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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