Robust predictive performance of indicator species despite different co-occurrence patterns of birds in natural and managed boreal forests

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ABSTRACT

Indicator species are widely used biodiversity surrogates that allow the assessment of biodiversity without the expensive and time-consuming construction of species inventories. The selection of indicator species often relies on species co-occurrence patterns, which may be altered by anthropogenic disturbance such as forest harvesting, imposing a unique challenge to their application in managed forest. Here, we studied boreal bird communities in natural forests originating from wildfire and managed forests originating from clearcutting. We aimed to (1) compare species co-occurrence patterns in natural and clearcut forest stands, (2) select indicator species based on species co-occurrence patterns to predict avian diversity, and (3) evaluate the predictive performance of indicator species under both natural and clearcutting disturbance regimes using the same training data set and an independent testing data set. We found that species co-occurrence patterns differ substantially between natural and clearcut stands, suggesting that forest harvesting alters species-environment relationships and/or interspecific interactions. Consequently, we selected different sets of species as indicators of avian diversity based on data from natural or clearcut stands. However, according to internal and external evaluation, selecting indicator species using data from both natural and clearcut stands produced surrogates that predicted avian diversity accurately and precisely in both types of forests. Our results suggest that, despite forest harvesting altering species co-occurrence patterns, a comprehensive understanding of species co-occurrence patterns across natural and managed forests can be used to develop robust biodiversity surrogates. Our study shows that small sets of indicator species can represent the biodiversity of a wide range of species in ecosystems undergoing anthropogenic disturbance, which has important implications for the application of biodiversity surrogates for conservation.

1. Introduction

The success of decision-making in biodiversity conservation and natural resource management relies upon a detailed understanding of spatial and temporal patterns of biodiversity (Heywood and Watson, 1995; Van Jaarsveld et al., 1998). However, thorough biodiversity assessments can be extremely expensive and time-consuming (Knight et al., 2006; Pressey et al., 2000), and conservation biologists frequently use biodiversity surrogates such as indicator species to assess biodiversity without detailed species inventories (Leal et al., 2010; Pearson, 1994; Thomson et al., 2007). Indicator species, which are small sets of species

whose presence or absence are correlated with the biodiversity of a larger group of species (Fleishman et al., 2005), have been successfully used to predict biodiversity of numerous taxa, including plants, invertebrates, and vertebrates, and across a variety of ecosystems (Azeria et al., 2009; Lindenmayer and Likens, 2011). One of the most important applications of indicator species is to assess the impacts of anthropogenic disturbance, such as forest harvesting, on biodiversity (Drever et al., 2008; Lindenmayer et al., 2000).

The selection of indicator species often relies on knowledge of species co-occurrence patterns (Azeria et al., 2009), which may be altered by anthropogenic disturbance. Habitats under anthropogenic disturbance tend to harbor different species communities compared to corresponding habitats in their natural state, even many years following disturbance events (Edwards et al., 2014; Kneitel and Chase, 2004; Zhao et al., 2013). Anthropogenic

disturbance can also disrupt patterns of interspecific associations (Azeria et al., 2011; Sarà et al., 2006). As a result, the performance of indicator species identified under natural conditions can be poor in ecosystems under anthropogenic disturbance due to alterations in environmental filtering, interspecific interactions, and, ultimately, species co-occurrence (Lindenmayer and Likens, 2011). This is a critical issue because the reliability of indicator species may be lowest where there is the greatest need for accurate assessments of anthropogenic impacts on biodiversity, thus imposing a unique challenge to the applications of indicator species. Surprisingly, few studies have investigated how the performance of indicator species in predicting biodiversity changes with anthropogenic disturbance (Lawton et al., 1998; Schulze et al., 2004).

Boreal forests are regularly harvested under sustainable forest management strategies, such as ecosystem-based management, with the goal of maintaining a balance between economic interests and biodiversity conservation. Despite the fact that ecosystem-based management aims to develop forestry practices that best emulate natural disturbance regimes such as wildfire (Bergeron et al., 2002), the practice of clearcutting is still widely used. Clearcutting strongly modifies the structure of boreal forest ecosystems by converting old-growth stands to young, even-aged stands (Cyr et al., 2009; Imbeau et al., 2001) and removing most standing trees and snags, which are key structural elements in post-fire conditions (Hutto, 2006). Consequently, managed forests often harbor contrasting species communities to natural forests, even many years following harvest (Azeria et al., 2011; Zhao et al., 2013). The potential for contrasting species co-occurrence patterns in managed and natural boreal forests means that indicator species could be ineffective for assessing the long term impacts of forestry on biodiversity.

Our overarching goal was to examine the effect of variation in bird species co-occurrence on the predictive performance of indicator species in natural and managed boreal forests. Indicator species may provide a practical and efficient measure for evaluating avian diversity in boreal forests, where poor visibility in dense forests and the cryptic nature of many species can make full inventories of diverse avian communities difficult to achieve (Drapeau et al., 2000; Zhao et al., 2013). We studied boreal bird communities in natural forests (originating from natural disturbances such as wildfire, disease and blow-downs) dominated by old-growth stands, and managed forests (originating from clearcutting for the timber industry) dominated by early successional stands. Our objectives were to (1) compare species co-occurrence patterns in natural and clearcut stands, (2) select indicator species based on co-occurrence patterns to predict species richness, and (3) evaluate the predictive performance of indicator species under both natural and clearcutting disturbance regimes using the same training data set and an independent testing data set.

2. Material and methods

2.1. Study area

The study was conducted in the boreal forest of the Côte-Nord region of Québec, Canada (49°-52°N, 65°-70°W) (Zhao et al., 2013). The climate in the region is humid, with a mean annual temperature of −2.5 to 0.0 °C and total annual precipitation of 1000–1400 mm, with 35% of this falling as snow (Grondin et al., 1996). Due to its high precipitation the area has a long fire cycle (average length >270 years), resulting in landscapes dominated by uneven-aged, old-growth stands (Bouchard et al., 2008). Dominant tree species include black spruce *Picea mariana* and balsam fir *Abies balsamea*. Several other tree species are common, including

white spruce *Picea glauca*, white or paper birch *Betula papyrifera*, trembling aspen *Populus tremuloides* and jack pine *Pinus banksiana* (Boucher et al., 2003). During the twentieth century, industrial forestry began in parts of the study region, in the form of clearcutting for pulp and paper (Bouchard et al., 2008).

2.2. Data collection

Breeding bird surveys were undertaken during two time periods. Firstly, between 2004 and 2007, a total of 185 sampling sites were surveyed, including 88 sites in natural forest and 97 sites in managed forest (Zhao et al., 2013). The data collected during the period of 2004–2007 were used to characterize bird community structure, select indicator species, and conduct an internal evaluation of the predictive performance of indicator species (hereafter, the training data set). Secondly, in 2011, 75 new sites were surveyed, including 29 sites in natural forest and 46 sites in managed forest, to provide an independent dataset for an external evaluation of the predictive performance of indicator species (hereafter, the testing data set). The natural forest stands originated from fire and had not been logged. They were aged 50–225 years, of which 65% were >120-years in the training data set, and 55–200 years in the testing data set. Clearcut forest stands had been cut with advance growth protection and <10% of tree retention. They were aged 5–70 years following harvest in the training set, and 20–65 in the testing set. For more details on the determination of stand ages, see Zhao et al. (2013). Each site was located >100 m from the forest edge, reducing the potential for edge effects, and >150 m from any other site, ensuring that sites were independent.

Presence-absence surveys were conducted at each site, using the fixed-radius point count method (Rosenstock et al., 2002). Each site in the training data set was visited in one year between 2004 and 2007. Each site was surveyed three times in its survey year during the early, middle, and late periods of the breeding season (June-July). Surveys were carried during the morning between 0500 and 1000 h, in the absence of wind or heavy rain. On each visit, all birds that were observed or heard within 50 m were recorded for 10 min. Data collated across the three visits represented the local bird communities in each site.

We considered cumulative detection probability to be high and homogeneous across space and over time due to each site being visited multiple times within a given season, the fine scale of survey areas, and the fact that surveys were conducted by well-trained observers, only in weather conditions favorable for detection.

The primary habitat associations of all species recorded were compiled according to prior knowledge (Drapeau et al., 2000; Poole, 2005). Birds were classified as mature forest species, young forest species, shrubland species or generalists (Table S1). For the analysis of species co-occurrence, species present in less than 1% of sites were excluded, as they provide limited information on species co-occurrence (Azeria et al., 2009). For the analyses focused on only natural or clearcut stands this threshold was increased to 2%, to account for the smaller number of sites analyzed. Rare species were included to evaluate the predictive performance of indicator species.

2.3. Data analysis

First, we examined the species co-occurrence patterns of boreal birds in all stands, natural stands only, and clearcut stands only. We characterized species co-occurrence using biodiversity deconstruction techniques, classifying communities into empirical groups of species exhibiting similar spatial distributions (Azeria et al., 2009; Marquet et al., 2004). Second, we selected species to represent the species richness of the empirical groups. We then