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Community structure and niche characteristics of upland and lowland western boreal birds at multiple spatial scales

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ABSTRACT

Direct and indirect effects of disturbance may cause the decline of specialist species and alter the condition of ecological communities. We characterized the community structure and niche characteristics (niche position, marginality, breadth) of upland and lowland boreal birds at scales relevant to both natural and human disturbance patterns in western boreal forests undergoing rapid and extensive multi-sector resource development. Our goal was to identify the degree of ecological specialization in order to inform activities directed at conserving a diversity of species (e.g. specialists and generalists) within the western boreal bird community. We used avian data (>5,220 point counts) and environmental variable data comprised of forest composition, stand, and landscape pattern metrics at local (7.1 ha), landscape (1,963 ha), and regional (11,310 ha) scales to determine boreal bird distribution and community-level associations using Canonical Correspondence Analysis (CCA) and Outlying Mean Index (OMI) analysis. OMI analysis explained a high proportion of variance in the dataset (71.8%) and separated boreal birds along two axes associated with moisture–productivity and age–structural complexity gradients. Niche position was influenced by local scale variables (height, age, area of mature-old forest, area of wet soil types), but also landscape and regional scale variables (total area of hardwood and conifer, mean nearest neighbour distance of conifer, and total core area of productive upland conifer). Only 15 of 67 species (22%) had marginal (atypical) niches and narrow niche breadths exhibiting specialization in old hardwood and white spruce forests and burned, open, and lowland habitats. Most species occupied typical or common habitats within the study area and exhibited generalist strategies typical of species in heterogeneous and disturbed habitats that undergo frequent change. Our results suggest the need to design and implement multi-species plans to conserve a diversity of western boreal bird species (e.g. specialists and generalists) at the regional scale.

1. Introduction

Hutchinson's (1957) concept of the realized niche of a species refers to the spectrum of resources and conditions that allows a species to maintain a viable population even in the presence of competitors and predators. A specialist species will utilize a narrow range of resources or environmental conditions within a region while a generalist species will utilize a broad range of resources or conditions. Evidence suggests that specialist species with narrow niches are more likely to occur in homogeneous environments (in space and/or time), while generalist species are more likely to occur in heterogeneous environments (in space and/or time) (Clavel et al., 2011; Devictor et al., 2008). Habitat disturbance and degradation should negatively affect specialist species leading to increased competition with generalists and increased extinction or extirpation risk (Clavel et al., 2011). This sensitivity to change may explain why direct and indirect effects of disturbance may cause the decline of specialist species (Clavel et al., 2011; Devictor et al., 2008, 2010; Julliard et al., 2006). Identifying (1) the degree of species specialization and, (2) the range of habitat conditions where specialist species are found at their highest densities is essential for developing management and conservation actions that maintain a diversity of species (e.g. specialists and generalists) within a community.

Habitat use and selection is thought to occur at multiple scales in a hierarchical framework (Johnson, 1980; Manly et al., 2002). During the breeding season, birds identify and select habitat at

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regional, landscape, and local scales. For example, birds within a population or sub-population may select a region because of the amount or configuration of suitable breeding habitat, the availability of food, and the presence of other breeding individuals (e.g. conspecific attraction), competitors, or predators (Jones, 2001). Individual breeding pairs may select a landscape or stand containing suitable home range habitat (e.g. nesting and foraging habitats). Within a home range, females may select a local site containing a suitable nest location (e.g. nest cover, proximity to perch trees and forage areas, distance from predator activity areas). Multi-scale habitat analyses are needed to identify key habitat variables at each scale and the spatial scale or scales influencing habitat associations for breeding birds. In western boreal forests, the range of habitats available to breeding birds is influenced by the distribution of natural and human disturbances that operate at a range of spatial scales. For example, natural disturbances range from single tree disturbances caused by stem or root disease and defoliating insects to >10,000 ha wildfires, while human disturbances range from 1 to 2 m seismic lines to 3.1 ha well sites to 40–60 ha forest harvest units to >40,000 ha bitumen mine sites. Understanding how the size, frequency, and intensity of disturbances influence habitat associations is critical because the pattern of natural and human disturbances in the western boreal has created a heterogeneous habitat mosaic composed of both natural openings and human-caused linear and polygonal stressors. We suggest that maintaining avian biodiversity in the western boreal will require documenting species–environment relationships in many community types and examining these associations at multiple spatial scales (Grand and Cushman, 2003; Jones, 2001; Kotliar and Wiens, 1990).

Multi-sector resource development in the western boreal is occurring at a rapid rate primarily as a result of industrial forestry, bitumen exploration and extraction, conventional oil and natural gas exploration and development, mineral mining, peat mining, agriculture, and infrastructure development (roads, railways, power and transmission lines, human settlements). In areas with intensive development, such as the Athabasca Oil Sands Area in Alberta, Canada, the density and area of land use stressors represent a gradient of disturbance that is changing the boreal landscape from an intact to a variegated or subdivided landscape (Holloway et al., submitted for publication). As landscape modification increases, additional native vegetation is lost and land use intensity in modified areas increases (Fischer and Lindenmayer, 2007; McIntyre and Hobbs, 1999). Landscape change in forest ecosystems has been correlated with declines in bird diversity and abundance (Andrén, 1992; Drapeau et al., 2000; for a review see Andrén, 1994; Fahrig, 2003). We expect some proportion of both upland and lowland boreal bird species to be threatened by continued landscape modification and the subsequent loss and subdivision of available breeding habitat. Specific mechanisms that may threaten boreal birds include a projected decrease in habitat supply (Mahon et al., 2014), synergistic effects (interactions of stressors) that increase the rate of species loss (Brown et al., 2013; Darling and Côté, 2008; Holloway et al., submitted for publication), and community shifts that replace specialist species with generalist species (e.g. biotic homogenization; Clavel et al., 2011; Julliard et al., 2006; Olden, 2006). Identifying specialist species found in the western boreal will allow land managers and conservation scientists to prioritize the monitoring, scientific study, and conservation initiatives of sensitive species which may be at higher risk of population declines, extinction, or extirpation.

In this paper we use the ecological concepts defined by Hutchinson to characterize the community structure and niche characteristics of both upland and lowland western boreal birds at scales relevant to both natural and human disturbance patterns in western boreal forests. Although several studies have focussed on the abundance (Sólymos et al., 2013), habitat associations (Cumming et al., 2014), and climate change impacts (Stralberg et al., 2015) of individual boreal species at local scales, there have been few attempts to describe and characterize community and habitat associations for boreal species at multiple spatial scales (but see Rempel, 2007). We characterized and compared boreal bird species using community structure and niche characteristics including niche position, breadth, and marginality. We define niche position as the typical conditions used by a species (Gregory and Gaston, 2000) which reflect the extreme or average nature of habitats used by the species relative to those available in the region. Niche marginality is used to describe niche position: species with marginal niches occur in atypical, specialized, or uncommon habitats within a region and species with non-marginal niches occur in typical or common habitats within a region. We define niche breadth (species tolerance) as the range of habitat conditions or the length of the environmental gradient over which the species occurs. Low values of species tolerance mean that a species is distributed across habitats with a limited range of environmental conditions (specialist species), while high values mean that a species is distributed across habitats with widely varying environmental conditions (generalist species). We suggest that these measures are critical to describing the western boreal bird community and have important implications for conservation biology. Niche width and niche marginality are associated with specialization along specific habitat or environmental gradients and can be used to identify specialist and generalist species within a community.

Our primary objective was to (1) describe the community structure of the boreal bird community in northern Alberta, Canada using species density and environmental variables summarized at local (7.1 ha), landscape (1,963 ha), and regional (11,310 ha) scales; and (2) describe the niche characteristics (position, breadth, marginality) of the boreal bird community to assess species specialization. We used data on vegetation structure and condition (composition metrics), stand characteristics (stand metrics), and landscape pattern (landscape pattern metrics) at local, landscape, and regional scales defined by animal (e.g. core area and territory sizes) and habitat structure data (e.g. natural disturbances like wildfire and human disturbances like well sites and aggregated harvest units). We determined boreal bird species distribution and community associations in a series of multivariate ordination analyses (Canonical Correspondence Analysis and Outlying Mean Index).

2. Methods

2.1. Study area

The Joint Oil Sands Monitoring area is comprised of three primary oil sands areas (hereafter OSA) located in Alberta, Canada (Athabasca, Cold Lake, and Peace River oil sands areas; Fig. 1). The OSA (107,000 km^2) encompasses the Boreal Plains ecozone and includes the Boreal Forest natural region. Natural subregions within the Boreal Forest natural region include the Central Mixedwood, Dry Mixedwood, Wetland Mixedwood, and Peace River Lowlands which are characterized by the Boreal Mixedwood ecological area (Beckingham and Archibald, 1996). The study area encompasses 36% of the Boreal Forest natural region in central and northern Alberta representing the range of ecological sites and natural and human-associated disturbances that exist within central and northern Alberta. Summer (May, June, July, August) mean temperature ranges from 7.2 to 20.2 °C and mean total precipitation is 2.4 cm. Within the Boreal Mixedwood, mesic sites in upland areas are dominated by mixed stands of trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). Beaked hazelnut (*Corylus cornuta*), prickly rose (*Rosa acicularis*), low-bush

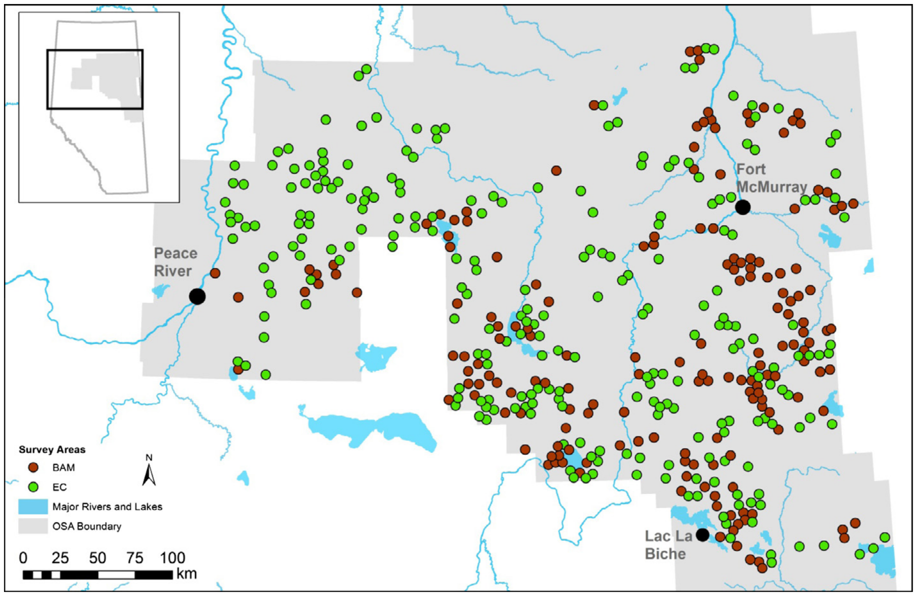

Fig. 1. The Joint Oil Sands Monitoring area is comprised of three primary oil sands areas located in northern Alberta, Canada (Peace River, Athabasca, and Cold Lake oil sands areas), which combined represent the oil sands area (OSA). Across the OSA region, 5,224 point counts were conducted between 2000 and 2013 within 419 survey areas by Environment Canada (EC) or Boreal Avian Modelling Project (BAM).

cranberry (*Viburnum edule*), Saskatoon (*Amelanchier alnifolia*), and twin-flower (*Linnaea borealis*) are typical understory shrubs while bunchberry (*Cornus canadensis*), wild sarsaparilla (*Aralia nudicaulis*), and dewberry (*Rubus pubescens*) are common forbs. Drier upland sites are dominated by jack pine (*Pinus banksiana*) with understory vegetation dominated by blueberry (*Vaccinium myrtilloides*), bearberry (*Arctostaphylos uva-ursi*), and reindeer lichens (*Cladina* species). Lowland areas are composed of wetlands in the form of marshes, treed swamps, and black spruce (*Picea mariana*) and tamarack (*Larix laricina*) dominated bogs and fens. Treed and shrubby bogs and fens are characterized by stunted tree growth and typical bog-type organic matter (peat moss) and fen-type organic matter (sedges, golden moss, tufted moss, and brown moss) (Beckingham and Archibald, 1996). The habitat composition of the western boreal is heterogeneous, typically comprised of a patchwork pattern of upland and lowland habitats. Within our study area, the mean size for the 41 identified habitat types (see Section 2.2 for details) was 10.8 ha (SE = 0.1; Fig. 1).

Within the OSA resource development is diverse, intensive at local scales, extensive at regional scales, and occurring at a rapid rate. Industrial forest harvesting and large-scale oil sands development involving bitumen exploration (seismic lines, pipelines, exploration well sites, industrial sites), extraction (mines, production well sites, pipelines, facilities associated with in-situ sites like Steam Assisted Gravity Drainage), and infrastructure construction (roads, railways, transmission and power lines, human settlements) are the two key resource sectors within the OSA. The operational forest harvesting within the Forest Management Agreements within the OSA is within its first forest rotation (rotation age is the number of years required to establish and grow trees to maturity) although planning to identify harvest levels (annual allowable cut) is being conducted for a period equivalent to two forest rotations (200 years).

2.2. Survey area selection, point count selection, and avian surveys-Environment Canada

We followed the steps outlined below to identify survey areas and collect avian survey data. First, we created a habitat classification system to describe, classify, and stratify habitat types within the OSA study area using Enhanced Alberta Vegetation Inventory data and Ducks Unlimited Wetland Inventory data (Appendices A–C). The Enhanced Alberta Vegetation Inventory is a forest resource inventory database provided by Alberta Environment and Sustainable Resource Development that is used for resource industry and land-use planning applications within Alberta. The inventory is created by interpreting medium-scale (1:60,000 or 1:40,000) aerial photographs to map vegetation cover types and determine the origin year (age) in forested stands and other vegetated and non-vegetated cover types. Vegetation plots, air calls (low elevation over-flights of area to be mapped), and past plots and surveys (temporary or permanent sample plots, regeneration surveys) are also used as information sources to map current vegetation conditions (Alberta Sustainable Resource and Development, 2005). Classification error is unknown but potential map classification errors exist for the two spruce-dominated forest types: white spruce and black spruce (upland black spruce and lowland black spruce or treed bog forest types). The vegetation inventory was used to derive forest stand and habitat type boundaries (polygons), forest type (composition), and forest age. Given limitations with the classification of subhygric–hygric forest types, wet areas were identified using the Ducks Unlimited Wetland Inventory, a proprietary spatial layer created by Ducks Unlimited, primarily for the purpose of identifying wetland habitats suitable for waterfowl. Forest polygons were reclassified to wet (subhygric–hygric) or lowland habitat types if >50% of forest polygons overlapped with bog, fen, or swamp habitat classes identified from this spatial layer.

The habitat classification system was developed to be comprehensive, both with respect to the range of ecological associations that occur in the OSA and the range of vegetation attributes that describe these areas. Classification was driven by two key habitat-related factors known to affect avian occurrence and abundance: (1) stand-level vegetation associations, and (2) structural stage. Based on vegetation associations (defined by forest composition and non-forested land categories), 12 vegetation types were identified (Appendix A). Wetland vegetation types followed the guidance of the Alberta Wetland Inventory Classification System (Halsey et al., 2004). For upland vegetation types, six structural stages based on forest stand development stages were defined using stand age (Appendix B). For lowland and non-forested

Table 1
Representation of current avian point count data and habitats within the oil sands areas (OSA) of Alberta, Canada.

Vegetation type	Habitat type	Representation of point counts		Representation of habitat types	
		Total point count sites	% of total point count sites	Area in OSA	% of area in OSA
Pine	Pine-pole sapling	83	1.3	135083.8	1.4
	Pine-young	113	1.8	281272.2	3.0
	Pine-mature	140	2.2	173895.8	1.8
	Pine-old	74	1.2	64859.7	0.7
Upland black spruce	Upland black spruce-pole sapling	10	0.2	16926.8	0.2
	Upland black spruce-young	26	0.4	73371.7	0.8
	Upland black spruce-mature	56	0.9	118459.0	1.2
	Upland black spruce-old	111	1.8	166907.7	1.8
White spruce	White spruce-pole sapling	8	0.1	5874.6	0.1
	White spruce-young	28	0.5	40411.0	0.4
	White spruce-mature	20	0.3	64704.6	0.7
	White-spruce-old	287	4.6	368670.8	3.9
Deciduous (mesic and hygric)	Deciduous-pole sapling	95	1.5	142093.6	1.5
	Deciduous-young	38	1.6	100155.0	1.1
	Deciduous-mature	727	11.6	1053650.6	11.0
	Deciduous-old	1393	22.2	1069442.7	11.2
Mixedwood (mesic and hygric)	Mixedwood-pole sapling	27	0.4	35742.9	0.4
	Mixedwood-young	19	0.3	15801.7	0.2
	Mixedwood-mature	80	1.3	124521.5	1.3
	Mixedwood-old	326	5.2	319260.9	3.3
Black spruce bog	Bog-open	4	0.1	20842.8	0.2
	Bog-shrub	681	10.8	1630425.9	17.1
	Bog-treed	409	6.5	969872.8	10.2
Larch fen	Fen-shrub	104	1.7	258330.7	2.7
	Fen-treed	123	2.0	359324.7	3.8
Swamp		150	2.4	769776.8	8.1
Marsh		4	0.1	15577.1	0.2
Shrubland		26	0.4	53376.7	0.6
Grassland		38	0.6	86579.8	0.9
Harvest	Harvest-herb[a]	150	2.4	97427.4	1.0
	Harvest-shrub[b]	305	1.3	135083.8	1.4
Burn	Burn-herb[c]	98	1.6	237757.7	2.5
	Burn-shrub[d]	538	8.6	532827.0	5.6

[a] Harvest-herb is harvest units 0–10 yrs old.
[b] Harvest-shrub is harvest units 11–20 yrs old.
[c] Burn-herb is wildfire 0–10 yrs old.
[d] Burn-shrub is wildfire 11–20 yrs old.

vegetation types, structural stages were defined as herb, shrub ($\leqslant$6 m), or treed ($\geqslant$6 m; Appendix C). A total of 41 habitat types were identified and mapped within the OSA (including dry and wet deciduous and mixedwood vegetation types).

Second, we conducted a representation analysis to (1) identify data gaps in the current avian data sets, and (2) determine the sampling intensity/effort per habitat type for 2012 and 2013 sampling plans. We first acquired the spatial locations of existing or historical point counts using the following data sources: Environment Canada, Boreal Avian Modelling Project, and Alberta Biodiversity Monitoring Institute. Since our objective was to assess which habitat types were generally under-represented in the current avian data repository, we selected a sub-set of the assembled point count data that met the following criteria: (1) a point count site was a 150 m radius circle (point count area = 7.1 ha) with no spatial overlap from adjacent point count sites; (2) vegetation inventory data was required for a minimum of 50% of the point count area; and (3) one habitat type comprised $\geqslant$50% of the point count area. Existing avian point count data was concentrated in mature and old deciduous habitat types (32% of avian point counts), old mixedwood and white spruce habitat types (5% of avian point counts), and black-spruce dominated lowland habitat types (treed and shrub; 17% of avian point counts). Given the disproportionate sampling effort among the 41 habitat types within the OSA (Table 1), sampling was targeted to (1) align the proportion of point counts per habitat type with the proportional area of each habitat type in the OSA (e.g. representation of each habitat type within the OSA), and/or (2) obtain at least 100 point count sites within each habitat type.

Third, we selected survey areas and point count sites to meet targeted sampling objectives in 2012 and 2013 by identifying large polygons of under-represented habitat types. We identified survey areas for sampling based on the (1) geographic location within the OSA; (2) accessibility based on the presence of roads and other linear features (e.g. seismic lines, pipelines, transmission lines); and (3) availability of vegetation inventory data. Survey areas were designed to cluster point count sites within one area to maximize sampling efficiency and minimize safety risks for field staff (Fig. 2). For ground-based sampling, an area was considered road accessible if it was within 7.5 km from an improved and/or maintained road (including major highways, paved roads, gravel roads, forestry access roads, energy access roads). Ground-based survey areas were 2,500 m radius circles and could be surveyed by two observers (total area = 1,963 ha). For helicopter-based sampling, an area was considered accessible by air if the centre of the survey area was located within a 120 km distance of the helicopter base location (e.g. Fort McMurray or Red Earth, Alberta, Canada) and suitable drop-off and pick-up locations could be located within the survey area. Helicopter-based survey areas were 5,000 m radius circles and could be surveyed by three observers (total area = 7,850 ha). We identified point count sites (spatial location of point count survey) and survey routes within each survey area by identifying habitat polygons >7 ha (minimum size required to accommodate a point count site with a radius of 150 m and a 25 m edge buffer distance) and placing point count sites in target habitat types and non-target habitat types to create continuous survey routes for each individual observer (e.g. a route of 8–12 point count sites was surveyed by one observer in one day). The

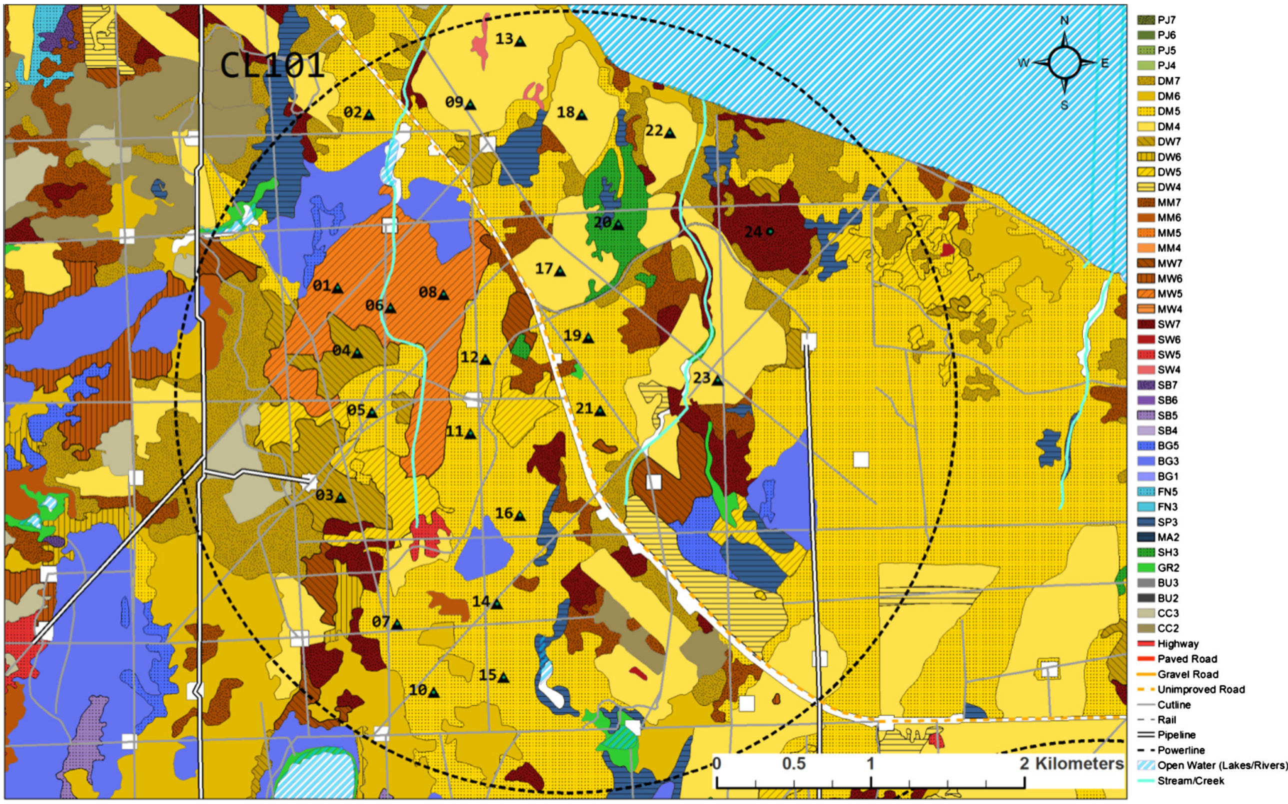

Fig. 2. Environment Canada field map showing the survey area boundary (2,500 m radius circle), habitat type and human footprint mapping, and clustered point count site locations. Up to 24 candidate point count sites were selected in each survey area to facilitate sampling by two independent observers. Point count sites were typically placed in the centre of small habitat patches (▲ for target habitat types; ● for non-target habitat types). Habitat type codes can be found in Appendix A.

majority of point count sites were placed entirely within one habitat type, but for rare habitat types, point count sites were positioned so that the target habitat type comprised a minimum of 75% of the 150 m radius circle (see Fig. 2). Within each ground-based survey area, we created a total of four survey routes to accommodate two observers over a maximum of two sampling days. Within each helicopter-based survey area, we created a total of six survey routes to accommodate three observers over a maximum of two sampling days.

Fourth, we conducted avian sampling within ground-based and helicopter-based survey areas during the 2012 and 2013 field seasons. Each observer walked a survey route in a pre-defined direction conducting surveys at designated point count sites separated by a minimum of 300 m within a survey area. Surveys were conducted during suitable weather conditions between official sunrise and 4–5 h after sunrise from the last week of May to the first week of July. Each observer conducted 8–12 point counts using a 10 min point count methodology where the point count was divided into three count periods (1–3 min, 3–5 min, and 5–10 min) to assess time to detection, and three distance bands (0–50 m, 50–100 m, and >100 m) to conduct distance sampling. This point count methodology follows standard recommended protocols (Matsuoka et al., 2014; Ralph et al., 1993, 1995).

2.3. Survey area selection, point count selection, and avian surveys-Boreal Avian Modelling Project

We obtained avian point count data compiled by the Boreal Avian Modelling Project within the OSA for the period 2000–2012. This large data set is a compilation of project-specific avian point count data from a variety of sources (North American breeding bird survey, academia, government, industry). A large proportion of the compiled data set (>70%) was collected between 2002 and 2004 so we backcasted the current 2013 vegetation inventory to 2003 and used this new vegetation inventory layer to extract and summarize composition, structure, and habitat polygon variables from the Enhanced Alberta Vegetation Inventory database for all point count sites with survey years between 2000 and 2004. To backcast the vegetation inventory to 2003 we (1) reset the stand age to be relative to 2003, (2) removed any forest harvesting, wildfire polygons, and other disturbances which occurred after 2003, and (3) reset the original stand composition. We followed the steps outlined below to identify survey areas and off-road point counts for use in our analysis.

First, we screened the compiled point count data for spatial overlap, temporal independence, and the availability of vegetation inventory data using the following criteria: (1) each point count site was an off-road point count separated by ⩾300 m; (2) vegetation inventory data was required for a minimum of 75% of the point count area (7.1 ha); (3) point counts for the most recent year were included for projects with time series data; and (4) any point count sites overlapping with Environment Canada point count sites were excluded. Second, we screened the point count data compiled in step one above using the following criteria: (1) at the 150 m radius scale, one habitat type had to comprise a minimum of 50% of the point count area (e.g. >3.53 ha); (2) at the 75 m radius scale, one habitat type had to comprise a minimum of 75% of the point count area (e.g. >1.05 ha) with the exception of conifer-dominated mixedwoods (stand composition 50–70% conifer) adjacent to white spruce stands of the same structural stage, and hardwood-dominated mixedwoods (stand composition 50–70% hardwood) adjacent to deciduous stands of the same structural stage; and (3) point counts where post-burn salvage harvesting occurred were removed (i.e. habitat type influenced by both fire and forest harvesting). This screening procedure enabled us to include point counts in similar habitat types and exclude the limited number of point counts (<100) in areas modified by more than two disturbance activities. We grouped point count sites from individual projects into survey areas (2,500 m radius circles) to ensure consistent methodologies were used for all point counts in the survey area.

This screening process resulted in a final analysis data set (Environment Canada and Boreal Avian Modelling Project) of 5,224 point count sites across 419 survey areas (246 survey areas sampled by EC and 173 survey areas from the BAM data set; Fig. 1). At a point count level, the analysis data set contained 3,491 point count sites collected by Environment Canada between 2012 and 2013, 1,616 point count sites sampled between 2000 and 2004 from the compiled BAM data set, and 117 point count sites sampled in 2011–2012 from the compiled BAM data set.

2.4. Local, landscape, and regional attributes

For each point count site (Environment Canada and Boreal Avian Modelling Project), we summarized environmental variables (composition metrics, stand metrics, landscape pattern metrics; Table 2) at local, landscape, and regional scales. We used animal and habitat structure data to define our three spatial scales (Wheatley and Johnson, 2009). The three scales examined were: (1) a 150 m radius circle (7.1 ha) centred on the point count site (hereafter local scale), an area comparable to landbird core area or territory sizes and small human disturbances like well sites in the region, (2) a 2,500 m radius circle (1,963 ha) centred on the point count site (hereafter landscape scale), an area comparable to small wildfires and aggregated harvest units in the region, and (3) a 6,000 m radius circle (11,310 ha) centred on each survey area (hereafter regional scale), an area comparable to large wildfires in the region (Wang and Cumming, 2010). The original helicopter survey areas used for field sampling (5,000 m radius circles) were modified in the analysis to ensure that each survey area represented a similar maximum potential sampling area (1,963 ha).

We first conducted an exploratory CART (Classification and Regression Tree) analysis to identify structured depictions of the key factors influencing species abundances and to evaluate the contribution of habitat types and vegetation composition variables. Based on our CART classification results and vegetation community descriptions for the western boreal (Rettie et al., 1997), we collapsed our 41 habitat types into 12 habitat classes (Table 3): white spruce/balsam fir (SWFB); trembling aspen/white birch (AWBW); balsam poplar (PB); black spruce/larch lowlands (LWLD); black spruce/uplands (SBUP), pine uplands (PINE); harvest unit (YGCC); burn (YGBU); open/non-forested (OPNF); open water (OPWA); and two anthropogenic categories, ANVG (vegetated human footprint, including seismic lines, pipelines) and ANHS (hard surface human footprint including industrial facilities, paved and gravel roads). We used these habitat classes to describe areas with consistent habitat characteristics for stand metrics at the landscape scale. At the regional scale, we further reduced habitat classes into eight habitat patch types: white spruce/balsam fir (SWFB); hardwood (combined trembling aspen, white birch and balsam poplar; HDWD); black spruce/larch lowlands (LWLD); combined black spruce/pine uplands (CON2); harvest unit (YGCC); burn (YGBU); open/non-forested (OPNF); and open water (OPWA). We collapsed hardwood species and upland-associated black spruce and pine because ordination results (see Ordination Analysis below), indicated that these habitats were strongly associated with respect to the bird species assemblages and environmental predictors. We used these habitat patch types to describe areas with consistent habitat characteristics for stand metrics and landscape pattern metrics at the regional scale.

We extracted vegetation composition metrics, stand metrics (Cumming and Vernier, 2002), and landscape pattern metrics (Wang and Cumming, 2010, 2011) for each point count site (see Table 2). At the local scale, we used the vegetation inventory data to extract vegetation composition metrics (Table 2). At the landscape scale, we used the vegetation inventory to extract a reduced subset of five vegetation composition metrics, and the 12 habitat classes to extract three stand metrics (total habitat area, mean habitat size, and standard deviation of habitat size). At the regional scale, we used the eight habitat patch types to extract the same three stand metrics and three landscape pattern metrics (normalized total core area, normalized mean shape index, and normalized mean nearest neighbour distance; Table 2). Stand and landscape pattern metrics followed the guidance of Cumming and Vernier (2002) and Wang and Cumming (2011). Total core area was calculated by applying a 25 m buffer to all habitat patch type polygons (Harper et al., 2004; López et al., 2006), while the mean nearest neighbour distance calculation was based on the average nearest neighbour tool in the spatial statistic extension in ArcGIS 10.2. Normalized metrics reduced correlations with habitat abundance in natural landscapes (Wang and Cumming, 2011). We also calculated the northing and easting coordinates associated with the centroid of each survey area to account for spatial location and any field sampling biases. All environmental, vegetation composition metrics, stand metrics, and landscape pattern metrics detailed above were extracted using Python scripting and ArcGIS 10.2.

2.5. Data analysis-standardizing bird species data

The Boreal Avian Modelling Project point count data is a heterogeneous data set where survey protocols varied among individual projects (Matsuoka et al., 2014). Point count survey effort varied with count period (e.g. 3 min, 5 min, or 10 min) and count radius (e.g. 50 m, 100 m, or unlimited). In this analysis, we only considered BAM point counts which were a minimum of 5 min, and had either 100 m or unlimited count radii to minimize the variability in field sampling protocols. However, because raw counts of birds typically increase with both count duration and count radius we used a new density estimator (Sólymos et al., 2013) to adjust raw counts for all point count data to control for the effects of survey protocol and temporal (date, time) and environmental (vegetation) covariates on detection probabilities. Left uncontrolled, these differences in avian counts due to protocol could obscure temporal and habitat-based trends in abundance. This density estimator (Sólymos et al., 2013) adjusts raw counts of avian relative abundance to density and accounts for two forms of detection bias: singing rate or the probability that a bird is singing (p) using a removal model, and detection distance or the probability of detecting a bird at distance r from the observer given that the bird is singing (q) using distance estimation. The raw counts were standardized by the density estimator where:

$$x_{ij}/\exp(y_{ij})$$

where x_{ij} = count for species i in site j, and y_{ij} = density estimator for species i in site j.

Species density estimators have not been calculated for some bird species groups, including all woodpeckers, Ruffed Grouse (*Bonasa umbellus*), and wetland associated waterbirds [Sandhill Crane (*Grus canadensis*)], and shorebirds [includes Greater Yellowlegs (*Tringa melanoleuca*), Wilson's Snipe (*Gallinago delicata*)]. As a result, raw counts were used in the analysis for these species.

2.6. Data analysis-ordination analyses

Initially, we combined all data sets and created two matrices for the ordination analyses: (1) a species matrix and (2) an environmental predictor matrix. The species matrix included 67 species

Table 2
Variable type, name, and description for composition metrics, stand metrics, and landscape pattern metrics at local (150 m/7.1 ha), landscape (2,500 m/1,963 ha), and regional (6,000 m/11,310 ha) scales. Composition metrics were calculated using forest habitat types.[a] Stand metrics and landscape pattern metrics were calculated using habitat classes at the landscape scale and habitat patch types at the regional scale.

Scale	Variable type	Variable name	Variable description
Survey area	Geography	Easting X_SA	Alberta map grid easting coordinate at the centre of each survey area
		Northing Y_SA	Alberta map grid northing coordinate at the centre of each survey area
Study area	Year	Survey year	Year of point count survey (2000–2004; 2011–2013)
Local (150 m)	Composition metric	WtAge	Area-weighted average age of a forest polygon
		MaxAge	Maximum age of a forest polygon
		SDAge	Standard deviation of the age of a forest polygon
		WtHeight	Area-weighted average height of a forest polygon
		PArea_AWBW	Proportion area of leading species within a forest polygon: trembling aspen/white birch (AWBW); balsam poplar (PB); white spruce (SW); jack pine (PJ); upland black spruce (SBU); lowland black spruce (SBL); larch (LT)
		PArea_PB	
		PArea_SW	
		PArea_PJ	
		PArea_SBU	
		PArea_SBL	
		PArea_LT	
		PArea_BURN	Proportion area of non-forested habitats: burn (BURN); harvest unit (HARV); bog or fen (BgFn); rich bog or fen (RBgFn); non-forested areas including shrubland, grassland, bog-open, marsh, swamp (NFor); open water (Wat)
		PArea_HARV	
		PArea_BgFn	
		PArea_RBgFn	
		PArea_NFor	
		PArea_Wat	
		PArea_For	Proportion area of forest
		PArea_YgFor	Proportion area of young forest <20 years old
		PArea_MOFor	Proportion area of mature and old forest. Includes forest stands >60 years for deciduous forests, >80 years for pine, white spruce, black spruce forests, and >90 years for treed bogs and fens
		PArea_CC	Proportion area of each crown closure class. Crown closure categories are: A = 6–30% (CC1); B = 31–50% (CC2); C = 51–70% (CC3); D = 71–100% (CC4)
		PArea_Wet	Proportion area of each soil regime category. Soil regime categories are: dry, mesic, or wet
		Harvest	Identifier of stand origin
		Burn	Factorial variable identifying the origin of forest stands where harvest = stand originating after forest harvest or burn = stand originating after wildfire
Landscape (2,500 m)	Composition metric	WtAge	Area-weighted average age of a forest polygon
		MaxAge	Maximum age of a forest polygon
		PArea_For	Proportion area of forest
		PArea_YgFor	Proportion area of young forest <20 years old
		PArea_MOFor	Proportion area of mature and old forest. Includes forest stands >60 years for deciduous forests, >80 years for pine, white spruce, black spruce forests, and >90 years for treed bogs and fens
	Stand metric	THA	Total habitat area. Total area of each habitat class (ha)
		MPS	Mean habitat size. Mean size of each habitat class (ha)
		PSSD	Standard deviation of size of each habitat class
Regional (6,000 m)	Stand metric	THA	Total habitat patch type area. Total area of each habitat patch type (ha)
		MPS	Mean habitat patch size. Mean patch size of each habitat patch type (ha)
		PSSD	Standard deviation of size of each habitat patch type
	Landscape pattern metric	NTCA	Normalized total core area. A measure of compactness. Sum of the core area for habitat patch types
		NMNN	Normalized mean nearest neighbour distance. A measure of spatial dispersion. Nearest inter-patch distance is measured as the minimum edge-to-edge Euclidian distance between a habitat patch type and its neighbours
		NMSI	Normalized mean shape index. A measure of the mean patch shape for habitat patch types

[a] Excludes shrubby bogs, shrubby fens, and all other non-forested habitats including swamp, marsh, shrubland, grassland, burns.

which occurred in >1% of point counts (minimum of 50 point count sites; all waterfowl species were removed from the data set). The standardized species data was relativized by the maximum value (see McCune and Grace, 2002). This transformation has been shown to be effective in detecting shifts in community composition, especially when the species data is dominated by species with low occurrence (76% of species had a percent occurrence value of <10%). The environmental matrix was comprised of local scale variables (23 composition metric variables), landscape scale variables (five composition metric and three stand metric variables), and regional scale variables (three stand metric and three landscape pattern metric variables). The distribution of all environmental predictors was examined using histograms, and where appropriate variables were square-root or ln-transformed to normalize the distribution of the predictor variable.

Given the large number of predictor variables and the three scales of analysis (local, landscape, and regional), we first conducted Canonical Correspondence Analysis (CCA) to determine the best predictor model set. CCA models were constructed in three iterative steps based on spatial scale and type of variables (defined below). Within each step, highly correlated variables were removed based on the variance inflation factor (VIF; all variables with values >10 were removed; Oksanen, 2009) and a visual examination of CCA plots. In step one, a CCA analysis was conducted for each spatial scale (e.g. local, landscape, and regional), to identify variables which were highly colinear within each spatial scale. This

Table 3
Habitat classes and habitat patch types used in ordination analyses in the oil sands areas (OSA) of Alberta, Canada.

Scale	Habitat classification	Habitat name	Description
Landscape (2,500 m)	Habitat classes	SWFB	White spruce/balsam fir. Stands dominated by white spruce; all ages and crown closure
		AWBW	Trembling aspen/white birch. Stands dominated by trembling aspen; all ages and crown closure
		PB	Balsam poplar. Stands dominated by balsam poplar; all ages and crown closure
		LWLD	Black spruce/larch lowlands. Stands dominated by black spruce in lowland habitat types including bog-shrub, bog-treed, fen-shrub, fen-treed
		SBUP	Black spruce/uplands. Stands dominated by black spruce in upland habitat types including mixed jack pine/black spruce stands, pure black spruce stands
		PINE	Pine uplands. Stands dominated by jack pine; all ages and crown closure
		YGCC	Harvest unit. Regenerating harvest units <20 years
		YGBU	Burn. Regenerating burns <20 years
		OPNF	Open/non-forested. Grassland, shrubland, bog-open, marsh, swamp
		OPWA	Open water. Open surface water
		ANVG	Vegetated human footprint. Vegetated human footprint including seismic lines, pipelines, well sites, transmission lines, cultivated areas
		ANHS	Hard surface human footprint. Hard surface human footprint including industrial facilities, paved and gravel roads, urban areas
Regional (6,000 m)	Habitat patch types	SWFB	As above
		HDWD	Hardwood. Combined stands dominated by trembling aspen, white birch, and balsam poplar
		LWLD	As above
		CON2	Black spruce/pine uplands. Combined stands dominated by upland black spruce and jack pine
		YGCC	As above
		YGBU	As above
		OPNF	As above
		OPWA	As above

analysis revealed high correlation among the three stand metric variables at both the landscape and regional scales. The total area of each habitat showed the strongest relationship (longest arrow on the CCA plot), and as a result, only the total area of each habitat patch was retained.

In step two, the three spatial scales (local, landscape, and regional) were combined. Model one contained all composition metric variables remaining at the local scale, plus all remaining variables at the landscape scale. The local scale composition metric variables were typically the strongest predictors based on an examination of the CCA plot and as a result several stand metrics at the landscape scale were dropped. Model two included all remaining variables in model one, plus all stand metric and landscape pattern metrics at the regional scale. Examination of model two revealed high correlation among the three stand metric and three landscape pattern metric variables for many of the landscape scale habitat classes and regional scale habitat patch types (e.g. total habitat patch area, mean habitat patch size, normalized total core area, normalized mean shape index, and normalized mean nearest neighbour distance). Variables were sequentially removed until all VIF values were <10 (see Table 4 for final CCA model variables).

Finally in step three, we investigated the relative importance of local, landscape, and regional variables using variance partitioning (Borcard et al., 1992; Cushman and McGarigal, 2004;) based on the final CCA model (model two). This analysis measures the variation in a community matrix, explained independently and jointly by different sets of predictor variables. We calculated the unique variation at each level (local, landscape, and regional) by partitioning variation (as a covariate) due to the other levels.

Following the CCA analysis, we performed an Outlying Mean Index (OMI) analysis (Doledec et al., 2000) using the same set of environmental predictors (model two). This technique addresses some of the limitations of other commonly used ordination analyses such as CCA and Redundancy Analysis, which are best suited to specific distributional data types (unimodel and linear respectively for CCA and Redundancy Analysis; Doledec et al., 2000; McCune and Grace, 2002). Moreover, CCA tends to over-emphasize rare species in the ordination results, while the reverse is true of Redundancy Analysis. The OMI approach makes no assumptions about the distribution of species responses to environmental variables, gives equal weight to both species-rich and individual-poor sampling units, and is particularly suited for data sets with low species occurrences (Thuiller et al., 2005; Tsiftsis et al., 2008). OMI analysis determines species marginality, by measuring the distance between the mean habitat condition used by a species (species centroid) and the mean habitat conditions in the study area (origin of the niche hyperspace). OMI analysis determines the magnitude of species habitat distributions where the position of the species depends on their niche deviation from a reference. Species with high OMI index values have marginal niches (occur in atypical, specialized, or uncommon habitats in a region), while those with low OMI index values have non-marginal niches (occur in typical or common habitats in a region). The analysis also determines niche breadth (species tolerance) defined as the range of habitat conditions or the length of the environmental gradient over which the species occurs. Species with low tolerance values indicate a specialist species (species is distributed across habitats with a limited range of environmental conditions). Species with high tolerance values indicate a generalist species (species is distributed across habitats with widely varying environmental conditions). We calculated Spearman's correlations between OMI axes and predictor variables. We also calculated mean adjusted counts across all habitat types for each bird species. We performed all classification, multivariate, and niche analyses using the rpart, vegan, and ade4 packages in R (Version 3.03).

3. Results

3.1. Vegetation ordination and community structure

The CCA ordination explained 31% (axis one) and 28% (axis two) of the variance in the bird community. The ordination results from the CCA and OMI analyses produced similar bird species associations and patterns among the environmental variables examined, and as a result, we included only figures for the OMI analyses (Figs. 3–6). The final CCA analysis included 54 environmental predictors (see Table 4). All habitat classes related to human footprint

Table 4
Final predictor set of environmental variables for Canonical Correspondence Analysis (CCA) and Outlying Mean Index (OMI) analysis including composition metrics, stand metrics, and landscape pattern metrics at local (150 m/7.1 ha), landscape (2,500 m/1,963 ha), and regional (6,000 m/11,310 ha) scales.

Scale	Variable type	Variable name	Variable description
Survey area	Geography	Easting X_SA	Alberta map grid easting coordinate at the centre of each survey area
		Northing Y_SA	Alberta map grid northing coordinate at the centre of each survey area
Study area	Study methodology	Survey year	Year of point count survey (2000–2004; 2011–2013)
		I_PA	Identifier for all point counts associated with Boreal Avian Modelling Project A
		I_PB	Identifier for all point counts associated with Boreal Avian Modelling Project B
		I_PC	Identifier for all point counts associated with Boreal Avian Modelling Project C
Local (150 m)	Composition metric	WtAge[a]	Area-weighted average age of a forest polygon
		WtHeight[a]	Area-weighted average height of a forest polygon
		PArea_AWBW	Proportion area of leading species within a forest polygon: hardwood (HW); white spruce (SW); jack pine (PJ); upland black spruce (SBU); lowland black spruce (SBL); larch (LT)
		PArea_PB	
		PArea_SW	
		PArea_PJ	
		PArea_SBU	
		PArea_SBL	
		PArea_LT	
		PArea_BURN	Proportion area of non-forested habitats: burn (BURN); harvest unit (HARV); bog or fen (BgFn); rich bog or fen (RBgFn); non-forested areas including shrubland, grassland, bog-open, marsh, swamp (NFor); open water (Wat)
		PArea_HARV	
		PArea_BgFn	
		PArea_RBgFn	
		PArea_NFor	
		PArea_Wat	
		PArea_YgFor	Proportion area of young forest <20 years old
		PArea_MOFor	Proportion area of mature and old forest. Includes forest stands >60 years for deciduous forests, >80 years for pine, white spruce, black spruce forests, and >90 years for treed bogs and fens
		PArea_CC1	Proportion area of each crown closure class. Crown closure categories are: A = 6–30% (CC1); B = 31–50% (CC2); C = 51–70% (CC3); D = 71–100% (CC4)
		PArea_CC3	
		PArea_CC4	
		PArea_Wet	Proportion area of each soil regime category. Soil regime categories are: dry, mesic, or wet
		Harvest	Identifier of stand origin. Factorial variable identifying the origin of forest stands where harvest = stand originating after forest harvest
Landscape (2,500 m)	Composition metric	WtAge_Lan	Area-weighted average age of a forest polygon
		MaxAge_Lan	Maximum age of a forest polygon
		PArea_For_Lan	Proportion area of forest
		PArea_YgFor_Lan[a]	Proportion area of young forest <20 years old
		PArea_MOFor_Lan[a]	Proportion area of mature and old forest. Includes forest stands >60 years for deciduous forests, >80 years for pine, white spruce, black spruce forests, and >90 years for treed bogs and fens
	Stand metric	THA_SWFB_Lan[b]	Total habitat area. Total area of each habitat class (ha)
		THA_AWBW_Lan[a]	
		THA_PB_Lan	
		THA_LWLD_Lan[a]	
		THA_SBUP_Lan[b]	
		THA_PINE_Lan[b]	
		THA_YGCC_Lan[b]	
		THA_YGBU_Lan[a]	
		THA_OPNF_Lan[a]	
		MPS_OPNF_Lan[b]	Mean habitat size. Mean patch size of each habitat class (ha)
Regional (6,000 m)	Stand metric	THA_SWFB_Reg[a]	Total habitat patch area. Total area of each habitat patch type (ha)
		THA_HDWD_Reg[a]	
		THA_LWLD_Reg[a]	
		THA_CON2_Reg[a]	
	Landscape pattern metric	NTCA_SWFB_Reg	Normalized total core area. A measure of compactness. Sum of the core area for habitat patch types
		NTCA_CON2_Reg	
		NTCA_OPNF_Reg	
		NMNN_SWFB_Reg	Normalized mean nearest neighbour distance. A measure of spatial dispersion. Nearest inter-patch distance is measured as the minimum edge-to-edge Euclidian distance between a habitat patch type and its neighbours
		NMNN_HDWD_Reg	
		NMNN_CON2_Reg	
		NMNN_OPNF_Reg	
		NMSI_HDWD_Reg	Normalized mean shape index. A measure of the mean patch shape for habitat patch types

[a] Variable square-rooted transformed.
[b] Variable ln transformed.

at the landscape scale (e.g. vegetated human footprint and hard surface human footprint) were removed from the final model due to high colinearity with habitat patch types related to harvesting and wildfires at the regional scale (e.g. harvest unit and burn). Variance partitioning for the CCA analysis indicated that of the explained canonical variance, 44%, 6%, and 12% respectively were

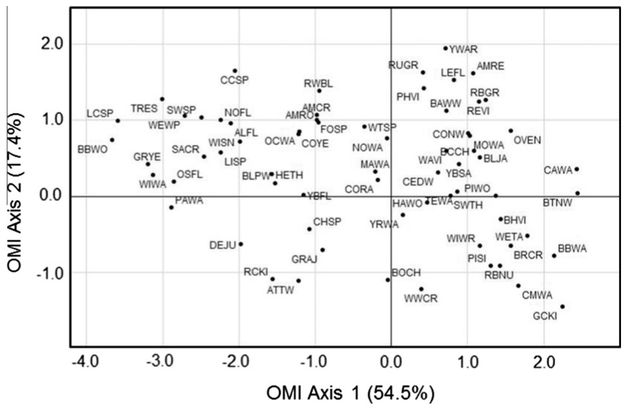

Fig. 3. Weighted positions of boreal bird species along the first two axes of the Outlying Mean Index (OMI) analysis. Species with non-marginal niches (typical habitats) were located near the origin and those with marginal niches (atypical, specialized, uncommon habitats) were located far from the origin. Species are identified by their codes (see Table 5 and Appendix D).

explained by local (150 m), landscape (2,500 m), and regional (6,000 m) scales respectively. The remaining 43% was combined variance (explained by all three spatial scales).

The OMI analysis explained a high proportion of the variance in the data set at 71.9% (54.5% for axis one and 17.4% for axis two; Fig. 3). Axis one of both ordination analyses (CCA and OMI) clearly separated bird species along a moisture–productivity gradient with species associated with high productivity open, graminoid wetland (marshes), and deciduous habitats occurring above the origin and species associated with lower productivity lowland conifer and upland conifer habitat types below the origin (Fig. 4). Productivity refers to site quality which is determined by soil type and condition, moisture regime, nutrient regime, and climatic conditions. Wet or hygric low productivity habitat types (lowland black spruce bogs and fens) and associated species occur to the lower left of the origin while mesic high productivity habitat types (deciduous forests) and associated species occur to the upper right of the origin. Axis two separated birds along an age–structural complexity gradient with species associated with high structural complexity deciduous and conifer habitats to the right of the origin and species associated with low structural complexity open habitats (burns, harvest units, marshes, grasslands, shrublands) and conifer habitats (lowland black spruce bogs and fens, upland black spruce and pine forests) to the left of the origin. Older, structurally complex habitat types (old conifer forest types in the gap phase dynamic stand development stage) and associated species occur to the lower right of the origin while younger or structurally simple habitat types (burns, harvest units, marshes, grasslands, shrublands) and associated species occur to the upper left of the origin. A few species appear as outliers on one or more axes (Fig. 3). The Black-throated Green Warbler and Canada Warbler had high positive scores on axis one (associated with mesic, high productivity

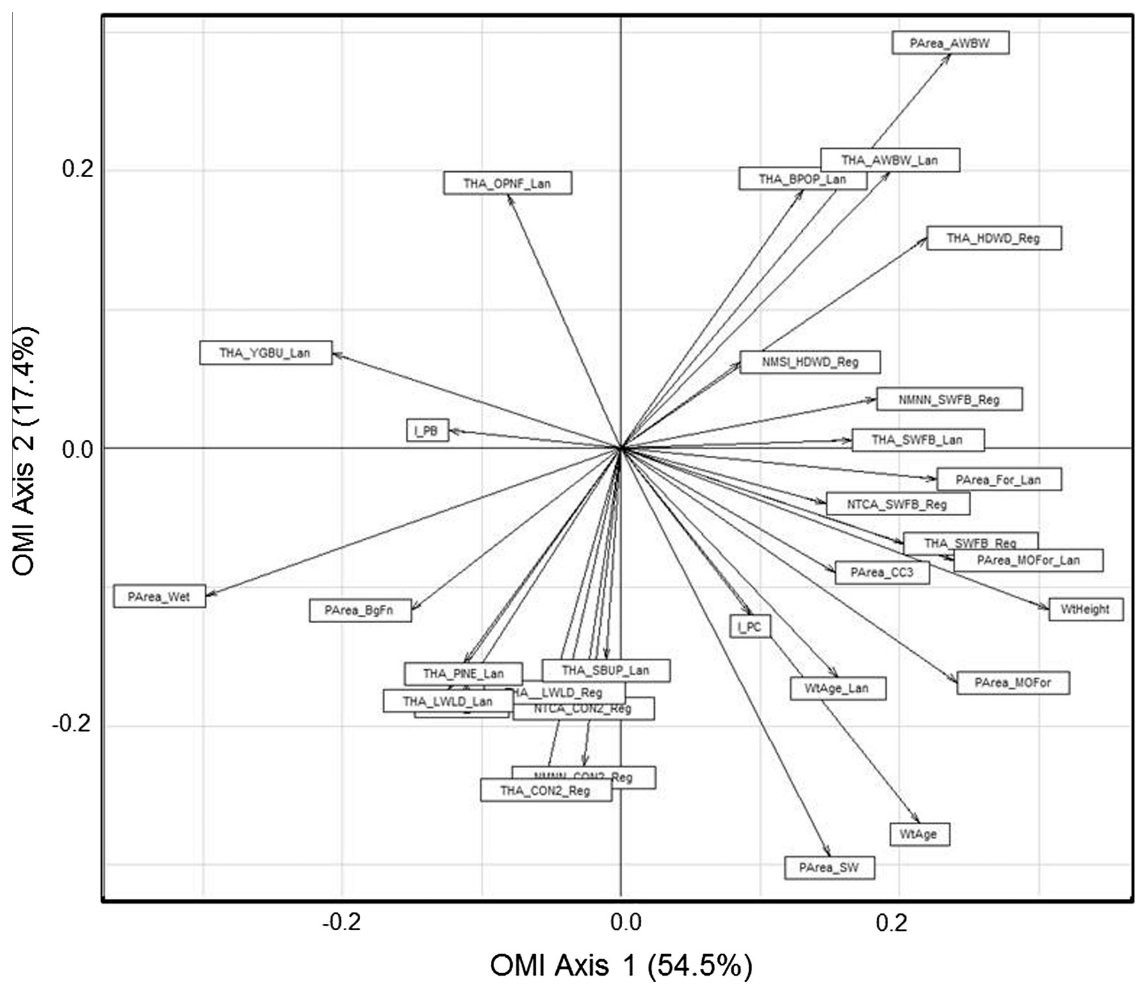

Fig. 4. Canonical weights of the environmental variables used in the Outlying Mean Index (OMI) analysis. For interpretation ease, arrows for environmental variables are only shown for variables which had correlation (r) values of >0.35 for either Axis 1 or Axis 2. The length of the arrow represents the relative importance of each variable in the analysis and the direction of the arrow indicates among-variable correlations. Environmental variables are identified by their codes (see Table 4).

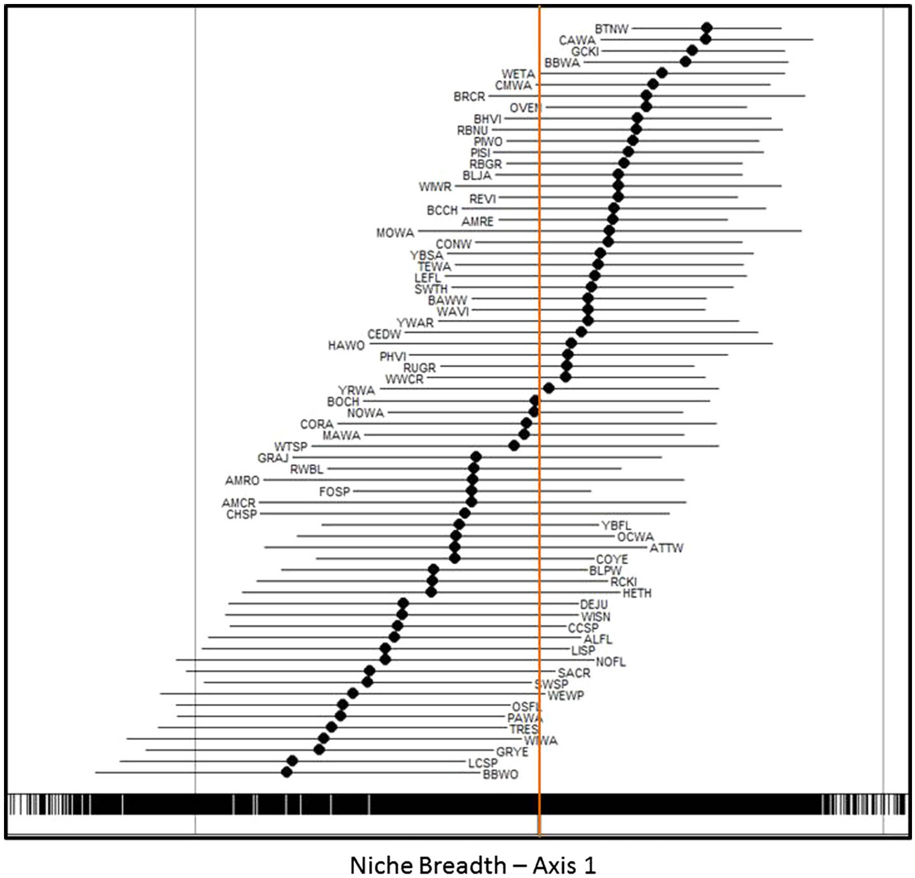

Fig. 5. Outlying Mean Index (OMI) analysis for axis one (moisture–productivity gradient) showing boreal bird species distribution. The black dot indicates the mean habitat condition within the study area for each species. The horizontal line represents the range of habitat conditions (described by the environmental variables) for each species. The vertical orange line represents the origin or the mean habitat condition within the study area. Species are identified by their codes (see Appendix D).

sites like old deciduous and mixedwood forests), while the Palm Warbler had negative scores on axis one (associated with wet, low productivity sites like shrubby black spruce bogs). The Boreal Chickadee had a high positive score on axis two (associated with old, high structural complexity sites like upland conifer forests). Spearman's correlations (>0.50) reveal that axis one was highly and significantly correlated with: five local scale variables [forest height (+0.77), forest age (+0.56), area of mature and old forest (+0.65), area dominated by trembling aspen and white birch (+0.51), area dominated by wet soil regimes (−0.56)]; four landscape scale variables [area of forest cover (+0.61), area of mature and old forest (+0.74), total habitat area dominated by trembling aspen and white birch (+0.54), and total habitat area dominated by white spruce and balsam fir (+0.54)]; and four regional scale variables [total habitat area dominated by hardwoods (+0.65), total habitat area dominated by white spruce and balsam fir (+0.66), mean nearest neighbour distance between polygons dominated by white spruce and balsam fir (+0.59), and total core area of white spruce and balsam fir (+0.52)]. Axis two was highly and significantly correlated with: one local scale variable [forest age (+0.57)] and two regional scale variables [total habitat area dominated by upland black spruce and pine (+0.57) and mean nearest neighbour distance between polygons dominated by upland black spruce and pine (+0.56)].

The position of each bird species along the first two OMI axes indicates niche position and the strength of the relationship between the species (species density) and environmental variables. Species that occur close to the origin show no strong association with environmental variables and have non-marginal niches, while species that occur far from the origin show strong associations with environmental variables and have marginal niches. Species such as Golden-crowned Kinglet (GCKI), Cape May Warbler (CMWA), Bay-breasted Warbler (BBWA), Red-breasted Nuthatch (RBNU), and Brown Creeper (BRCR) were strongly associated with white spruce and balsam fir forests (bottom right of Fig. 3), while species such as Yellow Warbler (YWAR), American Redstart (AMRE), Least Flycatcher (LEFL), Rose-breasted Grosbeak (RBGR), and Ovenbird (OVEN) were strongly associated with hardwood forests (top right of Fig. 3). The Canada Warbler (CAWA) appeared to be strongly associated with old hardwood forests while the Black-throated Green Warbler (BTNW) appeared to be strongly associated with old mixedwood forests (far right of Fig. 3). Several species exhibited strong associations with open/non-forested [Clay-coloured Sparrow (CCSP), Tree Swallow (TRES), Le Conte's Sparrow (LCSP)], burned [Black-backed Woodpecker (BBWO), Greater Yellowlegs (GRYE), Wilson's Warbler (WIWA), and Olive-sided Flycatcher (OSFL)], black spruce lowland habitats [Palm Warbler (PAWA), Dark-eyed Junco (DEJU)] and black spruce upland habitats [Ruby-crowned Kinglet (RCKI), Gray Jay (GRAJ), and American Three-toed Woodpecker (ATTW)]. A large group of bird species associated with mesic or wet non-forested and young forest habitats (e.g. recent and regenerating harvest units, marshes, grasslands, shrublands) exhibited weak habitat associations (top left corner of Fig. 3). For example, the weighted positions of the Red-winged Blackbird (RWBL), Fox Sparrow (FOSP), Orange-crowned Warbler (OCWA), Lincoln's Sparrow (LISP), Alder Flycatcher (ALFL), Northern Flicker (NOFL), Swamp Sparrow (SWSP), and Western Wood Peewee (WEWP) were widely distributed across the top left

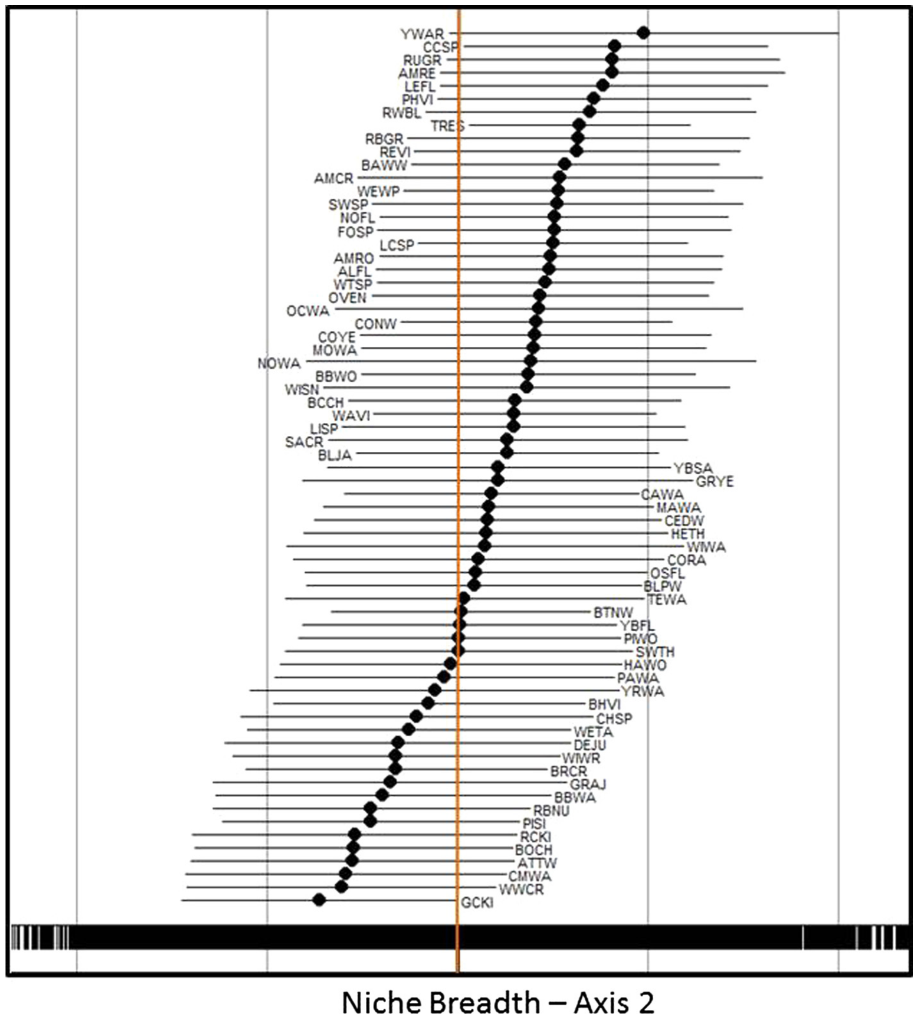

Fig. 6. Outlying Mean Index (OMI) analysis for axis two (age structural-complexity gradient) showing boreal bird species distribution. The black dot indicates the mean habitat condition within the study area for each species. The horizontal line represents the range of habitat conditions (described by the environmental variables) for each species. The vertical orange line represents the origin or the mean habitat condition within the study area. Species are identified by their codes (see Appendix D).

of the OMI plot. In contrast, species such as the White-throated Sparrow (WTSP), Northern Waterthrush (NOWA), Magnolia Warbler (MAWA), Common Raven (CORA), and Yellow-rumped Warbler (YRWA) were not strongly associated with any one habitat type. Across the three analysis scales (local, landscape, and regional), the related variables showed similar patterns and species associations (Fig. 4). For example, variables related to the proportional amount of hardwood forest at different scales [area dominated by trembling aspen at the local scale (PArea_AWBW), total habitat area dominated by trembling aspen and white birch at the landscape scale (THA_AWBW_Lan), and total habitat area dominated by hardwoods at the regional scale (THA_HDWD_Reg); top right corner of Fig. 4] all exhibited similar results.

3.2. Niche characteristics

The OMI analysis revealed that 22% or 15 of 67 species examined showed significant deviation from the mean habitat condition indicating marginal niches (Table 5). The majority of the species examined (78% or 52 of 67 species) had low OMI index values indicating non-marginal niches (typical or common habitats) and high residual tolerance index values suggesting that additional factors strongly affected species distribution. Most of the bird species included in the OMI analysis appeared to exhibit a wide niche breadth (e.g. wide range of conditions occupied by each species as indicated by the length of the horizontal lines for each species in Figs. 5 and 6) although some specialization is evident, particularly for species associated with old forest habitats and burned, open, and lowland habitats. Several bird species exhibited mean habitat conditions (black dot for each species) which deviated significantly from the origin or the mean habitat condition within the study area (vertical line), indicating a significant influence of the variables associated with the moisture–productivity gradient (Table 5 and Fig. 5). These species were split into two groups: (1) species at the top of Fig. 5 exhibit specialization in old hardwood and mixedwood forests [Black-throated Green Warbler, Canada Warbler, and Ovenbird (OVEN)] and white spruce and balsam fir forests [Golden-crowned Kinglet, Bay-breasted Warbler, Cape May Warbler, and Western Tanager (WETA)]; and (2) species at the bottom of Fig. 5 exhibit specialization in burned, open (e.g. marshes, grasslands, shrublands), and lowland habitat types (e.g. black spruce bog, black spruce–larch fen) including: Black-backed Woodpecker, Greater Yellowlegs, Wilson's Warbler, and Olive-sided Flycatcher in burned habitats; Le Conte's Sparrow, Tree Swallow, and Swamp Sparrow in open habitats; and Palm Warbler in lowland habitats. Few species exhibited significant influences of age–structural complexity gradients with the exception of the Clay-coloured Sparrow, Tree Swallow, and Golden-crowned Kinglet (Fig. 6).

Table 5
Mean adjusted count values and niche parameters for 67 species of boreal birds in the oil sands areas (OSA) of Alberta, Canada. The inertia (total variability), Outlying Mean Index (OMI), tolerance index (Tol), residual tolerance index (RTol) were computed for each species. Values in italics represent the corresponding percentages of variability. Species in bold show significant deviation from the origin indicating marginal niches. Full species names in Appendix D.

Code	Species name	Mean counts[a]	Inertia	OMI	Tol	RTol	*OMI*	*Tol*	*RTol*
ALFL	Alder Flycatcher	0.74	67.38	7.62	7.56	52.20	11.3	11.2	77.5
AMCR	American Crow	0.02	61.49	4.08	6.48	50.93	6.6	10.5	82.8
AMRE	American Redstart	1.36	51.73	5.16	3.55	43.01	10	6.9	83.1
AMRO	American Robin	0.32	58.50	3.22	8.11	47.16	5.5	13.9	80.6
ATTW	American Three-toed Woodpecker	0.19	55.94	5.29	7.03	43.62	9.5	12.6	78.0
BAWW	Black-and-white Warbler	1.25	48.39	2.52	2.46	43.41	5.2	5.1	89.7
BBWA	Bay-breasted Warbler	2.08	**40.73**	**5.86**	**2.72**	**32.15**	**14.4**	**6.7**	**78.9**
BBWO	Black-backed Woodpecker	0.23	**65.97**	**26.18**	**11.98**	**27.81**	**39.7**	**18.2**	**42.2**
BCCH	Black-capped Chickadee	0.74	47.77	1.82	3.79	42.16	3.8	7.9	88.3
BHVI	Blue-headed Vireo	0.70	50.07	2.93	3.75	43.40	5.8	7.5	86.7
BLJA	Blue Jay	0.06	43.76	3.14	2.00	38.62	7.2	4.6	88.3
BLPW	Blackpoll Warbler	0.32	61.04	9.20	2.90	48.93	15.1	4.8	80.2
BOCH	Boreal Chickadee	1.30	52.76	1.49	2.57	48.70	2.8	4.9	92.3
BRCR	Brown Creeper	0.80	47.17	4.67	3.00	39.50	9.9	6.4	83.7
BTNW	Black-throated Green Warbler	0.49	**48.65**	**8.32**	**1.41**	**38.92**	**17.1**	**2.9**	**80.0**
CAWA	Canada Warbler	0.38	**50.06**	**7.28**	**2.78**	**40.00**	**14.5**	**5.5**	**79.9**
CCSP	Clay-coloured Sparrow	0.35	68.07	9.26	4.23	54.59	13.6	6.2	80.2
CEDW	Cedar Waxwing	0.48	52.43	1.62	3.34	47.47	3.1	6.4	90.5
CHSP	Chipping Sparrow	3.50	59.18	1.47	6.78	50.93	2.5	11.5	86.1
CMWA	Cape May Warbler	1.74	**42.06**	**5.33**	**3.01**	**33.73**	**12.7**	**7.2**	**80.2**
CONW	Connecticut Warbler	0.33	44.25	3.31	2.95	37.98	7.5	6.7	85.8
CORA	Common Raven	0.22	52.48	0.68	2.17	49.63	1.3	4.1	94.6
COYE	Common Yellowthroat	0.32	63.25	5.78	3.25	54.23	9.1	5.1	85.7
DEJU	Dark-eyed Junco	2.15	62.57	4.84	4.20	53.53	7.7	6.7	85.5
FOSP	Fox Sparrow	0.08	61.17	12.86	1.20	47.12	21	2	77.0
GCKI	Golden-crowned Kinglet	0.99	**45.22**	**8.79**	**2.95**	**33.48**	**19.4**	**6.5**	**74.0**
GRAJ	Gray Jay	2.16	57.55	1.76	4.28	51.51	3.1	7.4	89.5
GRYE	Greater Yellowlegs	0.55	**69.84**	**11.19**	**6.52**	**52.13**	**16**	**9.3**	**74.6**
HAWO	Hairy Woodpecker	0.19	52.82	2.01	1.84	48.97	3.8	3.5	92.7
HETH	Hermit Thrush	1.56	57.96	3.00	5.81	49.15	5.2	10	84.8
LCSP	Le Conte's Sparrow	0.22	**70.59**	**18.31**	**6.98**	**45.30**	**25.9**	**9.9**	**64.2**
LEFL	Least Flycatcher	1.38	56.34	3.30	4.14	48.90	5.9	7.4	86.8
LISP	Lincoln's Sparrow	1.12	67.22	6.47	4.89	55.86	9.6	7.3	83.1
MAWA	Magnolia Warbler	1.37	51.49	1.94	3.69	45.87	3.8	7.2	89.1
MOWA	Mourning Warbler	0.49	54.62	3.85	3.20	47.57	7.1	5.9	87.1
NOFL	Northern Flicker	0.65	62.79	7.68	9.50	45.62	12.2	15.1	72.6
NOWA	Northern Waterthrush	0.16	60.66	4.07	7.53	49.06	6.7	12.4	80.9
OCWA	Orange-crowned Warbler	0.30	60.36	5.59	5.57	49.20	9.3	9.2	81.5
OSFL	Olive-sided Flycatcher	0.05	**62.70**	**9.76**	**7.17**	**45.76**	**15.6**	**11.4**	**73.0**
OVEN	Ovenbird	4.86	**43.35**	**3.49**	**2.16**	**37.70**	**8.1**	**5**	**87.0**
PAWA	Palm Warbler	1.75	**70.60**	**9.83**	**3.75**	**57.02**	**13.9**	**5.3**	**80.8**
PHVI	Philadelphia Vireo	0.51	55.66	3.05	3.21	49.41	5.5	5.8	88.8
PISI	Pine Siskin	1.42	48.86	3.49	3.45	41.92	7.1	7.1	85.8
PIWO	Pileated Woodpecker	0.31	44.80	3.04	2.74	39.01	6.8	6.1	87.1
RBGR	Rose-breasted Grosbeak	0.81	48.03	3.94	2.52	41.57	8.2	5.2	86.5
RBNU	Red-breasted Nuthatch	0.81	48.62	4.61	4.68	39.33	9.5	9.6	80.9
RCKI	Ruby-crowned Kinglet	2.40	61.97	4.34	5.49	52.14	7	8.9	84.1
REVI	Red-eyed Vireo	2.09	46.15	3.13	3.01	40.01	6.8	6.5	86.7
RUGR	Ruffed Grouse	0.52	51.64	3.94	3.49	44.21	7.6	6.8	85.6
RWBL	Red-winged Blackbird	0.04	64.40	8.46	7.54	48.41	13.1	11.7	75.2
SACR	Sandhill Crane	0.24	58.03	10.07	7.31	40.65	17.3	12.6	70.1
SWSP	Swamp Sparrow	0.46	**78.03**	**12.27**	**3.51**	**62.25**	**15.7**	**4.5**	**79.8**
SWTH	Swainson's Thrush	3.51	47.28	1.45	3.33	42.49	3.1	7	89.9
TEWA	Tennessee Warbler	10.97	47.69	1.23	3.40	43.07	2.6	7.1	90.3
TRES	Tree Swallow	0.21	**65.39**	**14.37**	**6.13**	**44.89**	**22**	**9.4**	**68.6**
WAVI	Warbling Vireo	0.48	44.83	4.63	2.22	37.99	10.3	4.9	84.7
WETA	Western Tanager	0.65	**47.99**	**4.39**	**3.72**	**39.88**	**9.1**	**7.8**	**83.1**
WEWP	Western Wood-Pewee	0.19	72.18	13.50	10.05	48.63	18.7	13.9	67.4
WISN	Wilson's Snipe	1.11	65.01	5.50	6.25	53.26	8.5	9.6	81.9
WIWA	Wilson's Warbler	0.23	**73.91**	**11.53**	**9.16**	**53.22**	**15.6**	**12.4**	**72.0**
WIWR	Winter Wren	0.67	48.10	2.81	5.28	40.01	5.8	11	83.2
WTSP	White-throated Sparrow	3.16	56.63	1.31	4.56	50.77	2.3	8	89.6
WWCR	White-winged Crossbill	0.28	56.96	3.99	4.03	48.94	7	7.1	85.9
YBFL	Yellow-bellied Flycatcher	0.56	57.29	5.28	3.47	48.54	9.2	6.1	84.7
YBSA	Yellow-bellied Sapsucker	0.97	48.50	1.55	2.55	44.41	3.2	5.2	91.6
YRWA	Yellow-rumped Warbler	9.11	51.93	0.65	3.21	48.06	1.3	6.2	92.6
YWAR	Yellow Warbler	0.50	67.15	7.05	9.81	50.28	10.5	14.6	74.9

[a] Mean Count is mean adjusted count. All values are raised to 10^{-2}.

4. Discussion

Our summary of niche characteristics for western boreal birds revealed that: (1) most species do not have marginal niches or narrow niche breadths; (2) specialized species are associated with both rare and abundant upland and lowland habitats; (3) and species are influenced by environmental variables operating at multiple spatial scales.

4.1. Community and niche characteristics at multiple spatial scales

We found that 22% or 15 of 67 species we examined had marginal niches (i.e. associated with atypical or uncommon habitats) and narrow niche breadths indicating specialization in either rare or abundant habitats within our study area. Our specialist species include both provincial species at risk (http://esrd.alberta.ca) like the Black-throated Green Warbler (species of special concern), Bay-breasted Warbler (species status recommendations), and Cape May Warbler (species status recommendations) and federal species at risk (www.sararegistry.gc.ca) like the Canada Warbler (threatened). Each of these wood warblers are found at their highest densities in the increasingly rare old forest types that are targeted for harvesting by licence holders seeking resources for pulp and paper and sawtimber. Future landscape simulations using multiple scenarios (including the base case or business as usual) suggest that the total area of old conifer, mixedwood, and deciduous forest types will decline during the next 30 years (Mahon et al., 2014). The Swamp Sparrow, Tree Swallow, and Le Conte's Sparrow are also species associated with rare habitat types within our study area: Swamp Sparrows are associated with marsh habitats (Mowbray, 1997); Tree Swallows are associated with open grasslands or water but also require either nest boxes, natural cavities, or cavities created by primary cavity excavators in adjacent woodland or forest habitats (Winkler et al., 2011); and Le Conte's Sparrows are associated with open wet grasslands (Lowther, 2005). Both marsh and grassland habitats are uncommon at northern latitudes within the boreal forest natural region in northeastern Alberta. Other specialized species are associated with temporally rare habitat types like natural burns which undergo shifts in vegetation structure and prey abundance in the years post-fire. These temporal shifts alter habitat suitability and habitat quality for fire-associated species like the Black-backed Woodpecker (Dixon and Saab, 2000; Hoyt and Hannon, 2002; Hutto, 1995; Nappi and Drapeau, 2011) and Olive-sided Flycatcher (Altman and Sallabanks, 2012; Hutto, 1995). The Palm Warbler is typically associated with black spruce bogs and fens in the western boreal forest (Wilson, 2013), which often form large peatland complexes in northern Alberta. This species exhibits high specialization when selecting breeding habitat in northern Alberta (author and T. Carpenter, Unpublished results) and is sensitive to habitat disturbance (Desrochers et al., 1998) and peatland size and isolation (Calmé and Desrochers, 1999, 2000; Calmé et al., 2002).

Our results suggest that most boreal bird species have adopted generalist strategies in order to persist within the heterogeneous and unstable environments typical of northern boreal forests (e.g. a mosaic of upland and lowland habitats characterized by natural disturbances, climate change, and human disturbance). Our results agree with other avian niche analyses which have found non-marginal niches and wide niche breadths indicating generalist characteristics or strategies for the majority of the songbird community in Brazil (Marsden and Whiffen, 2003) and Britain (Gregory and Gaston, 2000) and the diurnal raptor community in Peru (Piana and Marsden, 2012). Our habitat associations for individual species align with existing empirical habitat models (Boreal Avian Modelling Project; www.borealbirds.ca) and documented habitat associations (Schieck and Song, 2006; Hannon et al., 2004) but in addition provide the first quantitative representation of species–environment relationships for the terrestrial bird community in the western boreal as a whole.

Our results suggest that western boreal birds respond to habitat characteristics at multiple spatial scales. We compared our results to those of Rempel (2007), who examined species associations for 30 boreal species using both local and landscape scale environmental variables in northern Ontario, Canada. We also found a significant influence of forest height, forest age, area of mature and old forest, and area dominated by trembling aspen at the local scale (150 m/7.1 ha). In addition, we also found a significant influence of soil moisture at the local scale and a series of stand and landscape pattern metrics summarized at the landscape (2,500 m/1,963 ha) and regional (6,000 m/11,310 ha) scales including: area of total forest cover, area of mature and old forest, area of deciduous and conifer forest, mean nearest neighbour distance of white spruce–balsam fir and total core area of white spruce–balsam fir.

We included stand and landscape pattern metrics at larger scales (landscape, regional) in addition to vegetation composition metrics at the local scale because we wanted to represent both the amount and the spatial arrangement (configuration) of habitat classes and patches. This is particularly important in areas where habitat is subdivided by natural and human disturbance into small spatial units (Andrén, 1994; Fahrig, 1997; Wang and Cumming, 2011). Western boreal forest ecosystems in Alberta are naturally complex and heterogeneous landscapes composed of a patchwork of upland and lowland habitats. Operating within this diverse landscape are multiple disturbances including wildfire, insects, forest harvesting, and energy sector development which create additional habitat subdivision. Our results suggest a strong influence of habitat composition and structure variables at the local scale and a weak influence of habitat amount (e.g. total habitat area of hardwood and white spruce–balsam fir) and spatial arrangement (e.g. nearest neighbour distance of white spruce–balsam fir) at landscape and regional scales. Both empirical and theoretical evidence suggest that both habitat amount and habitat configuration influence bird species richness and abundance (for reviews see Andrén, 1994; Fahrig, 2003; Tscharntke et al., 2012). Habitat configuration appears to have a higher influence on species at intermediate values (i.e. 20–50%) of habitat amount (Villard and Metzger, 2014). Documenting the threshold value of habitat amount below which patch size and isolation effects emerge has proven complex primarily due to the challenges associated with implementing study designs using the whole landscape as the unit of study (Lindenmayer, 2009; Radford et al., 2005) as opposed to patches within landscapes as the unit of study (Donovan et al., 1995; Schmiegelow et al., 1997; for a review see Lindenmayer and Fischer, 2006). In addition, understanding (1) processes associated with area, edge effects, shape, isolation, and matrix structure, (2) interdependence of effects and responses, and (3) confounding factors (e.g. differences in species-specific responses, time lags, and synergies that magnify impacts like human-modified disturbance and climate change) complicates the detection of species responses to habitat subdivision (Didham et al., 2012; Ewers and Didham, 2006). We suggest that total habitat area, total core area, and mean nearest neighbour distance (measure of spatial dispersion) of hardwood and conifer forest types contributed significantly to boreal bird community structure within the boreal system we studied because these variables likely influenced (1) the frequency and scale of breeding season dispersal among bird populations; (2) birth, death, and dispersal rates; and (3) habitat selection patterns (Donovan and Flather, 2002). Maintaining mixedwood and conifer-dominated forest types in proportions that mimic the spatial and temporal distribution of forest types found in historical or undeveloped boreal regions appears critical to maintaining conifer-associated specialists like the Golden-crowned Kinglet, Bay-breasted Warbler, Cape May Warbler, and Western Tanager in the western boreal (Hobson and Bayne, 2000). We support simulating the size range, amount, and spatial arrangement of all age classes of upland and lowland habitat types associated with natural disturbance regimes in the western boreal (e.g. wildfire, insects, disease). Although this goal forms the basis for ecosystem management approaches that aim to maintain ecosystem integrity and biological diversity, achieving these objectives in multi-use, intensively managed landscapes in the western boreal will be challenging because future resource development activities will alter the amount and configuration of habitats within landscapes and regions across time and space. Land use simulations for this region suggest that future hypothesized resource development (predominantly forestry and oil sands) will alter the forest age class distribution, reduce forest habitat supply, and in turn impact regional bird populations (Mahon et al., 2014).

4.2. Conservation implications

These results have implications for conservation planning because maximizing the effectiveness of conservation strategies or plans (e.g. Bird Conservation Region Strategies; Environment Canada, 2013) depends on identifying species that are sensitive to threats and disturbance and targeting the appropriate scale or scales of management (Grand and Cushman, 2003). Regional changes in biodiversity do not occur at random. Human-caused environmental change acts as a non-random filter selecting for those species best able to survive within modified or disturbed ecosystems (Devictor et al., 2008; Smart et al., 2006). These changes have consequences for natural communities as increasing generalists (the winners) replace decreasing specialists (the losers) (Clavel et al., 2011; McKinney and Lockwood, 1999). This process of biotic homogenization (the genetic, taxonomic, or functional similarity of two or more species assemblages increasing over space and/or time; Olden, 2006) occurs when local species are replaced by more widespread species effectively "reshuffling" existing species distributions and reducing spatial diversity (Clavel et al., 2011). Our results suggest that there are specialized upland and lowland bird species in the western boreal associated with rare (e.g. old conifer forests, Bay-breasted Warbler), temporally rare (e.g. burns, Black-backed Woodpecker), and abundant habitats (e.g. bogs and fens, Palm Warbler). Regional status and trend monitoring data from multiple sources (Environment Canada, Alberta Biodiversity Monitoring Institute) suggests that the process of biotic homogenization is occurring in boreal Alberta. Of the 15 upland and lowland boreal species we identified as specialist species, six have declining populations in the Alberta portion of Bird Conservation Region 6-Boreal Taiga Plains (www.ec.gc.ca) and nine have declining species intactness indices and are less abundant than expected in the Alberta Athabasca Oil Sands Area (www.abmi.ca). The species intactness index ranges from 0% to 100% and at 100% represents the abundance one would expect in an area with no human disturbance. Declines in species intactness occur because the species is more or less abundant relative to an undisturbed area (Alberta Biodiversity Monitoring Institute, 2013, 2014). In Alberta and other regions where human disturbance is pervasive, we need to: (1) manage and mitigate the habitat effects of multi-scale, multi-sector resource development; (2) implement multi-species conservation plans to maintain a diversity of boreal bird species at the regional scale; (3) explore innovative approaches to accommodate specialist species and meet regional bird conservation objectives; and (4) understand how changes at the community level (i.e. replacement of specialists by generalists) alter the maintenance of ecosystem services and ecosystem productivity and function (Clavel et al., 2011).

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Appendix A. Vegetation type descriptions for the oil sands areas (OSA) of Alberta, Canada

Vegetation type	Code	Description
Pine	PJ	Upland. Stands where combined jack pine and lodgepole pine are the leading species and deciduous species comprise ⩽20%
Upland black spruce	SB	Upland. Stands where black spruce is the leading species, the soil regime is dry or mesic, and larch = 0% or; stands where black spruce is the leading species, the soil regime is wet, and the combined species trembling aspen + balsam poplar + balsam fir + jack pine >0%
White spruce	SW	Upland. Stands where combined white spruce and balsam fir comprise ⩾80%
Deciduous	DM/ DW	Upland. Stands where combined trembling aspen, balsam poplar, and white birch comprise ⩾80%. Mesic (M) and hygric (W) stands are differentiated
Mixedwood	MM/ MW	Upland. Stands where deciduous >20%, and combined conifer species (jack pine, lodgepole pine, white spruce, balsam fir, and black spruce) >20%. Mesic (M) and hygric (W) stands are differentiated
Black spruce bog	BG	Lowland–wetland. Stands where black spruce is the leading species and the soil regime is aquatic or; stands where black spruce is the leading species, the soil regime is mesic, and larch >0 or; stands where black spruce is the leading species, the soil regime is wet, and the combined species trembling aspen + balsam poplar + balsam fir + jack pine = 0

(continued on next page)

Appendix A (*continued*)

Vegetation type	Code	Description
Larch fen	FN	Lowland–wetland. Stands where larch is the leading species
Swamp	SP	Lowland–wetland. Open shrub or closed shrub and soil regime is wet or aquatic
Marsh	MA	Lowland–wetland. Herbaceous grassland or herbaceous forbs and soil regime is aquatic
Shrubland	SH	Non-forested land. Open shrub or closed shrub and soil regime is dry or mesic
Grassland	GR	Non-forested land. Herbaceous grassland or herbaceous forbs and soil regime is dry, mesic, or wet
Harvest	CC	Forest modifier-clearcut. Clearcut harvest units <20 yrs (CC)
Burn	BU	Forest modifier-burn. Stand-replacing burn <20 yrs (BU)

Appendix B. Structural stage descriptions for upland vegetation types in the oil sands areas (OSA) of Alberta, Canada. Stand age for herb, shrub, and pole/sapling are the same for all forest types. Stand age for young, mature, and old forests differed by forest type

Structural stage (stand development stage)	Code[a]	Vegetation type[b]	Description
Herb (post-disturbance stage)	2	All forest types	Stand age 0–10 yrs
Shrub (stand initiation stage)	3	All forest types	Stand age 11–20 yrs
Pole/sapling (stem exclusion stage)	4	All forest types	Stand age 21–40 yrs
Young forest (stem exclusion stage)	5	DM/DW, MM/MW	Stand age 41–60 yrs
		PJ/SB/SW	Stand age 41–80 yrs
Mature forest (understory reinitiation stage)	6	DM/DW, MM/MW	Stand age 61–80 yrs
		PJ/SB/SW	Stand age 81–100 yrs
Old forest (old growth/gap phase dynamics stage)	7	DM/DW, MM/MW	Stand age >80 yrs
		PJ/SB/SW	Stand age >100 yrs

[a] Codes for structural stages in upland vegetation types are: herb (2); shrub (3); pole/sapling (4); young forest (5); mature forest (6); old forest (7).

[b] Codes for upland vegetation types are: deciduous mesic (DM), deciduous hygric (DW), mixedwood mesic (MM), mixedwood hygric (MW), pine (PJ), upland black spruce (SB), white spruce (SW).

Appendix C. Structural stage descriptions for lowland and non-forested vegetation types in the oil sands areas (OSA) of Alberta, Canada

Vegetation	Structural stage			Structural stage criteria
	Herb	Shrub	Treed	
Black spruce bog		x	x	Tree height
Larch fen		x	x	Tree height
Swamp		x		Dominant vegetation
Marsh	x			Dominant vegetation
Shrubland		x		Dominant vegetation
Grassland	x			Dominant vegetation
Burn		x		Dominant vegetation

Appendix D. Boreal bird species common name, code, and scientific name

Code	Species common name	Species scientific name
ALFL	Alder Flycatcher	*Empidonax alnorum*
AMCR	American Crow	*Corvus brachyrhynchos*
AMRE	American Redstart	*Setophaga ruticilla*
AMRO	American Robin	*Turdus migratorius*
ATTW	American Three-toed Woodpecker	*Picoides dorsalis*
BAWW	Black-and-white Warbler	*Mniotilta varia*
BBWA	Bay-breasted Warbler	*Setophaga castanea*
BBWO	Black-backed Woodpecker	*Picoides arcticus*
BCCH	Black-capped Chickadee	*Poecile atricapillus*
BHVI	Blue-headed Vireo	*Vireo solitarius*
BLJA	Blue Jay	*Cyanocitta cristata*
BLPW	Blackpoll Warbler	*Setophaga striata*
BOCH	Boreal Chickadee	*Poecile hudsonicus*
BRCR	Brown Creeper	*Certhia americana*
BTNW	Black-throated Green Warbler	*Setophaga virens*
CAWA	Canada Warbler	*Cardellina canadensis*
CCSP	Clay-coloured Sparrow	*Spizella pallida*
CEDW	Cedar Waxwing	*Bombycilla cedrorum*
CHSP	Chipping Sparrow	*Spizella passerina*
CMWA	Cape May Warbler	*Setophaga tigrina*
CONW	Connecticut Warbler	*Oporornis agilis*
CORA	Common Raven	*Corvus corax*
COYE	Common Yellowthroat	*Geothlypis trichas*
DEJU	Dark-eyed Junco	*Junco hyemalis*
FOSP	Fox Sparrow	*Passerella iliaca*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
GRAJ	Gray Jay	*Perisoreus canadensis*
GRYE	Greater Yellowlegs	*Tringa melanoleuca*
HAWO	Hairy Woodpecker	*Picoides villosus*
HETH	Hermit Thrush	*Catharus guttatus*
LCSP	Le Conte's Sparrow	*Ammodramus leconteii*
LEFL	Least Flycatcher	*Empidonax minimus*
LISP	Lincoln's Sparrow	*Melospiza lincolnii*
MAWA	Magnolia Warbler	*Setophaga magnolia*
MOWA	Mourning Warbler	*Geothlypis philadelphia*
NOFL	Northern Flicker	*Colaptes auratus*
NOWA	Northern Waterthrush	*Parkesia noveboracensis*

Appendix D (*continued*)

Code	Species common name	Species scientific name
OCWA	Orange-crowned Warbler	*Oreothlypis celata*
OSFL	Olive-sided Flycatcher	*Contopus cooperi*
OVEN	Ovenbird	*Seiurus aurocapilla*
PAWA	Palm Warbler	*Setophaga palmarum*
PHVI	Philadelphia Vireo	*Vireo philadelphicus*
PISI	Pine Siskin	*Spinus pinus*
PIWO	Pileated Woodpecker	*Dryocopus pileatus*
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
RBNU	Red-breasted Nuthatch	*Sitta canadensis*
RCKI	Ruby-crowned Kinglet	*Regulus calendula*
REVI	Red-eyed Vireo	*Vireo olivaceus*
RUGR	Ruffed Grouse	*Bonasa umbellus*
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*
SACR	Sandhill Crane	*Grus canadensis*
SWSP	Swamp Sparrow	*Melospiza georgiana*
SWTH	Swainson's Thrush	*Catharus ustulatus*
TEWA	Tennessee Warbler	*Oreothlypis peregrina*
TRES	Tree Swallow	*Tachycineta bicolor*
WAVI	Warbling Vireo	*Vireo gilvus*
WETA	Western Tanager	*Piranga ludoviciana*
WEWP	Western Wood-Pewee	*Contopus sordidulus*
WISN	Wilson's Snipe	*Gallinago delicata*
WIWA	Wilson's Warbler	*Cardellina pusilla*
WIWR	Winter Wren	*Troglydytes hiemalis*
WTSP	White-throated Sparrow	*Zonotrichia albicollis*
WWCR	White-winged Crossbill	*Loxia leucoptera*
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*
YRWA	Yellow-rumped Warbler	*Setophaga coronata*
YWAR	Yellow Warbler	*Setophaga petechia*

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