

An experimental study of how variation in deer density affects vegetation and songbird assemblages of recently harvested boreal forests

Etienne Cardinal, Jean-Louis Martin, Jean-Pierre Tremblay, and Steeve D. Côté

Abstract: Intense browsing by abundant large herbivores can threaten the ecological integrity of ecosystems by inducing modifications in the structure and composition of vegetation that trigger trophic cascades affecting plant and animal communities. We investigated the relationships between density of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), forest succession after clear-cut, and songbird communities on Anticosti Island, Quebec, Canada. We hypothesized that lower deer densities would alter the trajectory of forest succession after clear-cutting and lead to a rapid recovery of habitat attributes favorable to songbirds associated with a dense complex shrub layer. Six years after establishing a controlled browsing experiment (0, 7.5, 15, and >27 deer·km⁻²) in recent clearcuts, reducing deer densities ≤ 7.5 deer·km⁻² initiated the restoration of balsam fir (*Abies balsamea* (L.) Mill.) forests and increased the regeneration of paper birch (*Betula papyrifera* Marshall). Increasing birch ground cover from 10% to 20% increased songbird total abundance, species richness, and diversity by 17%, 39%, and 31%, respectively. Alder Flycatcher (*Empidonax alnorum* Brewster, 1895) was only present at ≤ 7.5 deer·km⁻² and strongly associated with birch regeneration. The regeneration of browse-resistant plants such as white spruce (*Picea glauca* (Moench) Voss) in some areas at high deer density favored the maintenance of many shrub-dependent songbirds but also species usually associated with forest canopy. Active management of deer populations in Canadian harvested boreal forests will mitigate losses in vegetation and songbirds caused by over-browsing.

Key words: white-tailed deer, *Odocoileus virginianus*, over-browsing, active management, controlled-browsing experiment, Anticosti Island.

Résumé : Le broutement intensif par de nombreux grands herbivores peut menacer l'intégrité écologique d'écosystèmes en induisant des modifications de la structure et de la composition de la végétation qui déclenchent des cascades trophiques ayant des incidences sur les communautés végétales et animales. Nous nous sommes penchés sur les liens entre la densité du cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)), la succession forestière après la coupe à blanc et les communautés d'oiseaux chanteurs sur l'île d'Anticosti (Québec, Canada). Nous avons émis l'hypothèse que de plus faibles densités de cerfs modifieraient la trajectoire de succession forestière après une coupe à blanc et mèneraient au rétablissement rapide des attributs d'habitat favorables aux oiseaux chanteurs associés à une strate arbustive complexe et dense. Six ans après l'établissement d'une expérience de broutement contrôlé (0, 7,5, 15 et >27 cerfs·km⁻²) dans des coupes récentes, la réduction des densités de cerfs à $\leq 7,5$ cerfs·km⁻² s'est traduite par le début du rétablissement des forêts de sapin baumier (*Abies balsamea* (L.) Mill.) et une régénération accrue du bouleau à papier (*Betula papyrifera* Marshall). Un passage de la couverture de bouleau de 10 % à 20 % s'est traduit par des augmentations de l'abondance totale d'oiseaux chanteurs, de la richesse spécifique et de la diversité de 17 %, 39 % et 31 %, respectivement. Le moucherolle des aulnes (*Empidonax alnorum* Brewster, 1895) n'était présent qu'à des densités $\leq 7,5$ cerfs·km⁻² et était fortement associé à la régénération du bouleau. La régénération de plantes résistantes au broutement, telles que l'épinette blanche (*Picea glauca* (Moench) Voss) dans certaines zones à forte densité de cerfs a favorisé le maintien de nombreux oiseaux chanteurs dépendants des arbustes, mais également d'espèces généralement associées à la canopée. La gestion active des populations de cerfs dans les forêts boréales canadiennes exploitées atténuera les pertes de végétation et d'oiseaux chanteurs causées par le surbroutement.

Mots-clés : cerf de Virginie, *Odocoileus virginianus*, surbroutement, gestion active, expérience de broutement contrôlé, île d'Anticosti.

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Introduction

Several populations of large wild herbivores in Europe and North America have reached abundance levels likely exceeding their natural range of variability (Côté et al. 2004). They have become a major perturbation affecting the dynamics of forest ecosystems (Horsley et al. 2003; Hester et al. 2006; Tremblay et al. 2007). Selective foraging on herbs, shrubs, and young trees have changed local plant diversity and species composition, progressively excluding browse-sensitive species to the benefit of more tolerant species (Horsley et al. 2003; Rooney and Waller 2003; Royo et al. 2010). In addition, high herbivore density has modified biogeochemical cycles (Pastor et al. 1998; Persson et al. 2005), reduced primary productivity (Hobbs 1996; Persson et al. 2005), and modulated tree regeneration and forest structure (Alverson et al. 1988; Rooney 2001; Tremblay et al. 2007). Such changes can lead to alternate succession pathways (Healy 1997; Augustine et al. 1998) and alter the attributes of ecosystems (Augustine et al. 1998; Suding et al. 2004; Royo et al. 2010). They also trigger indirect effects on food webs (e.g., Berger et al. 2001; Côté et al. 2004; Martin et al. 2010; Ripple and Beschta 2006; Suominen and Danell 2006) such as decreasing the abundance and diversity of songbirds (Casey and Hein 1983; Allombert et al. 2005a), small mammals (McShea and Rappole 1992; Moser and Witmer 2000), and some invertebrates (Stewart 2001; Allombert et al. 2005b).

In songbirds, the bulk of the documented effects in North America and Europe have shown that understory species have suffered the most from the simplification of the vertical structure and the reduction of the density of understory vegetation (Fuller 2001; Perrins and Overall 2001; Allombert et al. 2005a; Gill and Fuller 2007; Holt et al. 2010; Martin et al. 2011; Mathisen and Skarpe 2011). Little is known, however, on how large herbivore densities interfere with the recovery from other major perturbations in managed forests such as fires or clearcut harvesting (deCalesta 1994).

This study is the first attempt to assess how varying levels of densities of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) affect the use of regenerating cutover areas by songbirds in boreal forest. We focused on the early successional stage 6 years after tree harvest. We used a controlled browsing experiment that had been set up on Anticosti Island, Quebec, Canada, (Tremblay et al. 2006) to assess how bird communities varied in relation to the relative abundance of deer. We already showed using this experiment a dramatic change in the field layer and regeneration dynamics of forests (Tremblay et al. 2006, 2007). At densities >15 deer·km⁻², deer-preferred species such as fireweeds (*Chamerion angustifolium* (L.) Holub), balsam fir (*Abies balsamea* (L.) Mill.), or paper birch (*Betula papyrifera* Marshall) are replaced by resistant plants such as thistle (genus *Cirsium* Mill.), bluestem grass (*Calamagrostis canadensis* (Michx.) P. Beauv.), and white spruce (*Picea glauca* (Moench) Voss).

We hypothesized that in the absence of deer, or at low deer densities, the onset of forest succession after clear-cutting would rapidly reestablish habitat attributes favorable to songbirds associated with a dense complex shrub layer and deciduous saplings. We predicted that songbirds with higher dependence on the shrub layer would be the most affected by intensive deer browsing, which would lead to lower song-

bird species richness, abundance, and (or) diversity under high deer densities. We also expected that the presence of species with little dependence on the shrub layer would be unrelated to deer density. We interpreted results on songbirds in relation to changes in composition and structure of the plant communities.

Materials and methods

Study area

Anticosti Island (7943 km²) is located in the Gulf of St. Lawrence (49°28'N, 63°00'W), Quebec, Canada. The forests of Anticosti are located in the boreal zone and are part of the eastern balsam fir – paper birch bioclimatic region (Saucier et al. 2009). In the late 19th century, white-tailed deer were introduced on Anticosti Island in a predator-free environment. The lack of predators led to a rapid increase in deer numbers with population levels now averaging >20 deer·km⁻² (Rochette and Gingras 2007). Sustained heavy browsing dramatically modified the composition and structure of Anticosti forests (Potvin et al. 2003). Palatable shrubs were virtually eradicated (Tremblay et al. 2005) and balsam fir dominated stands were gradually converted into white spruce (Potvin et al. 2003).

Controlled browsing experiment

The experimental design consisted of three replicated blocks each containing four experimental units with controlled deer densities (0, 7.5, 15 deer·km⁻², and ambient density). The blocks were established during the summer of 2001 in balsam fir dominated forest clearcuts where regeneration was achieved through natural regrowth. About 30% of the area was left as residual forest patches in each experimental unit. From 2002 to 2008, in each block, we excluded all deer from a 10 ha enclosure and introduced three deer inside a 40 ha and three deer in a 20 ha enclosure (7.5 and 15 deer·km⁻², respectively). We also monitored an unfenced 20 ha clearcut area with ambient deer densities varying between 27 and 56 deer·km⁻² (for a complete description of the controlled browsing experiment see Tremblay et al. 2006). We maintained deer number constant in each experimental unit by culling deer in autumn and restocking them each spring. Deer densities were estimated with distance sampling of pellet groups calibrated with known deer densities from the enclosures (details in Tremblay et al. 2006, 2007). Animal handling protocols were approved by the Université Laval Animal Care Committee of the Canadian Council on Animal Care (UL 2008017-1).

Vegetation compositional responses to treatments

In 2002, we randomly distributed 20 permanent vegetation-sampling stations in clearcuts within each experimental unit to investigate the responses of field-layer plants and tree regeneration ($n = 240$) to the deer density treatment. At each sampling station, we measured field-layer plants in July 2007. Measurements were taken in two 1 m × 1 m plots randomly distributed in a 10 m × 10 m grid centered on each sampling station (cluster sampling). We visually estimated percent ground cover of grasses, sedges, forbs, ferns, and heaths at the species level. Following Tremblay et al. (2006, 2007), we coded plant species as sensitive (decreasing with

increasing deer density) or tolerant or resistant (increasing or neutral) to browsing and used the sum of the percent ground cover of each species within a plant group as an index of abundance for that functional assemblage. We surveyed tree regeneration in September 2007 in three 4 m² circular (1.13 m radius) plots systematically distributed at 5 m intervals north from the center of each sampling station. Within these plots, we counted the number of paper birch, balsam fir, and spruce stems >10 cm tall.

Songbird surveys

We used point-counts to assess songbird relative abundance, richness, and diversity during the nesting period (Bibby et al. 2000). We centered point-counts ($n = 36$, i.e., 3 per experimental unit) on randomly selected vegetation sampling stations separated by at least 100 m (234 ± 99 m, mean \pm SD) in each experimental unit (McWethy et al. 2009). We excluded sampling stations within 50 m of a fence or edge of residual forest patches. We counted the number of individuals for each species seen or heard during a 20 min period within a 30 m radius (Drapeau et al. 1999). We visited each point-count station six times in 2007 and four times in 2008. We conducted songbird surveys from 5 to 30 June 2007 and 2008, between 0430 and 1000, and always started under weather conditions with no rain or strong winds. Observers and time of visits were balanced and alternate to minimize potential biases in species detection associated with these parameters. Moreover, extensive training was done to calibrate abilities among observers and no difference in songbird detection was observed (Cardinal et al. 2012).

For each point-count station, we defined the abundance of songbird species as the highest count of individuals of a given species among all visits at that point-count within a year, which is a reliable proxy of true abundance (Toms et al. 2006). Species richness was defined as the number of species recorded over all visits. We used the Shannon–Wiener index ($H' = -\sum p_i \ln(p_i)$, where p is the proportion of total abundance occupied by a given species i) as a measure of diversity. Like Allombert et al. (2005a), we used data from the literature to score the expected dependence of each songbird species to the structure of the shrub layer (<2 m) according to their use of different vegetation types for foraging and nesting (Table 1). We created groups of species with strong (score of three or above), medium (score of two), and low (score of one or zero) dependence to the understory.

Songbird habitat structure

In June and July 2008, we visited each point-count station to characterize songbird habitat structure at a scale better reflecting the songbird–habitat associations than the scale used for investigating the vegetation compositional responses to deer density treatments. We sampled a 10 m radius plot centered on each point-count station and three other plots of the same dimension located 40 m away in three equidistant directions (Smith et al. 2008). At each plot, we visually estimated the percent ground cover of the total field-layer vegetation and the tree cover for conifers and paper birch below 1 m and in the 1–2 m height class; tree regeneration above 2 m was scarce. We considered that, from a bird perspective, the structure offered by fir and spruce regeneration was similar. For this reason, we pooled fir and spruce regeneration to-

gether as conifer structure available to birds at the point-count scale. We summed the values of tree cover per height classes, separating conifers and paper birch to generate distinct indices of vertical cover (Allombert et al. 2005a).

Statistical analyses

We used a principal components analysis (PCA) using the CANOCO software (ter Braak and Šmilauer 2002) to examine relationships between deer density and vegetation composition following tree harvesting. We included the sum of percent ground covers of browse-tolerant and browse-sensitive field-layer species and the number of stems of paper birch, balsam fir, and spruce as variables in the analysis. We applied the square-root transformation option available in CANOCO (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003) to all vegetation variables. Changes to the results were subtle, but improved their presentation by reducing the influence of extreme values. We first analyzed the variation of vegetation data across samples with the PCA and subsequently assessed the relationships between variation in deer density and variation in vegetation composition by the addition of deer density as a supplemental variable (Palmer 1993; Lepš and Šmilauer 2003). Supplemental variables do not influence the ordination and are only related to the resulting components by simple regressions (Lepš and Šmilauer 2003). We controlled for the block structure of the experimental design and for sampling year using dummy covariates (Lepš and Šmilauer 2003).

We investigated the relationships among deer density, habitat structure, and songbird community composition with a canonical correspondence analysis (CCA; ter Braak 1986; Palmer 1993; CANOCO software: ter Braak and Šmilauer 2002). We conducted the analysis on bird species abundance and excluded species occurring in fewer than 5% of the point-count stations (Greenacre 1984). We included cover indices estimated for paper birch and conifers, as well as field-layer vegetation cover, as structure explanatory variables. We added deer density as a supplemental variable to visualize and measure how much of the relationship between songbird composition and vegetation variables deer density could explain. We controlled for block structure and sampling year using dummy covariates. We tested the significance of the relationships between songbird species and vegetation variables with Monte Carlo permutation test (9999 permutations using the reduced model option; Lepš and Šmilauer 2003).

We examined the effects of deer density and habitat structure on bird species total abundance, richness, and diversity using mixed-model ANOVAs (Littell et al. 2002) for a complete random block design with block ($n = 3$) as random factors and year ($n = 2$) as repeated measures (SAS Institute Inc. 2003; Tremblay et al. 2006). We avoided pseudo-replication by including point-count stations within experimental units as repeated measures in space and time (Littell et al. 2002). For each response variable, we built two sets of statistical models to test our predictions. The first set of models included only deer density as a fixed effect. The second set of models included deer density with paper birch and conifer cover indices as fixed effects. We did not include field-layer cover in any model because it was highly negatively correlated ($r = -0.69$) with the conifer cover index. We only considered the interaction between deer density and

Table 1. Songbird species tallied in clearcuts 6–7 years after the beginning of a controlled browsing experiment by white-tailed deer (*Odocoileus virginianus*) in boreal forests of Anticosti Island, Quebec, Canada.

Species name	Species acronym	Dependence scores*			Dependence on the shrub layer vegetation	
		Foraging	Nesting	Total		
Alder Flycatcher, <i>Empidonax alnorum</i> Brewster, 1895	ALFL	2	3	5	Strong	
Common Yellowthroat, <i>Geothlypis trichas</i> (L., 1766)	COYE	2	2	4		
Magnolia Warbler, <i>Setophaga magnolia</i> (Wilson, 1811)	MAWA	1	3	4		
Yellow-bellied Flycatcher, <i>Empidonax flaviventris</i> (Baird and Baird, 1843)	YBFL	3	1	4		
Lincoln's Sparrow, <i>Melospiza lincolni</i> (Audubon, 1834)	LISP	2	1	3		
White-throated Sparrow, <i>Zonotrichia albicollis</i> (Gmelin, 1789)	WTSP	2	1	3		
Wilson's Warbler, <i>Wilsonia pusilla</i> = <i>Cardellina pusilla</i> (Wilson, 1811)	WIWA	2	1	3		
Winter Wren, <i>Troglodytes troglodytes</i> (L., 1758)	WIWR	2	1	3		
American Robin, <i>Turdus migratorius</i> L., 1766	AMRO	1	1	2		Medium
Blackpoll Warbler, <i>Setophaga striata</i> (Forster, 1772)	BLPW	0	2	2		
Dark-eyed Junco, <i>Junco hyemalis</i> (L., 1758)	DEJU	1	1	2		
Fox Sparrow, <i>Passerella iliaca</i> (Merrem, 1786)	FOSP	1	1	2		
Ruby-crowned Kinglet, <i>Regulus calendula</i> (L., 1766)	RCKI	2	0	2		
Savannah Sparrow, <i>Passerculus sandwichensis</i> (Gmelin, 1789)	SAVS	1	1	2		
Tennessee Warbler, <i>Vermivora peregrina</i> = <i>Oreothlypis peregrina</i> (Wilson, 1811)	TEWA	1	1	2		
Yellow-rumped Warbler, <i>Setophaga coronata</i> (L., 1766)	MYWA	1	1	2		
Black-and-white Warbler, <i>Mniotilta varia</i> (L., 1766)	BAWW	0	1	1	Low	
Black-throated Green Warbler, <i>Setophaga virens</i> (Gmelin, 1789)	BTNW	0	1	1		
Boreal Chickadee, <i>Poecile hudsonica</i> Forster, 1772	BOCH	0	0	0		
Brown Creeper, <i>Certhia americana</i> Bonaparte, 1838	BRCR	0	0	0		
Cape May Warbler, <i>Setophaga tigrina</i> (Gmelin, 1789)	CMWA	0	0	0		
Golden-crowned Kinglet, <i>Regulus satrapa</i> Lichtenstein, 1823	GCKI	0	0	0		
Red-breasted Nuthatch, <i>Sitta canadensis</i> L., 1766	RBNU	0	0	0		

Note: Species in boldface type were present in at least 5% of point-count stations. Species are ordered following their dependence on the shrub-layer vegetation structure during nesting and foraging activities.

*Dependence scores are as follows. Foraging scores: (3) exclusive dependence on the shrub-layer vegetation structure; (2) most foraging activities 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 placing nests; (2) most nests placed in the shrub layer or exclusive use of the shrub layer to hide nests on the ground; (1) possible use of the shrub layer for nesting 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 et al. 2005a; foraging and nesting information is based on Gauthier and Aubry 1995 and Poole 2005).

conifer cover because the interaction between deer density and paper birch caused collinearity issues (variance inflation factor >10; Belsley et al. 1980). We applied a square-root transformation to species richness to meet the assumptions of normality and homogeneity of variance. For the presentation of figures, we inverted predicted values from the transformed scale back to the original scale. 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).

Results

Vegetation compositional responses to treatments

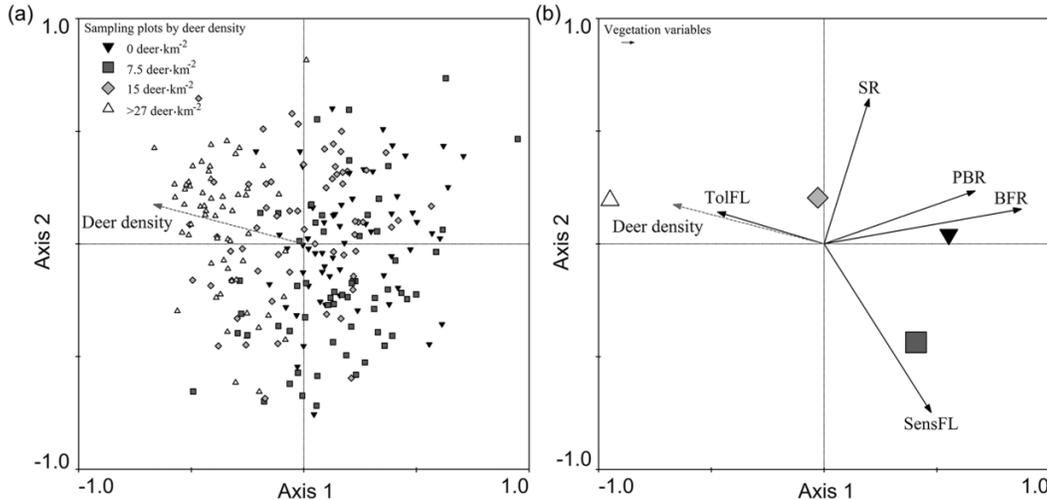
The general pattern of vegetation composition was correlated with deer density in clearcuts, but variability was high within deer density treatments (Figs. 1a, 1b). We restricted the analysis to the first two PCA components because they explained 99.6% of the variability in the relationship between vegetation variables and deer density (axis 1 alone explained 95.4% of the variability). The first two axes summarized 38.1% and 23.9% of the total variance explained by vegeta-

tion variables, respectively (Figs. 1a, 1b). The cover of browse-sensitive field-layer species and the regeneration of paper birch and balsam fir were associated with reduced deer densities (positive scores on axis 1). On the other hand, the cover of browse-tolerant field-layer species was associated with high deer densities (negative scores on axis 1; Fig. 1b). The mean scores of the different samples (centroids) indicated that vegetation structure at 15 deer·km⁻² was intermediate between vegetation structure observed in clearcuts at ambient versus lower deer densities (0 and 7.5 deer·km⁻², respectively). Sites at 15 deer·km⁻² had also relatively high scores for white spruce seedlings. Spruce regeneration scored low on axis 1 but high on axis 2 (Fig. 1b) and was independent of deer density as indicated by the orthogonal position of the respective vectors and by the low variance of the relation between vegetation and deer density explained by axis 2 (4.2%).

Songbird response to deer density

Thirteen bird species were present in at least 5% of the point-counts and were included in the CCA (Table 1). The first two axes summarized only a small proportion of the to-

Fig. 1. (a) Sample plots and (b) plot centroids for scores of density of white-tailed deer (*Odocoileus virginianus*) and vegetation variables for axes 1 and 2 of a principal components analysis in relation with deer density in a controlled browsing experiment on Anticosti Island, Quebec, Canada. The sum of the percent ground cover of the field-layer plant species, coded as browse-tolerant (ToIFL) and browse-sensitive (SensFL), was used as an index of abundance for that functional assemblage. The number of seedlings >10 cm of white spruce (*Picea glauca*; SR), paper birch (*Betula papyrifera*; PBR), and balsam fir (*Abies balsamea*; BFR) regeneration were also included in the analysis. A square-root transformation was applied to all vegetation variables. Deer density (broken line) was added post hoc as a supplemental variable to visualize its relationships with vegetation structure.



tal variance in the composition of bird communities (8.5%). However, both axes contributed to explain variance in the relation between habitat structure variables and bird species composition (axis 1: 64.1%; axis 2: 30.2%); we therefore restricted the analysis to these two axes. For this relation, the Monte Carlo permutation test was significant when considering all canonical axes ($P = 0.002$). Axis 1 represented an ecological gradient going from high field-layer vegetation cover with negative scores to high conifer cover with positive scores. High conifer cover, however, was the only variable associated with particular bird species on this axis (Fig. 2a). These species (Red-breasted Nuthatch (*Sitta canadensis*), Boreal Chickadee (*Poecile hudsonica*), Ruby-crowned Kinglet (*Regulus calendula*), and Yellow-bellied Flycatcher (*Empidonax flaviventris*)) were all forest-dwelling species. Two of them had either medium or strong dependence on the shrub-layer vegetation (Table 1). Axis 2 segregates plots with no deer, cover of paper birch, and presence of Alder Flycatcher (*Empidonax alnorum*) (positive scores) from plots with high deer densities (negative scores; Figs. 2a, 2b). Adding deer density as a post hoc supplemental variable explained little variance of the species-vegetation relationships on axis 1 (4.0%) but explained considerably more variance on axis 2 (56.7%). On axis 2, high deer density was opposed to high paper birch cover and high Alder Flycatcher abundance (Fig. 2a). Most species did not show any specific associations with vegetation variables (Fig. 2a).

Three point-counts (shown as pairs of points for the 2 years sampled on Fig. 2b) had somewhat high scores on the axes (Fig. 2b). These points had either a high conifer ground cover (one pair of points at >27 deer-km⁻² on axis 1) or a high paper birch ground cover (two pairs of points at 0 deer-km⁻² on axis 2). Ignoring the point with high conifer cover excluded three of the forest-dwelling species listed above using the 5% occurrence threshold (Boreal Chickadee remained). The two pairs of points with high paper birch cover both supported

Alder Flycatcher, but this species was also present in 14% of the remaining samples. Excluding those three points did not change the conclusions of the CCA.

Deer density as such did not affect bird species total abundance, richness, and diversity whether it was tested alone or with vegetation covariates (Table 2). Paper birch and conifer cover indices had positive effects on bird total abundance, richness, and diversity, but the effect was stronger for paper birch (Fig. 3). Predicted values from the mixed-model ANOVAs show that doubling paper birch ground cover from 10% to 20% resulted in 17%, 39%, and 31% increases in total abundance, species richness, and diversity, respectively. A threefold increase of conifer cover was required to obtain a similar gain (31%, 32%, and 29% for total abundance, species richness, and diversity, respectively). The results remained similar and conclusions did not change when excluding the three points with high ground cover values.

Discussion

Deer density, vegetation, and songbirds

Our results confirmed that reducing deer density after clear-cutting can reset the succession pathway of boreal forests and enhance songbird diversity even after 80 years of chronic heavy browsing. As expected from results obtained at year 3 of this experiment (Tremblay et al. 2006, 2007), browse-sensitive plant species in the field and shrub layers were more abundant and the complexity of the vertical structure was greater under reduced deer density. High cover of browse-sensitive plants in the field layer, regenerating paper birch and balsam fir, which are both characteristic features of forests from the eastern balsam fir – paper birch bioclimatic region (Saucier et al. 2009), were associated with the lowest deer densities. Sites under heavy browsing pressure were dominated by browse-tolerant field-layer plants such as grasses and thistles. The recovery of the shrub layer

Fig. 2. Mean bird species abundance (a) and point-count plot (b) scores for axes 1 and 2 of a canonical correspondence analysis in relation to vegetation structure and density of white-tailed deer (*Odocoileus virginianus*). The relative abundance of songbird species was measured at point-counts in a controlled browsing experiment involving four deer density levels on Anticosti Island, Quebec, Canada. Bird species are represented according to their dependence on the shrub-layer vegetation. Vegetation structure variables are an index of ground cover of paper birch (*Betula papyrifera*; PBC), conifer (CC), and field-layer plant species (FLC). Deer density (broken line) was added post hoc as a supplemental variable to visualize how it explains the relationships between songbird composition and vegetation variables. For acronyms of bird species see Table 1.

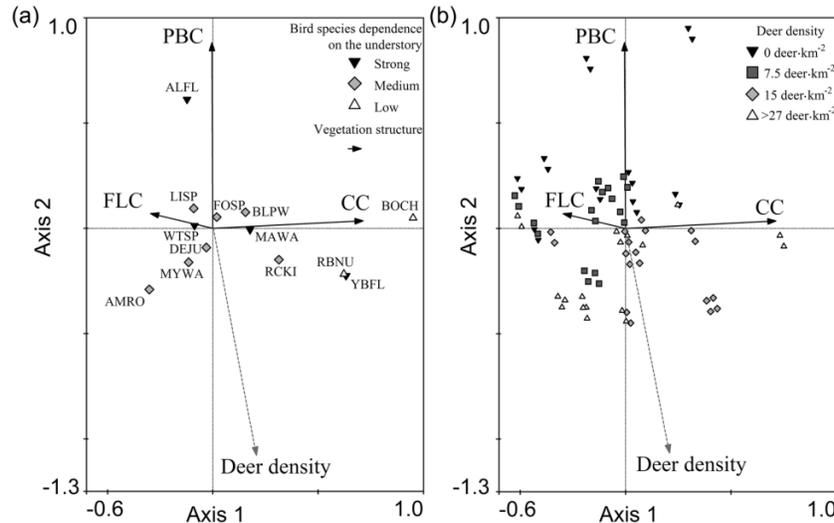


Table 2. Responses of songbird species total abundance, richness, and diversity measured at point-counts 6–7 years after reducing density of white-tailed deer (*Odocoileus virginianus*) in clearcuts in boreal forests of Anticosti Island, Quebec, Canada.

Dependent variable	R ²	Fixed effects	Numerator df	Denominator df	F	P
Total abundance	0.02	Deer density only	3	6	0.40	0.8
		Deer density*	3	6	0.57	0.65
	0.28	Conifer index	1	19	7.62	0.01
		Deer density × conifer index	3	19	0.93	0.4
		Paper birch index	1	19	6.91	0.02
Species richness	0.01	Deer density only	3	6	0.12	0.9
		Deer density*	3	6	0.13	0.9
	0.45	Conifer index	1	19	8.69	0.008
		Deer density × conifer index	3	19	1.47	0.2
		Paper birch index	1	19	7.17	0.01
Diversity index	0.02	Deer density only	3	6	0.19	0.9
		Deer density*	3	6	0.32	0.8
	0.35	Conifer index	1	19	8.38	0.009
		Deer density × conifer index	3	19	1.34	0.3
		Paper birch index	1	19	9.16	0.007

Note: Fixed effects in boldface type are significant at $P \leq 0.05$.

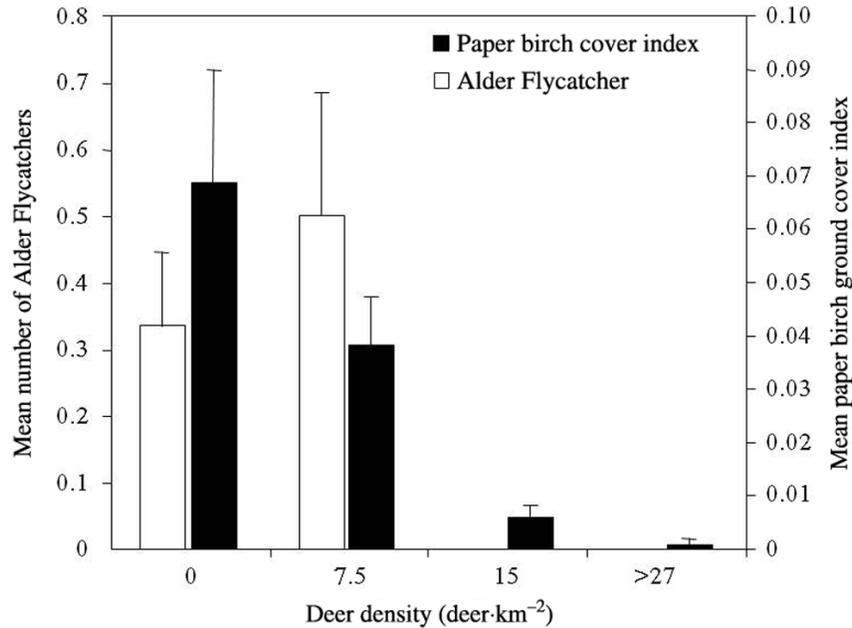
*The effects of a combination of deer density with covariables related to the structure of the shrub layer tested with mixed-model ANOVAs.

under reduced browsing pressure, especially for deciduous species at deer densities ≤ 7.5 deer·km⁻², was associated with higher songbird species total abundance, richness, and diversity. However, as observed by Tremblay et al. (2007), the abundance of spruce was unrelated to deer density. Because the experiment was set into a restoration scheme following over eight decades of chronic browsing, there were some strong cohorts of advanced spruce regeneration within forest gaps (Potvin et al. 2003). The vertical structure made avail-

able in some areas under heavy browsing pressure by this advanced spruce regeneration provided foraging or nesting opportunities likely to benefit several songbird species. It accommodated species dependent on the shrub layer, but also species that are usually associated with forest canopy such as the Boreal Chickadee and the Red-breasted Nuthatch.

Six years of deer control after tree harvest had measurable and significant indirect, vegetation-mediated, positive effects on songbird richness and diversity. These changes were es-

Fig. 3. Alder Flycatcher (*Empidonax alnorum*) and paper birch (*Betula papyrifera*) responses to four density levels of white-tailed deer (*Odocoileus virginianus*) in a controlled browsing experiment on Anticosti Island, Quebec, Canada. Bars are the number of individual Alder Flycatchers observed (mean \pm SE) and paper birch (*Betula papyrifera*) ground cover index (mean \pm SE) measured at point-counts.



essentially correlated to the marked increase in paper birch regeneration under the lowest browsing regimes. This effect was strongest for the Alder Flycatcher, a specialist species breeding in shrub thickets and young stands of deciduous trees (Lowther 1999). Chestnut-sided Warbler (*Setophaga pensylvanica* (L., 1766)) and Yellow Warbler (*Setophaga petechia* (L., 1766)) were also seen in experimental units with reduced deer density where paper birch regeneration was present but were not detected during point-count sampling. More generally, our results show that the provision of suitable habitat to songbirds that depend on deciduous shrubs typically present in the early successional stage of boreal forests (Schlossberg and King 2009) is lost under heavy browsing pressure. This is consistent with results obtained in riparian shrublands of the western US where reduced browsing pressure by elk (*Cervus elaphus* L., 1758) and moose (*Alces alces* (L., 1758)) was positively correlated to willow (genus *Salix* L.) regeneration and to bird species richness and diversity, especially deciduous shrub specialists (Berger et al. 2001; Anderson 2007; Olechnowski and Debinski 2008). The results of our analyses on total abundance, diversity, and richness failed to reveal a direct effect of deer abundance.

In comparison to the effect on vegetation, the magnitude of the positive effects of deer density reduction on songbirds was not as striking considering the relation between deer density, vegetation, and birds observed in Figs. 1a, 1b, 2a, and 2b. The unequal dimension and shape of the experimental units may partly explain these results. Larger units with lower deer density covered greater habitat heterogeneity, possibly increasing beta diversity and species abundance, than small enclosures where larger perimeter to area ratio with a poor-quality neighboring habitat could also possibly decrease abundance or diversity. More likely, the lower overall effect of deer density among treatments reflects the presence in the

boreal forest of avian communities composed of many resilient generalist species adapted to frequent disturbances (Mönkkönen and Welsh 1994; Schmiegelow et al. 1997), especially considering that some structural components were maintained when forests were converted from balsam fir to white spruce dominated stands (Tremblay et al. 2007).

In a companion study, we demonstrated that in mature boreal forests that had been exposed to severe deer browsing for over a century, a whole suite of forest species depending on a lush understory were reduced when compared with mature forests on the nearby Mingan islands where deer are absent (Cardinal et al. 2012). The simplification of the vegetation structure from deer over-browsing resulted in the homogenization of the composition of songbird communities in balsam fir stands on Anticosti Island (Cardinal et al. 2012). The results we obtained here show that three of the six species with strong dependence on understory vegetation common in Mingan's mature forests (Magnolia Warbler (*Setophaga magnolia*), Yellow-bellied Flycatcher, and White-throated Sparrow (*Zonotrichia albicollis*)) were able to use the ground layer vegetation found in recently harvested forest blocks on Anticosti, even when deer densities were high. The same is true for all species with medium dependence on understory vegetation (Blackpoll Warbler (*Setophaga striata*), Fox Sparrow (*Passerella iliaca*), Ruby-crowned Kinglet, and Yellow-rumped Warbler (*Setophaga coronata*)) that were negatively affected by deer in mature forests on Anticosti Island (Cardinal et al. 2012). As a result, for some mature forest understory bird species negatively affected by deer in mature forests on Anticosti Island, forest harvesting may temporarily provide alternative breeding habitat. As the forest will grow, however, their persistence will more and more depend on the control of the deer population allowing the presence of a complex understory structure (Millington et al. 2011; Cardinal et al. 2012). This suggests that deer and forest manage-

ment will ideally need to be integrated into forest ecosystem management strategies wherever deer are present.

In another companion study, the abundance and richness of Apoidea and macro Lepidoptera were associated with plants mostly found under reduced browsing pressure (Brousseau 2011). These invertebrates provide additional food resources to songbirds, especially for foliage gleaners such as flycatchers (Lowther 1999). Moreover, Tremblay et al. (2006) reported an exponential increase of the reproductive structures of grazed plants under reduced browsing pressure (≤ 7.5 deer-km⁻²). Fruit-bearing plants dominated by blackberries (genus *Rubus* L.) increase at low deer density and can provide easily accessible food for birds during the fledging and postfledging periods when energy requirements are high for molting and before migration (Rubolini et al. 2002).

Implications for conservation and management

Earlier in the same experiment, Tremblay et al. (2006, 2007) showed that reducing local deer densities under 15 deer-km⁻² allows the natural regeneration dynamics of native balsam fir dominated forests. However, they also pointed out that lower deer densities may be required for the conservation of browse-sensitive plant species. Similar density levels were prescribed for the management of hardwood forests in Pennsylvania (7–9 deer-km⁻²; Tilghman 1989; Horsley et al. 2003). Still, these densities may be too high to restore the diversity of all plants and animals in forests (Alverson et al. 1988). Our results suggest that local deer densities ≤ 7.5 deer-km⁻² may be a conservative deer management target to regenerate balsam fir dominated forests after clear-cutting and habitat attributes required by most songbird species to complete their life cycles. Sylvicultural treatments may also help the recovery process (Tanentzap et al. 2009; Royo et al. 2010). On Anticosti, for instance, experiments have shown that soil scarification favored paper birch regeneration (Beguín et al. 2009), which as shown here would increase songbird richness and diversity provided birches are not browsed. Nonetheless, exploring potential nonlinearities in the relationships between deer density and biodiversity would allow a better understanding of these relationships to establish more effective management strategies (e.g., Fuller and Gill 2001; Tremblay et al. 2007).

Active management of deer populations combined with less intensive forest management strategies may be an effective conservation avenue to reduce future losses in biodiversity (Rooney 2001; Côté et al. 2004; Millington et al. 2011), but should also be seen as a way to increase the persistence of key habitat attributes required by some species. Our study is not only the first to observe indirect effects of abundant herbivore populations on songbirds in North American boreal forests, but it is also the first to measure songbird responses to the control of deer abundance in this ecosystem after tree harvesting. Because songbirds are considered indicators of ecosystem integrity (Niemi and McDonald 2004), understanding their responses to active management of herbivores in a context of forest harvesting could also improve our ability to mitigate detrimental effects of forest harvesting on boreal forest birds (Venier and Pearce 2004). The successful increase in songbird richness and diversity observed in this short-term experiment is promising for other efforts to understand and mitigate the negative effects of heavy chronic

browsing on plant and animal communities in managed forests.

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