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Biodiversity and Conservation

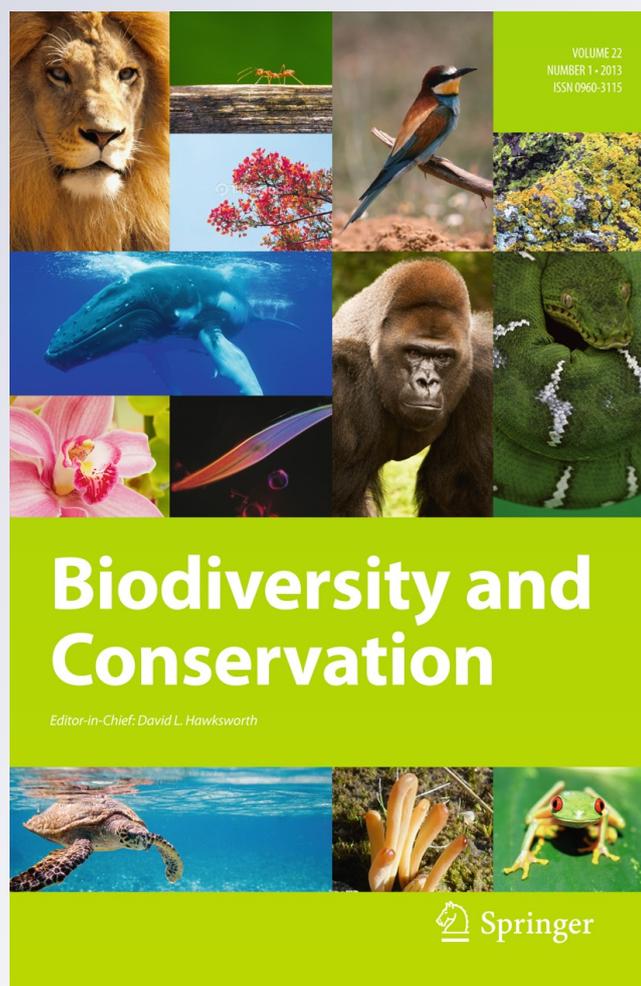
ISSN 0960-3115

Volume 22

Number 1

Biodivers Conserv (2013) 22:77-92

DOI 10.1007/s10531-012-0400-5



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Short-term effects of reduced white-tailed deer density on insect communities in a strongly overbrowsed boreal forest ecosystem

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Received: 22 March 2012 / Accepted: 12 November 2012 / Published online: 9 December 2012
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Abstract Browsing by overabundant deer modifies plant communities and alters forest regeneration, which can indirectly impact associated insect fauna. We tested the hypothesis that the response of insect communities to changes in deer abundance should depend on the strength of their association with plants, which we considered as a key functional trait. Seven years after a deer density control experiment was established in partly harvested forests on Anticosti Island (Quebec, Canada), we evaluated the effects of reducing white-tailed deer (*Odocoileus virginianus*) density from >20 down to 15, 7.5 and 0 deer km⁻², on four insect taxa representing different levels of dependence on plants. As predicted by our hypothesis, the sensitivity of insect taxa to deer density decreased along a gradient representing their degree of association with plants. Carabidae remained unaffected, while Apoidea and Syrphidae communities differed between uncontrolled and reduced deer densities, but not as clearly as for Lepidoptera. As expected, insect communities responded faster in harvested than in forested areas because vegetation changes more rapidly in open habitats. For most insect taxa, dominant species were the most strongly affected by deer density reduction, but it was clearly stronger for predator taxa (Syrphidae and Carabidae). A fast recovery of rare species was observed for macro Lepidoptera. Reducing deer density down to 15 deer km⁻² is sufficient to restore insect diversity on Anticosti Island, but it is unlikely to be efficient in all situations, particularly when competing tree regeneration is firmly established.

Keywords Functional traits · Restoration · Perturbation · Dominance · Rare species

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Introduction

Since the beginning of the 20th century, populations of cervids have been increasing in many parts of the world, mainly because of reductions in predators and in hunting pressure, as well as increasing forage availability (reviewed in Côté et al. 2004). The overabundance of cervids has important ecological consequences because selective overbrowsing can be detrimental to forest regeneration (Watson 1983; Côté et al. 2004) and can modify plant communities (Rooney and Waller 2003; Côté et al. 2004). Also, the direct effect of high cervid density on vegetation is known to indirectly impact populations of invertebrates (Stewart 2001), birds (McShea and Rappole 2000), small mammals (McShea 2000) and even large omnivores such as black bear (*Ursus americanus*) (Côté 2005).

Large herbivores can indirectly affect invertebrates by removing their host plants or by reducing plant biomass or quality, as well as by simplifying vegetation structure, soil microclimate and litter quantity and quality (reviewed in Stewart 2001; Suominen and Danell 2006). Studies on different herbivorous insect taxa have generally shown that they were negatively affected by high ungulate density (Gibson et al. 1992; Baines et al. 1994; Kruess and Tschardt 2002; Martin et al. 2010), while studies on predators yielded variable responses. For instance, web-spiders, which highly depend on vegetation architecture (Greenstone 1984), were shown to be negatively affected by high ungulate density (Miyashita et al. 2004; Takada et al. 2008) while ground beetles (Carabidae) were more abundant at high grazing intensity (Suominen et al. 2003; Melis et al. 2006; 2007). However, few empirical studies considered multiple guilds showing different functional relationships with plants in assessing the impact of ungulate density on arthropods (see Allombert et al. 2005). Furthermore, some groups such as pollinators have rarely been studied, except while observing their activity on flowers (Vázquez and Simberloff 2003, 2004).

Based on these results, we hypothesized that arthropods respond to ecosystem changes resulting from overbrowsing as a function of the strength of their association with plants. We consider dependence on plants for feeding and reproduction as a key functional trait linking arthropods to terrestrial communities, which could help in predicting the impact of mammal browsing (or other similar perturbations) on arthropod fauna in different ecological situations. For example, it has been shown that vegetation changed more rapidly in harvested than in forested areas following deer density reduction (Tremblay et al. 2006). Thus, considering the close link between arthropods and vegetation, a similar effect of forest harvesting can be expected on insect fauna. Moreover, based on the ecological niche theory, if deer density reduction modifies plant communities or microclimate sufficiently, a shift in interspecific competition among a guild could occur (Chase and Leibold 2003). As dominant species are those that benefited from the environmental conditions generated by overabundant deer, a shift in interspecific competition is more likely to affect these species, resulting in abundance reduction of dominant species and augmentation of less abundant ones.

In this study, we evaluate the short-term effects on insect communities of reducing the density of overabundant white-tailed deer (*Odocoileus virginianus*) in strongly overbrowsed balsam fir forests on Anticosti Island, Quebec, Canada in spatially close forested and harvested areas. We aim to determine the highest deer density compatible with the objective of restoring insect communities in unbrowsed stands. We predicted that: (1) sensitivity to deer density would be stronger for herbivores and decrease along a guild gradient representing the degree of association with plants (from Lepidoptera, which are mostly herbivores, to Carabidae, which are not directly dependent on plants), (2) short-

term responses would be stronger in harvested areas than in forested areas, and (3) the abundance of the dominant species would decrease, while the abundance of less abundant species would increase.

Materials and methods

Study area

Study sites were located on Anticosti Island (7,943 km²) in the Gulf of St. Lawrence (49°30'N 63°00'W), Quebec, Canada. The north coast of the island is 35 km from the mainland compared with 72 km for the south coast. White-tailed deer were introduced on Anticosti Island between 1896 and 1900. Without predators, the deer population increased rapidly and its density is now estimated at >20 deer km⁻² across the island (Potvin and Breton 2005). The forest of Anticosti Island is in the boreal zone and is mostly composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*) and black spruce (*Picea mariana*). The dynamics of Anticosti forest ecosystems are strongly disturbed by deer overabundance. Old-growth forests originating prior to the time when deer became overabundant are mostly dominated by balsam fir while recent forests are almost entirely dominated by white spruce because of browsing selectivity on balsam fir and deciduous trees (Potvin et al. 2003). The proportion of balsam fir dominated stands across the landscape has decreased from approximately 40 to 20 % over the last century and many plant species that were once abundant are now rare, such as fireweed (*Chamaerion angustifolium*), raspberry (*Rubus idaeus*) and yellow clintonia (*Clintonia borealis*) (Potvin et al. 2003).

Experimental design

A permanent deer enclosure system, where deer density was controlled, was established in 2001 (Tremblay et al. 2006). The experiment formed a factorial design, where deer density was controlled at 0, 7.5 and 15 deer km⁻² in fenced enclosures in three replicated blocks (A, B and C) located in different parts of the island. Each block also included an additional experimental unit with the local uncontrolled deer density (>20 deer km⁻²).

To control deer density in experimental units, all deer were removed from a 10 ha enclosure (0 deer km⁻²), whereas three deer (>11 months old) were stocked in enclosures of 40 ha (7.5 deer km⁻²) and 20 ha (15 deer km⁻²), for the other controlled densities. Deer used in the controlled densities were captured in early spring, released within enclosures and euthanized in late fall. Deer were equipped with VHF radio transmitters with mortality and activity sensors (Lotek Wireless, Newmarket, ON) to ensure constant monitoring of deer density during the summer treatment period.

In each experimental unit (four densities x three blocks), ~70 % of the forest was harvested just before the onset of the experiment in 2001, leaving ~30 % of the mature balsam fir forest. The deer density was controlled in each experimental unit between 2002 and 2007. In the unharvested residual forested areas of the experimental units, most of the vegetation biomass was represented by mature trees almost unaffected by the reduction of deer density as they only browse on lower branches of fir during winter, thus the main changes were in herbaceous plants density, such as dwarf cornel (*Cornus canadensis*) (Tremblay et al. 2006). However, in harvested areas, pioneering species such as fireweed and *Rubus* spp. rapidly established. In some parts of block B, a high level of white spruce regeneration was observed, probably resulting from partial fir mortality caused by an

outbreak of the hemlock looper (*Lambdina fiscellaria*) in the early 1970's (Jobin and Desautniers 1981; Potvin et al. 2003). Uncontrolled deer density in each block was estimated each year between 2002 and 2007 using line transect surveys of summer fecal pellet clusters using a distance sampling protocol (Buckland et al. 2001) and computed with DISTANCE 5.0 software (Thomas et al. 2010). For details about the estimation protocol, see Tremblay et al. (2006). Through the years, uncontrolled deer densities were estimated at 26 deer km⁻² for block B and 57 deer km⁻² for blocks A and C.

Vegetation data

Vegetation was inventoried during summer 2007 in 20 plots of 10 × 10 m randomly distributed in both the harvested and forested areas of each experimental unit. The percentage cover of shrubs was visually evaluated by several observers in each 10 × 10 m plot, while that of other vascular plant species was estimated in each of two randomly selected quadrats of 1 × 1 m inside the larger plot; for trees, only seedlings were considered (2 quadrats × 20 plots × 2 cover types = 80 quadrats per experimental unit). The technique was similar to that used by Tremblay et al. (2006). The mean percentage cover of each species across all quadrats of each experimental unit was used for the analyses.

Insect sampling

Four taxonomic groups belonging to different ecological guilds along a gradient of association with plants were sampled. Nocturnal macro Lepidoptera (i.e. Bombycoidea, Drepanoidea, Geometroidea, Noctuoidea) represent mostly herbivorous insects such as caterpillars; Apoidea (excluding former Sphecoidea) (Hymenoptera) represent the most important insect pollinator specialists and are also seasonal nesting insects; Syrphidae (Diptera) are pollinators (polliniphage) when adults, while presenting diverse feeding behaviours at the larval stage such as predators, saprophages, herbivores or inquilines with ants or bees (Foote 1991). The absence of nesting behaviour also makes Syrphidae less affected by landscape structure (such as forest fragmentation) than Apoidea (Jauker et al. 2009). Finally, Carabidae were selected because they represent a broad diversity of mostly epigeal predators, often considered as useful bioindicators (Rainio and Niemelä 2003). These four taxa represent a gradient relative to their degree of association with plants: macro Lepidoptera (close relationship with plants and numerous cases of mono- and oligophagy) > Apoidea > Syrphidae > Carabidae (no direct relationship).

Luminoc[®] traps (BIOCOM, Quebec City, QC) (Jobin and Coulombe 1992) equipped with a 1.8 W blue light tube were used as pitfall traps to sample Carabidae (Hébert et al. 2000). In each experimental unit, two pitfall traps at least 100 m apart from each other were installed at random locations in both harvested and forested areas. Traps were placed at least 100 m away from enclosure fences and whenever possible (i.e. when the forest patch was large enough), at least 50 m from the forest edge. Trapping periods were separated into two phases so that Carabidae and Lepidoptera were not caught concurrently. First, traps were operated as pitfall during 9–11 day periods using 40 % ethyl alcohol as a preservative. In the second phase, the Luminoc[®] traps were raised and placed on a post 3 m above the ground to sample macro Lepidoptera for 3 day periods with Vapona[®] strips instead of ethyl alcohol. Traps set 3 m high were operated when three consecutive non-rainy days were forecasted by Environment Canada. Five trapping periods were carried out between mid-June and mid-August 2007.

Flying adult Apoidea and Syrphidae were sampled using one Malaise trap (Gressitt and Gressitt 1962) in each experimental unit, installed in the harvested area, 50 m away from the forest edge and at least 100 m away from the enclosure fence. These traps were operated between 15 June and 19 August 2007. A solution of 40 % ethyl alcohol was used as a preservative and samples were collected at intervals of ~ 14 days.

All specimens were identified at the species level whenever possible except for a few genera: i.e. *Andrena* (Apoidea: Andrenidae), *Cheilosia* and *Microdon* (Syrphidae), *Eupithecia* (Lepidoptera: Geometridae) and most female *Heringia*, *Platycheirus* and *Sphaerophoria* (Syrphidae). Furthermore, specimens of the subgenus *Lasiglossum* (*Dialictus*) (Apoidea: Halictidae) were identified as morphospecies. Specimen identifications were cross-checked at the Canadian National Collection (CNC) of insects, arachnids and nematodes in Ottawa, Canada and at the Insectarium René-Martineau (IRM) of the Canadian Forest Service in Quebec City, Canada.

Statistical analyses

For each major taxon (macro Lepidoptera, Apoidea, Syrphidae and Carabidae), we used mixed model ANOVAs (PROC mixed) (SAS 9.1, SAS Institute 2003) to examine variation in species richness (R), the Shannon–Wiener index and the overall abundance of each major taxon in relation to deer density. Deer density was considered a fixed effect and blocks a random effect. For macro Lepidoptera and Carabidae, a split-plot model with cover (forested or harvested) included as a subplot was used. To meet the assumptions of ANOVA (i.e. normality, homogeneity of variances), abundance and species richness data were square-root transformed. Furthermore, for the abundance of each major taxon, the relative contribution of blocks to the total variance among experimental units was calculated as follows:

$$\sigma_B^2 / (\sigma_B^2 + \sigma_\epsilon^2)$$

where σ_B^2 is the estimated variance of the block effect and σ_ϵ^2 is the estimated variance of residuals (Fleiss et al. 2003). Raw species richness was preferred to rarefaction because our sampling effort was the same in all experimental units. This is in agreement with Collins and Simberloff (2009) who suggest using standardized sampling protocols rather than rarefaction when possible. Rossi (2011) also argued that the use of rarefaction to compare sites sampled with the same effort, but where abundance differs can lead to misinterpretation.

To investigate how dominant and rare species responded to deer density reductions, we classified all species of each major taxon into four groups based on their ordered total abundance in uncontrolled deer densities. For Carabidae and macro Lepidoptera, this was done for both harvested and forested areas. A dominant species was defined as a species representing at least 25 % of the total abundance of the taxon; common species were those that composed the first 75 % of the total abundance, but were not dominant; uncommon species were present in the interval between 75 and 95 %; and rare species were the remaining 5 %. A mixed ANOVA was used to compare the abundance of each group between deer densities using the model previously described.

Variations in community composition were examined using redundancy analysis (RDA) based on Hellinger transformed species data (Legendre and Gallagher 2001) performed with the software R (function *rda* of the library *vegan*, version 1.15–4) (Oksanen et al. 2009). They were conducted for each major taxon and also separately for harvested and forested areas for macro Lepidoptera and Carabidae considering only the vegetation from

these specific areas. All RDAs included the twelve experimental units (four deer densities x three blocks), all insect species identified in the taxon and a number of explanatory variables selected using the two-steps forward selection procedure described by Blanchet et al. (2008), using the function *forward.sel* of library *packfor* in R (Dray et al. 2007), with $\alpha = 0.1$. Explanatory variables included deer density, % cover of each common plant species (i.e. representing ≥ 5 % of total cover in at least one experimental unit) and the Shannon–Wiener index (based on the percentage ground cover of each species) estimated for all vascular plants. Non-normal variables (based on the Shapiro test) were square-root or fourth-root transformed; if they could not be normalized, they were removed from the analysis. Multicollinearity among explanatory variables was assessed by calculating tolerance value (Quinn and Keough 2002); if tolerance was < 0.2 for one or more variables, the one with the lower score was removed from the pool and the forward selection was run again until a result > 0.2 was obtained for all variables. The list of retained explanatory variables for each RDA is available in Table 1. RDA results were interpreted using distance triplots (scaling 1) where the eigenvectors are scaled to unit length, as described in Legendre and Legendre (1998), p. 586.

Results

Diversity and abundance

A total of 260 specimens of macro Lepidoptera were collected in the harvested areas and 1,343 in the forested areas. They belong to five families (Arctiidae, Drepanidae, Geometridae, Lymantriidae and Noctuidae) and to 105 species (56 in the harvested areas and 90 in the forested areas). Only four species representing 0.03 % of the total abundance were associated with lichens, forest litter or ant nests, with all others being herbivores. Apoidea totalled 1,308 specimens representing 35 species that belong to five families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae). The Syrphidae were represented by 7,481 specimens belonging to 109 species, of which 63, representing 88 % of the total abundance, were predators of herbivorous insects (mainly on aphids) at the larval stage. Larval stages of other syrphid species were saprophagous on litter or wood (5.4 % of total abundance), epigeal predators (3.3 %), aquatic saprophages (2.3 %), inquiline with ants or bumblebees (0.2 %) or herbivores (0.1 %). Finally, 1,878 Carabidae belonging to 30 species were caught; 875 in the harvested areas and 1,003 in the forested areas. Twenty-one carabid species, representing 58 % of total abundance, were epigeal predators. One species (*Synuchus impunctatus*) representing 37 % of total abundance was both predator and granivorous. Pure granivorous species represented only 5 % of total abundance.

Although significant ANOVAs were obtained for most taxa, the block effect was high, explaining from 18.2 % to 95.8 % of variance in the abundance of the four major insect taxa (Table 2). The block effect was not significant for Syrphidae while the strongest effect was observed for Carabidae in forested areas. For both macro Lepidoptera and Carabidae, a significant block effect was found in both harvested and forested areas (Table 2).

Mixed ANOVAs did not reveal any significant effect of deer density on total abundance of any major taxa (Table 3; Fig. 1a). However, the effect of deer density was significant on the number of species of macro Lepidoptera (Table 3; Fig. 1b), for which more species were captured at 7.5 and 15 deer km^{-2} than in uncontrolled densities. At 0 deer km^{-2} , the number of species was lower than at mid densities, but not significantly so. No effect of

Table 1 Vegetation explanatory variables selected using the two-steps forward selection procedure and used in redundancy analyses (RDA) on insect communities on Anticosti Island (Québec, Canada), with their mean % cover and range for 'H'arvested and 'F'orested areas

Explanatory variables	Percentage cover		Macro Lepidoptera (H)	Macro Lepidoptera (F)	Apoidea	Syrphidae	Carabidae (H)	Carabidae (F)
	Harvested areas							
	Mean ± SD	Range						
<i>Abies balsamea</i> (L.) Mill.	2.4 ± 0.5	<0.1, 6.2	3.1 ± 0.5	0.2, 5.4	X			
<i>Coptis groenlandica</i> (Oeder) Fern.	3.7 ± 0.6	1.2, 7.1	4.0 ± 0.4	1.5, 5.7	X	X	X	X
<i>Cornus canadensis</i> L.	15.7 ± 1.8	4.4, 28.0	14.5 ± 1.2	6.4, 18.9			X	
<i>Dryopteris disjuncta</i> (Ledeb.) Morton	2.4 ± 0.7	0.2, 8.7	1.9 ± 0.4	0.5, 6.5		X		
<i>Oxalis montana</i> Raf.			2.5 ± 0.7	0, 7.7				X
<i>Picea glauca</i> (Moench) Voss	17.5 ± 3.7	3.0, 36.7	14.1 ± 2.4	0.8, 30.6			X	X
<i>Picea mariana</i> (Mill.) B.S.P.	2.0 ± 0.8	0, 9.0	6.5 ± 1.9	0, 22.7				X
<i>Rubus idaeus</i> L.	4.1 ± 1.7	0, 18.1				X		
<i>Rubus pubescens</i> Raf.	8.3 ± 1.7	1.7, 22.8	4.0 ± 0.6	0.1, 7.0	X			
Shannon index of all vascular plants	2.7 ± 0.1	2.2, 3.0	2.9 ± 0.1	2.4, 3.3			X	
<i>Betula papyrifera</i> Marsh.	2.3 ± 0.6	<0.1, 8.0						
<i>Cirsium arvense</i> (L.) Scop.	2.8 ± 0.5	0.5, 5.7						
<i>Dicentra canadensis</i> (L.) Bernh.			1.8 ± 0.3	0.7, 5.2				
<i>Chamaerion angustifolium</i> (L.)	7.4 ± 2.3	0, 19.2						
<i>Fragaria virginiana</i> Duchesne	2.2 ± 0.5	0.5, 5.9						
<i>Gaultheria hispida</i> (L.) Muhl.			1.9 ± 0.6	0, 6.2				
<i>Linnæa borealis</i> L.	3.2 ± 0.7	0.1, 6.8						
<i>Maianthemum canadense</i> Desf.	4.5 ± 0.7	0.7, 9.6	4.9 ± 0.3	3.4, 6.5				

Plant species unselected, but present in the original data pool are presented in the lower part of the table

Table 2 Proportion of variance explained by the block effect based on type 3 mixed ANOVA on the abundance of the four major insect taxa in ‘H’arvested and ‘F’orested areas (df = 2/6) of a white-tailed deer controlled browsing experiment on Anticosti Island (Québec, Canada)

Taxon	% Variance	F	P
Macro Lepidoptera (H)	87.2	28.28	0.001
Macro Lepidoptera (F)	57.3	6.36	0.03
Apoidea	54.7	5.83	0.04
Syrphidae	18.2	1.89	0.23
Carabidae (H)	63.2	7.86	0.02
Carabidae (F)	95.8	73.30	< 0.0001

Significant variances are in bold

Table 3 Variation in the abundance and species richness of Apoidea, Syrphidae, Carabidae and macro Lepidoptera in three blocks (random factor), four experimental white-tailed deer densities and two vegetation cover areas (harvested or forested) for Carabidae and macro Lepidoptera on Anticosti Island (Québec, Canada) (mixed ANOVA)

Source of variation	Apoidea			Syrphidae			
	df	MS	F	P	MS	F	P
Abundance							
Density	3	77.12	1.35	0.34	96.47	2.40	0.17
Error	6	39.71			152.99		
Richness							
Density	3	0.46	1.65	0.27	0.25	0.32	0.74
Error	6	0.28			0.78		
Carabidae							
Abundance							
Density	3	6.99	2.24	0.18	3.67	0.29	0.83
Residual	6	3.13			1.24		
Cover	1	2.17	0.85	0.38	201.58	62.72	<0.0001
Density × Cover	3	2.16	0.85	0.51	0.57	0.83	0.51
Error	8	2.56			2.47		
Richness							
Density	3	0.21	0.83	0.53	1.17	5.62	0.035
Residual	6	0.25			0.21		
Cover	1	0.01	0.12	0.74	31.63	82.59	<0.0001
Density × Cover	3	0.02	0.27	0.84	0.25	0.67	0.60
Error	8	0.09			0.38		

deer density was observed on the diversity of any taxon based on Shannon–Wiener index (Fig. 1c). The abundance of the dominant species of Syrphidae (*Melanostoma mellinum*) and Carabidae (*S. impunctatus*) in both harvested and forested areas, decreased at reduced deer densities (Fig. 2a). No dominant species was identified in forested areas for macro Lepidoptera, while the dominant species in harvested areas, the noctuid *Leucania multilinea*, did not vary significantly with deer density (Fig. 2a). The dominant species of Apoidea, *Bombus borealis*, did not vary significantly with deer density but, nevertheless,

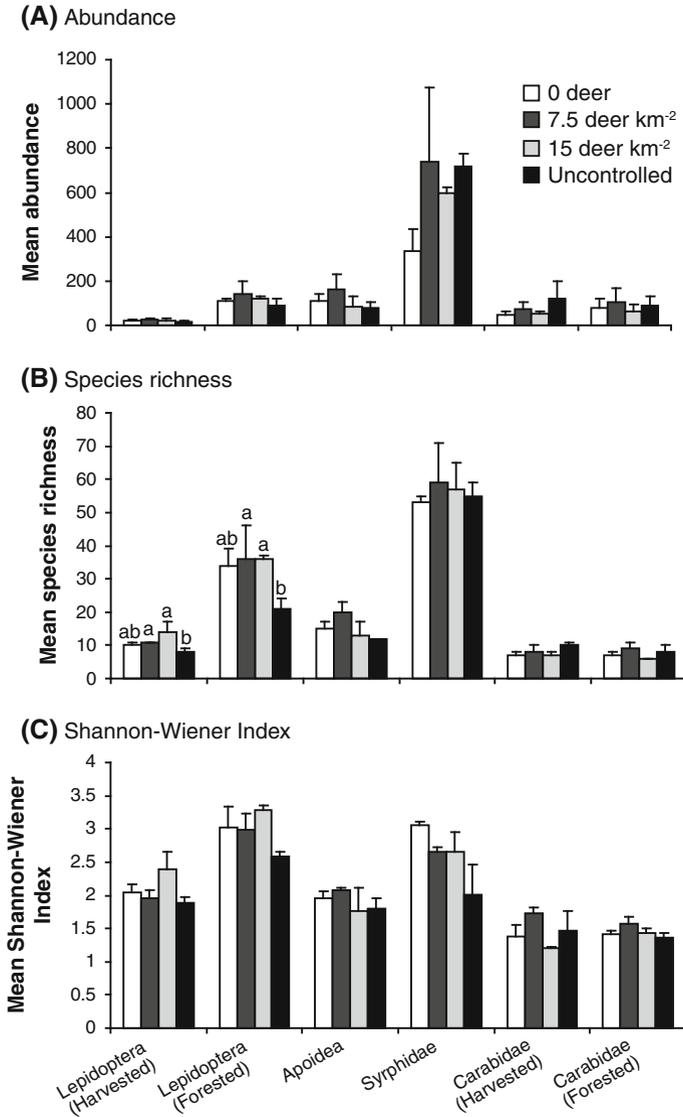


Fig. 1 **a** Mean abundance, **b** mean species richness and **c** mean Shannon–Wiener Index (with standard error) of macro Lepidoptera, Apoidea, Syrphidae and Carabidae in harvested and forested areas along an experimental white-tailed deer density gradient (0, 7.5 and 15 deer km⁻² and uncontrolled) replicated in three blocks on Anticosti Island (Québec, Canada). Within each group and for each area, different letters indicate significant differences between deer densities based on mixed ANOVAs at $\alpha = 0.05$

its abundance decreased in all reduced deer density sites by 25–79 % while *Bombus frigidus* became the dominant species in these sites. Total abundance of common and uncommon species did not vary for any taxa as a function of deer density (Fig. 2b, c). The abundance of rare species of macro Lepidoptera was significantly higher at reduced deer densities than in uncontrolled densities in both harvested and forested areas (Fig. 2d). An a posteriori test revealed that the number of rare species was also significantly higher in

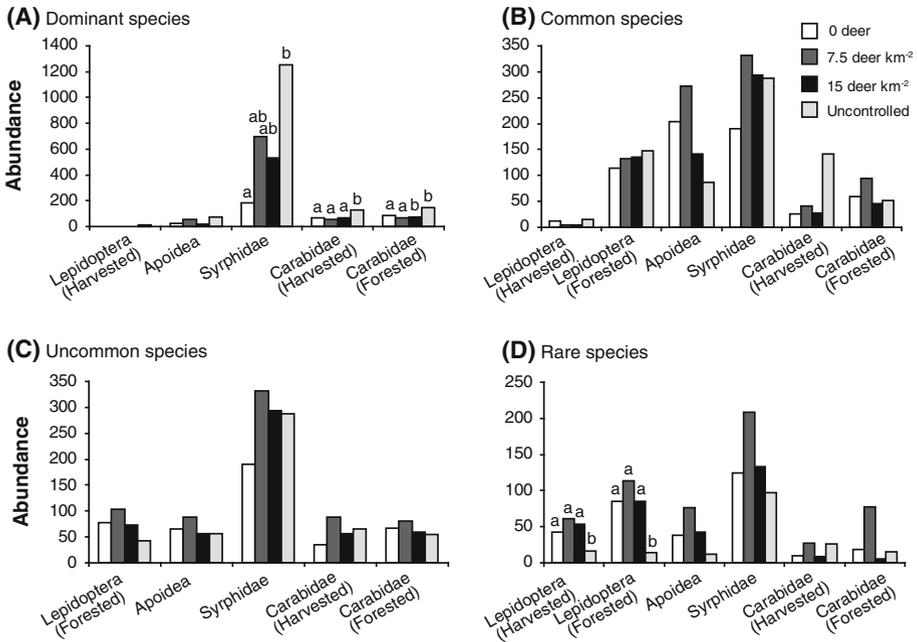


Fig. 2 Total abundance of **a** dominant, **b** common, **c** uncommon and **d** rare species based on their relative abundance in uncontrolled deer density sites for macro Lepidoptera, Apoidea, Syrphidae and Carabidae along an experimental white-tailed deer density gradient (0, 7.5 and 15 deer km⁻² and uncontrolled) in harvested and forested areas on Anticosti Island (Québec, Canada). Dominant species was not identified for macro Lepidoptera in forested areas, as well as uncommon species for Lepidoptera in harvested areas. Within each group and for each area, different letters indicate significant differences between deer densities based on mixed ANOVAs at $\alpha = 0.05$

reduced deer density sites than in uncontrolled deer densities, suggesting that the change in the overall number of species was related to the change in the number of rare species.

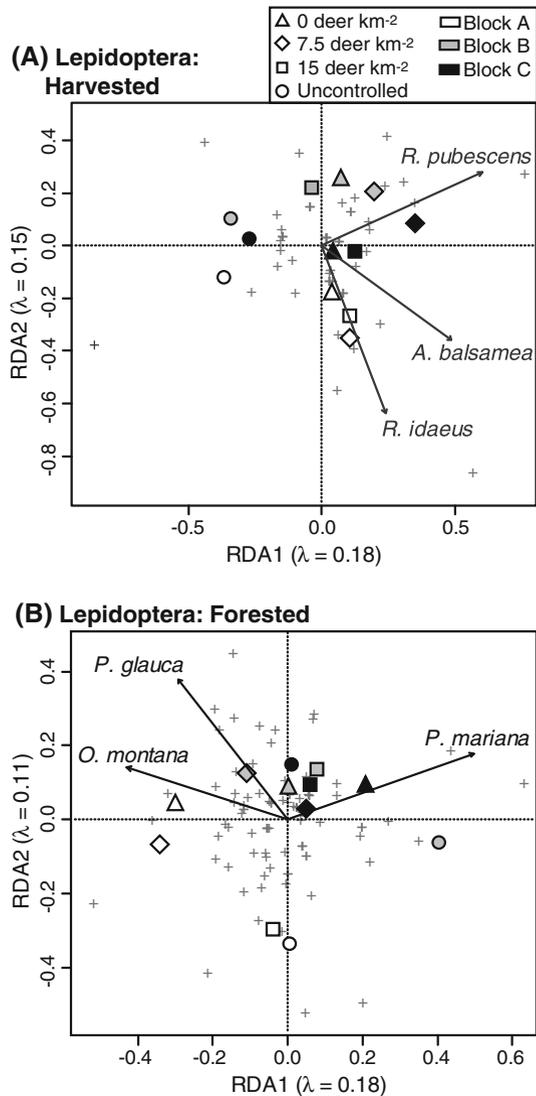
Community assemblages

Community analyses carried out with RDAs showed markedly different responses by the four studied insect taxa. For macro Lepidoptera, in harvested areas, the three uncontrolled deer density sites had negative values on axis 1 along with the 15 deer km⁻² density of block B, while other experimental units had positive values (Fig. 3a). The second axis mostly separated block A from blocks B and C. In forested areas, community patterns were not as clear as in harvested areas (Fig. 3b). However, sites of block A, except for the 0 deer km⁻² site, had negative values on the second axis along with uncontrolled density of block B, which was far from other densities in this block.

For Apoidea (Fig. 4a), experimental units of block A had negative values on axis 1 while those of blocks B and C were on the positive side, confirming the aforementioned substantial block effect on insect abundance (Table 2). Uncontrolled deer densities of blocks A and C were clearly separated from reduced deer densities of the same blocks, but this was not observed in block B.

Uncontrolled deer densities of the three blocks clearly shared a similar syrphid community, which was also shared with the 15 deer km⁻² density of block B (Fig. 4b). The

Fig. 3 Distance triplots (scaling 1) of redundancy analyses (RDA) on species data of macro Lepidoptera in **a** harvested areas (species richness $R = 56$) and **b** forested areas ($R = 90$) at all experimental sites (4 deer densities \times 3 blocks) of a white-tailed deer controlled browsing experiment on Anticosti Island (Québec, Canada). Species are represented by a cross symbol (+). Arrows represent percent cover of each plant species retained as explanatory variables with the two-steps forward selection procedure



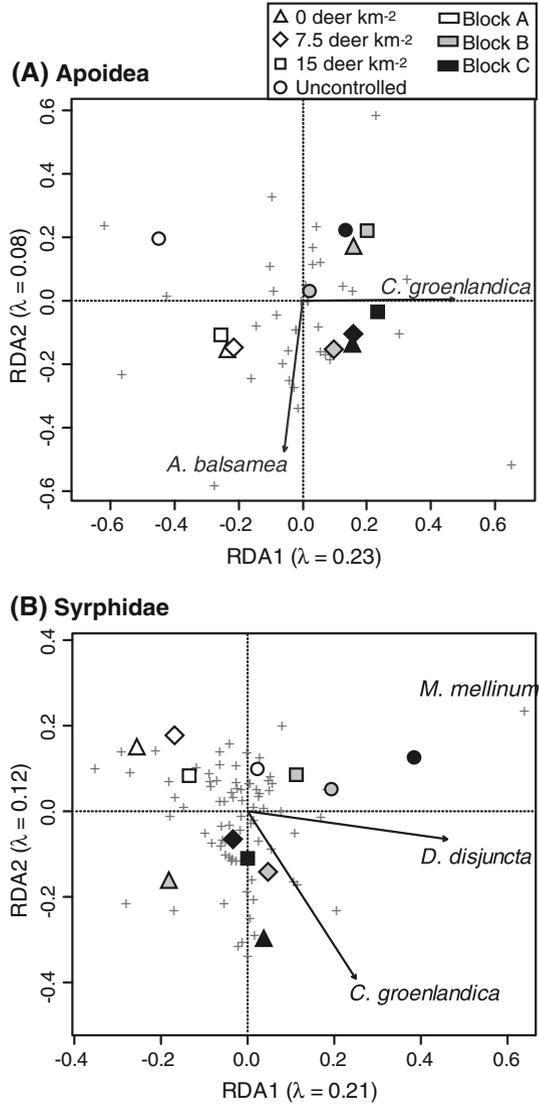
dominant species (*M. mellinum*) was strongly associated with this group of experimental units. Experimental units with reduced deer densities of block A were far from those of blocks B and C.

Finally, for Carabidae, no significant RDA could be obtained either for the harvested or the forested areas.

Discussion

Our results showed that the sensitivity of different insect taxa and feeding guilds to deer density decreased along a gradient representing their degree of association with plants. Epigeal Carabidae, which do not have any direct relationship with plants, did not vary with

Fig. 4 Distance triplots (scaling 1) of redundancy analyses (RDA) on species data of **a** Apoidea ($R = 35$) and **b** Syrphidae ($R = 109$) at all experimental sites (4 deer densities \times 3 blocks) of a white-tailed deer controlled browsing experiment on Anticosti Island (Québec, Canada). Species are represented by a cross symbol (+). Arrows represent percent cover of each plant species retained as explanatory variables with the two-steps forward selection procedure



deer density. Communities of Apoidea and Syrphidae differed in uncontrolled and reduced deer density sites but were not separated as clearly as for the macro Lepidoptera, which is the group most intimately linked to vegetation. Moreover, macro Lepidoptera was the only taxon with significantly higher abundance of rare species and higher species richness overall at reduced than at uncontrolled deer densities.

Insect communities

Because our study sites were located far from the shore, and Anticosti Island itself is located at least 35 km from the continent, we assume that the species pool here was composed of resident species that were present on the island at the start of the experiment

in 2001. This implies, on one hand, that the most common species must be those that were adapted to conditions generated by deer overabundance and were already abundant locally and thus were available to colonize the new habitats. On the other hand, rare species are more likely to be those inhabiting restricted areas on the island, such that their colonizing potential depends on the distance between the source populations and the new habitats (Littlewood et al. 2009). Dominant species of each group decreased in abundance with decreasing deer density, but it was significant only for Syrphidae and Carabidae, i.e. the two taxa that are least strongly associated with the plants among the four studied. In addition to their degree of association with plants, trophic level could also be important; Syrphidae and Carabidae are mostly predators, at least in their larval stages. Indeed, predators may be slower to colonize new habitats than herbivorous species (Brown and Southwood 1983) as they depend on the recovery of herbivorous insect prey.

Deer density reduction seems to have generated less favourable conditions for dominant species and, as no significant modification in total abundance of any major group studied was observed, we can speculate that less abundant species benefited from these new conditions. Community changes were fast, particularly for macro Lepidoptera in which we observed a rapid return of rare species, suggesting a higher colonization capacity than expected for this taxon. The increasing abundance of rare species and higher species richness of macro Lepidoptera in reduced deer density sites are in agreement with ecological niche theory. Thus, deer density reduction could increase the number of niches per unit area, which is reflected in the higher number of rare Lepidoptera species. Among predator taxa, rare species may recover over a longer time frame, which remains to be determined.

Our experiment was designed to study the impact of deer browsing on regeneration. In Norway, winter browsing by deer on *Vaccinium* spp. has been associated with increases in Carabidae abundance. However, winter browsing was not considered in our study. During winter on Anticosti Island, deer feed mainly on the lower branches of mature balsam fir and have only a small impact on the total foliage biomass of trees (Lefort 2002). In fact, winter browsing has virtually no impact on the forest structure and thus it is unlikely to have an impact on insects. The main impact of deer browsing on forest structure is caused by summer feeding when they browse on most fir seedlings, which results in the quasi absence of balsam fir saplings in Anticosti forests and a conversion from balsam fir to white spruce forests.

Several studies have already shown the positive impact of high Cervid density on Carabidae abundance (Melis et al. 2006; 2007) and diversity (Suominen et al. 2003), while we only observed a positive impact on the abundance of the dominant species *S. impunctatus*. In both Melis et al. (2007; 2006) studies, the dominant species *Pterostichus oblogopunctatus* represented respectively 45 % and 33 % of the total abundance of Carabidae. When we look closely at the data, this species seems to be the main cause of the variation in the abundance of the whole family. These results are thus similar to ours and are in agreement with our hypothesis on the dominant species. Suominen et al. (2003) observed no dominant species, which might result from the smaller scale of their study, with enclosure dimensions $< 50 \times 50$ m, compared with 0.5×1 km in Melis and >10 ha in ours.

Forested vs. harvested areas

For macro Lepidoptera, results of the RDAs agree with our hypothesis that changes occur faster in an ecosystem fully exposed to sunlight by forest harvesting, which allows rapid

establishment and growth of colonizing plants. However, the abundance of rare species was higher at reduced deer densities than in uncontrolled densities in both harvested and forested areas. This suggests that moth communities can rapidly benefit from new vegetation growth in both open and forested areas. In temperate deciduous forests, it has been shown that rare Lepidoptera species were mostly associated with understory vegetation (Hirao et al. 2009), which could explain why rare species were also affected in forested areas. Alternatively, it could also suggest that Lepidoptera in our relatively small residual forest patches benefit from the fast regeneration of the surrounding harvested areas.

Conservation

Our results support the suggestion of Hébert and Jobin (2001) that regeneration of balsam fir forests and of pioneering plant species such as raspberry are important for restoring insect communities on Anticosti Island. These plants, once very abundant on the island, are now endangered by deer overabundance and only a marked decrease in deer density could make it possible to restore them (Tremblay et al. 2006; 2007). Insect communities in the 15 deer km⁻² of block B differed from those in other sites with the same deer densities and were more similar to uncontrolled density sites. We speculate that the high level of regeneration of white spruce in this site may have reduced sunlight penetration and adversely affected herbaceous plant regeneration. In any event, this indicates that deer reduction to 15 deer km⁻² could be sufficient to restore insect diversity, but is unlikely to be effective in all situations. Unfortunately, unlike plants, no historical data are available for insects of Anticosti Island before deer overbrowsing became noticeable in the mid 20th century (Potvin et al. 2003) and thus it is difficult to determine how reducing deer density can actually help to restore original natural insect communities.

Conclusion

Our results show that even in highly perturbed environments, restoration of plant communities can rapidly benefit insects and particularly rare herbivorous species with high dispersal ability. More specifically, our results are consistent with our hypothesis that the impact of deer density on insect communities strongly depends on their degree of association with plants. This hypothesis was tested here in the context of a recent density reduction experiment involving Anticosti's overabundant deer population. More support for the hypothesis could become available from future studies of ungulate overbrowsing impact on insect diversity and abundance, where a range of insect guilds and functional traits are studied. Considering finer and more diverse traits than trophic relationships (e.g. related to insect behaviour or reproductive strategy), could also lead to a deeper understanding of the impact of mammal browsing on arthropod communities.

Acknowledgments Our research was financed by the Natural Sciences and Engineering Research Council of Canada (NSERC), Produits forestiers Anticosti Inc. (PFA), Natural Resources Canada (NRCan) and Université Laval. We would like to thank M. Poulin, S. Pellerin and M. Bachand for vegetation data; N. Giasson for help in field work and Y. Paiement for help in laboratory work. We also thank Y. Dubuc for technical assistance and G. Pelletier for his taxonomic expertise, both from NRCan and S. de Bellefeuille from the NSERC-Produits forestiers Anticosti Industrial Research Chair for logistical assistance. We are grateful to Y. Bousquet from the Eastern Cereal and Oilseed Research Center in Ottawa for confirming identification of Carabidae and G. Daigle of the Département de Mathématiques et de Statistiques at Université Laval and E. Azeria from NRCan for statistical advice. We also thank I. Lamarre and P. Cheers from NRCan for editing the manuscript.

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