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Research Paper

Bicknell's Thrush (*Catharus bicknelli*) habitat occupancy in Québec's Laurentian Highlands

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ABSTRACT. In North America, several migratory bird species inhabiting boreal and eastern forests are declining. Habitat loss is frequently cited as a limiting factor. We estimated occupancy of suitable nesting habitat by Bicknell's Thrush (*Catharus bicknelli*), a forest dwelling threatened species, in the Laurentian Highlands of Québec. Forests in this region are shaped by intensive forestry activities and natural disturbances. The species was found primarily in stands of about 20 years or more, with higher occupancy in older stands on hilltops where recent forestry activities and natural perturbations have been much less prevalent. Bicknell's Thrush occupancy was significantly associated with high elevations in landscapes with relatively low amounts of precommercial thinning. Occupancy and multivariate niche approaches indicated that a large extent of potential habitat (> 80%) was unoccupied by breeding Bicknell's Thrushes. We conclude that maintaining sufficient amounts of suitable breeding habitat in this exploited forest landscape remains important to enable the species' recovery, but that an increase in its numbers may not materialize without further measures unrelated to availability of breeding habitat.

Taux d'occupation de l'habitat par la Grive de Bicknell (*Catharus bicknelli*) sur le plateau Laurentien du Québec

RÉSUMÉ. En Amérique du Nord, les populations de plusieurs espèces d'oiseaux migrateurs nichant dans les forêts boréales et de l'Est sont en diminution. La perte d'habitat est souvent soulevée comme facteur limitant. Nous avons estimé le taux d'occupation d'habitats favorables par la Grive de Bicknell (*Catharus bicknelli*), une espèce forestière menacée, sur le plateau Laurentien du Québec. Les forêts de cette région ont été façonnées par des activités forestières intenses et des perturbations naturelles. L'espèce a surtout été trouvée dans des peuplements âgés de 20 ans et plus, et le taux d'occupation le plus élevé a été observé dans de vieux peuplements au sommet de montagnes, où est advenu beaucoup moins d'activités forestières récentes et de perturbations naturelles. L'occupation par la Grive de Bicknell était associée aux hautes élévations où les éclaircies précommerciales étaient moins fréquentes. Tant le taux d'occupation que l'analyse multivariée ont indiqué que de grandes étendues d'habitats favorables (> 80 %) n'hébergeaient pas de Grives de Bicknell. Nous concluons que le maintien d'habitats de nidification favorables dans ce paysage de forêts exploitées demeure important pour le rétablissement de l'espèce, mais la hausse des effectifs risque de ne pas se matérialiser si des mesures additionnelles de protection non liées à la disponibilité d'habitats de nidification ne sont pas mises en place.

Key Words: *Bicknell's Thrush; Catharus bicknelli; forest management; habitat use; occupancy; Quebec; threatened species*

INTRODUCTION

In North America, several migratory bird species inhabiting boreal and eastern forests are declining (Sauer et al. 2013). Habitat loss, impairment, and fragmentation on breeding or wintering grounds or at stopover sites may play a significant role in these declines. The endangered status of several species has been directly linked to forest management issues. Those species include Olive-sided Flycatcher (*Contopus cooperi*; Robertson and Hutto 2007), Rusty Blackbird (*Euphagus carolinus*; Powel et al. 2010), Cerulean Warbler (*Setophaga cerulea*; Buehler et al. 2008), Kirtland's Warbler (*Setophaga kirtlandii*; Long 2009), and Barrows Goldeneye (*Bucephala islandica*; Vaillancourt et al. 2009, Gouvernement du Québec 2013). Forest management impacts, proven or hypothesized, have triggered calls for action by the scientific, philanthropic, and environmental advocacy communities, as exemplified by the "Boreal Birds Need Half" campaign (Wells et al. 2014), which aims to prevent habitat limitation from becoming a pervasive issue affecting boreal birds. Accordingly, forestry operators on breeding grounds are being asked to adopt more sustainable and bird-friendly practices (Booth et al. 1993, Franklin et al. 2002, Cyr et al. 2009, Bélanger 2010, Marzluff et al. 2000, Drapeau et al. 2016).

An essential requirement for effective and efficient recovery planning for a species at risk is the identification of the key limiting factors through its annual cycle (Faaborg et al. 2010, Rushing et al. 2016). Habitat availability is one of the most frequently cited limiting factors for a wide range of taxa (Hoekstra et al. 2005, Maxwell et al. 2016). This may be especially true for migratory species that depend on different habitats, each potentially under

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different threats, at different times through their annual cycle. Habitat may be limiting for a species at risk because it is rare, of low quality, inaccessible, or for more subtle reasons as in the case of species with spatially aggregated social systems (Macedo and Bianchi 1997, Bourque and Desrochers 2006) or a highly biased sex-ratio (Donald 2007).

To determine whether habitat availability limits a population, a logical first step is to determine how much suitable habitat is available yet unoccupied (Nelson and Buech 1996, Rappole et al. 2003, Gibson et al. 2007, Engler et al. 2014). High vacancy rates, i.e., low occupancy, would generally negate the hypothesis that habitat availability is limiting, at least in the geographic area considered (Hoekstra et al. 2005, Nielsen et al. 2006). However, apparently unoccupied areas could also reflect inadequacies of the survey method, i.e., low detection probability of the focal species (Gu and Swihart 2004) or of the habitat sampling design, i.e., failure to include important habitat variables for the species under consideration.

Bicknell's Thrush (*Catharus bicknelli*) has one of the most restricted breeding ranges of all North American forest-breeding migratory birds (COSEWIC 2009, McFarland et al. 2013, Townsend et al. 2015, Hill and Lloyd 2017). At the continental scale, the species ranks as one of the highest conservation priorities (Rich et al. 2004, Rosenberg et al. 2014), while it is legally considered as threatened in Canada (Government of Canada 2012) and vulnerable in Québec (Gouvernement du Québec 2009). Most of Bicknell's Thrush breeding habitat in Canada occurs in southern Québec in the Appalachian Range and on the Laurentian Highlands north of the St. Lawrence River (COSEWIC 2009). In the latter region, breeding habitat occurs primarily at high elevation in dense balsam fir dominated stands within industrial forestland where clear-cuts and forest management practices aimed at reducing stem density (hereafter called precommercial thinning) may affect habitat quality (Higdon et al. 2006, Chisholm and Leonard 2008, COSEWIC 2009, Aubry et al. 2011, 2016). Habitat loss and impairment on breeding grounds have been suggested as the major threats to the species (COSEWIC 2009, Lloyd and McFarland 2017). Consequently, there have recently been pressures and efforts to limit the extent and intensity of precommercial thinning throughout the species' breeding range (Chisholm and Leonard 2008, BSC 2009, Gouvernement du Québec 2014, Lambert et al. 2017). Such changes can be costly to the industry, directly and indirectly affecting regional economies and, if misguided, impinge the credibility of science conservation advisors.

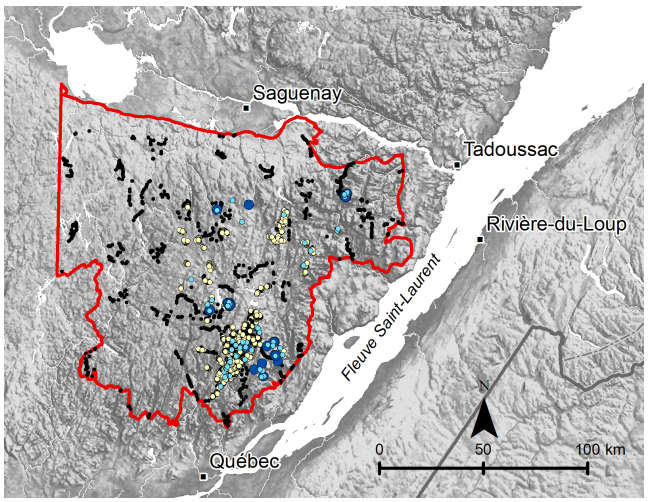
To better guide Bicknell's Thrush conservation efforts, we studied habitat occupancy in Québec's Laurentian Highlands. Our primary objective was to test whether maximum breeding habitat occupancy approached saturation (100%). We also tested the hypothesis that precommercial thinning is associated with lower occupancy of Bicknell's Thrush breeding habitat, as found in other regions (Aubry et al. 2011). The species needs dense stands as a concealment for its nest and to avoid potential predation. Therefore, we predict that thinned stands are less occupied than unthinned stands. To test those two hypotheses, we performed site occupancy modeling as per Mackenzie et al. (2002). However, Bicknell's Thrushes have large home ranges on their breeding grounds and a spatially aggregated social system (Aubry et al. 2011, Townsend et al. 2015), likely due to their polygynandric mating system (Goetz et al. 2003, Townsend et al. 2015), which may undermine the assumption of closure of the occupancy state required by occupancy models (MacKenzie et al. 2003). Thus, we also assessed occupancy using a graphical approach that represents Bicknell's Thrush niche space based on a two-dimensional reduced projection of topographic and vegetation variables.

METHODS

Study area

The 17,350-km² study area is located north of the St. Lawrence River, centered approximately 75 km north of Quebec City, Québec, at the southeast edge of the Laurentian Highlands. It is part of the balsam fir-white birch bioclimatic domain (Grondin et al. 1998; Fig. 1) lying between 47° and 48.35°N and 70° and 72.30°W. The elevation varies from 130 to 1100 m and the mean annual temperature is 0° C. Abundant precipitations (1.2–1.6 m/year) are associated with a long fire cycle (> 500 years; Boucher et al. 2014). The vegetation is dominated by balsam fir (*Abies balsamea*) and paper birch (*Betula papyrifera*); black spruce (*Picea mariana*) occurs increasingly toward the north of the study area, and deciduous trees are often abundant in regenerating clear-cuts and recently burned areas (Grondin et al. 1998). Disturbances are mostly from anthropic origin, with forestry activities having occurred at all elevations since 1900 but more intensively at low elevation (Boucher and Grondin 2012, Boucher et al. 2014).

Fig. 1. Study area, delimited by the red line, in the Laurentian Highlands, Québec, Canada. Beige and blue dots represent point count stations with no, or at least one Bicknell's Thrush (*Catharus bicknelli*) reported, respectively. Light and dark blue dots represent detections of one or multiple Bicknell's Thrushes, respectively. Black dots represent point counts eliminated from the analyses. (Map sources: Digital elevation model© Government of Quebec, all rights reserved, 2004, and Natural Resources Canada for waterways)



We determined stand age, the proportion of deciduous, and the extent of precommercial thinning over the study area from forest inventory data (Gouvernement du Québec 2015). We converted the original forestry and topographic map layers to rasters with a 10-m resolution, with the Spatial Analyst extension of ArcGIS (ESRI 2010). We calculated stand ages based on documented years of clear-cutting and other stand-renewing events, i.e., fire and major spruce budworm outbreaks. In places where only age classes were known, we determined stand age as the midpoint of the age class for even-aged stands, or as the lowest age class for heterogeneous stands. We extracted elevation at point counts and its variation within 1000 m from the Canadian Digital Elevation Data 2000 (available from https://open.canada.ca/data/en/dataset?organization=nrcan-rncan). We considered a habitat as suitable when it was at elevations greater than 550 m, composed of balsam fir-dominated stands, and had not been thinned (Lambert et al. 2005, Chisholm and Leonard 2008, Aubry et al. 2011, 2016).

Point counts

We compiled data from 7830 fixed radius point counts conducted for different projects in the study area between 1995 and 2016 (Fig. 1). Those projects focused on all bird species (> 98% of sites randomly selected) and covered a broader range of altitudes, while surveys targeting Bicknell's Thrush covered sites with elevation > 800 m. The projects were the second Québec Breeding Atlas, Forêt Montmorency bird monitoring program, regional environmental impact assessments, Mountain BirdWatch monitoring scheme, Huron-Wendat Bicknell's Thrush monitoring project, and provincial and federal governments' Bicknell's Thrush surveys. We retained 4818 point counts for analysis based on three criteria: a duration of 15 to 30 min (mean = 18 min), conducted before 9:00 (n = 4700) or after 19:00 (n = 118), and between 22 May and 25 July. Those periods correspond to high Bicknell's Thrush vocal activity (Ball 2000). Nine percent of the point counts used playbacks of Bicknell's Thrush calls and songs. Retained point counts were distributed among 2500 stations separated by at least 150 m, often (54%) along forestry roads. We surveyed 31% of the point count stations more than once in a year (Appendix 1), and surveyed 38 and 114 stations on two and three different years, respectively. Forty observers, all with experience with Bicknell's Thrush vocalizations, participated in the point counts. We recorded all Bicknell's Thrushes within 75 or 100 m-radii, depending on the data source. We assumed that the radius difference was sufficiently small across surveys, and that the distance between point counts was sufficient across the study areas, to prevent major biases (Yip et al. 2017).

Site occupancy

We fit nine competing single-season site occupancy models (Mackenzie et al. 2006) to measure site occupancy by Bicknell's Thrush, given imperfect detection during point counts. Models were fit by maximum likelihood with the unmarked package 0.11-0 in R Version 3.3.1 (Fiske et al. 2011, R Development Core Team 2016). The models considered various combinations of 11 site-related occupancy and four point count-related detection variables, identified from our experience with the species, the published literature, and the habitat data generally available. (Table 1; Aubry et al. 2011, 2016, Lambert et al. 2005, Townsend et al. 2015). We introduced the variable Year in the models to account for a possible population trend. Further annual variation could result from nest predation by red squirrel (*Tamiasciurus hudsonicus*; Townsend et al. 2015), which may affect recruitment and demographic parameters, and hence occupancy. However, we have no quantitative information on cone crops or squirrel population densities throughout the duration and spatial extent of the study. Elevation was selected because the species is known to be associated with montane habitat (Townsend et al. 2015, Aubry et al. 2016) and we used the standard deviation of elevation within 1 km of point count as an index of terrain ruggedness. Proportion of deciduous within 1000 m along with proportion of precommercial thinning were selected as proxies for recent forestry activities and habitat structure. Bicknell's Thrushes often establish their home range in regenerating or young forest stands (Townsend et al. 2015) ≥= 1.5–2 m high (*personal observation*). To account for a possible nonlinear response to forest age (Ter Braak and Looman 1986), we included a quadratic stand age term in the models. We used the standard deviation of stand age as an index of habitat heterogeneity. Some variables were estimated at local and/or at the landscape scale (within 100 and 1000 m of point count center, respectively) to explore the sensitivity of the species at those two scales. In the full model we included distance of point count from nearest road in view of concerns of a possible edge effect expressed earlier (Hanowski and Niemi 1995, but see Hutto et al. 1995, Lituma and Buehler 2016). Moreover, Bicknell's Thrush may respond to edges, as shown in a recent study where the species was not avoiding stand edges in an industrial forest (Aubry et al. 2011), or as in a ski trail study where a higher nest density was observed in forest edges where vegetation was dense (Rimmer et al. 2004). In another study, in the White Mountains (New Hampshire, USA), the presence of hiking trails did not affect Bicknell's Thrush abundance and detection probabilities (Deluca and King 2014). Models (Table 2) were selected to estimate site occupancy according to predation by squirrels (model 6), to habitat structure along with elevation (model 3) and year (model 1), to elevation (model 4) and topography (model 5) and to spatial variation in habitat structure (model 7) and habitat composition (model 8).

We computed Goodness-of-Fit for the best occupancy model using a parametric bootstrap approach (MacKenzie and Bailey 2004) with 100 replicates. The best, single-season model fit the data well with no apparent over dispersion (function parboot of package unmarked, p = 0.21). To facilitate convergence and parameter estimation, all numerical variables were standardized before analysis. We evaluated the degree of support for each model using Akaike's Information Criteria (AIC_c) and standardized Akaike weights. The models with $\Delta AIC_c \leq 2$ were considered as supported models (Table 2).

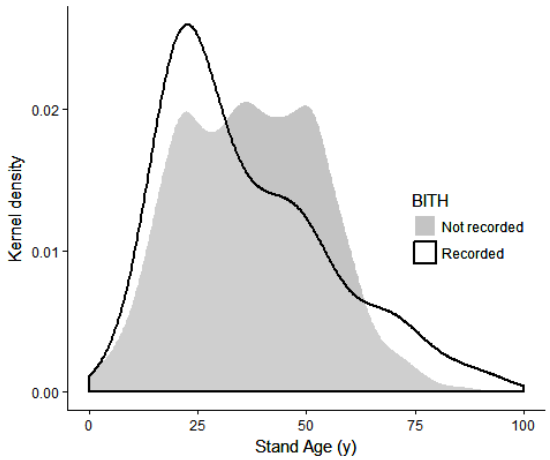
Niche space occupancy

We conducted a Principal Component Analysis (function prcomp in R) using the three vegetation and topography variables that were identified as significantly related to Bicknell's Thrush occupancy in the best performing occupancy model (Table 3), along with mean stand age (within 100 m of point count) that also appeared to be associated with occupancy (Fig. 2). We used the first two principal components to represent Bicknell's Thrush niche space, and calculated two-dimensional kernel densities of Bicknell's Thrush occurrences (R package MASS, function kde2d; Venables and Ripley 2002). The proportions of occupied point count stations falling in each kernel density category provided estimates of Bicknell's Thrush occupancy.

Table 1. Site-related occupancy, and point count-related detection variables included in Bicknell's Thrush (*Catharus bicknelli*) occupancy models for the Laurentian Highlands, Québec, Canada.

Variable	Description
Occupancy	
Year	Year of point count
Longitude	Easting (meters, MTM7 projection)
Latitude	Northing (meters, MTM7 projection)
Elevation	Elevation of point count, above sea level (m)
ElevationSD1000	Standard deviation of elevation within 1 km of point count
% Deciduous	Proportion of raster with deciduous-dominated stands, within 1 km of point count
Age100	Mean stand age within 100 m of point count
Age100quad	Quadratic term of the stand age within 100 m of point count
Age1000	Mean stand age within 1 km of point count
AgeSD1000	Standard deviation of stand age within 1 km of point count
PCT1000	Proportion of raster with precommercial thinning in the last 20 years, within 1 km of point count
DistRoad	Distance to nearest road (m)
Detection	
Playback	Use of Bicknell's Thrush playback during point count (dichotomous)
Date (Julian)	Days since 1 January
Time of Day	Evening or morning (dichotomous)
Duration	Duration of point count (minutes)

Fig. 2. Kernel density distribution of stand ages (Age 100; Table 1) for point count stations where Bicknell's Thrush (*Catharus bicknelli*) were recorded, or not recorded, in the Laurentian Highlands, Québec, Canada. Data from 2500 point count stations surveyed between 1995–2016.



RESULTS

Bicknell's Thrush were reported at 121 (2.5%) of the 4818 point counts, and at 115 (4.6%) of the 2500 point count stations (Fig.1). The best-performing occupancy model included Year (+), Elevation (+), Elevation interactions with stand age (linear and quadratic), as well as the percentage of deciduous forest (+) and precommercial thinning (-) at the landscape scale (Table 2, Table 3). Given that estimate for forest stand age was positive and the age x elevation interaction estimate negative (Table 3), we interpret the significant interaction as a lower effect of stand age on occupancy at higher elevations. The best performing occupancy model as well as the other models, identified three point count-related detection variables that were significantly associated with the probability of detecting Bicknell's Thrush (Table 3): date (increasing from May to July), duration (+), and use of playback (+). Detection probabilities in the morning were 0.16 ± 0.04 without playback and rose significantly to 0.63 ± 0.15 with playbacks. Detection probabilities were higher, but not significantly so (Table 3), in the evening, both without or with playbacks (0.36 ± 0.24, 0.83 ± 0.15, respectively). Occupancy increased significantly between 1995 and 2016 in the study area (Table 3, Fig. 3). An analysis where all variables except Year were set to their mean value over the entire study area, thereby removing confounding factors revealed that the temporal trend was consistent through time. Bicknell's Thrushes were seldom reported below 800 m elevation (n = 6/121), and site occupancy was greater than 0.7 at only a handful of stations (n = 10) at the highest elevations (Fig. 4).

Fig. 3. Bicknell's Thrush (*Catharus bicknelli*) site occupancy in relation to year in the Laurentian Highlands, Québec, Canada. To prevent confounding effects, occupancy estimates were obtained by setting all other variables fixed at their mean value over the entire study area. Data from 2500 point count stations surveyed between 1995–2016. Error bars are ± 1 SE.

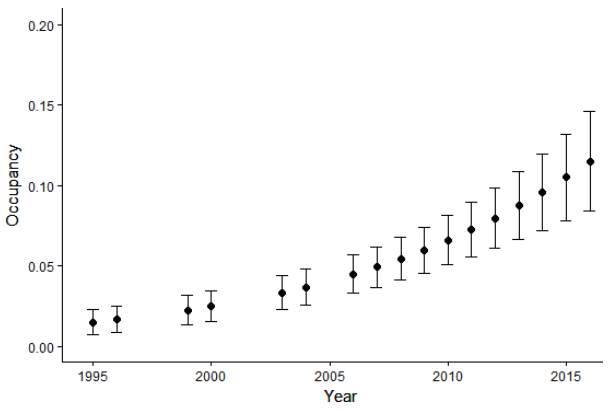
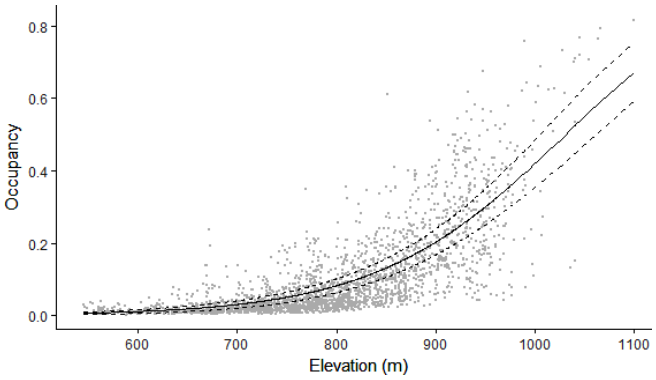


Table 2. Comparison of nine models for Bicknell's Thrush (*Catharus bicknelli*) occupancy in the Laurentian Highlands, Québec, Canada, using combinations of topographic, vegetation, landscape, and temporal variables (see Table 1). All models included the four point count-related detection variables: playback, Julian date, time of day, duration. Data from 2500 point count stations surveyed between 1995–2016.

Model	K	AICc	Delta AICc	AICc Weight	Cum. Wt	Log Likelihood
1-Year, Elevation x (Age100, Age100quad), % Deciduous, PCT1000	14	855.91	0	0.99	0.99	-413.87
2-Full	18	865.15	9.24	0.01	1	-414.44
3-Elevation x (Age100, Age100quad), ElevationSD1000, PCT1000	13	872.54	16.63	0	1	-423.2
4-Elevation	7	876.73	20.82	0	1	-431.34
5-Elevation, ElevationSD1000	8	876.93	21.01	0	1	-430.43
6-Year (trend)	7	921.04	65.13	0	1	-453.5
7-Latitude, Longitude, Age100, Age100quad, PCT1000	11	922.1	66.19	0	1	-450
8-Latitude, Longitude, % Deciduous, PCT1000, AgeSD1000	11	926.39	70.48	0	1	-452.14
9-Null	6	935.62	79.71	0	1	-461.79

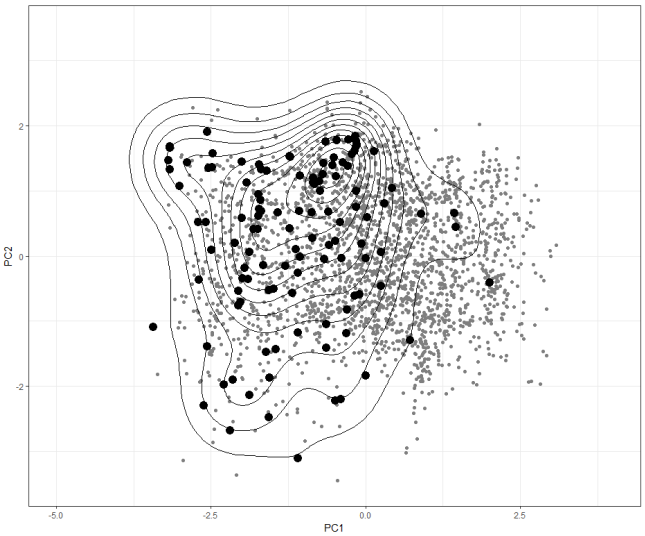
Fig. 4. Bicknell's Thrush (*Catharus bicknelli*) site occupancy in relation to elevation in the Laurentian Highlands, Québec, Canada. The vertical scatter in occupancy estimates comes from the effect of other variables included in the best performing occupancy model presented in Table 3. The solid line represents occupancy estimated from model with elevation as the sole covariate, and other covariate values set at the mean of all point count stations. Data from 2500 point count stations surveyed between 1995–2016. Error bands are ± 1 SE.



To better understand the relationship between stand age and occupancy, we contrasted the kernel density distributions of stand age at stations where Bicknell's Thrushes were observed and not observed (Fig. 2). The distributions were substantially different, revealing higher occupancy of the youngest (20–30 years old) and oldest (> 70 years old) stands, and lower occupancy of mid-age stands.

In the niche space occupancy analysis, the first two axes of the principal component analysis accounted for 71% of the total variance (PC1: 0.44; PC2 0.27; Table 4). High values for the first factor reflected low elevation, but high deciduous and precommercial thinning cover. High values for the second factor reflected high elevation and young stands, independent of deciduous dominance or precommercial thinning. Of the 2500 point count stations surveyed, 1969 fell within the two-dimensional niche space defined by kernel density > 0.05 (Fig. 5).

Fig. 5. Kernel density estimates of Bicknell's Thrush (*Catharus bicknelli*) occurrence in the Laurentian Highlands, Québec, Canada, based on a principal component analysis of topographic and vegetation variables (Table 4). Contour lines represent increments in kernel density from 0.01 to 0.12 by increments of 0.01. Grey and black dots represent point counts with Bicknell's Thrush not reported and reported, respectively. Data from 2500 point count stations surveyed between 1995–2016.



Unoccupied sites were dispersed throughout the biplot (Fig. 5) while occupied sites were mostly concentrated on the two left quadrants. Bicknell's Thrush was largely unreported at stations in the lower right quadrant of the biplot, corresponding to lower elevation, high thinning, and more deciduous stands (Table 4). Bicknell's Thrush reporting rate was consistently low, reaching less than 8% at point count stations in the most suitable habitat (i.e., kernel density estimates > 0.10; Fig. 6).

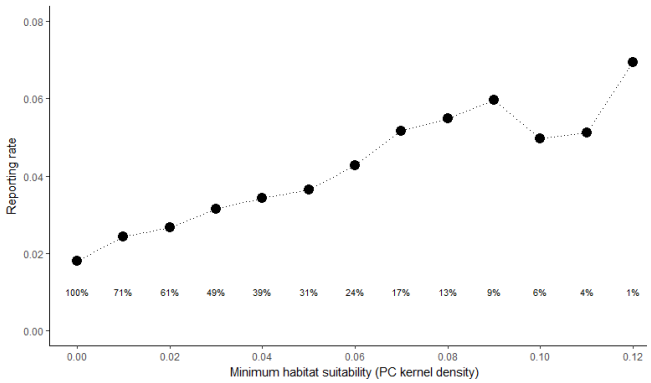
Table 3. Parameter estimates for the best performing occupancy model for Bicknell's Thrush (*Catharus bicknelli*) in the Laurentian Highlands, Québec, Canada. Data from 2500 point count stations surveyed between 1995–2016.

Variable	Estimate	SE	*z*	P(>|*z*|)
Occupancy				
(Intercept)	-2.874	0.27	-10.7	< 0.001
Year (trend)	0.659	0.20	3.43	< 0.001
Elevation	1.036	0.16	6.4	< 0.001
Age100	6.2	7.77	0.80	0.4
Age100 (quadratic)	9.068	9.29	0.986	0.3
% Deciduous	0.428	0.13	3.26	0.001
PCT1000	-0.304	0.12	-2.45	0.015
Elevation x Age100	-15.117	6.49	-2.33	0.02
Elevation x Age100 (quadratic)	-4.017	8.47	-0.47	0.6
Detection				
(Intercept)	-7.5853	2.29	-3.32	0.0009
Playback	2.1695	0.60	3.61	0.0003
Julian Date	0.0261	0.01	2.22	0.03
Time of Day (evening)	1.065	0.98	1.09	0.3
Duration	0.0749	0.037	2.00	0.045

Table 4. Factor loadings for the first two factors of a principal component analysis of topographic and vegetation variables at Bicknell's Thrush (*Catharus bicknelli*) point count stations in the Laurentian Highlands, Québec, Canada. Data from 2500 point count stations surveyed between 1995–2016.

Variable	PC1	PC2
Elevation	-0.60	0.31
% Deciduous	0.58	0.03
PCT1000	0.53	0.17
Age1000	-0.08	-0.93

Fig. 6. Reporting rates of Bicknell's Thrush (*Catharus bicknelli*) at point count stations within available suitable habitat in the Laurentian Highlands, Québec, Canada. Large kernel density estimates can be interpreted as an increase in habitat suitability. Sample sizes are shown below each density point. Data from 2500 point count stations surveyed between 1995–2016.



DISCUSSION

Our study of Bicknell's Thrush site occupancy in the Laurentian Highlands of Québec, using two contrasted approaches, revealed that a large extent of potential habitat was unoccupied. Similar conclusions were reached from studies of several other avian species at risk, such as the Golden-cheeked Warbler (*Setophaga chrysoparia*; Rappole et al. 2003), Kirtland's Warbler (Nelson and Buech 1996), Lesser Kestrel (*Falco naumanni*; Serano and Tella 2003), and White-browed Treecreeper (*Climacteris affinis*; Radford and Bennett 2004).

There is an apparent discrepancy between the positive regression estimate of % deciduous in Table 3, and the low reporting rates in the right quadrants of Fig 5, corresponding to high % deciduous values. We attribute this apparent discrepancy to the fact that occupancy estimates accounted for other covariables such as elevation, which was not the case in the principal component analysis. The significant negative interaction between forest age and elevation effects in the best occupancy model indicates that the occupancy of young forests, where deciduous stems are prevalent, is not as pronounced at high elevations as it is at lower elevations. Furthermore, the amount of deciduous forest was estimated within 1000 m around point count. At that scale and in an environment where forestry activity is ubiquitous, young deciduous dominated stands are common in the early stages of regenerating balsam fir forest. In our study area, below 800 m elevation, deciduous stands represented 40% (± 24) of the area within 1000 m of point count, and 28% (± 10) over 800 m. Despite that Bicknell's Thrush is known as a balsam fir specialist, notable presence in deciduous stands has also been documented in New Brunswick (Nixon et al. 2001), in young regenerating stands where fir has not surpassed deciduous in height yet.

Our site occupancy models likely overestimated occupancy rates because the large home ranges of Bicknell's Thrush (≥ 10 ha; Aubry et al. 2011) likely resulted in violations of the closure assumption (MacKenzie et al. 2006, Rota et al. 2009). On the other hand, imperfect detection may have led us to underestimate

occupancy rates in the niche space occupancy analysis. This is unlikely since in a companion study (Aubry and Mazerolle, *unpublished data*), we estimated detection probabilities at ≥ 0.74 and ≥ 0.88 using point count techniques similar to those used here, i.e., 3 x 5 min. survey periods without and with an additional playback period, respectively. Biased occupancy rate estimates can also result from uneven accessibility of habitat patches across a study area, e.g., less access to high elevation sites. This was not at play in our research because the study area was covered by forestry roads, with almost no site beyond 300 m from a road, i.e., beyond the audible range of Bicknell's Thrush calls. It is thus unlikely that imperfect detection has introduced a bias of sufficient importance to alter our conclusion.

Bicknell's Thrush nesting habitat quality seems to be mostly driven by elevation and associated vegetation dynamics (e.g., wind throw, fir waves *sensu* Sprugel 1976) in both the northeastern United States (Lambert et al. 2005, Hale 2006) and in Québec (Aubry et al. 2016). In Vermont, in mostly protected areas, occupancy of high-elevation habitat approaches 100% (Frey et al. 2012). Extrapolating from Lambert et al.'s (2005) elevational habitat model, we should have recorded Bicknell's Thrush as low as 550 to 600 m in our study area. A similar model adapted for Québec latitudes predicted occurrences at even slightly lower elevations (Rimmer, *unpublished report*). However, we recorded the species below 800 m (641–777 m) in only six occasions, corresponding to an estimated occupancy rate of < 8%. The discrepancy between model predictions and our observations may be due to habitat quality impairment at low elevation resulting from major fires and intensive logging through the 20th century (Boucher and Grondin 2012), the prevalence of precommercial thinning, and possibly nest predation by red squirrel. A similar effect was observed by Whitaker et al. (2015; D. Whitaker, *personal communication*), who noted that on Newfoundland the closely related Gray-cheeked Thrush (*Catharus minimus*) became confined to high elevation forests following the introduction of squirrels (Payne 1976), which are restricted to lower elevations.

Even at higher elevations, site occupancy by Bicknell's Thrush was generally well below saturation (Fig. 4). The most parsimonious explanation for this is an insufficient number of birds due to limiting factors acting outside of the breeding grounds. However, alternative phenomena may lead to a lack of breeders in optimal habitat. First, as for lower elevation, territory abandonment may occur over a large scale because of nest predation by red squirrels (McFarland et al. 2008). Second, polygynandry in Bicknell's Thrush may lead to clustering through conspecific attraction (Nocera and Forbes 2010) and, in turn, reduce the suitability of small habitat patches, as is the case with several other forest songbirds (Bourque and Desrochers 2006, Desrochers et al. 2010). Third, incomplete occupancy of suitable habitat at higher elevation may be a constraint of dispersal because of insufficient numbers of females. Considering the highly male-biased sex-ratio of the species, unoccupied habitat can remain unoccupied for a long time because of the lack of conspecifics to attract dispersers (Schlossberg and Ward 2004). Last, we cannot rule out that some habitat attributes may have been overlooked because of our selection of variables, which was based on what was available at the time of the study.

During the study period, in New Hampshire (1993–2003; Lambert et al. 2008), an annual decline (-7%) was reported while recent analyses from data across its United States range (2011–2016) produced a nonsignificant decline (Hill and Lloyd 2017). Bicknell's Thrush numbers were declining in the Canadian Maritimes and southeastern Québec where the species became extirpated from several locations (Whittam 2015, Québec Breeding Bird Atlas 2018). Contrastingly, we documented a significant increase in occupancy in the spatiotemporal bounds of the current study. We can only speculate on the causes of this local increase, but it may result from a nonlinear functional response to the strong increase in early-successional dense balsam fir forest stands following a major spruce budworm outbreak that began in the early 1970s (Hardy et al. 1983) and lasted for over two decades in our study area (Gray et al. 2000).

Although large areas of apparently suitable Bicknell's Thrush habitat appear to be unoccupied in the Laurentian Highlands of Québec, habitat conservation efforts and thrush-friendly forestry practices should not be abandoned. Habitat availability can rapidly become a concern if management of successional dynamics and forest structure pushes large areas of forest outside the suitable stand age and density for the species. This appears to be the case in northwestern New Brunswick where, if current forest management plans are maintained, Bicknell's Thrush potential habitat will have entirely disappeared by 2027 (Higdon et al. 2006). Similarly, a proposal to vastly expand old-growth areas in support of the conservation of woodland caribou (*Rangifer tarandus caribou*) in the Laurentian Highlands of Québec (Équipe de rétablissement du caribou forestier du Québec 2013) may conflict with the maintenance of suitable habitat for Bicknell's Thrush. Considering the ephemeral habitat suitability status, it is therefore prudent to preserve more habitat than what a target population may occupy at a specific time (Rompré et al. 2010, Frey et al. 2012). This rationale underlies the recent publication by the Government of Québec of guidelines aimed at reducing precommercial thinning in Bicknell's Thrush occupied and potential habitat, as well as avoiding incidental destruction of nests, eggs, and young (Gouvernement du Québec 2014).

In the Laurentian Highlands of Québec, there appears to be a shortage of Bicknell's Thrushes rather than its breeding habitat. But considering that the population seems to have increased over the period of the study, there are good conservation-based reasons to maintain more habitat at higher elevation (> 800 m) than is required to allow the population to grow to the recovery target as prescribed by the Species at Risk Act. Without discontinuing efforts to conserve breeding habitat, greater attention should be paid to other potential limiting factors. Current challenges for the species outside the breeding range are habitat loss and degradation due to anthropogenic and natural causes on its wintering grounds in the Greater Antilles (Hill and Lloyd 2017, Lloyd et al. 2017).

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1226

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Appendix 1. Frequency of first, second, and later visits to point counts conducted in the study area, 1995-2016. Laurentian Highlands, Quebec, Canada.

Year	Visit sequence number				
	1	**2**	**3**	**4**	**5**
1995	164	138	0	0	0
1996	110	2	0	0	0
1999	134	124	75	0	0
2000	150	86	0	0	0
2003	143	98	0	0	0
2004	123	102	71	25	4
2006	170	52	0	0	0
2007	143	61	23	8	2
2008	16	0	0	0	0
2009	120	87	30	0	0
2010	130	124	110	90	0
2011	143	132	121	110	19
2012	258	0	0	0	0
2013	200	116	70	0	0
2014	203	132	32	0	0
2015	153	105	29	0	0
2016	140	113	27	0	0