



Habitat geometry, a step toward general bird community assembly rules in mature forests



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ABSTRACT

Community ecology has often been criticized because it seldom defines general rules that can be exported outside of the studied system. Although much progress has been achieved by studying functional traits instead of species identities *per se*, environmental gradients defined in terms of local resources can be measured only on a subset of ecosystems and, thus, are not deemed general. Here, we used state-of-the-art statistical approaches for modeling the interaction between species functional traits (body size, feeding substrate) and habitat geometry (object size, shape and color; packing, layering and texturing), such as to derive general assembly rules for bird communities in an even-aged mature forest (La Mauricie National Park, Québec, Canada). Our results show that habitat geometry filters the species pool through its interaction with bird body size and feeding substrate, both at the species, and even more so at the community level. We found comparable assembly rules using only photographic (image-based) descriptors of habitat geometry, thus providing forest managers with a fast, reliable, standardized and cost-effective protocol for characterizing forest stands. Because bird functional groups respond differently to environmental gradients, we conclude that mature forest should be managed to preserve a spatial mosaic of successional states.

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1. Introduction

Community ecology has often been criticized because it seldom defines general rules (e.g. Lawton, 1999; Simberloff, 2004). McGill *et al.* (2006) revived an approach focused on functional traits and environmental gradients that emphasized the importance of testable rules, and yet a final step is still missing to truly general rules in local community assembly. In order to be described as general or not, assembly rules need to be defined in a way that makes them testable outside of the original study area. That is, in addition to species functional traits, the environmental gradient also needs to be described with variables that can be measured in the broadest range of ecosystems possible. While in practice one can assign functional traits like body size or preferred feeding substrate to nearly all living organisms, environmental gradients defined in terms of local resources (e.g., lichen cover, biomass of wildberries, etc.) can be measured only on a subset of ecosystems.

Habitat geometry is a physical representation of the environment using descriptors that are measurable at several observation scales (e.g. object size, shape and color; packing, layering and

texturing). In wilderness areas where environmental filtering is not overridden by human activities, both guild proportion and species diversity of bird communities have been related to forest geometry (e.g. Arriaga-Weiss *et al.*, 2008; Naidoo, 2004). Stem density, tree size and foliage cover are among the most common stand descriptors reported to structure bird communities (Table 1). One could thus expect that directing the description of forest habitat to these three axes should provide enough environmental gradients to assemble bird communities.

Previous studies have shown that the feeding substrate of bird species can be used to define guilds (e.g. De Graaf *et al.*, 1985) and that these guilds converged on three continents in association with habitat geometry (Korňan *et al.*, 2013). Other studies also found that the proportion of each feeding guild presents a turnover along environmental gradients such as tree density (e.g. Hanspach *et al.*, 2011; Mac Nally, 1994 and see Table 1). Hence our first specific hypothesis that (H1) forest stand geometry should affect bird species presence differently depending on their feeding substrate.

Because animals use physical structures adapted to their size, body size could also be an important trait structuring local bird communities. Several studies support this idea, where coarser habitat structures (e.g., thinned maquis, low tree densities in an agricultural landscape, etc.) supported higher densities of large birds than finely textured ones, while the opposite pattern was

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Table 1

Literature review of the interaction between forest stand descriptors of habitat geometry and both bird feeding substrate and diversity in wilderness areas.

Feeding substrate	Related forest geometry	Sources
Ground	Tree size	Arriaga-Weiss et al. (2008) Castaño-Villa et al. (2014)
	Stem density	Arriaga-Weiss et al. (2008)
Understory/shrubs	Stem density	Cockle et al. (2005)
	Cover	Ding et al. (2008)
Foliage/canopy	Tree size	Arriaga-Weiss et al. (2008) Nikolov (2009) Castaño-Villa et al. (2014)
	Cover	Castaño-Villa et al. (2014) Ding et al. (2008)
Bark	Tree size	Arriaga-Weiss et al. (2008) Laiolo et al. (2003) Nikolov (2009)
	Stem density	Castaño-Villa et al. (2014) Laiolo et al. (2003)
Air	Cover	Castaño-Villa et al. (2014)
Species richness/diversity	Tree size	Martin and Blackburn (2012) McDermott et al. (2011)
	Cover	Castaño-Villa et al. (2014) Martin and Blackburn (2012) Ding et al. (2008)
	Stem density	Naidoo (2004)

Understory height and undergrowth density were categorized as cover. Tree height, density of large trees and basal area were grouped into tree size.

observed for smaller birds (de la Montaña et al., 2006; Fischer et al., 2008; Hanspach et al., 2011). Therefore, we expect that (H2) the size of objects composing the habitat should interact with body size to filter out species presence.

The combination of different environmental (geometric) filters should make some stands appropriate for some functional traits syndromes only. Although species sharing similar traits should be found in the same stands, they might avoid sharing similar physical stands because of interspecific competition or niche pre-emption processes. In such case, we hypothesize (H3) that bird traits–habitat geometry interaction should make better predictions about species richness at the community level.

This study tests the above species sorting hypotheses (H1–H3) using either classic (direct) forest stand descriptors, or photographic (image-based) descriptors of habitat geometry (Macfarlane et al., 2007; Meyer and Camargo Neto, 2008; Proulx and Parrott, 2008). We propose that the interaction between species functional traits and habitat geometry describes general assembly rules for forest bird communities.

2. Methods

2.1. Study area

To test the effect of forest geometry on bird communities, we selected La Mauricie National Park (Québec, Canada), an even-aged forest conservation area (536 km²). This allowed us to control for other confounding effects that are known to structure bird communities (e.g. anthropic activity, loss of habitat, fragmentation, etc.), but also to use multiple years of bird data to account for the variability of bird communities at the patch scale (see Section 2.2. BIRD DATA). The park's forest was harvested from the beginning of the 19th century, for lumber and then for pulpwood, until the 1950s and then protected in 1970. Stands in the study area are dominated by either balsam fir (*Abies balsamea*), sugar maple (*Acer*

saccharum), black spruce (*Picea mariana*) or yellow birch (*Betula alleghaniensis*).

2.2. Bird data

We used bird survey data collected from 2011 to 2014 by the Park staff as part of their monitoring program. Each year, all stands were visited by the same team of two observers at the peak of the breeding season (May 18 to July 2) between 5 AM and 10 AM. Following the Québec Breeding Bird Atlas point count protocol (Regroupement Québec Oiseaux et al., 2011), every bird seen or heard within a 5-min stop was recorded. Bird counts were then converted to species presence–absence and filtered to keep only singing forest bird species ($n = 68$).

We compiled bird functional traits from the literature, that is, individuals from the same species were assigned the same trait value. We extracted body size (g) from the Quebec Breeding Bird Survey Atlas (Gauthier and Aubry, 1995). We retrieved the feeding substrate from De Graaf et al. (1985) and assigned each bird species to one of five categories: ground, lower-canopy, upper-canopy, bark and air (see Table S1 for a complete list of bird species and their functional traits).

2.3. Direct forest descriptors

To represent all habitat types available along the survey paths, we measured habitat geometry in a subset of 57 stands. In each stand, we evenly spaced four subplots on an 85 m radius around the point count position. This distance was selected as to both minimize habitat perturbations due to the path opening, while being close enough from the point count position as to remain half-way to the average distance where 50% of the birds are heard in a forest setting (mean $D_{50} = 151$ m; Wolf et al., 1995).

In each subplot, we measured the size (DBH, cm) and distance (m) of four trees and four saplings. We used these data to calculate the average tree size (DBH, cm) and applied the point centered quarter technique (Cottam and Curtis, 1956) to estimate stem density (stem ha⁻¹). A correction was applied to stem density to account for missing trees in open spaces or near lakes (Warde and Petranka, 1981). We also measured lateral vegetation cover at 15 m in the four cardinal directions using a cover board (Nudds, 1977) and 20% cover classes in four height bands (0–50 cm, 50–100 cm, 100–150 cm and 150–200 cm). All these measures (tree size, stem density, lateral cover) were then aggregated at the stand level to define a 3×57 environment matrix. Variance inflation factors (VIF; Neter et al., 1996) were computed on this matrix to ensure that colinearity was below the usually recommended threshold (all values were <5).

2.4. Image-based forest descriptors

In each subplot, we took photographs using an EOS Digital Rebel XS camera (Canon Inc., Tokyo, Japan) mounted with a 15–85 mm lens (EF-S f/3.5–5.6 IS USM, Canon Inc., Tokyo, Japan). Photos were taken in four cardinal directions, both horizontally and at a 45° angle (Fig. 1; see Table 2 for camera settings). On each of the horizontal photographs, we calculated mean information gain (MIG, Proulx and Parrott, 2008) on the hue and intensity color space bands, as well as a green index (ExG-ExR, Meyer and Camargo Neto, 2008). On each 45° picture, we calculated an indirect leaf area index (LAI) measure following the method described by Macfarlane (2011). All these measures were aggregated at the stand level to form a second 4×57 environment matrix. VIF values were computed on this second matrix and were also below the recommended threshold.

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