

Large herbivore effects on songbirds in boreal forests: lessons from deer introduction on Anticosti Island¹

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Abstract: Over recent decades, deer populations have reached densities exceeding their natural range of variability in several regions worldwide. Abundant deer populations can change the composition and structure of understory plant communities in forests and trigger trophic cascades affecting animal communities. To investigate such indirect effects on boreal forest songbirds we compared the understory vegetation and songbird communities of balsam fir stands on Anticosti Island (Quebec, Canada), where white-tailed deer (*Odocoileus virginianus*) were introduced, to those of the neighbouring Mingan Archipelago, where deer are absent. Mean cover of trees at 0–2 m height was on average sevenfold higher on Mingan than on Anticosti, and songbirds dependent on the understory were more common on Mingan than on Anticosti. Songbird community composition was more variable on Mingan, suggesting that the opening of the forest understory on Anticosti through intensive browsing homogenized the songbird community by reducing the occurrence of understory-dependent species. These indirect effects on songbirds were similar, although less dramatic, than those described in temperate forests. We interpret this as a consequence of lower productivity and complexity in understory vegetation of boreal forests. Our results emphasize the negative effects of abundant deer populations on animal diversity and underline the role played in the dynamics of communities by top down factors that regulate herbivore populations.

Keywords: deer browsing, indirect effects, overabundance, songbird communities, white-tailed deer.

Résumé: Plusieurs populations de cervidés ont récemment atteint des densités élevées dans différentes régions du monde. Ces populations abondantes peuvent modifier la composition végétale et la structure des forêts et engendrer des cascades trophiques affectant les communautés animales. Nous avons vérifié l'étendue de ces effets sur les oiseaux chanteurs en forêt boréale en comparant le sous-étage forestier et les communautés aviaires des sapinières de l'île d'Anticosti (Québec, Canada), où le cerf de Virginie (*Odocoileus virginianus*) a été introduit, à celles de l'archipel de Mingan où le cerf est absent. Le recouvrement arborescent entre 0 et 2 m était en moyenne sept fois plus élevé à Mingan qu'à Anticosti et les oiseaux dépendant de cette strate étaient plus communs à Mingan. La composition des communautés aviaires étant plus variable à Mingan, l'ouverture du sous-étage forestier par le broutement intensif à Anticosti a vraisemblablement homogénéisé les communautés aviaires en réduisant la présence d'espèces associées à cette strate forestière. Ces effets indirects étaient similaires à ceux observés en forêt tempérée, mais moins contrastés. Nous interprétons ceci comme une conséquence de la faible productivité et complexité de la végétation de sous-étage des forêts boréales. Nos résultats mettent en évidence les effets des populations abondantes de cervidés sur la diversité animale et le rôle des facteurs descendants dans la dynamique des communautés.

Mots-clés: broutage par le cerf, cerf de Virginie, communautés d'oiseaux chanteurs, effets indirects, surabondance.

Nomenclature: Integrated Information Taxonomic System (ITIS), 2011.

Introduction

Over recent decades, deer populations have reached densities exceeding their natural range of variability in several regions of Europe and North America (McShea, Underwood & Rappole, 1997; Fuller & Gill, 2001; Côté *et al.*, 2004). These abundant deer populations can severely affect ecosystem characteristics such as

biogeochemistry and plant diversity (Hobbs, 1996; Rooney & Waller, 2003; Côté *et al.*, 2004). Selective browsing can change plant species composition by progressively excluding browse-sensitive species from the landscape to the benefit of more tolerant species (Tilghman, 1989; Rooney & Waller, 2003), and intense browsing pressure can affect tree regeneration and simplify forest structure (Alverson, Waller & Solheim, 1988; Rooney, 2001).

These changes in plant species composition or stand structure can trigger trophic cascades (Côté *et al.*, 2004;

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Suominen & Danell, 2006; Martin *et al.*, 2010) with effects on invertebrates (Stewart, 2001; Allombert, Stockton & Martin, 2005), small mammals (McShea & Rappole, 1992; Moser & Witmer, 2000), and songbirds (Casey & Hein, 1983; deCalesta, 1994; Allombert, Gaston & Martin, 2005). These effects may ultimately lead to a loss in biodiversity (van Wieren & Bakker, 2008), emphasizing the key role of large herbivores in ecosystems (McShea & Rappole, 1992).

Songbird species most dependent on the understory vegetation are especially exposed to reductions in vegetation density (McShea & Rappole, 1997; Fuller, 2001) and habitat structure (van Wieren & Bakker, 2008) caused by intensive browsing. Declines in understory-dependent songbirds were correlated with increasing deer populations in numerous deciduous forests of Europe and North America (England: Perrins & Overall, 2001; Gill & Fuller, 2007; USA: Casey & Hein, 1983; McShea & Rappole, 2000). Similar conclusions were reached in lush coastal forests of western Canada and USA (temperate rainforest: Allombert, Gaston & Martin, 2005; Douglas fir forest: Martin, Arcese & Scheerder, 2011). Conversely, experiments conducted in American hardwood forests have shown that reductions of deer density can lead to the recovery of some of these birds and increase total bird abundance and species richness (Pennsylvania, USA: deCalesta, 1994; Virginia, USA: McShea & Rappole, 2000). Such results emphasize not only the range of effects that large herbivores can have in ecosystems, but also, indirectly, the importance of top-down factors in controlling their populations (McShea & Rappole, 1992; Martin *et al.*, 2010).

The existence of long-term and broad-scaled ecosystem effects of browsing by abundant deer populations, however, has often been met with skepticism (Martin *et al.*, 2010). One reason for skepticism is that in most such situations, changes in deer populations typically occurred simultaneously with changes in land use and other confounding factors. Another reason is that few natural habitats exist that provide reference data: abundant deer populations have become common, but natural habitats without deer, or habitats that still have fully functioning top-down deer regulation by carnivores, are rare. For the former, isolated islands provide valuable settings in which different histories of deer presence occur in proximity. On the Haida Gwaii Archipelago (British Columbia, Canada), for example, dramatic decreases in vegetation cover in the lower strata on islands where deer had been present for > 50 y (Stockton *et al.*, 2005) led to significant reductions in the abundance of invertebrate and songbird species (Allombert, Stockton & Martin, 2005; Allombert, Gaston & Martin, 2005). By contrast, bird communities on islands without deer were dominated by understory-dependent songbirds (Allombert, Gaston & Martin, 2005).

While evidence of widespread negative impacts of abundant deer populations on segments of the forest songbird communities have accumulated in different temperate forest ecosystems of Europe and North America, we still know little about the potential extent of this phenomenon in boreal forests. Anticosti Island and the Mingan

Archipelago (Quebec, Canada) provide a natural experiment to start filling this knowledge gap. These neighbouring islands have similar vegetation and geology but represent 2 extremes in deer browsing histories. On Anticosti, white-tailed deer (*Odocoileus virginianus*) introduced at the end of the 19th century have reached and maintained unusually high densities despite the existence of sport hunting and severe winters. On Mingan islands deer are absent. The prolonged and intense browsing history in the understory of Anticosti Island forests has resulted in a dramatic reduction in regenerating trees (Potvin, Beupré & Laprise, 2003). We therefore predicted a higher prevalence of dense understory vegetation on Mingan islands and a correlated higher prevalence of understory-dependent songbirds on these islands when compared to Anticosti Island.

Methods

STUDY AREA

Located in the Gulf of St. Lawrence (Quebec, Canada), Anticosti Island and the Mingan Archipelago form a single ecological unit (Figure 1; Grondin *et al.*, 2007). All of the islands have the same underlying bedrock mainly composed of Ordovician and Silurian limestone. They were separated by erosion. They belong to the eastern balsam fir–paper birch (*Betula papyrifera*) bioclimatic region and have typical boreal vegetation (Saucier *et al.*, 2009). The climate is maritime and characterized by cool summers and long but relatively mild winters, with mean temperatures ranging from $-13\text{ }^{\circ}\text{C}$ in January to $14\text{ }^{\circ}\text{C}$ in July (Grondin *et al.*, 2007).

Approximately 200 white-tailed deer were introduced on Anticosti Island (7943 km²) in 1896. In the absence of large predators, the population rapidly increased, and densities now average > 20 deer·km⁻² (Rochette & Gingras, 2007). The abundant deer population has considerably modified the composition and structure of Anticosti forests (Potvin, Beupré & Laprise, 2003). Palatable shrubs are virtually eradicated, the understory is generally sparse and very open (Côté *et al.*, 2008), and stands once dominated by balsam fir (*Abies balsamea*) are gradually being replaced by white spruce (*Picea glauca*) forests (Potvin, Beupré & Laprise, 2003). The nearby Mingan Archipelago includes over 66 islands, all of which are devoid of white-tailed deer. With a total area of 88 km², it is located approximately 30 km north of Anticosti Island (Figure 1). The archipelago has remained mostly free of large herbivores, with exceptional sporadic incursions of moose (*Alces alces*) on some islands close to the mainland.

Earlier studies have used the Mingan Archipelago as a reference to evaluate the impacts of long-term deer browsing on the vegetation of Anticosti Island (Viera, 2004; Pellerin, Huot & Côté, 2006). For example, plant diversity in fens on Mingan was greater than on Anticosti, especially for shrubs, sedges, and liverworts (Pellerin, Huot & Côté, 2006). When comparing balsam fir stands between Mingan and Anticosti, Viera (2004) found no differences in large tree densities but much denser understory vegetation on Mingan.

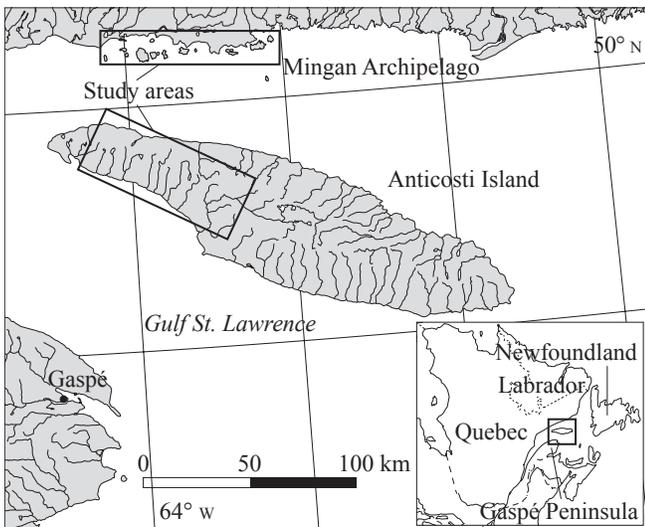


FIGURE 1. Study sites were located on Anticosti Island and the Mingan Archipelago in the Gulf St. Lawrence, Quebec, Canada.

SONGBIRD SURVEYS

Songbirds on the Mingan Archipelago were extensively surveyed in 1998–1999 by Environment Canada and Parks Canada (G. Falardeau, S. Paradis & J.-P. Savard, unpubl. data). We collected similar data on Anticosti Island in 2008. Because of difficult logistics and limitations in observer time, sampling these 2 bird communities during the same year was not possible and we decided to use the existing Mingan data. We started with the assumption that the presence/absence of bird species did not vary in the natural and protected environment of the Mingan Archipelago between the 2 surveys. The 2 sets of data were collected following the same methodology: standard point-counts (Bibby *et al.*, 2000). Singing birds detected at point-counts within a 50-m radius during a 10-min survey were recorded. Census points were distributed along sampling routes established on each site and visited twice a year from 5 June to 30 June between 0430 and 1000 h on days without rain or strong winds.

On the Mingan Archipelago, sampling routes started from island campgrounds or boat drop-offs and were designed to form a loop, taking observers back to their starting points and maximizing the number of habitats covered by point-counts separated by at least 250 m from each other. We only considered point-counts situated in balsam fir stands. There was an average of 10 point-counts per sampling route. These were distributed on 6 islands, totalling 58 point-counts. These islands ranged from 5 to 24 km² (mean = 11 km²) and were on average at 3 km from the coast.

On Anticosti Island, 3 sampling routes of 8 point-counts each were distributed in forest types similar to the balsam fir stands sampled on Mingan. One route was located in the western part of the island (Lake Macray), approximately 67 km east from the other 2 routes which were located in the centre of the island (Jupiter River). The latter routes were separated by 3 km. Deer densities varied between 27 and 56 deer-km⁻² in the areas sampled (Tremblay, Huot & Potvin, 2007). We used forest type

maps to locate point-counts in mature balsam fir stands accessible from the road and easy to reach from the other sites studied in the course of this project. This and the need to find stands of sufficient size to fit point-counts and to have > 200 m between points were the major constraints in selecting stands.

The sampling routes on Anticosti and on Mingan were visited by different observers (3 on Anticosti, 6 on Mingan). On Anticosti, extensive training was done on site to calibrate abilities among observers. In 2008, the 3 observers sampled 22 training point-counts simultaneously and noted their own songbird detections. A multivariate analysis of variance (MANOVA general linear models; SAS Institute, 2003) indicated that songbirds detected did not differ between observers (Wilks's Lambda test, abundance: Wilks = 0.42, $P = 0.7$; presence/absence: Wilks = 0.39, $P = 0.6$). Such simultaneous point-counts were not performed on Mingan, but we assumed little difference in species detection considering that observers were highly experienced ornithologists. Moreover, on both Anticosti and Mingan, observers and time of visits were balanced and alternated to minimize potential biases in species detection associated with these parameters. In the absence of sufficient repetitions on Mingan we could not estimate variation in detection probabilities among observers (MacKenzie *et al.*, 2006). To be conservative with respect to potential observer-related biases we only used presence/absence data. Birds were considered present at a point-count station when detected at least once.

As did Allombert, Gaston, and Martin (2005), we used the literature (Gauthier & Aubry, 1995; Poole, 2005) to score the expected dependence of forest birds towards the understory and ground-layer vegetation (Table I). We assigned a score between 0 (no use of understory and ground layer vegetation) and 3 (exclusive use of understory and ground-layer vegetation) for both nesting and foraging dependence on the understory. The scores were given equal weights and summed to generate an overall score for each bird species' dependence on understory vegetation (Allombert, Gaston & Martin, 2005). This led to 3 groups of species: those with strong, medium, and low dependence on understory vegetation (Table I).

HABITAT CHARACTERIZATION AND VEGETATION COVER ESTIMATES

We visually estimated the percent cover of the ground layer and tree foliage in different height strata (Mingan: 0–2 m, 2–6 m, and > 6 m; Anticosti: 0–1 m, 1–2 m, 2–4 m, 4–8 m, and > 8 m). On each census point we surveyed the vegetation the same year as we surveyed birds between 9 June and 4 July (median = 27 June) on Mingan and between 2 and 5 July (median = 3 July) on Anticosti Island. On Mingan, vegetation cover had been estimated within a 50-m radius around the centre of the point-counts by walking the entire plot to ensure good coverage. On Anticosti, cover was estimated in four 10-m radius plots (Drapeau *et al.*, 2000; Smith *et al.*, 2008): the first plot was positioned at the centre of the point-count, while the 3 other plots were placed 40 m away in 3 equidistant directions (0°, 120°, and 240°). We used the mean value of the 4 plots

TABLE I. Songbird species encountered on the Mingan Archipelago in 1998-1999 and on Anticosti Island in 2008 were grouped according to their dependence-scores on understory vegetation for foraging and nesting based on the scientific literature. Foraging and nesting scores were given equal weights and summed to provide a total understory dependence score. The species in parenthesis was present in less than 5% of the samples.

Species common names	Species scientific names	Acronym	Dependence scores*			Species understory dependence groups
			Foraging	Nesting	Total	
Magnolia warbler	<i>Dendroica magnolia</i>	MAWA	1	3	4	Strong
Swainson's thrush	<i>Catharus ustulatus</i>	SWTH	1	3	4	
Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>	YBFL	3	1	4	
Hermit thrush	<i>Catharus guttatus</i>	HETH	2	1	3	
Nashville warbler	<i>Vermivora ruficapilla</i>	NAWA	2	1	3	
White-throated sparrow	<i>Zonotrichia albicollis</i>	WTSP	2	1	3	
Winter wren	<i>Troglodytes troglodytes</i>	WIWR	2	1	3	
American robin	<i>Turdus migratorius</i>	AMRO	1	1	2	Medium
Blackpoll warbler	<i>Dendroica striata</i>	BLPW	0	2	2	
Dark-eyed junco	<i>Junco hyemalis</i>	DEJU	1	1	2	
Fox sparrow	<i>Passerella iliaca</i>	FOSP	1	1	2	
Ruby-crowned kinglet	<i>Regulus calendula</i>	RCKI	2	0	2	
(Blue-headed vireo)	<i>Vireo solitarius</i>	BHVI	0	2	2	
Tennessee warbler	<i>Vermivora peregrina</i>	TEWA	1	1	2	
Yellow-rumped warbler	<i>Dendroica coronata</i>	MYWA	1	1	2	
Bay-breasted warbler	<i>Dendroica castanea</i>	BBWA	0	1	1	
Black-throated green warbler	<i>Dendroica virens</i>	BTNW	0	1	1	Low
Boreal chickadee	<i>Poecile hudsonica</i>	BOCH	0	0	0	
Brown creeper	<i>Certhia americana</i>	BRCR	0	0	0	
Golden-crowned kinglet	<i>Regulus satrapa</i>	GCKI	0	0	0	
Red-breasted nuthatch	<i>Sitta canadensis</i>	RBNU	0	0	0	

* Foraging scores: 3) exclusive dependence on the shrub layer vegetation structure; 2) most foraging activities occurring in the shrub layer; 1) partial use of the shrub layer during foraging and/or foraging on the ground; 0) almost no use of the shrub layer. Nesting scores: 3) exclusive dependence on the shrub layer for nesting site; 2) most nests in the shrub layer or exclusive use of the shrub layer to hide nests; 1) possible use of the shrub layer for hiding nests and/or nesting on the ground; 0) no use of the shrub layer during nesting. Total scores are the sum of foraging and nesting scores (adapted from Allombert, Gaston & Martin, 2005; foraging and nesting information is based on Gauthier & Aubry, 1995 and Poole, 2005).

to characterize vegetation cover at each point-count. The plot area sampled on Anticosti Island was smaller than that on Mingan, but we are confident that both data sets represent a valid sample of vegetation cover in the lower strata.

STATISTICAL ANALYSES

VEGETATION COVER AND HABITAT STRUCTURE

To test for differences in the percent cover of understory vegetation between Anticosti and Mingan we performed *t*-tests for unequal variances (Ruxton, 2006) on vegetation cover in the vegetation strata directly exposed to deer: ground cover and vegetation < 2 m. Because the protocols of cover estimation in the layers below 2 m differed between Mingan and Anticosti, data had to be made comparable. As the 0–1 m and 1–2 m strata on Anticosti were strongly correlated ($r = 0.8$) and did not significantly differ (paired *t*-test: $t_{23} = 1.82$, $P = 0.08$), we decided to use the mean cover of the 2 strata as an estimation of cover in the 0–2 m stratum in the comparison with the data from Mingan. We square root-transformed the ground layer cover and arcsine-transformed tree cover at the 0–2 m height stratum in order to respect normality of residuals (Sokal & Rohlf, 1995).

We analyzed variation in habitat structure separately for Anticosti and Mingan by Principal Component Analyses (PCA) with the SAS statistical software (SAS Institute, 2003). PCA scores summarized variation amongst sampling points in percent vegetation cover in the different vegetation

layers. We used PCA scores along the first axis to establish indexes of habitat structure (see Results).

ASSOCIATION OF BIRD SPECIES AND HABITAT STRUCTURE

We limited all analyses to songbirds and excluded corvids (common raven [*Corvus corax*], American crow [*Corvus brachyrhynchos*], gray jay [*Perisoreus canadensis*]), tree swallow (*Tachycineta bicolor*), pine siskin (*Carduelis pinus*), red crossbill (*Loxia curvirostra*), and woodpeckers (*Picoides* spp. and *Colaptes auratus*) because these species were poorly censused by point-counts (see Bibby *et al.*, 2000).

To validate our classification of songbirds according to understory dependence, we looked for consistency between the *a priori* classification and the observed association of species with habitat structure in the PCA on Mingan, our reference site. We also compared the response of songbird communities to variation in vegetation structure between Mingan and Anticosti. To look for correlations between habitat structure and species richness on Mingan and Anticosti we used mixed model ANOVAs (Littell *et al.*, 2002; SAS Institute, 2003). We included sampling routes as random factors to control for possible spatial autocorrelation between point-counts of the same route. We tested the relationships between the habitat structure index and 1) the number of songbird species in each of the 3 species groups and 2) total bird species richness. We square root-transformed the response variables to meet assumptions of normality and homogeneity of variance when needed.

For the presentation of results, we back-transformed all predicted values to the original scales. As mixed models do not provide R^2 values, we computed variance explained by fixed effects with the square of the correlation coefficient between predicted and observed values (Xu, 2003).

SONGBIRD COMPOSITION AND DIVERSITY

To compare the composition of bird communities between Mingan and Anticosti we used Correspondence Analysis (CA; Hill, 1974; CANOCO software, Ter Braak & Šmilauer, 2002). We excluded species occurring in less than 5% of the point-counts to limit potential problems caused by rare species (Greenacre, 1984). We included Mingan *versus* Anticosti as an explanatory nominal variable added *post hoc* to estimate its relation with the variability in species composition explained by the ordination axes (Palmer, 1993). We then produced an ordination diagram to visualize community composition and species association with the 2 island categories. Species occurring on the same point-counts have similar positions on the diagram (Lepš & Šmilauer, 2003). Hence, we inferred associations between species and study sites using distances between species and island category centroids (mean position of site samples).

We defined alpha diversity of songbirds as the species composition at the point-count scale and beta diversity as the relative changes in species composition among point-counts (Jost, 2007). Because we used songbird presence/absence data and could not account for species abundance at point-counts, the ordination diagram provided approximate indications of alpha and beta diversity. Point-counts close to each other have similar alpha diversity, while their dispersion indicates beta diversity at each study site.

POTENTIAL TEMPORAL BIASES

To assess potential biases due to the 10-y gap between bird censuses on Mingan and Anticosti, we used the Breeding Bird Survey (BBS; Sauer, Hines & Fallon, 2008) analytical tools based on linear route-regressions and compared the results of the species trend analysis to the differences in observation frequency of bird species between island categories. For species that had populations that increased or decreased regionally over the period, we examined if these trends were likely to bias our conclusions.

Results

VEGETATION DENSITY AND HABITAT STRUCTURE

Cover of the ground layer did not differ between Mingan and Anticosti ($t_{76,7} = -0.78$, $P = 0.4$). The mean tree cover at the 0–2 m height stratum differed significantly between the 2 island categories ($t_{76,7} = -10.05$, $P < 0.0001$) and was on average sevenfold larger on Mingan (mean \pm SE: 41.7% \pm 3.6) than on Anticosti (5.7% \pm 0.8).

On both study sites, the first axis of the PCA summarized habitat structure and explained over 50% of the variance in vegetation strata (Table II). Eigenvector values along axis 1 opposed understory density to canopy closure and ground layer vegetation (Table II). On Mingan, the first axis of the PCA described a habitat structure gradient

TABLE II. Gradients of habitat structure at songbird point-counts on Mingan Archipelago and Anticosti Island can be summarized by the first axis of a principal component analysis (PCA) performed on the mean ground cover (\pm SE) of vegetation strata measured at point-counts.

Study sites	Vegetation strata	Ground cover (%)	SE	PCA axis 1	
				Variance explained	Eigen vectors
Mingan				0.52	
(n = 58)	Trees 0–2 m	41.7	3.6		0.37
	2–6 m	28.3	2.9		0.61
	> 6 m	63.5	3.1		-0.57
	Ground layer	24.3	3.2		-0.41
Anticosti				0.53	
(n = 24)	Trees 0–1 m	6.3	1.1		0.48
	1–2 m	5.1	0.7		0.49
	2–4 m	9.2	1.2		0.41
	4–8 m	49.5	2.3		0.21
	> 8 m	33.3	2.8		-0.42
	Ground layer	17.2	1.8		-0.39

where positive scores were associated with an open canopy (> 6 m tree stratum) and a dense understory (0–6 m tree strata), while negative scores were associated with a dense canopy and an open understory (Table II). On Anticosti, the understory was less variable than on Mingan and generally very open, and the first axis of the PCA on habitat structure described a gradient of canopy closure (positive scores = open canopy, negative scores = closed canopy).

SPECIES ASSOCIATIONS WITH HABITAT STRUCTURE

The relationships between the habitat structure index obtained from PCA scores and our *a priori* species classification of songbirds according to understory dependence yielded consistent results (Figure 2). On Mingan, species classified as strongly or moderately dependent on the understory were associated to census plots with a dense understory and an open canopy (strong dependence: $F_{1,51} = 4.95$, $P = 0.03$, $R^2 = 0.07$; medium dependence: $F_{1,51} = 7.79$, $P = 0.007$, $R^2 = 0.12$; Figure 2). Species with a low dependence on the understory vegetation tended to be associated with sampling plots that had an open understory and a closed canopy ($F_{1,51} = 3.60$, $P = 0.06$, $R^2 = 0.06$; Figure 2). Overall, species richness per point count increased as the canopy opened and the understory became denser ($F_{1,51} = 4.35$, $P = 0.04$, $R^2 = 0.05$; Figure 2). These results suggest that changes in local bird richness associated with variations in habitat structure were mostly generated by understory-dependent species.

On Anticosti Island, the number of species per point count with a low dependence on the understory vegetation increased with increasing canopy closure ($F_{1,20} = 8.52$, $P = 0.009$, $R^2 = 0.28$; Figure 2), while the number of species with a medium ($F_{1,20} = 0.39$, $P = 0.5$) or strong ($F_{1,20} = 0.67$, $P = 0.4$) dependence on the understory did not vary with habitat structure (Figure 2). Although a non-linear relationship seems to occur for the medium-dependence group (Figure 2), this apparent relationship is the result of differences between sampling routes controlled by a random factor in the mixed model analyses. Bird species richness per point count declined with increasing

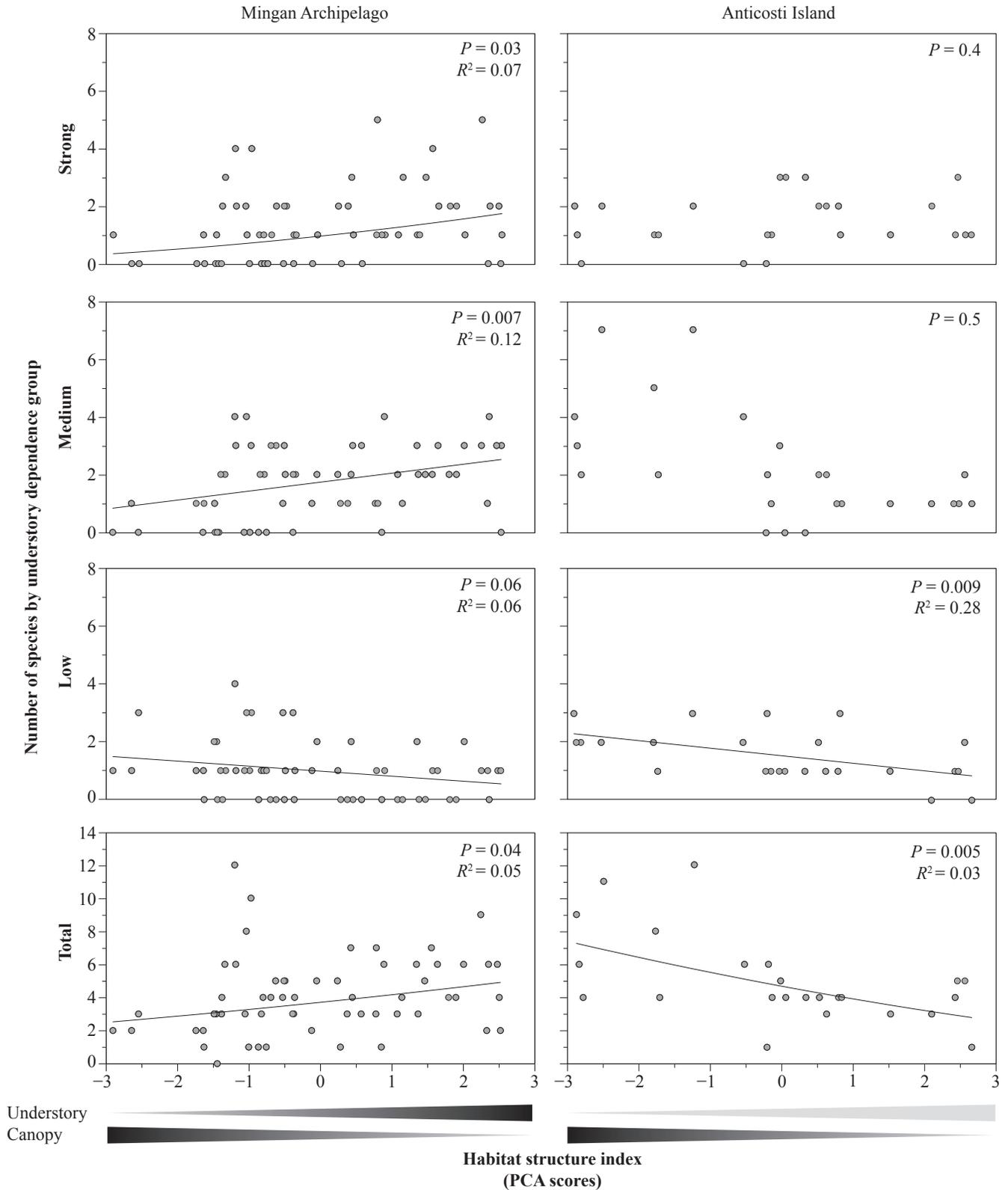


FIGURE 2. Number of songbird species of each understory dependence group (Table I) and total richness in relation with habitat structure on Mingan Archipelago and Anticosti Island. Relations were tested with mixed model ANOVAs where sampling routes were included as random factors. Scores of the first PCA axis (Table II) were used as a habitat structure index gradient illustrated at the bottom (shadiness and width symbolizes the intensity of the gradient). Mingan: negative scores = dense canopy and open understory; positive scores = open canopy and dense understory. Anticosti: negative scores = dense canopy; positive scores = open canopy (understory remained mostly open along gradient). Dots represent observed data at each point-count, and lines were drawn from the predicted values.

scores on PCA axis 1, *i.e.*, with increasing canopy closure ($F_{1,20} = 10.09, P = 0.005, R^2 = 0.03$; Figure 2). Because habitat structure in the understory on Anticosti Island varied little between sampling points (Table II), variation in habitat structure mostly reflected variation in canopy closure. Thus, changes in songbird community structure in presence of deer were mainly attributable to variation in the occurrence of species with low dependence on the understory and not to variation in the occurrence of species that depend on the understory. Low R^2 values for both Mingan and Anticosti (Figure 2) reflect the importance of other factors than habitat structure index and songbird species habitat preference in explaining the actual occurrence of a species at a given census point.

SONGBIRD COMPOSITION AND DIVERSITY

Twenty species were present in at least 5% of the point-counts and were included in the multivariate analysis (Table I). All species were present on Mingan (6, 7, and 7 species with low, medium, and strong understory-dependence, respectively), while 19 species occurred on Anticosti (5, 8, and 6 species with low, medium, and strong understory-dependence, respectively). The first 2 axes of the CA summarized 11.5% and 9.4% of the total variance in species composition and 21.2% and 26.6% of the variance in the species–island category relationship, respectively. Except for Swainson’s thrush (*Catharus ustulatus*), all species classified as strongly dependent on the understory were more often associated with Mingan than with Anticosti (Figure 3a). Most species with a low dependence on the understory were more frequently observed in the samples from Anticosti than in those from Mingan. Species with a medium dependence were intermediate and varied in their association with one of the 2 island categories (Figure 3a). On the CA ordination diagram (Figure 3b) the point-counts from Anticosti overlapped (*i.e.*, similar alpha diversity) with a subset of point-counts from Mingan that were characterized by species not dependent on the understory (closed canopy sites on Mingan). The overall scatter of points on Mingan was about twice the size of the one observed for Anticosti, indicating greater variation in species composition between point-counts on Mingan (higher beta diversity; Figure 3b).

POTENTIAL TEMPORAL BIAS

According to the BBS population trend analyses (see Sauer, Hines & Fallon, 2008 for details), the red-breasted nuthatch (*Sitta canadensis*) is the only species that was more abundant on Anticosti (the most recent sample) and that had increased in the province of Quebec since the sampling of the Mingan birds (estimated equation parameter: $\beta = 7.94, P < 0.001$). The Magnolia warbler (*Dendroica magnolia*) also increased over the period ($\beta = 4.02, P < 0.0001$), but despite this it was more frequently recorded in the earlier sample of Mingan. One species, the winter wren (*Troglodytes troglodytes*), declined during the period considered ($\beta = -4.32, P = 0.004$). It showed a slight trend for being more frequently recorded on Mingan than on Anticosti (Figure 3a), a trend that could be the result of a temporal bias. In sum, there was no general temporal trend of increase or decrease in abundance that

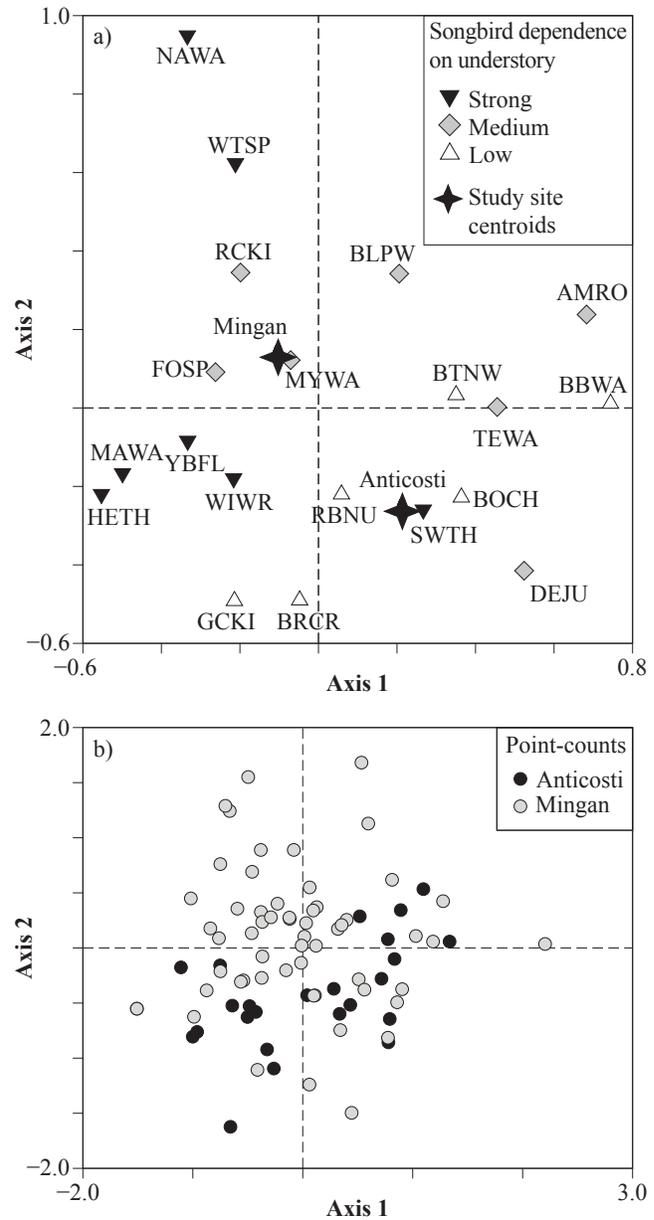


FIGURE 3. Correspondence analysis (CA) ordination diagram illustrating the composition of songbird communities sampled on Mingan Archipelago in 1998–1999 and Anticosti Island in 2008. The diagram shows the projection of a) songbird species scores along axes 1 and 2 and b) point-counts dispersion with site overlap. Species are shown according to their dependence on understory vegetation. Refer to Table I for bird species acronyms and understory dependence groups. Stars represent site centroids (*i.e.*, mean position of point-counts).

could account for the differences we observed between the bird communities of Mingan and Anticosti.

Discussion

In studies on direct and indirect ecological effects of browsing by large herbivores, the occurrence of a reference site close by with no incidence of browsing is a rare opportunity (Martin *et al.*, 2010). The existence of a comparable data set on Mingan to match with data from Anticosti was

such an opportunity. It enabled us, despite the differences in sampling year and observers involved, to compare 2 contrasted situations in the interaction between deer and their boreal environment, *i.e.*, their absence against their prolonged presence at high density.

Our results suggest that abundant deer populations affected songbird communities in the boreal forests of Anticosti Island through their effect on the density of the vegetation. As expected, the assemblage of songbird species on Mingan, where dense understory vegetation was available in a subset of census-points, was more characterized by understory-dependent birds than on Anticosti. Alpha diversity was similar in both study areas, especially so in census points with a dense canopy, where songbird communities were dominated by species with low dependence on the understory. Species composition varied more among sampling points on Mingan than on Anticosti, suggesting that the low density of understory vegetation in balsam fir stands of Anticosti Island resulted in a more homogenous songbird community by decreasing songbird beta diversity (Figure 3b) and variability in community composition.

Although species dependent on the understory in boreal forests were more frequent on the islands without deer, especially in sampling points where a dense understory was present under an open canopy, most of these species were still present, although at a low observation frequency, in our intensively browsed study site (Anticosti). Consistent with the lack of variability in the understory vegetation structure in presence of deer, there was little variation in bird presence among sampling points on Anticosti (Figure 2; and low beta diversity in presence of deer: Figure 3b). The estimated 4% average ground cover of trees in the 0–2 m stratum (Table II) may be sufficient to maintain small populations of these species in Anticosti's balsam fir forests.

Homogenization of the understory vegetation and its associated bird communities has been a general feature associated with browsing by abundant deer populations in non-boreal forests (McShea & Rappole, 2000; Rooney *et al.*, 2004; Allombert, Gaston & Martin, 2005; Martin *et al.*, 2010; Martin, Arcese & Scheerder, 2011). In coastal temperate forests of western Canada (Haida Gwaii: Allombert, Gaston & Martin, 2005; Gulf Islands: Martin, Arcese & Scheerder, 2011) understory-dependent species dominated bird communities on islands without deer (73% of individuals) while understory-independent birds dominated on islands with a long browsing history (79% of individuals). In these western coastal forests, in the absence of (over-)browsing, the understory vegetation is dominated by a suite of tall shrubs (*Rubus* spp. and *Erica* spp.) and very large ferns that are rare or less common in boreal forests. These plants produce lush and dense stands favoured by mild and short winters, providing a distinct and structurally complex habitat to understory birds. Such a diverse understory rarely develops in boreal forests even in the absence of over-browsing (Saucier *et al.*, 2009), which probably accounts for a lower dominance of understory birds even in the absence of deer.

However, among the different forest systems studied, there is a negative correlation between deer presence and the occurrence or abundance of understory-dependent bird species, while overall species richness in the samples appears less affected (*e.g.*, Casey & Hein, 1983; McShea & Rappole, 2000; Allombert, Gaston & Martin, 2005). In most situations, understory-dependent species may be able to maintain reduced populations even in the presence of abundant deer populations by taking advantage of the remnant understory vegetation in refuges less accessible to deer. They may also take advantage of the artificial structure formed by fallen trees or the dense ground layer of vegetation that can temporarily establish in short-lived clearings created by windfalls (Lain *et al.*, 2008). It has also been suggested that the ecological plasticity of songbirds is higher in boreal forests than in more temperate forests owing to their adaptation to the large-scale perturbation dynamics of boreal forests (Mönkkönen & Welsh, 1994; Schmiegelow, Machtans & Hannon, 1997). This could make them more resilient to habitat modifications caused by intensive browsing. On Anticosti, 2 other factors may play in favour of understory songbirds by somewhat mitigating the ability of deer to affect the understory: sport hunting and, more important, the severity of the winters. Both affect deer demography (Simard *et al.*, 2010), and the latter reduces their access to the ground layer and understory vegetation when snow covers the ground. Nonetheless, understory vegetation remains scarce on Anticosti, suggesting again that the different species may be less specific than expected regarding habitat requirements.

Although based on correlations, our study provides the first insights on the impacts of long-term deer browsing on songbird communities in North American boreal forests. Our results echo recent concerns about songbird population declines in North American forests (Robbins *et al.*, 1989; Stutchbury, 2007) and shrublands (Askins, 2001; Dettmers, 2003). The role of abundant herbivores in these declines may have been underestimated (McShea *et al.*, 1995; Allombert, Gaston & Martin, 2005; Holt, Fuller & Dolman, 2010; Martin, Arcese & Scheerder, 2011). As large herbivore populations have increased over recent decades in many regions of the world (Côté *et al.*, 2004), conservation issues related to long-term browsing impacts on biodiversity should become increasingly common (Rooney, 2001; Mysterud, 2006). Ecosystem management needs to integrate the ecological relationships between abundant herbivores and other animal communities such as songbirds (deCalesta & Stout, 1997). Long-term monitoring of different herbivore–forest systems will prove increasingly important not only to improve our understanding of the effects of herbivores on ecosystems, but also to evaluate the effects of any mitigation measures that will be attempted. The extreme impact of introduced deer on the vegetation of Anticosti and the indirect effects of that impact on the local songbird communities also underline the role played in the dynamics of communities by top-down factors that regulate herbivore populations, including the occurrence of functional populations of their predators.

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