



Local forest structure, climate and human disturbance determine regional distribution of boreal bird species richness in Alberta, Canada

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ABSTRACT

Aim It is challenging to disentangle how local habitat structure, climate, and human disturbance interplay to determine broad-scale variation of species richness. Here, we separated various measures of local forest structure and composition, abiotic factors, and human land cover that constrain species richness of bird guilds in the boreal forest.

Location Boreal forest, western Canada.

Methods Data on breeding birds, habitat structure, climate and human footprints in 206 sites were sampled, with each site centred on an area of 1 ha in size. The 206 sites cover a large geographical extent with a distance of c. 1000 km between the most distant sites. We modelled bird guild species richness in relation to forest structure and composition (woody plant richness, forest biomass, number of vegetation layers, canopy openness), abiotic environment (temperature, precipitation, elevation), and percentage area of human land cover. We classified bird species into different guilds based on dietary preference, habitat specialization and migratory status, and used structural equations to quantify effect strengths of predictor variables.

Results We found that temperature, low levels of human land cover, woody plant richness and number of vegetation layers had strong positive correlations with overall bird species richness in the boreal forest. Moreover, local forest structure and composition showed a pronounced variation in their relationships with species richness of different guilds. Insectivores, old-growth forest specialists, forest generalists, long-distance migrants and winter residents showed strong positive correlations with woody plant richness, whereas old-growth forest specialists and winter residents were strongly related to forest biomass as well. The number of vegetation layers was positively related to species richness of most guilds, whereas the response to canopy openness was most pronounced for old-growth forest specialists and winter residents (being negatively correlated).

Main conclusions In addition to climate and human disturbance, local forest structure and composition are important determinants of broad-scale variation of bird species richness in boreal forest. However, the strength and direction (positive/negative) of determinants is guild-specific, suggesting a strong functional component to community structure.

Keywords

Bird richness, boreal forest, functional trait, guild assembly, habitat heterogeneity, species–energy theory, structural equation modelling, taiga, vegetation structure.

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INTRODUCTION

Understanding the mechanisms and determinants of species diversity patterns is of central interest in ecology and biogeography. For birds and other terrestrial vertebrates, geographical variation in species richness across broad spatial extents is related to abiotic and biotic variables, including climate and energy availability (Wright, 1983; Currie, 1991; Hawkins *et al.*, 2003; Hurlbert & Haskell, 2003; Hansen *et al.*, 2011), habitat heterogeneity (Kerr & Packer, 1997), food resources (Kissling *et al.*, 2007), and human disturbance (Devictor *et al.*, 2008; Lepczyk *et al.*, 2008; Desrochers *et al.*, 2011). At local spatial scales, the importance of habitat conditions and vegetation structural complexity has long been emphasized (MacArthur & MacArthur, 1961). However, the relative importance of determinants of species richness varies widely, possibly because mechanisms are scale-dependent, i.e. they vary with the grain size and spatial extent of the sampling units (Levin, 1992; Willis & Whittaker, 2002; Qian & Kissling, 2010). While climatic variables have been widely examined as determinants of species richness across scales, the importance and scale-dependence of biotic drivers remains less clear (Field *et al.*, 2009).

Variation and scale-dependence in the relative importance of broad-scale biotic determinants of species richness is reflected in contrasting findings of plant–bird richness analyses. For example, in North American forests, James & Wamer (1982) showed a positive relationship between woody plant and bird richness using local bird census data, while Currie (1991) found that birds showed weak associations with tree species richness when using coarse-grained grid cells. One possible reason for these inconsistencies is that detailed and accurate information on several key variables (e.g. plant species distributions and vegetation structure) is incomplete (Willison & Comet, 1996). Also, spatial scale (i.e. the spatial grain or resolution of analysis units) matters (Willis & Whittaker, 2002; Qian & Kissling, 2010). At local spatial scales, i.e. within habitat patches (Willis & Whittaker, 2002) or at grain sizes $< 10 \text{ km}^2$ (Field *et al.*, 2009), previous studies have looked into determinants of forest bird species richness at one or a few study sites, while analyses of local (i.e. fine-grained) data across broad-scale gradients have been scarce. In contrast, most studies on large-scale patterns of bird species richness have used coarse grain sizes (e.g. $50 \text{ km} \times 50 \text{ km}$ grid cells) for which the quantification of local habitat structure and composition is largely overlooked. Hence, it remains essential to link local-scale observations across large geographical extents for understanding bird diversity across scales. Few studies have analysed local-scale forest bird data across such broad spatial extents with the aim of testing for the relative importance of local habitat structure and composition versus broad-scale environmental gradients.

To improve our understanding of species richness patterns it is important to quantify whether, and to what extent, determinants vary with specific traits or natural history

characteristics of species (Carnicer & Díaz-Delgado, 2008; Kissling *et al.*, 2012). Bird-specific traits, such as dietary preference, habitat specialization and migratory behaviour, constrain demographic dynamics and population parameters and thus influence species distributions and richness variation across large geographical extents (Carnicer *et al.*, 2012). For example, the dietary preference of a bird species represents a fundamental aspect of its ecological niche, and determines a species' functional role in an ecosystem (Kissling *et al.*, 2012). Similarly, the degree of habitat specialization can strongly constrain the presence/absence and abundance of bird species along broad-scale environmental gradients (Devictor *et al.*, 2008). While some previous broad-scale studies have examined the relative importance of predictor variables for species richness of some selected guilds (e.g. dietary guilds: Kissling *et al.*, 2012), comprehensive assessments of those determinants for various bird guilds across broad geographical extents are rare.

In this study we used a spatially fine-grained ($< 1 \text{ km}^2$ resolution) data set covering a large geographical extent (almost 1000 km between the most distant sites) to analyse biotic and abiotic determinants of spatial variation in bird species richness across the boreal forest in Alberta, Canada. The boreal forest is the largest terrestrial biome in the world, containing about one third of the Earth's forest. Birds are the richest vertebrate taxon in the forest, comprising c. 75% of all terrestrial vertebrate species (Niemi *et al.*, 1998). In contrast to tropical and temperate forests, the proportion of migratory bird species generally exceeds that of permanent residents (Niemi *et al.*, 1998). However, our understanding of the determinants of boreal bird species diversity is still limited in comparison with that of other forest ecosystems (Cumming *et al.*, 2010), largely owing to the limited availability of comparable data for bird species and the shortage of standard sampling techniques in the boreal region. We examined bird species richness in relation to abiotic environment (temperature, precipitation and elevation), human land cover, and local forest structure and composition (woody plant richness, forest biomass, number of vegetation layers and canopy openness), and classified bird species into different guilds based on dietary preference, habitat specialization and migratory status. We were specifically interested to test how the relationships between bird species richness and biotic and abiotic variables vary among guilds, and how various measures of local forest structure and composition are related to guild species richness after statistically accounting for abiotic environmental determinants across a large spatial extent.

MATERIALS AND METHODS

Study sites

The study was conducted at 206 sites in the boreal forest region in Alberta, Canada (Fig. 1), and included all the boreal forest sites maintained by the Alberta Biodiversity

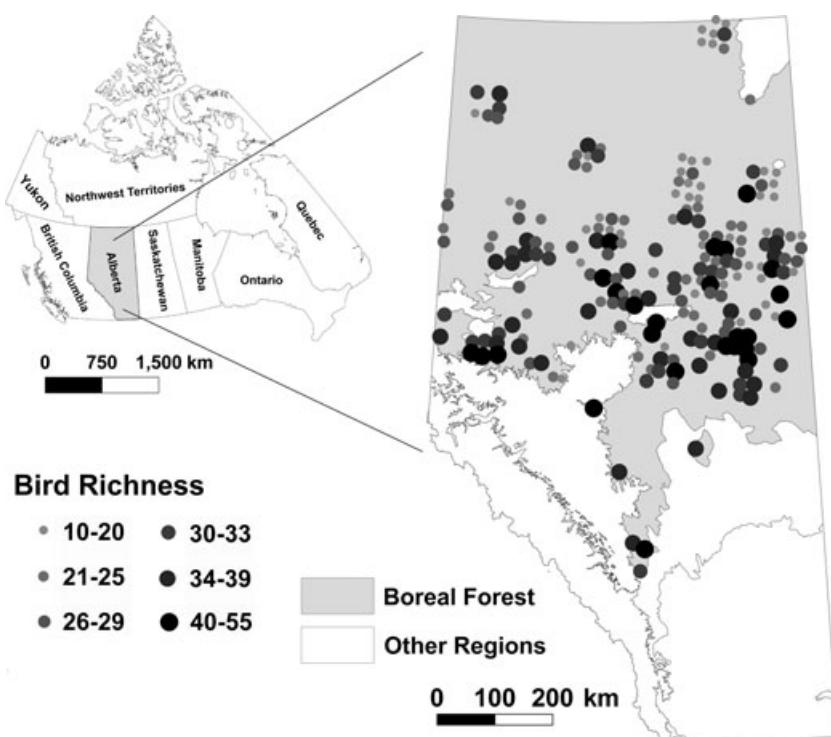


Figure 1 The distribution of the 206 study sites and their breeding bird species richness across the boreal forest in Alberta, western Canada. Quantile classification was used for species richness, and NAD83 (North American Datum of 1983) for map projection.

Monitoring Institute (ABMI). ABMI conducts a broad-scale, long-term monitoring programme on tracking biodiversity status and trends in Alberta (<http://www.abmi.ca/abmi/home/home.jsp>). The boreal region has short summers (only 1 or 2 months have average daily temperatures exceeding 15 °C) and long and cold winters (average daily temperatures are below -10 °C for 4 months or more) (Natural Regions Committee, 2006). Precipitation follows a summer-high continental pattern, with peak rainfalls occurring in July and about 60–70% of the annual precipitation falling between April and August. The dominant landform is fine textured lacustrine and till plains. Elevations range from c. 150 m near the Alberta–Northwest Territories border to over 1100 m near the Alberta–British Columbia border. The region is vegetated by deciduous, mixedwood and coniferous forests. Aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are the most common deciduous species, while white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are the dominant conifers.

Data collection

We recorded the presence of breeding birds and characterized the abiotic environment, human land cover, and several measures of local forest structure and composition for each of the study sites. The predictor variables used have previously been shown to influence bird species richness at various spatial scales (MacArthur & MacArthur, 1961; Cody,

1985; Hawkins *et al.*, 2003; Kissling *et al.*, 2008, 2012). Descriptive statistics of those variables across our study sites are provided in Table 1.

Breeding birds were surveyed at nine point count stations at each ABMI site during the breeding season (June) in the years 2003–2010. Point count stations were arranged in a gridded pattern with one point count station located at the centre and the remaining stations located 300 m apart surrounding the centre. An omnidirectional microphone (Compression Zone Microphone, developed by River Forks Research Corporation, Chilliwack, BC, Canada) was used to digitally record singing birds for 10 min at each of the nine stations. All audio recordings were later interpreted by a single expert in a standardized laboratory setting. We used the number of recorded bird species to indicate species richness at each site.

To characterize the abiotic environment we included mean annual temperature (TEMP, related to ambient energy), mean annual precipitation (PREC, related to water availability), and absolute elevation (ELEV, characterizing topography) (Table 1). Climate data for the temperature and precipitation variables were derived from the program CLIMATEAB 3.22 (Wang *et al.*, 2006). This program uses baseline climate data derived from monthly precipitation and temperature grids (Daly *et al.*, 2008) based on interpolated climate data from weather stations for the period 1961–1990 (only for USA and Canada). The program includes a lapse-rate based down-sampling to 1-km resolution and estimation of biologically relevant climate variables (Wang *et al.*, 2006).

Table 1 Descriptive statistics of abiotic environment, human land cover, local forest structure and composition, and bird guild species richness in the 206 study sites in Alberta, Canada. Mean \pm standard deviation (SD) are given. Note that total numbers are only available for species richness data.

Variables	Abbreviation	Total	Mean	SD	Range
Abiotic environment					
Mean annual temperature ($^{\circ}$ C)	TEMP	–	0.95	1.06	–1.75–3.35
Mean annual precipitation (mm year $^{-1}$)	PREC	–	440.35	40.60	296.10–529.00
Elevation above sea level (m)	ELEV	–	593.04	155.25	192.20–1190.50
Human land cover					
Percentage human land cover types (%)	HUMAN	–	7.89	13.25	0.00–74.47
Local forest structure and composition					
Woody plant richness (no. of species)	WOODY	101	17.55	6.28	3–36
Stand biomass (kg ha $^{-1}$)	BIOMASS	–	492.73	391.28	0.09–1973.87
Number of vegetation layers	LAYERS	–	3.52	0.61	0.67–4.56
Canopy openness (%)	CANOPY	–	46.08	26.30	1–96
Overall bird species richness					
All birds (no. of species)	BIRDS	134	28.43	9.85	10–55
Dietary guild richness					
Insectivore (no. of species)	Diet_INS	72	15.85	6.26	4–35
Omnivore (no. of species)	Diet_OMN	42	11.50	3.96	3–22
Carnivore (no. of species)	Diet_CARN	12	0.15	0.41	0–3
Habitat guild richness					
Old-growth forest specialist (no. of species)	Hab_FORSPEC	37	10.10	4.07	2–22
Forest generalist (no. of species)	Hab_FORGEN	43	11.46	4.25	3–24
Habitat generalist (no. of species)	Hab_GENERAL	17	2.10	1.66	0–8
Migratory guild richness					
Long-distance migrants (no. of species)	Mig_LONG	54	12.14	5.19	1–27
Short-distance migrants (no. of species)	Mig_SHORT	53	11.91	4.16	4–27
Winter residents (no. of species)	Mig_RESI	26	4.37	2.31	0–12

Based on input values for longitude and latitude of each ABMI site, we localized the annual climate variables (PREC and TEMP) from the last 10 years (2000–2009) and then used the average values across the 10 years to describe local climatic conditions of each site. ELEV was extracted from Alberta Digital Elevation (DEM) data with the resolution of 100 m for each site.

To characterize the influence of human disturbance (HUMAN) on bird species richness we used land cover data derived from manually interpreting aerial photography of photoscale 1:30,000 and SPOT satellite imagery within 500 m distance from the centre of each ABMI site. Land cover types considered to characterize strong human influence on forest bird species richness included agriculture, forest harvesting, roads, and urban and industrial areas. The percentage area of these land cover types within a 500 m radius from the centre of each site was used to quantify human influence.

We derived four variables to describe local forest structure and composition for birds at our study sites (Table 1). Woody plant richness (WOODY) was surveyed within a 1-ha (hectare) square plot (100 m \times 100 m) in the centre of each ABMI site. The plot was divided into four 0.25-ha subplots, and all vascular plants were surveyed during July for each subplot using 20-min area-restricted searches. We only included the number of woody plant species (trees and shrubs) as they are the most important plant species to characterize bird habitat in forested ecosystems (Cody, 1985).

As a second habitat variable we quantified stand biomass (BIOMASS) in the 1-ha plot at each site. BIOMASS reflects the accumulative effect of past growth of trees (Elo *et al.*, 2012) with larger BIOMASS possibly implying a higher production rate of many critical resources for birds, such as invertebrate prey, seeds and other plant food resources, cover from predators, as well as nesting and roosting sites. All trees with ≥ 25 cm diameter at breast height (d.b.h.) in 25 m \times 25 m plots, all trees with ≥ 7 cm d.b.h. in 10 m \times 10 m subplots, and all trees regardless of size in 5 m \times 5 m subplots were measured for d.b.h. Above-ground biomass was then estimated for each site using d.b.h.-based biomass equations and tree species-specific parameters as provided by Lambert *et al.* (2005) and Ung *et al.* (2008). These equations were derived from thousands of trees sampled across Canada and allow the calculation of tree biomass (foliage, branches, stem bark, and stem wood) based on d.b.h. measurements (for details see Lambert *et al.*, 2005 and Ung *et al.*, 2008). Total biomass of each site was summed up from three parts: the biomass per hectare of trees with ≥ 25 cm d.b.h. in 25 m \times 25 m plots, the biomass per hectare of trees with 7–25 cm d.b.h. in 10 m \times 10 m subplots, and the biomass ha $^{-1}$ of trees with < 7 cm d.b.h. in 5 m \times 5 m subplots.

As a third habitat variable we included the number of vegetation layers (LAYERS) as recorded in a 150 m radius around each bird point count station at each ABMI site. A total of five vegetation layers were distinguished: veteran

layer (defined as the layer of trees older than the rest of the stand and usually a remnant from a previous forest), dominant canopy layer, suppressed canopy layer, upper shrub layer (> 1.3 m), and lower shrub layer (< 1.3 m). We determined the number of vegetation layers for each point count station and then used the average values of the nine point count stations as the number of vegetation layers at each site.

As a fourth measure of bird habitat structure and composition we included canopy openness (CANOPY) estimated with a spherical (concave) densitometer held at elbow height (i.e. with arm bent at a right angle). Canopy openness was measured at eight locations per site (two readings at each of the four 10 m \times 10 m quadrats). We calculated the average canopy openness at each site by averaging values of the four quadrants: values for canopy openness ranged from 0 (closed canopy) to 96 (high canopy openness).

Bird guild classification

We classified all bird species (BIRDS) into functional groups (termed 'guilds' here) according to their dietary preferences, habitat specialization, and migratory status. Similar to previous publications (Carnicer & Díaz-Delgado, 2008; Kissling *et al.*, 2012), species were classified according to the major fraction of their diet. Dietary guilds were distinguished following their major food types during the breeding season (De Graaf *et al.*, 1985; Canadian Wildlife Service, 2005): (1) insectivores (Diet_INS, feeding predominantly on insects); (2) omnivores (Diet_OMN, feeding on both animals and plants); and (3) carnivores (Diet_CARN, feeding predominantly on vertebrates). Nine species ('not classified' in Appendix S1 in Supporting Information) were not included because they belonged to other dietary guilds (e.g. granivores, piscivores, frugivores) for which sample sizes were too small for our analysis. Habitat guilds were distinguished based on species' preferences and dependence on forest habitat (ABMI, 2009): (1) old-growth forest specialists (Hab_FORSPEC, defined as species which depend on forests older than 80 years for living/reproduction during the breeding season and have higher densities in old-growth forests than in other vegetation types); (2) forest generalists (Hab_FORGEN, defined as species depending on forests for living/reproduction and having higher densities in forest than in other vegetation types, but excluding Hab_FORSPEC); (3) habitat generalists [Hab_GENERAL, defined as species inhabiting various habitat types during the breeding season, but excluding (1) and (2)]. We finally distinguished migratory guilds depending on the migratory behaviour of species (Godfrey, 1986; Canadian Wildlife Service, 2005; ABMI, 2009): (1) long-distance migrants (Mig_LONG, i.e. Neotropical migrants defined as birds breeding in North America during the spring and early summer but spending the winter in Mexico, the Caribbean, and Central and South America); (2) short-distance migrants (Mig_SHORT defined as birds that migrate to southern Canada, coastal Canada, or the

USA for the winter); and (3) winter residents (Mig_RESI defined as birds remaining in Alberta during the winter). Species that did not fit into a guild category were excluded from guild-specific analyses.

Statistical analysis

We first used simple Pearson correlations to explore covariation among variables (Table S1 in Appendix S2). We then used structural equation models (SEMs) (Grace, 2006) to investigate direct and indirect effects of abiotic environment, human land cover, and local forest structure and composition on species richness of terrestrial breeding birds and of dietary, habitat and migratory guilds. SEMs allow partitioning of the correlations between predictor and response variables into direct and indirect effects and thus enable the evaluation of hypothesized causal relationships in data sets with more than one dependent variable and effects of dependent variables on one another (Grace, 2006). Based on previous analyses of broad-scale patterns of bird and vertebrate species richness (e.g. Kissling *et al.*, 2007, 2008; Qian & Kissling, 2010), we designed a set of SEMs with the aim of specifically assessing the relative importance of local forest structure and composition (and environmental and human determinants) on terrestrial bird and guild species richness across our study sites. We developed four *a priori* theoretical SEMs (Fig. S1 in Appendix S3) with abiotic environmental variables (TEMP, PREC, ELEV), human land cover (HUMAN), and the four measures of forest structure and composition (WOODY, BIOMASS, LAYERS, CANOPY). The structures of the four *a priori* SEMs were the same except for the local forest structure variable which was substituted in each model (Fig. S1). This was carried out to specifically test the influence of different forest structure and composition variables on bird richness. To test how abiotic environment, human land cover, and local forest structure and composition influence the species richness of guilds, we used the same *a priori* theoretical SEM structure (Fig. S1), but interchanged BIRDS with the respective guild richness variable (Diet_INS, Diet_OMN, Diet_CARN, Hab_FORSPEC, Hab_FORGEN, Hab_GENERAL, Mig_LONG, Mig_SHORT, or Mig_RESI; see Figs S2–S5 in Appendix S3).

To develop the final SEMs, we started with the initial *a priori* SEMs and then evaluated their residual correlations, modification indices, and model fits when implementing them for a specific bird guild. Missing paths were identified from large residuals and high modification indices and subsequently accounted for by adding error covariances between pairs of variables. This was repeated until satisfactory measures of model fit were obtained. We used the chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit. The following criteria were used to indicate SEMs with a satisfactory fit: (1) *P*-values of chi-square tests > 0.05 ; (2) lower 90% confidence intervals of RMSEA < 0.05 ; and

(3) CFIs > 0.90 . In a final step, we deleted non-significant paths (with $P > 0.05$) in SEMs with satisfactory model fit and reassessed model fits. All final SEMs had P -values of chi-square tests > 0.1 , lower 90% confidence intervals of RMSEA equal to 0, and CFIs > 0.98 .

Because the presence of spatial autocorrelation in model residuals violates the assumption of data independence, we additionally assessed to what extent residual spatial autocorrelation exists and whether its inclusion would change the relative importance and statistical significance of explanatory variables (Bini *et al.*, 2009). To assess spatial autocorrelation we calculated Moran's I values on the residuals of non-spatial multiple regression models (ordinary least squares, OLS) using the same variables as in the SEMs (i.e. abiotic environment, human land cover and forest structure and composition as predictors, and bird richness as the response), and then fitted spatial linear models [here 'spatial simultaneous autoregressive error models (SARs)'; Kissling & Carl, 2008], which allow the inclusion of the residual spatial autocorrelation of the data. We then compared the relative importance of predictor variables from OLS models with those of SARs by calculating the standardized partial regression coefficients of all predictor variables (cf. Kissling *et al.*, 2008). For the non-spatial (OLS) models, these standardized partial regression coefficients are equivalent to the direct effects on species richness in our SEMs.

All statistical analyses were carried out using R 2.15.0 software (R Development Core Team, 2012). Pearson correlation coefficients after accounting for spatial autocorrelation were calculated with the R library MODTEST 1.4 (José Manuel Blanco Moreno, Universitat de Barcelona, Catalonia, Spain, pers. comm.), the SEMs were calculated with the R library LAVAAN 0.4–13, and Moran's I values and SARs were calculated using the R library SPDEP 0.5–33. The spatial weight matrices of the SARs and the Moran's I values were calculated with the nearest neighbour and a row-standardized coding style (Kissling & Carl, 2008). To improve normality and linearity in our models, we log-transformed species richness of overall birds and bird guilds, TEMP, PREC and WOODY; and square-root-transformed ELEV, HUMAN, BIOMASS and CANOPY for all statistical analyses.

RESULTS

Geographical variation of bird species richness and environment

A total of 134 breeding bird species were recorded across the 206 boreal sites (Appendix S1). Overall bird species richness per site ranged from 10 to 55, with an average of nearly 29 species per site (Table 1) and about 80% of the sites having > 20 species (Fig. 1). The species richness of guilds per site ranged from 0 to 35 species (Table 1), with only two guilds (Diet_CARN and Hab_GENERAL) having < 20 species. Spatial patterns of species richness of some guilds (e.g. Diet_INS, Diet_OMNI, Hab_FORGEN) were similar to

overall bird richness whereas most other guilds showed idiosyncratic patterns (Fig. S6 in Appendix S3). Abiotic environmental conditions across our study sites were characterized by a mean TEMP of c. 1 °C, almost 440 mm PREC, and a mean absolute ELEV of c. 590 m (Table 1). However, there was a clear spatial trend in TEMP and PREC decreasing from the south to the north (Fig. S7 in Appendix S3). On average, human-modified land cover types covered about 8% of the 500 m radius centred at the site (Table 1), but peaked at some sites with HUMAN $> 70\%$ (Fig. S7). Measures of forest structure and composition also showed a large variation across sites (Fig. S7) with on average 18 woody plant species, a stand biomass of about 493 kg ha $^{-1}$, 3.5 vegetation layers and a canopy openness of 46% (Table 1).

Determinants of overall bird species richness

We examined the direct and indirect effects of predictor variables on overall bird species richness using four SEMs (Fig. 2a–d). In all SEMs, TEMP had the strongest direct (and positive) correlation with BIRDS among all predictor variables followed by HUMAN (positive effect) and ELEV (negative effect) (Fig. 3). The correlation between PREC and BIRDS was statistically not significant and thus removed in the final SEMs (Fig. 2). Among the four forest structure variables, WOODY showed the strongest (positive) effect followed by LAYERS (positive), but BIOMASS and CANOPY were unimportant for BIRDS in the boreal forest (Figs 2a,d & 3). Overall, the results for the overall bird species richness supported our hypotheses except for HUMAN, BIOMASS and CANOPY. The effect of HUMAN was positive (instead of negative) and the strength of BIOMASS and CANOPY was much less pronounced than expected.

Determinants of guild species richness

Simple Pearson correlations between guild species richness and our predictor variables indicated a large variation in the correlations between them (Table S2). SEM models with guild species richness similar in structure to those of BIRDS confirmed this variation of guild-specific responses (Figs S2–S5). Overall, the direction of the relationships between guild richness and abiotic environment (TEMP, PREC, ELEV) and HUMAN were similar to those of BIRDS in most cases although the strength of the correlations varied markedly among guilds (Fig. 4). For instance, TEMP was markedly related to species richness of most guilds, PREC had weak or no correlation to all guilds, ELEV showed the strongest (negative) correlation on long-distance migrants, and HUMAN showed strong positive correlations on most guilds (except carnivores). The local forest structure and composition variables also showed a pronounced variation in their relationships with species richness of the various bird guilds (Fig. 4). Insectivores, old-growth forest specialists, forest generalists, long-distance migrants and winter residents showed strong positive correlations with WOODY, whereas old-growth

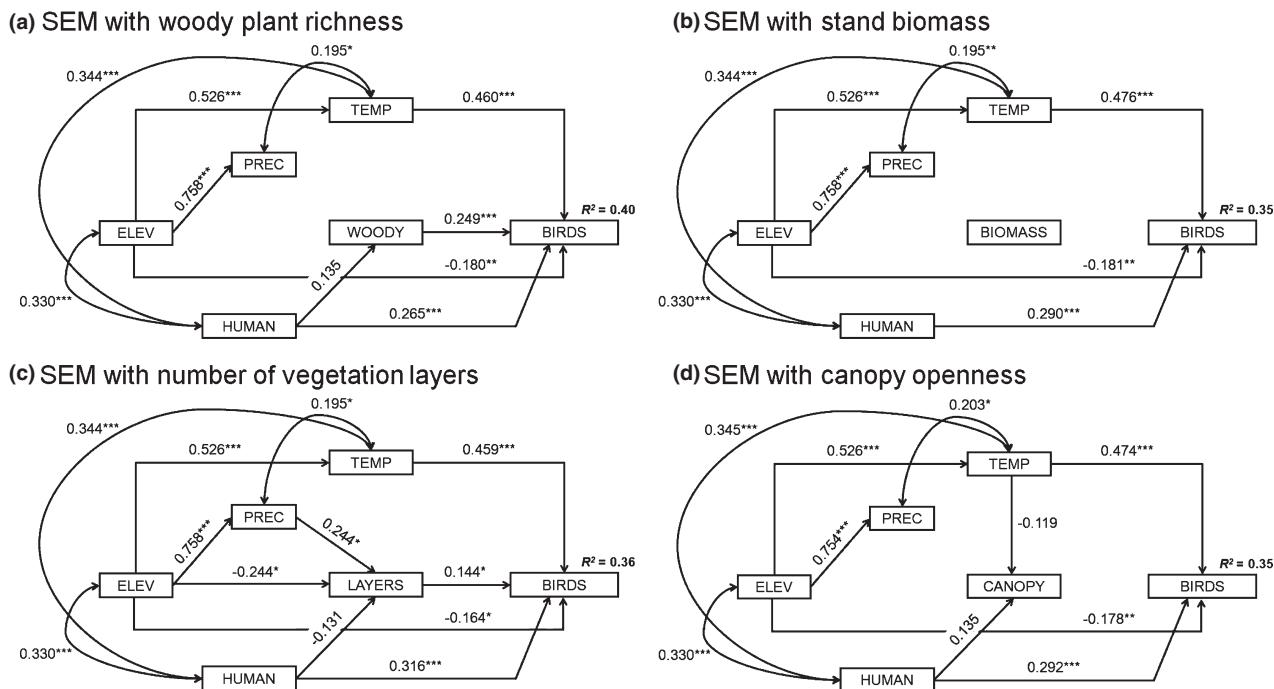


Figure 2 Structural equation models (SEMs) examining the influence of abiotic environment, human land cover, and local forest structure and composition on overall bird species richness in the boreal forest of Alberta. Measures of local forest structure and composition include: (a) woody plant species richness, (b) stand biomass, (c) number of vegetation layers, and (d) canopy openness. Note that the *a priori* structure of all four SEMs was initially the same (see Fig. S1 in Appendix S3), but that non-significant paths were removed and missing error covariances (curved arrows) added to improve model fits. All final SEMs had *P*-values of chi-square tests > 0.1, lower 90% confidence intervals of the root mean square error of approximation equal to 0, and the comparative fit index > 0.98. Straight arrows illustrate standardized path coefficients and their significance levels (**P* < 0.05, ***P* < 0.01, ****P* < 0.001). Abbreviations of variables are explained in Table 1.

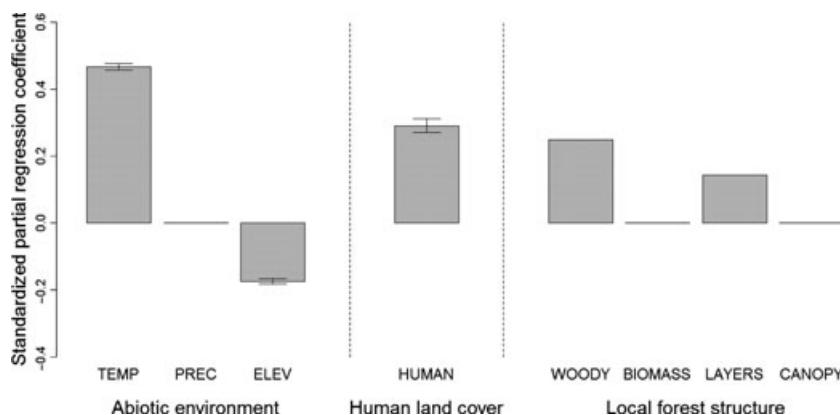


Figure 3 Direct effects of abiotic environment, human land cover and local forest structure and composition on species richness of all birds in the boreal forest study area in Alberta, as derived from structural equation models (SEMs, Fig. 2a–d). Mean ± SD is given for standardized path coefficients of environmental and human predictor variables across four SEMs (Fig. 2a–d). For local forest structure variables only one standardized path coefficient is available (cf. Fig. 2). Abbreviations of variables are explained in Table 1. Other symbols and explanations are as in Fig. 2.

forest specialists and winter residents were strongly related to BIOMASS as well (Fig. 4). LAYERS showed positive correlations with almost all guilds (except carnivores and short-distance migrants), whereas the correlations with CANOPY varied markedly among guilds, with old-growth forest

specialists being most strongly negatively related (Fig. 4). Overall, the results supported the idea that bird guilds with different dietary, habitat and migratory preferences showed differential or contrasting responses to environmental and habitat structure conditions.

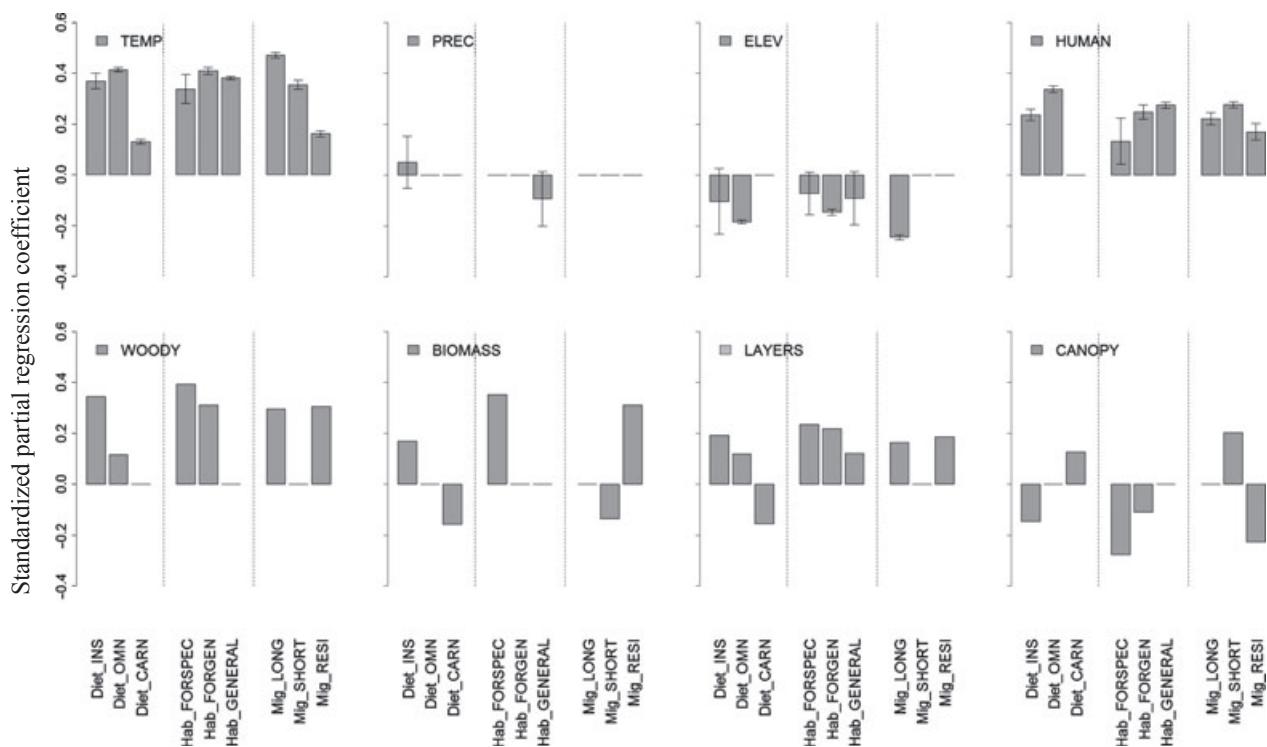


Figure 4 Direct effects of abiotic environment, human land cover, and local forest structure and composition on bird species richness of dietary, habitat, and migratory guilds in the boreal forest, Alberta. Standardized path coefficients are derived from structural equation models (SEMs) similar to those in Fig. 2 where the species richness of birds was replaced by the species richness of guilds (see Figs S2–S5 in Appendix S3). Other symbols and explanations are as in Fig. 3.

Effects of spatial autocorrelation

Some of the non-spatial multiple (OLS) regression models (equivalent to the SEMs) showed a statistically significant spatial autocorrelation structure in model residuals (Table S2a–d in Appendix S2). When spatial regression models (SARs) were used, the spatial autocorrelation structures in species richness were removed as indicated by non-significant Moran's *I* values (Table S2a–d). In almost all cases, the relative importance and ranks of predictor variables, based on standardized partial regression coefficients, did not change between spatial and non-spatial models (Table S2a–d). Therefore, the effects of spatial autocorrelation on the results of our analyses are negligible.

DISCUSSION

Our analyses clearly show that bird species richness patterns in the boreal forest are related to a combination of climate, human land cover, and local forest structure and composition. The importance of these determinants varies markedly among guilds. For instance, our results suggest that some determinants (e.g. forest biomass and canopy openness) are guild-specific, whereas other determinants (e.g. temperature, elevation, human land cover) have similar effects across most guilds. This indicates that the overall response of bird community composition to biotic and abiotic drivers is

guild-specific, suggesting a strong differentiation in behaviour of the guilds and their varied adaptation to different habitats; there is no unified mechanism linking these drivers with species richness.

Among predictor variables, mean annual temperature (TEMP) was found to be a key determinant of bird species richness in the boreal forest across guilds (Figs 3 & 4, S2–S5). These results support the ambient energy hypothesis (Wright, 1983; Hawkins *et al.*, 2003) and suggest that bird diversity at high latitudes is directly controlled via an effect of ambient energy [e.g. temperature or potential evapotranspiration (PET)] at the individual organism level (Currie, 1991; Hawkins *et al.*, 2003). This effect could be mediated via the physiological tolerances of individual species (Hawkins *et al.*, 2003), via an increase of bird population growth and reproduction at high temperatures (Hawkins *et al.*, 2003), or via accelerated evolutionary rates over evolutionary time-scales (Gillman *et al.*, 2012). For some guilds (e.g. winter residents) the direct effects of temperature on species distributions might be even more pronounced if seasonal climatic extremes (e.g. severe winter conditions) are directly considered (Carrascal *et al.*, 2012). Overall, the strong direct effects of temperature on bird richness of almost all guilds indicate that variation in guild species richness in the boreal forest is strongly temperature dependent. This suggests that future climate change (i.e. rising temperatures) is likely to have strong effects on bird guild species richness in the

boreal forest. Compared with other terrestrial ecosystems in the tropics, subtropics, and temperate zones, the boreal forest is expected to experience the greatest increase in temperature (Houghton *et al.*, 1996), which may result in pervasive impacts on temperature-dependent bird distributions (Hitch & Leberg, 2007; Brotons & Jiguet, 2010). In contrast, the direct effect of precipitation in our models was less pronounced (Figs 3 & 4, Figs S2–S5), indicating that climate change in relation to temperature could be more important for boreal bird diversity than precipitation changes. However, future precipitation changes could also act indirectly on bird diversity, e.g. via woody plant richness and forest biomass, and such indirect effects could even occur with strong time-lags (Kissling *et al.*, 2010), making precise predictions of future bird species composition and diversity challenging.

Bird species richness was strongly affected by the footprint of human disturbance, as measured by the percentage of agriculture, forest harvesting, roads, and urban and industrial areas in the surroundings. For almost all guilds, species richness increased with increasing human influence. One possible explanation of this positive (rather than negative) relationship in our study is that most of our study sites have relatively low levels of human land cover (Table 1, Fig. S6). For instance, 78% of study sites have < 10% human land cover and 86% of sites have < 20% human land cover. At such low levels of human disturbance, it is possible that an increase in habitat heterogeneity is positively related to bird species richness. For instance, analyses of northern temperate forest landscapes across Ontario, Canada, show that almost half of the natural land cover can be converted to human-dominated forms before avian richness started to decline (Desrochers *et al.*, 2011), although the abundance of individual species populations can be negatively affected by low levels of anthropogenic land cover (Lepczyk *et al.*, 2008). Another possible explanation of this positive relationship is that human settlements may provide additional food resources for birds (Marzluff, 2001). Also, it is possible that bird species may select environments that are similar to those of humans (Hansen *et al.*, 2011).

In addition to broad-scale climatic gradients and human influence via land cover, local forest structure and composition emerged as an important driver of breeding bird species richness in the boreal forest. We detected a strong and positive relationship between woody plant richness and overall bird richness, supporting previous findings of local (i.e. fine-grained) studies from North America (James & Wamer, 1982) and western Canada (Hobson & Bayne, 2000) and results from broad-scale (i.e. coarse-grained) studies from China (Qian & Kissling, 2010) and Kenya (Kissling *et al.*, 2008). However, there were pronounced differences between bird guilds in the magnitude of responses to plant richness. Among dietary guilds, insectivores showed a much stronger association with WOODY than omnivores and carnivores, possibly because there is a larger number and higher abundance of insect species with increasing plant species richness (Danks & Footit, 1989; Blondel *et al.*, 1991). Among habitat

and migratory guilds, WOODY showed stronger effects on old-growth forest specialists, forest generalists, long-distance migrants and residents than on habitat generalists and short-distance migrants, respectively. Diverse food supplies and more nesting habitats for birds in the forests with high woody plant richness might be the main reason for these positive relationships.

Direct effects of stand biomass on overall bird species richness and most guilds (except old-growth forest specialists and residents) were weak in our study (Figs 3 & 4), suggesting that stand biomass does not strongly limit bird species diversity in the boreal forest of Alberta. These findings appear in contrast to several other studies which find strong effects of stand biomass on species richness of birds (Mitchell *et al.*, 2001; Honkanen *et al.*, 2010; Elo *et al.*, 2012), but are not inconsistent when analysed on the basis of guilds. For guild-specific analyses, we found that stand biomass is a strong determinant of bird species richness of old-growth forest specialists and residents, being even stronger than temperature (Fig. 4). These results are in line with those of Honkanen *et al.* (2010) who found that species richness of old-growth forest specialists and residents in boreal forests of Finland is strongly related to total volume and total growth of trees (compare our results with their results for 'observed species richness'; Honkanen *et al.*, 2010, their Tables 4 and 5). Old-growth forest specialists and residents are further strongly related to woody plant richness (positive), the number of vegetation layers (positive), and canopy openness (negative), suggesting that both guilds predominantly occur in closed and locally undisturbed forests.

The number of vegetation layers and canopy openness played a less important role in determining overall bird species richness although their relative importance was pronounced for some guilds (Fig. 4). The species richness of old-growth forest specialists and forest generalists was most strongly (and positively) related to the number of layers, suggesting that those guilds strongly depend on the vertical structure and diversity of forest habitat (*sensu* MacArthur & MacArthur, 1961). In contrast, canopy openness had a relatively strong negative effect on old-growth forest specialists and residents, especially when compared with the other direct effects in these SEMs (Fig. S5). This highlights that these guilds depend on dense wood stands with little disturbance at a local scale. A possible mechanism could be that structural diversity provides a great array of nesting locations and increases nesting success by reducing the ability of predators to find nests (Cody, 1985). Overall, these results highlight the importance of vegetation structural diversity at a local scale for maintaining variation in bird richness across large spatial extents.

Our findings have wide implications for the prediction of bird community composition, for biodiversity conservation, and for forest management. First, our study highlights the importance of local forest structure and composition (i.e. woody plant richness, forest biomass, number of vegetation layers, and canopy openness) in complementing climate and

land cover as determinants of bird species diversity across large spatial extents. This means that local influences (e.g. via forest management regimes) can substantially affect bird community composition and species richness distribution in addition to, or in conjunction with, broad-scale trends in climate and human disturbance. Second, our study further highlights the importance of spatially fine-grained data for assessing and measuring the relative effects of biotic versus abiotic determinants of species richness across large spatial extents, which might otherwise not be revealed (Field *et al.*, 2009). In contrast to many previous macroecological studies, our analysis at < 1 km² grain size shows that the effect of local habitat structure is readily detectable across large geographical extents.

In conclusion, our findings emphasize that biotic and abiotic determinants of bird species richness depend on spatial grain sizes of sampling units and the life history traits of species. Thus, guidelines for biodiversity conservation and forest management should pay attention to the combined influence of local and regional factors, and to the specific requirements of diverse bird guilds. Beyond diet, habitat preference and migratory behaviour, other traits related to demographic rates, natal and breeding dispersal, competitive abilities or predator avoidance may also need consideration (Blaum *et al.*, 2011; Carnicer *et al.*, 2012). We see great potential for better understanding and predicting spatial variation in bird species richness and community composition by using data on species' traits and life history and by measuring local conditions across large geographical extents.

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SUPPORTING INFORMATION

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

Appendix S1 Species list of breeding birds in the boreal forest of Alberta.

Appendix S2 Pearson correlation coefficients (Table S1) and standardized partial correlation coefficients (Table S2) for all birds and bird guilds.

Appendix S3 Additional figures of structural equation models (SEMs) examining the influences of local forest structure, climate and human disturbance on bird guild richness (Figs S1–S5), and spatial patterns of bird species richness and predictor variables (Figs S6–S7).

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