eastway Road, South Euclid, OH 44118, USA.
‡Present address: US Environmental Protection Agency, Mid Continent Ecology Division, 6201 Congdon Boulevard, Duluth, MN 55804, USA.
§Present address: Center for Tropical Research, University of California Los Angeles, Los Angeles, CA 90095-1469, USA.*

tropics are most accessible from the eastern end of the Palaearctic boreal zone, in terms of distance and the absence of geographical barriers. Based on comparisons with Canadian sites, we recommend that future comparative studies between Palaearctic and Nearctic faunas be focused more on Siberia and the Russian Far East, as well as on central and western Canada.

INTRODUCTION

Increasingly, a biogeographical perspective has been brought to the classic ecological question of what determines the distribution and abundance of organisms. Broad comparisons between regions, or even entire continents, can illuminate processes and patterns that cannot be discerned in more local studies. However, such broad comparisons may themselves be limited because of the restricted geographic scope of data sets. Such is the problem that faces students of the distribution of faunas in temperate forests. Although considerable research has focused on describing patterns and hypothesizing processes underlying the distribution of temperate-zone faunas in both the Nearctic and the Palaearctic, these analyses have often suffered from incomplete coverage, particularly of the Palaearctic east of Europe (Haila *et al.*, 1987; Morse, 1989; Mönkkönen, 1994; Mönkkönen & Viro, 1997; Böhning-Gaese, 2005).

For example, a number of studies have been published in the past few decades that explore patterns of the species richness and abundance of birds with different migration patterns (residents, within-Temperate Zone, and tropical migrants in Palaearctic and Nearctic forests: Herrera, 1978; Helle & Fuller, 1988; Newton & Dale, 1996; Mönkkönen & Forsman, 2005). Most of the studies, particularly those that attempt inter-continental comparisons, are based on studies of the Western Palaearctic (Europe) and the eastern Nearctic. Studies that look at avifaunal relationships between different portions of the boreal forest within each continent are few and are generally qualitative analyses based on regional species lists (Wiens, 1975; Erskine, 1977; Preobrajenskaya, 1982; Mönkkönen & Helle, 1989; Haila & Järvinen, 1990).

The boreal forest is a compelling biome for comparative studies of the composition and structure of faunal assemblages (Haila & Järvinen, 1990; Mönkkönen & Welsh, 1994). The biome is distributed in an almost continuous band across the northern continental masses and consists of relatively homogeneous, low-diversity stands of conifers, birches, and aspens throughout. Within each continent, the boreal forest belt extends north-west to south-east, so that equivalent climatic zones and associated vegetation tend to be at higher latitudes in the western portions (Haila & Järvinen, 1990). Although boreal forests show important spatial variation, they arguably form the most comparable band of vegetation both across and between continents. Because of the broad distribution and similar composition of boreal forests, the study of the distribution of organisms across the boreal zone provides an excellent opportunity to evaluate the roles that climate, physical geography, and historical process have in shaping local assemblages found at different ends of continents and on different continents.

Boreal forests are both floristically undiverse and climatically harsh, often experiencing extreme differences in temperature between summer and winter. Because of this, most animal groups must adapt to the extreme seasonality in climate and resource availability. Birds are often surprisingly abundant and diverse in boreal habitats because of their mobility and their ability to exploit the seasonal summer peak in arthropod abundance, while avoiding the cold harsh winters. It is not surprising, therefore, that previous studies have often focused on the distribution and abundance of species with differing migratory strategies.

Ecologists have attempted to understand the factors that control the abundance, diversity, and ecological composition of bird assemblages through the analysis of divergence and convergence. Studies of divergence examine how particular shared taxa respond to variation in climate, geography, and history. Research in convergence examines how largely unrelated faunas respond to habitats that are similar in climate and geography. The boreal forest affords opportunities to use and integrate both approaches. Despite this, studies of factors that determine the abundance, diversity and composition of boreal forest avifaunas are few.

In this paper, we use a data set of simple quantified surveys from across the Russian boreal forest to: (1) describe the geographic patterns in abundance, species richness, and the composition of the avifauna with respect to overall abundance, species richness, and the distribution of migratory strategies; (2) determine whether the distribution of birds and their different migratory strategies is predictably related to continental position and gradients of climate and primary productivity; and (3) test the hypothesis that the variation abundance, diversity of boreal forest birds and the distribution

of migration strategies is at least as strongly related to location within a continent as it is to the differences between the Nearctic and Palaearctic *per se*. The study, although limited to data from only 1 to 2 years from each site, represents the only attempt known to us to discern patterns across the entire Eurasian boreal zone, and therefore should provide a working hypothesis for longer-term studies in the future.

MATERIALS AND METHODS

Study sites

Russian Bird Surveys were conducted primarily at Zapovedniks or Scientific Nature Reserves (Colwell *et al.*, 1997). Sites were selected based on whether there were available local ornithologists to conduct the surveys. Exceptions to this consist of fieldwork conducted near the Kostromskaya field station in Kostroma Province, and Myrnoe, Fomka, and Fir Island sites along the Yenesei River in Central Siberia. The locations and approximate elevations of the sites are provided in Appendix S1, and their locations are plotted in Fig. 1. In addition, studies using similar methodologies were conducted in the western and eastern Canadian boreal forest (see Greenberg *et al.*, 1999a,b), and these data are used in these analyses as well.

Bird surveys

Bird surveys were conducted from 05:00 to 09:00 h on 1–20 June at each of the study sites (see Fig. 1 and Appendix S1), a period that corresponds to the peak of singing for most boreal forest species. The data were all collected during the summer of 1994, with the exception of data gathered in eastern Canada during the 1996 field season and in Central Siberia and Kostroma during the 1993 and 1995 field seasons, respectively.

All of the observers, with the exception of those for the Central Siberian and Kostroma study areas, were experienced Russian ornithologists. Some of the observers at the two excepted study areas were North Americans, who went through extensive pre-field and field training on Palaearctic bird identification before conducting the surveys. At each study site, the major accessible forest types were identified, and transects were established along which point counts (Hutto *et al.*, 1986; Petit *et al.*, 1995) were conducted at 200-m intervals. In this way, up to fifteen 5-min point counts were conducted per morning. All birds detected visually or audibly within 50 m of the observer were recorded. For the analysis, we excluded nocturnal birds and birds flying over the plot. In addition, we did not include data from waterfowl, shorebirds, or species that are characteristically nomadic and gregarious (crossbills). For further analysis, birds were classified as resident (most of the population remains resident in the surveyed region throughout the year); tropical migrant (most of the population winters south of the Tropic of Cancer); and short-distance migrant (most of the population migrates from the region of the surveys, but remains north of the Tropic of Cancer). The classification of the species is presented in Appendix S2.

Climate data, global vegetation index values, and habitat classification

Climate data consist of 20-year averages obtained from the nearest meteorological sites to the study sites that could be found on the International Research Institute for Climate and Society C (IRI) data base (IRI/LDEO, 2003). This data base provides monthly average temperatures, precipitation, and the number of frost-free days. From these data, we derived six climatic variables: average maximum temperature in July, average minimum temperature in January, average difference between the two previous measures, total precipitation per
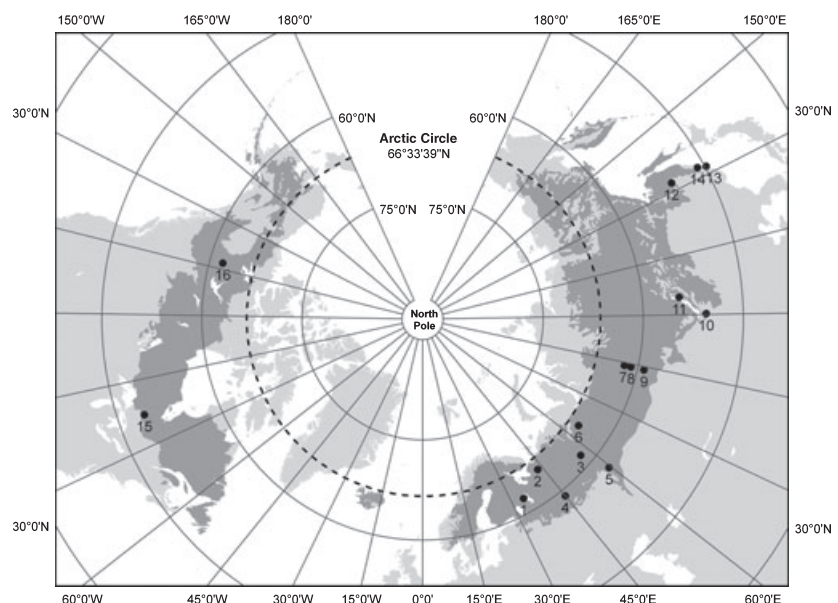
Figure 1 Locations of study sites in Russian and Canadian boreal forest. 1, Kivach; 2, Pinejskyi; 3, Pechoro-Ilichskiy; 4, Kostroma; 5, Visimskiy; 6, Malaya Solosva; 7, Myrnoe; 8, Fir Island; 9, Fomka; 10, Bay Kalskiy; 11, Barguzinskiy; 12, Komsomolskiy; 13, Sichote-Alin; 14, Amur; 15, Mackenzie; 16, Ontario (see Appendix S1 for further details).

year, summer precipitation (May–August), and number of frost-free days. In order to reduce the redundancy and multicollinearity among the climate variables we used principal components analysis (PCA) on the six variables listed above and used the site-specific loadings of the first two principal components (PC1 and PC2) as climatic explanatory variables.

Normalized difference vegetation index (NDVI) values were obtained from the NOAA National Environmental Satellite, Data, and Information Service (Kineman & Hastings, 1992). NDVI values are remotely sensed values based on the overall photosynthetic activity of a habitat. The NDVI has been used to represent habitat productivity in a number of studies of bird distribution (Hurlbert & Haskell, 2003; Szép & Møller, 2005; Ding *et al.*, 2006). Latitude and longitude (to the nearest 0.1°) were entered into the program, and the interpolated monthly averages (1985–88) were downloaded. We obtained two parameters from the NDVI data: the maximum monthly value (usually June or July, $NDVI_{max}$); and an index of seasonality, which was calculated as the difference between the monthly maximum and minimum divided by the maximum ($NDVI_{ratio}$, based on Hurlbert & Haskell, 2003). This value ranges from 0 to 1, so we multiplied it by 100 to obtain a value between 0 and 100. Finally, we ranked habitats for relative productivity in the following order (from greatest to least): 1 = riparian; 2 = broad-leafed upland (aspen–birch); 3 = mixed upland (spruce, fir, aspen, birch etc.); and 4 = pine, larch, black spruce (Erskine, 1977).

Statistical analysis

We calculated the mean number of birds per individual point count as an index of relative abundance. For each habitat we derived the Chao I estimate of total species richness based on a sample size of 50 point counts (Colwell, 2003). We calculated these same parameters for tropical migrant, short-distance, total migrant, and resident species within each habitat surveyed at each site. We thus had 10 response variables (species richness and number of individuals in each of five classes: total birds, tropical migrants, short-distance migrants, total migrants, and residents) that we wished to test against the four continental gradients described above, namely climate (PC1 and PC2), primary productivity ($NDVI_{max}$ and $NDVI_{ratio}$), longitude, and latitude, which resulted in a total of 40 regression equations. Note that all models included habitat (HAB) as a fixed effect because we were certain that our response variables would vary by habitat.

Many previous analyses of continental-scale patterns of the density and species richness of birds (e.g. Diniz-Filho *et al.*, 2003; Bini *et al.*, 2004) and of other organisms (Selmi & Boulinier, 2001) have shown spatial autocorrelation both in the response variables and in common explanatory variables (e.g. climate and primary productivity). The existence of spatial autocorrelation may result in negatively biased estimates of standard errors around estimated regression parameters and in inflated Type I error rates (Legendre *et al.*,

2002). However, when autocorrelation is caused by the underlying environmental gradient under study, the fitting of a regression model should remove the autocorrelation, leaving uncorrelated residuals, and reliable error rates (Diniz-Filho *et al.*, 2003).

To investigate autocorrelation in our data we generated spatial correlograms using Moran's *I* (Legendre & Fortin, 1989) calculated for 10 distance classes (with upper bounds at 240, 622, 1396, 1707, 2254, 2880, 3490, 4683, 5279, and 6244 km) for all 10 response variables and for PC1, PC2, $NDVI_{max}$, and $NDVI_{ratio}$. We interpreted a correlogram as showing significant autocorrelation when at least one of the individual estimates of Moran's *I* had an associated *P*-value of < 0.005 (α = 0.05 with Bonferroni correction for 10 distance classes tested). Because multiple habitats were sampled within a site and the transects were not geo-positioned at the time of the surveys, we arbitrarily set the habitats to be separated by 1 km within each site. Although this introduced some artificial structure at local scales, we did not think it would affect the macro-scale patterns in which we were primarily interested because sites were separated by hundreds to thousands of kilometres. All correlogram data were generated using the software Spatial Analysis in Macroecology (SAM, Rangel *et al.*, 2006) and plotted using MATLAB 7.0 (Mathworks, 2006).

To test the explanatory power of the four continental gradients of interest, namely climate, primary productivity, longitude, and latitude, we used simple linear regression (often referred to as ordinary least squares, or OLS, although we fitted all models using maximum likelihood) to fit 10 sets of four models each, corresponding to the 10 response variables tested against each of the four continental gradients described above. Because we were certain that our response variables would vary with habitat, all models included habitat as a main effect, and each model treated habitats within sites as repeated measures on the same subject. Upon examination of scatter plots of bird data, we determined that a continental pattern was often evident, in that the data in the centre of the continent differed from those in the western and eastern regions. Therefore, for location variables (latitude and longitude) we also included a quadratic term (Table 1).

For each of the 10 sets of four models, we used AIC_c (Akaike's information criterion, adjusted for small sample size; Burnham & Anderson, 2002) to choose the best regression model (i.e. the gradient that best explained the variation in the

Table 1 Four fixed-effects models of the continental distribution of birds by migratory status.

Name	Model[a]
PC	Response = HAB + PC1 + PC2
NDVI	Response = HAB + $NDVI_{max}$ + $NDVI_{ratio}$
LONG	Response = HAB + Longitude + Longitude^2
LAT	Response = HAB + Latitude + Latitude^2

[a]'Response' refers to one of the 10 categories of species or individuals by migratory status. LONG, longitude; NDVI, normalized difference vegetation index; PC, principal component; HAB, habitat.

response variable). For this best model we generated a second set of correlograms on the residuals to determine whether the model fitting procedure reduced or removed spatial autocorrelation in the response variable.

When spatial autocorrelation cannot be removed through simple regression modelling, it may be possible to incorporate it directly into the residual error structure during model fitting (Littell *et al.*, 2006) and thereby avoid biased error rates. These models are often referred to as generalized least squares (GLS), although again we fit all models using maximum likelihood to ensure that our fixed-effects models would be comparable using AIC_c. We used GLS to fit all 40 of the previous fixed-effects models assuming a spherical structure to the error residuals (Littell *et al.*, 2006). To account for multiple measurements of the response variable (habitats) within a site we included a local nugget effect (Littell *et al.*, 2006), which allows an abrupt discontinuity in the pattern of autocorrelation at very local scales. As above, we ranked all four models for each of the 10 response variables using AIC_c. All regression analyses were performed using Proc Mixed in sas 9.0 (SAS Institute, 2002).

RESULTS

PCA analysis of climate data

The first two principal components explained 87% of the variance in climate data from the study sites. The first component (59% of variance) was correlated primarily with data indicating temperature extremes (temperature difference, $r = -0.87$). The second component (28% of variance) was correlated primarily with summer rainfall (-0.78). We used only these components in the regression analysis.

The relationship between the first two PC scores and degrees longitude from the eastern coast shows that the first principal component is a good index of continentality (Fig. 2a). Note that the two Canadian sites fit well within the Eurasian relationship (e.g. Northwest Territory points fall near Central Siberia, and Ontario is found near the Russian Far East). The second PCA shows the east–west gradient (Fig. 2b), primarily in precipitation, and the Canadian points are, once again, consistent with the Eurasian pattern.

Spatial autocorrelation and effects on model selection

Analysis of Moran's *I* indicated significant autocorrelation for all variables tested. In general, the four predictor variables for which we generated correlograms (Fig. 3a–d) showed a greater degree of autocorrelation than did the 10 response variables (Fig. 3e–n), as judged by the extreme values of Moran's *I* observed at some spatial scales. For each of the 10 response variables, the best-fit model usually greatly reduced spatial autocorrelation, in most cases eliminating it at large distances (> 2000 km, Fig. 3). After fitting the linear models, the residuals retained some positive autocorrelation at very local scales (< 500 km), and, for
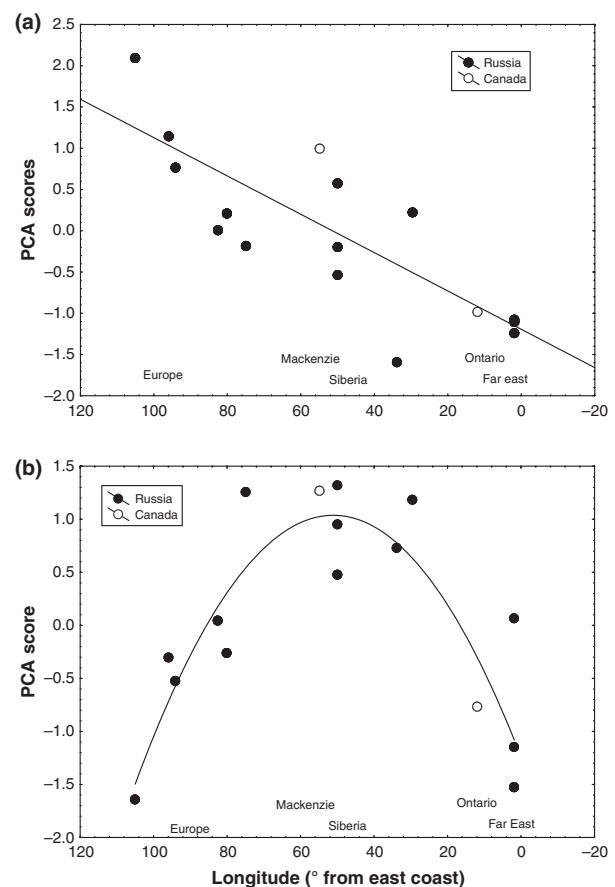

Figure 2 PCA climate scores for study areas plotted against degrees longitude from the eastern edge of the continent for (a) Factor 1 (continentality of temperature increasing from bottom to top of axis) and (b) Factor 2 (precipitation increasing from top to bottom of axis). The locations of the regions of Russia are indicated at the bottom of the graphs.

some variables, negative autocorrelation at intermediate scales (500–2000 km). The further imposition of spherical structure on model residuals had little effect on the AIC_c scores or model ranks for any of the 10 response variables (Tables 2 and 3).

Patterns of abundance

The model containing a quadratic effect of longitude (LONG, Table 1) was the best description for overall abundance (Tables 2 and 3), which followed a clear continental pattern (Fig. 4a) with the lowest abundance towards the centre of the Eurasian continents and the highest abundances in the European and Far Eastern sites. Abundance also varied with the first principal component of climate data (Fig. 4b), although the PC model was clearly inferior to the LONG model (Tables 2 and 3) based on AIC_c scores. The LAT and NDVI models both performed very poorly (Tables 2 and 3). Examining Fig. 4, the data points from the Canadian sites fall within the pattern for the Russian sites.
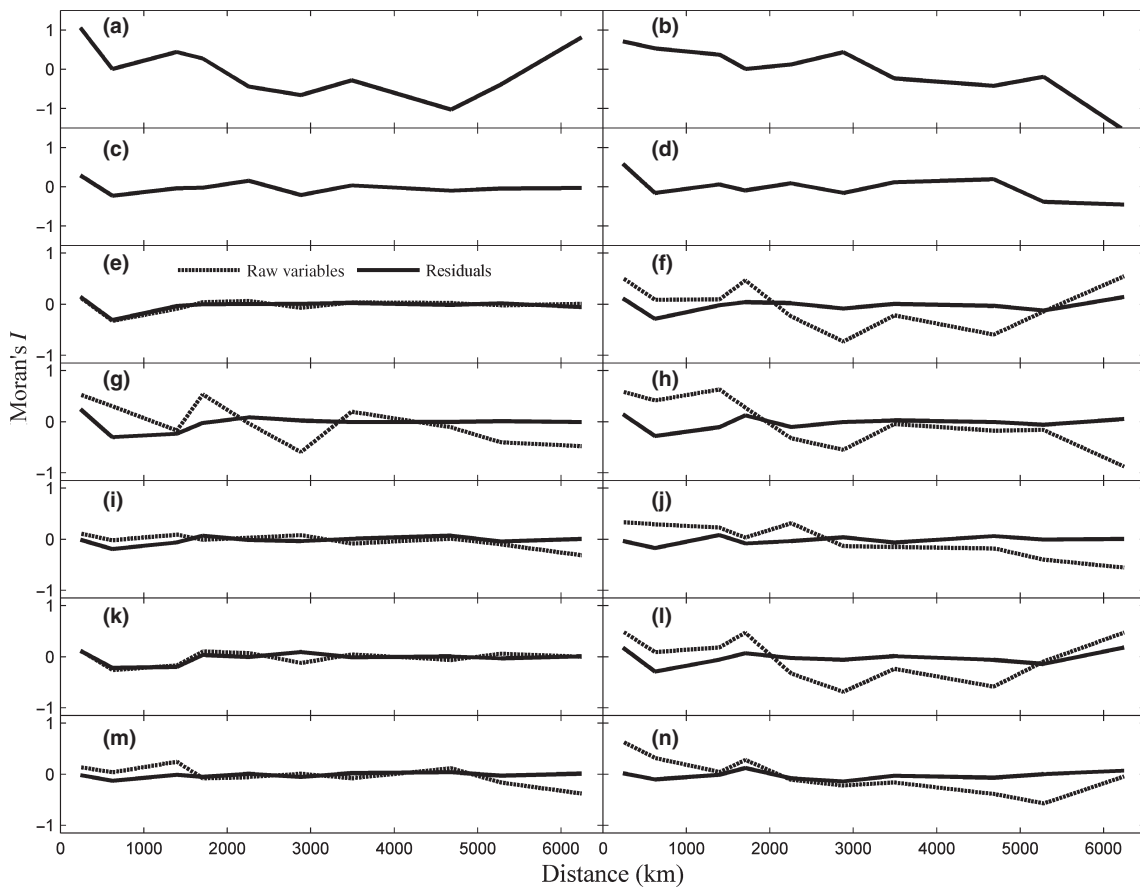
Figure 3 Spatial correlograms for raw predictor variables (a) PC1, (b) PC2, (c) NDVI$_{ratio}$, (d) NDVI$_{max}$, and for all 10 response variables both as raw variables (dashed lines) and as residuals after fitting the best model (solid lines). See text for details on the best models. Response correlograms are species richness of (e) all birds, (g) short-distance migrants, (i) residents, (k) all migrants, and (m) long-distance migrants, and total individuals of (f) all birds, (h) short-distance migrants, (j) residents, (l) all migrants, and (n) long-distance migrants.

Response	TOSP	RSP	SDSP	TRSP	MGSP	TOIND	RIND	SDIND	TRIND	MGIND
Climate PC	1.3	1.7	13.4	0	3.2	5.9	14.7	15	9.6	5.3
NDVI	0	5.9	11.6	13.2	1.3	22	13.3	39.8	23.4	22.4
LONG	2.7	0	0	2.8	3.5	0	0	0	2.8	0
LAT	1.2	3.3	13.2	5.5	0	20.6	8.9	36.8	0	20.6

Table 2 AIC$_c$ differences for simple regression analyses between the mean abundance and estimated species number for components of the Russian boreal avifauna and potentially explanatory ecogeographic variables.

TO, total; R, residents; SD, short-distance migrants; TR, tropical migrants; MG, migrants; IND, individuals per survey; SP, estimated number of species per habitat; PC, principal component; NDVI, normalized difference vegetation index; LONG, longitude; LAT, latitude.

Response	TOSP	RSP	SDSP	TRSP	MGSP	TOIND	RIND	SDIND	TRIND	MGIND
Climate PC	1.4	1.6	3.5	0	3.2	3.2	11.4	5.2	9.5	1.4
NDVI	0	8.3	5.5	13.6	1.2	6.5	10.8	7.6	8.1	5
LONG	2.8	0	0	2.9	3.4	0	0	0	2.7	0
LAT	1.2	3.3	2.9	5.6	0	10.6	8.8	8	0	7.4

Table 3 AIC$_c$ differences for regression analyses between the mean abundance and estimated species number for components of the Russian boreal avifauna and potentially explanatory ecogeographic variables assuming spatially autocorrelated (spherical) residuals.
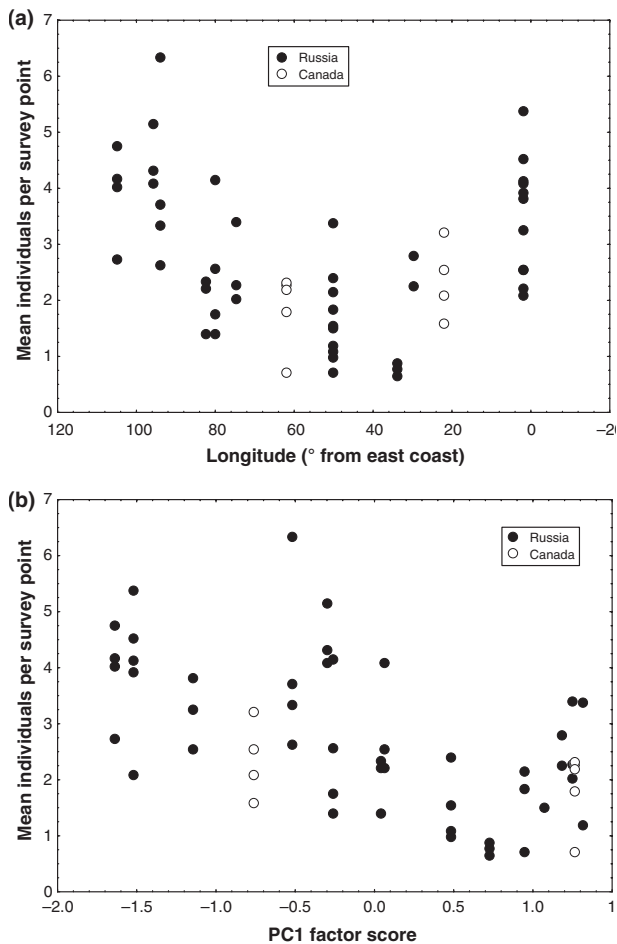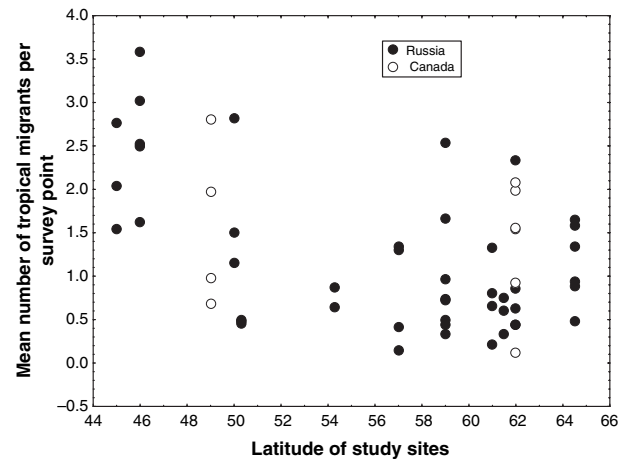
For key to acronyms see Table 2.

The relative abundance of tropical and short-distance migrants

The vast majority of the birds in the boreal forest sites were migrants, accounting for an average of 81% (± 13 SD) of the surveyed birds; tropical migrants averaged 43% (± 26); and short-distance migrants 36% (± 21) of the samples. The abundance of birds classified by migration types was best explained by a quadratic model of longitude for residents, short-distance migrants, and overall migrants (LONG,

Figure 5 Mean individuals of tropical migrants per point for each habitat/site plotted against degrees latitude.

model (Table 2; see Fig. 6c,d for abundance and species richness vs. longitude for short-distance migrants). However, when the residuals were assumed to be spatially autocorrelated, the relative strength of this model for short-distance migrants was weakened considerably (Table 3).
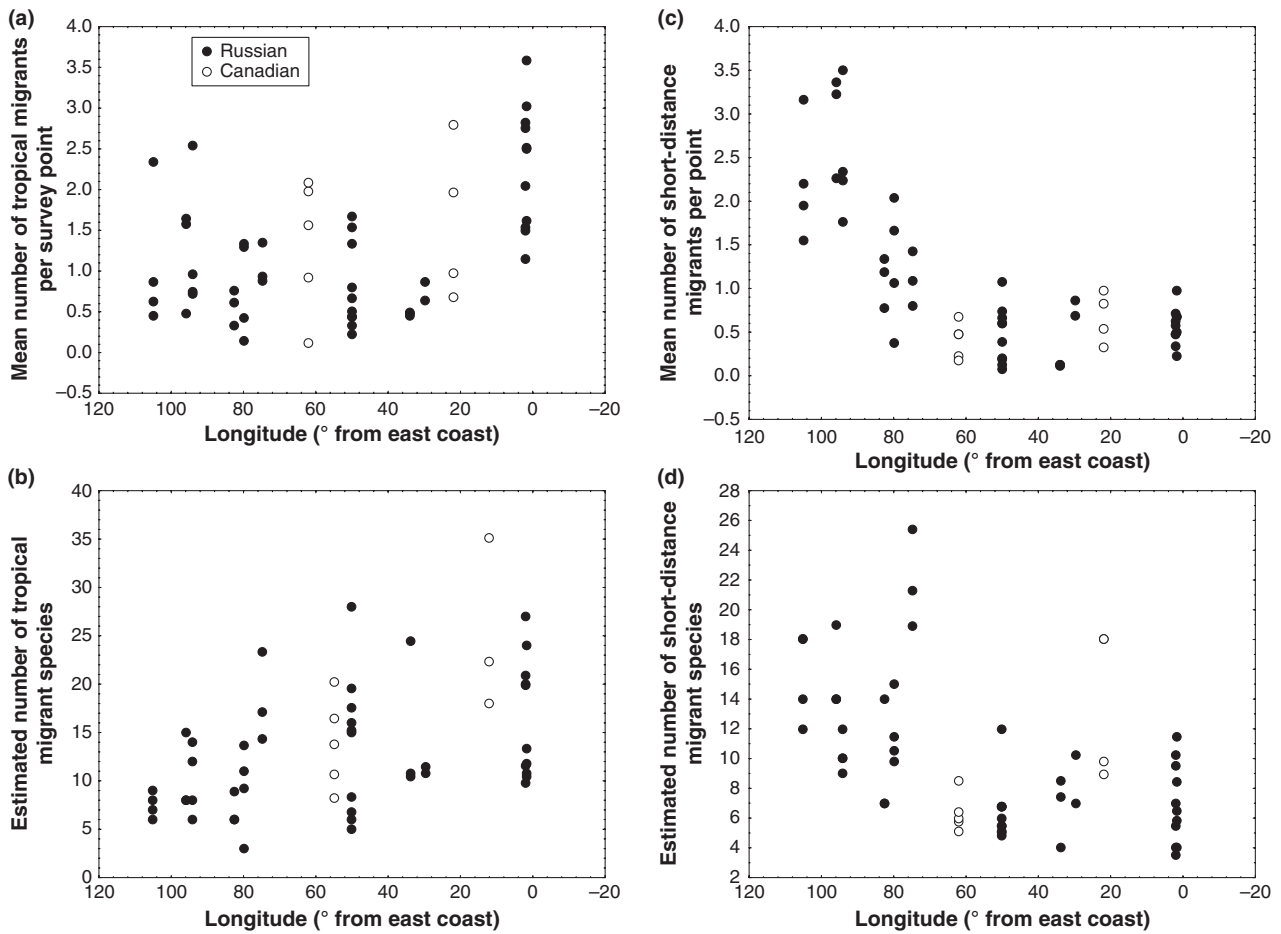
DISCUSSION

Geographic patterns

The abundance data from the Russian sites showed two distinct patterns. First, overall abundance showed a continental-scale pattern, with the average number of birds per survey point depressed in Siberia compared with European Russian and Far Eastern sites. Second, the numerical dominance of tropical migrants increased along a gradient from west to east, whereas the numerical dominance of short-distance migrants increased from east to west. The pattern was less clear for residents, which accounted for a small portion (< 20%) of the birds surveyed.

Explanatory power of climate, NDVI and geographic variables

For the 10 response variables considered (five classes each of species richness and number of individuals), either the LONG or the LAT model performed best in eight cases. LONG or LAT was always the best model for the total number of individuals detected, either for total birds or for each migratory class. Thus, our data suggest that patterns in the distribution of avian abundance and, to a lesser degree, species richness, across the Russian boreal forest are best explained by simple geographic position. We offer three possible explanations for this. First, the data quality for climate and NDVI may have been too low. We used time periods and spatial scales that were dictated by the available data sets. More exploration of data gathered at varying temporal and spatial scales may improve their fit in these models. Second, with predictable geographic

Figure 4 Abundance (mean individuals/point) per study site/habitat plotted against (a) degrees longitude from the eastern edge of the continent, and (b) climate-based PC1 factor scores.

Tables 2 and 3). None of the other models considered performed well compared with the LONG model. For tropical migrants, both the LONG and LAT models performed well, with the LAT model slightly outperforming the LONG model (Tables 2 and 3, Figs 5 & 6a). Thus, all of the migratory classes showed a relationship with longitude, with tropical migrant and resident abundances increasing to the east (Fig. 6), but short-distance migrants decreasing to the east.

Species richness

Species richness (Chao I) showed inconsistent patterns over our set of candidate models. The NDVI model performed best for overall species richness. Beyond that, each model was selected as the best model for at least one migratory class (Tables 2 and 3). However, the differences among top models were generally small, within a range (≤ 4 AIC_c units, Burnham & Anderson, 2002) that meant they could be considered as serious competitors. The exception was short-distance migrant species richness in the simple regression analysis, for which the quadratic longitudinal model (LONG) was the only reasonable

Figure 6 Mean individuals per point (a) and estimated species richness (b) of tropical migrants, and mean individuals per point (c) and estimated species richness (d) of short-distance migrants for each habitat/site plotted against degrees longitude from the eastern edge of the continent.

patterns in climate, the geographic variables may include both climate effects and the additional direct influence of geography as it affects the accessibility of winter habitats. Finally, the geographic configuration of boreal forest may have an overarching direct effect on abundance and migration patterns. In a speculative manner, we explore the possible underlying causal hypotheses below.

Explanatory hypotheses: climatic regimes in the breeding grounds or accessibility of wintering grounds

We present two hypotheses for the explanatory effect of the variables on the overall distribution of birds and the pattern for the component migratory classes. First, bird populations are responding to the two major climatic gradients as indicated in the PCA analysis: a continental pattern in temperature regimes resulting in more extreme temperatures and shorter growing seasons in the mid-continent, and a gradient of summer precipitation from west to east. Second, the accessibility of tropical and non-tropical wintering areas plays a role either in patterns of overall abundance or in the relative
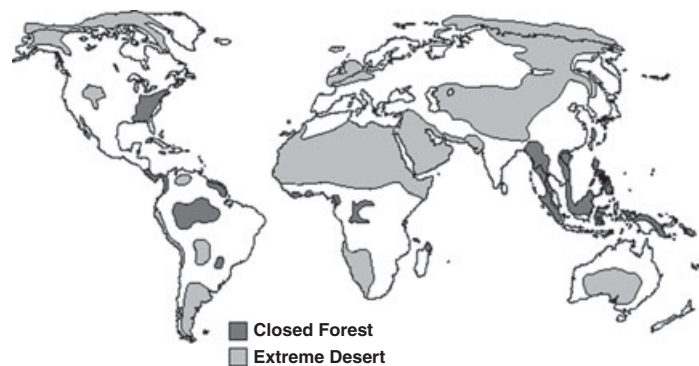
importance of tropical vs. within-temperate migration patterns.

The climatic conditions hypothesis would suggest that climate drives either resource abundance or the amount of time that habitat is available for reproduction, and that these in turn affect bird abundance. Arguments have been made for why climate might affect the proportion of migrants vs. residents in temperate breeding assemblages (MacArthur, 1959; Herrera, 1978; Newton & Dale, 1996; Hockey, 2005). However, it is unclear why breeding-location climate should affect the relative abundance of short-distance vs. long-distance migrants (Willson, 1976).

The wintering-ground accessibility hypothesis is based on a growing amount of research that suggests that the distribution of migratory birds and their flyways can be strongly shaped by barriers, such as deserts and high mountains, particularly if they are located close to the potential breeding area (Bensch, 1999; Alerstam, 2001; Henningsson & Alerstam, 2005). In the Palaearctic, the western and eastern ends of the boreal forest have no major barriers to non-boreal wintering areas, which allows for the over-winter survivorship of a large population of birds (Fig. 7a,b). Siberia has both a greater area of boreal forest

(a) Present Potential Vegetation

■ Closed Forest (> 70% canopy cover)
□ Extreme Desert (< 2% vegetation cover)
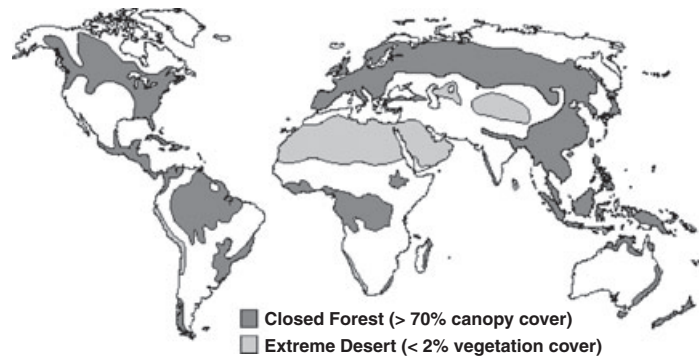
(b) Last Glacial Maximum (18 000 ^{14}C years ago)

■ Closed Forest
□ Extreme Desert

Figure 7 Estimated distribution of desert and closed forest: (a) present-day potential and (b) Latest Glacial Maximum (from Adams, 1997, with permission).

than Europe and the Russian Far East and a series of profound barriers to migration south of boreal habitats, including both extremely arid areas, depicted in Fig. 6, and the Himalayas (Irwin & Irwin, 2005). The major barrier (the Sahara Desert) between Europe and tropical Africa will favour boreal species that winter within the temperate and Mediterranean regions of Europe. Some of these species, such as the chaffinch, have adapted to the human-transformed environment, which provides enhanced winter resources, and they occur at extremely high abundances (Greenberg *et al.*, 1999a), thus explaining the high abundance of short-distance migrants in the Western Palaearctic. In contrast, the Russian Far East differs from Europe and Siberia in having a historically stable, barrier-free corridor to the tropics of Southeast Asia, thus favouring tropical migration.

The pattern of overall abundance could be explained by the climate or accessibility of wintering grounds hypotheses, as the abundance is lowest in Siberia where the climate is most continental and the present-day barriers to both temperate/ Mediterranean and tropical wintering areas are the most profound. The shift between migration types is probably best explained by the wintering ground accessibility hypothesis, as it is unclear why a gradient in summer rain would shift the migration strategies of breeding species.

Inter-continental comparisons

Most previous work comparing Palaearctic and Nearctic boreal biota has focused on Europe and Eastern North America. A few studies have included Siberia and the Russian Far East, but these are based on regional species lists (Mönkkönen & Helle, 1989; Haila & Järvinen, 1990). This study is the first to be based on habitat-specific survey data, and can examine abundance and local patterns of species richness. With only two regions in North America surveyed in this study, it is difficult to conduct formal statistical analyses. However, the values for both climate and metrics characterizing avian assemblages at the Canadian sites are more similar to those from the central and eastern portions of the Palaearctic than they are to those from the European boreal forest, and hence the Asian boreal forest might be an appropriate region for future avifaunal comparisons with Nearctic sites.

First, as Fig. 2 shows, both major gradients in climate (PC factors 1 and 2 vs. longitude) show that the eastern Canadian site is closest in climate to sites in the Russian Far East, and that the western Canadian site is similar to those in Central Siberia. Large-scale patients of habitat distribution, particularly the connectivity of tropical and temperate forest since the late Pleistocene (Huntley, 1993), is also similar between the two continents if the appropriate regions are compared. Patterns of overall abundance and the abundance and species richness of tropical and short-distance migrant species (Fig. 6) in the Canadian sites appear to be consistent with the overall geographic patterns found in the Eurasian samples. Therefore, the characterization of the differences in the abundance of tropical and short-term migrants between the Palaearctic and Nearctic boreal forest is largely dependent on where in the continent the data from the comparison are obtained. Based

on these preliminary surveys, it would appear that a comparative intercontinental research programme should focus more on Siberia and the Russian Far East (see also Mönkkönen, 1994), where current information is the most sparse. Finally, the generality of patterns of bird density and species richness described in this paper should be tested by conducting a similar analysis based on sites distributed widely across the New World boreal forest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location, climate, NDVI, and bird abundance and species richness data for Russian and Canadian survey sites.

Appendix S2 Latin names (Sibley & Monroe, 1990) and migratory bird classes for species of (a) Russian and (b) Canadian birds included in the analyses.

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BIOSKETCHES

Russell Greenberg received his PhD from the University of California in 1981 and has been the director of the Smithsonian Migratory Bird Center since 1992.

Anna Kozlenko earned her doctorate from the Russian Academy of Science in 1987, worked as a researcher for the Russian Institute for Nature Protection for 8 years, and is currently working on information technology for a private firm.

Matthew Etterson received his PhD in conservation biology from the University of Minnesota in 2000 and is currently a senior research associate at the Mid Continent Ecology Division of the US Environmental Protection Agency in Duluth, MN, and an adjunct assistant professor of biology at the University of Minnesota Duluth.

Thomas Dietsch received his PhD from the University of Michigan and has gone on to post-doctoral positions at the Smithsonian Migratory Bird Center and UCLA's Center for Tropical Research.

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