A generalist rodent benefits from logging regardless of deer density[1]

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Abstract: Landscape homogenization resulting from high browsing pressure or forest management practices can impact plant and animal diversity. Large herbivores and logging may therefore influence small mammal populations, which are known to strongly respond to forest disturbances. We assessed the influence of white-tailed deer (*Odocoileus virginianus*) density and forest harvesting on deer mice (*Peromyscus maniculatus*) in the boreal forest of Anticosti Island (Quebec, Canada). We expected mice to be favoured by logging and thus that their abundance and body mass would increase in cutblocks, due to a greater availability of grasses providing food, shelter from predators, and improved thermoregulation. Mice may also benefit from an increase in deer density, especially at intermediate densities, where food (insects and seeds) availability is the highest. In 2 consecutive summers, we live-captured mice within a large, controlled deer browsing experiment where deer were maintained at 4 different densities (0, 7.5, and 15 deer·km^{-2} and ambient density, 27 to 56 deer·km^{-2}) in forest and in cutblocks. We found higher mice abundance in logged habitat regardless of deer density, but body mass was unaffected by deer density and forest harvesting. While plant, insect, and bird communities have all been shown to respond to deer density reduction, the interspecific relationships between deer and mice appear neutral in this system.
Keywords: browsing, forest management, habitat disturbance, interspecific interactions, large herbivores, small mammals.

Résumé: L'homogénéisation du paysage résultant d'une forte pression d'herbivorie ou de pratiques de gestion forestière peut influencer la diversité végétale et animale. Les grands herbivores et la coupe forestière pourraient ainsi influencer les populations de petits mammifères que l'on sait être très sensibles aux perturbations de la forêt. Nous avons évalué l'influence de la densité de cerfs de Virginie (*Odocoileus virginianus*) et de l'exploitation forestière sur les souris sylvestres (*Peromyscus maniculatus*) sur l'île d'Anticosti (Québec, Canada). Nous nous attendions à ce que les souris soient favorisées par les coupes forestières et donc que leur abondance et leur masse corporelle augmentent du fait d'une plus grande disponibilité en graminées fournissant de la nourriture, des refuges face aux prédateurs et une meilleure thermorégulation. Les souris devraient aussi bénéficier d'une augmentation de la densité de cerfs, surtout à densité intermédiaire, où la disponibilité en nourriture (insectes et graines) est la plus grande. Pendant 2 étés consécutifs, nous avons capturé des souris au sein d'un dispositif de broutement contrôlé dans lequel les cerfs ont été maintenus à 4 densités différentes (0, 7,5 et 15 cerfs·km^{-2} et à densité ambiante: 27 à 56 cerfs·km^{-2}) en forêt et dans des coupes. Nous avons trouvé que l'abondance de souris a augmenté dans les coupes indépendamment de la densité de cerfs, mais leur masse corporelle n'a pas été affectée par la densité de cerfs ou la coupe forestière. Alors que les communautés végétales, d'insectes et d'oiseaux ont toutes montré une réponse à la réduction de la densité de cerfs, les relations interspécifiques entre les cerfs et les souris apparaissent neutres dans ce système.
Mots-clés: broutement, gestion forestière, grands herbivores, interactions interspécifiques, perturbation de l'habitat, petits mammifères.

Nomenclature: Integrated Information Taxonomic System (ITIS), 2013.

Introduction

Small mammals perform important roles in ecosystem functioning, for example as seed dispersers, as prey, or in structuring vegetation (Pearson, 1999; Carey & Harrington, 2001; Austrheim *et al.*, 2007). However, they may be especially sensitive to habitat changes caused by natural or anthropogenic disturbances, since they rely heavily on habitat heterogeneity and micro-habitats to access food and to find shelter for improved thermoregulation and predation avoidance (*i.e.*, Pearce & Venier, 2005; Zwolak, 2009).

High deer population densities are increasingly being observed in many regions (Fuller & Gill, 2001; Côté *et al.*, 2004) and may have considerable effects on the vertical and

horizontal heterogeneity of vegetation communities (Olff & Ritchie, 1998; Rooney, 2001; Russell, Zippin & Fowler, 2001). By decreasing the regeneration rate, abundance, and diversity of palatable understory plant species, intensive browsing can lead to the gradual replacement of the original plants by species resistant to herbivores (Côté *et al.*, 2004; Tanentzap *et al.*, 2011; Hidding, Tremblay & Côté, 2012). These changes in resource availability may indirectly influence other large herbivore species, either positively through facilitation (Arsenault & Owen-Smith, 2002) or negatively through exploitative competition (Tilman, 1994). They may also lead to cascading effects on other animal functional groups, especially those associated with the affected plant species and vegetation strata (van Wieren, 1998; *e.g.*, in birds: Allombert, Gaston & Martin, 2005; or in insects: Allombert, Stockton & Martin, 2005; Loe *et al.*, 2007).

Habitat opening and modifications in the composition of plant and insect communities induced by high browsing pressure can affect small mammal communities by influencing their food availability and detectability by predators. Responses to deer browsing are likely to be species-specific, depending on the ecological requirements of species for food and vegetation cover (Flowerdew & Ellwood, 2001; Buesching *et al.*, 2011). Some species, like field voles (*Microtus agrestis*), may be favoured by an increase in food plant species unpalatable to deer (Flowerdew & Ellwood, 2001), while other species, such as bank voles (*Myodes glareolus*), may be negatively influenced by a loss of ground cover (Buesching *et al.*, 2011; Bush *et al.*, 2012). In slowing plant succession (Speed *et al.*, 2013), high deer density may favour small mammal species associated with forest early successional stages (Flowerdew & Ellwood, 2001).

Anticosti Island (Quebec, Canada) provides an excellent natural laboratory to study the impact of browsing by white-tailed deer (*Odocoileus virginianus*) on deer mice (*Peromyscus maniculatus*). The latter is the only small mammal species present on the island: consequently, confounding factors of interspecific interactions within rodent assemblages are non-existent. Following their introduction to the island in the late 19th century, white-tailed deer quickly established high density populations (>20 individuals·km^{-2} locally on average). As a keystone species (McShea & Rappole, 1992; Waller & Alverson, 1997), white-tailed deer have strongly modified the composition of boreal forest on the island (Potvin, Boots & Dempster, 2003; Tremblay *et al.*, 2005; Hidding, Tremblay & Côté, 2013). As deer mice abundance has been shown to increase in disturbed habitats, such as in logged areas (Martell *et al.*, 1983a; Pearce & Venier, 2005), they are likely to be influenced by both deer density and logging.

Using a large-scale controlled browsing experiment (3 blocks of 110 ha each), we tested the combined and separate effects of 4 different deer densities (from 0 to ambient, 27−56 deer·km^{-2}) and 2 different habitat types (forest and cutblocks) on deer mice. We assessed whether differences in habitat types and white-tailed deer density may cause indirect effects leading to changes in deer mice abundance, body mass (as a proxy of fitness), sex, and population age structure. Deer mouse abundance should

be favoured in cutblocks because of the woody debris produced by logging, which may be used as shelter for thermoregulation and protection against predators (Tallmon & Mills, 1994; Fauteux *et al.*, 2012). Deer mice may also be positively influenced by deer density because of the natural disturbance induced by browsing, which may maintain attributes of early succession in forests (Potvin, Boots & Dempster, 2003; Tremblay, Huot & Potvin, 2006). Given that the diversity and abundance of major food resources like seedlings and insects (Desrosiers, Morin & Jutras, 2002; Lobo & Millar, 2011) appear highest at deer densities of 7.5−15 individuals·km^{-2} (Tremblay, Huot & Potvin, 2006; Brousseau *et al.*, 2013), deer mice should mostly be favoured at these deer densities.

Methods

STUDY AREA

Anticosti Island (7943 km^2) is located in the Gulf of St. Lawrence in Quebec, Canada (49°28'N, 63°00'W). The climate is classified as cold maritime, with a total annual precipitation of 917 ± 130 mm (mean ± SD, Environment Canada, 2006), with a third falling as snow (Environment Canada, 1982). Mean temperatures vary from a minimum of −11.5 ± 1.9 °C in February to a maximum of 16.1 ± 1.1 °C in July (Environment Canada, 2006).

About 220 white-tailed deer were introduced to the island in 1896. The deer population reached high densities in the 1930s and is currently estimated at >20 individuals·km^{-2}, locally exceeding 50 individuals·km^{-2}. Deer have had no natural predators on Anticosti Island since the black bear (*Ursus americanus*), the only predator species previously observed on the island, became extirpated (Côté, 2005). The only other mammalian herbivores are introduced moose (*Alces alces*, <1 individual·10 km^{-2}) and snowshoe hares (*Lepus americanus*) (Potvin, Boots & Dempster, 2003).

The forest ecosystem belongs to the eastern balsam fir (*Abies balsamea*)–white birch (*Betula papyrifera*) bioclimatic sub-domain (Saucier *et al.*, 2003). Since the introduction of deer, the forest composition has changed in such a way that deciduous trees and the shrub layer have largely disappeared (Potvin, Boots & Dempster, 2003; Tremblay *et al.*, 2005). About a century after the introduction of deer, balsam fir has lost more than 50% of its original cover, progressively being replaced by the less palatable white spruce (*Picea glauca*) through apparent competition (Potvin, Boots & Dempster, 2003; Tremblay, Huot & Potvin, 2007).

The deer mouse is the only small mammal species that has ever been recorded on Anticosti Island (Potvin, Boots & Dempster, 2003). The deer mouse is a nocturnal species, occupying a home range of about 500–590 m^2 (Wolff, 1985). Being a generalist, the deer mouse is associated with a number of different habitat types, but most specifically with recently disturbed forests (Pearson, 1999; Pearce & Venier, 2005; Zwolak, 2009). Deer mice are omnivorous, mainly eating seeds, fruits, leaves, mushrooms, arthropods, and snails when available (Desrosiers, Morin & Jutras, 2002). Potential natural predators include foxes (*Vulpes vulpes*) and birds of prey.

EXPERIMENTAL DESIGN

CONTROLLED DEER BROWSING

In 2001, 3 replicated blocks (a, b, and c) of 110 ha each were established, each containing 3 enclosures with a 3-m-high fence in which deer density was controlled. These 3 enclosure types differed in their size and controlled deer density, and are denoted as follows: zero deer density in 10-ha enclosures (0 deer·km^{-2}; hereafter denoted as "zero"); 7.5 deer·km^{-2} in 40-ha enclosures (denoted as "low"); and 15 deer·km^{-2} in 20-ha enclosures (denoted as "high"). The deer densities in the latter 2 enclosure types were achieved by introducing 3 individuals into each enclosure. The remaining 40 ha in each block were left unfenced. Deer density in the surrounding environment (denoted as "ambient") was estimated at 56 deer·km^{-2} in block a and at 27 deer·km^{-2} in blocks b and c (details in Tremblay, Huot & Potvin, 2006). In the summer of 2001, approximately 70% of the surface of each enclosure was logged (harvesting of trees with diameter at breast height >9 cm; DBH, 1.3 m). Each treatment was thus composed of both forested areas and cutblocks. The experimental design hence corresponded to a split-block experiment, with habitat type varying within enclosures, and with each of the 3 enclosure types occurring in each of the 3 replicate blocks.

The habitat composition changed over time after logging in the experimental blocks. In cutblocks, 2 to 3 y after logging, field layer plants started to recover exponentially in the enclosures with reduced deer density (Tremblay, Huot & Potvin, 2006). The biomass of balsam fir, paper birch, and herbs and shrubs palatable to deer (*e.g.*, *Chamerion angustifolium* and *Rubus* sp.) increased in cutblocks at densities below 15 deer·km^{-2}, whereas regeneration remained low at higher density levels. The abundance of browse-tolerant species such as grasses increased with deer density. Seven years after logging, almost no balsam fir saplings taller than 30 cm were observed at ambient deer densities, but regeneration was present below 15 deer·km^{-2} (Hidding, Tremblay & Côté, 2012). After 7 y of deer exclusion in other experimental sites on Anticosti Island, balsam fir, deciduous species, and palatable herbs still struggled to regenerate, while white spruce tended to persist (Hidding, Tremblay & Côté, 2013).

CAPTURE OF SMALL MAMMALS

Captures were performed in 2007 and 2008, 6 and 7 y after logging and fencing. Within each treatment, 49 Sherman traps were placed 15 m apart to form a grid (90 × 90 m) distributed over the 3 habitat types (Figure 1). The grids were placed at the same location at each capture session. The 196 traps per block (*i.e.*, 49 traps at 4 different deer densities) were simultaneously activated during 4 consecutive nights from dusk to dawn, in 2 successive months (July and August) each year. In 2008, an additional capture session was performed in June (3920 trap-nights in total). For logistic reasons, 2 different Sherman trap sizes, both commonly used to trap deer mice (Kaufman & Kaufman, 2007), were employed: 19 large traps (76 × 89 × 229 mm) and 30 small traps (51 × 64 × 165 mm) per grid. The 2 types of traps were equally alternated within each grid (Figure 1).

Traps were baited with pieces of apple dipped in peanut butter. Cotton wool was systematically placed in each trap to limit the risk of hypothermia. Individuals were placed in a bag and weighed using a Pesola balance (precision 1 mg). Animals were tagged with a metal ear-tag (model 1005-1, National Band & Tag Co., Newport, Kentucky, USA) and differentiated according to their sex and age (adult males, adult females, juveniles [<18 g], and undetermined; after Martell, 1983a). The habitat type was specified for each trap. To avoid misattribution, we also considered the edge between forest and cutblocks as a third habitat type (Figure 1).

STATISTICAL ANALYSES

First, we evaluated deer mice fidelity for each habitat type and the dispersion between habitat types by evaluating the number of recaptures in cutblocks of individuals initially captured in cutblocks or in forest, and similarly for the number of recaptures in forest. Secondly, we evaluated whether deer density and habitat type affected mice abundance and body mass with mixed effect models, using the nlme library (Pinheiro & Bates, 2000) in R (R version 2.12.1, R Development Core Team, 2012). In line with other studies (*e.g.*, Fauteux *et al.*, 2012), we calculated the mean number of mice caught per 100 trap-nights (trap number × trapping nights) for each session of 4 nights as a proxy of mice density (minimum number of mice known to be alive). We omitted all recaptures within sessions to avoid pseudo-replication and over-estimation of mice density. Following the method
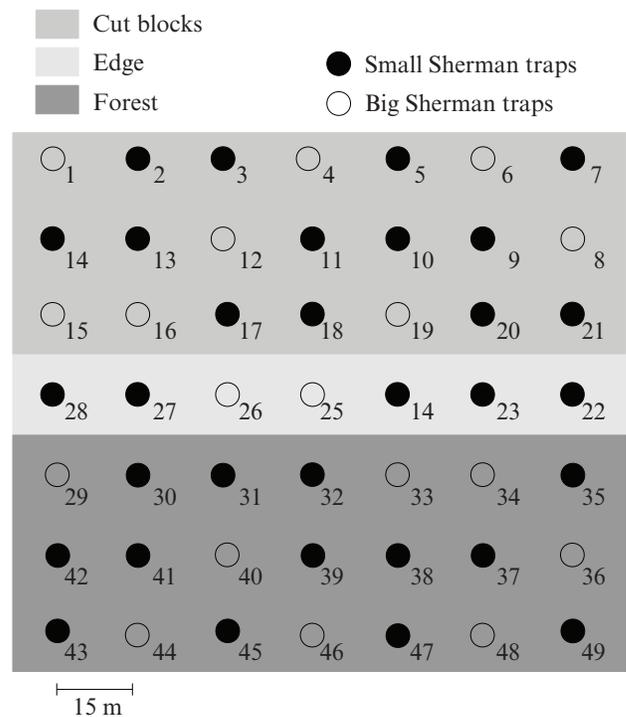

FIGURE 1. Configuration of the trapping grid (90 × 90 m) used to capture deer mice in each treatment combination (3 blocks, 4 deer densities, and 3 habitat types) on Anticosti Island (Quebec, Canada). Small (51 × 64 × 165 mm) and large (76 × 89 × 229 mm) Sherman traps were used for captures.

of Fauteux *et al.* (2012), we corrected trapping effort for traps that were triggered but empty by multiplying them by 0.5. To test whether mice abundance and body mass depended on deer density (main plot) and habitat type (secondary plot), we considered the complete model containing the interaction between deer density (levels "zero", "low", "high", "ambient") and habitat type ("cutblocks", "forest", "edge"). We included 3 factors as random variables in the models: block, year, and month. Month was included because abundance and body mass are likely to increase over the course of the summer due to the seasonal increase in resource availability and the accompanying increase in mouse reproductive success (Desrosiers, Morin & Jutras, 2002). The relative abundances calculated for each sampling period were square-root transformed to normalize the data, a result verified using a Shapiro–Wilk test. Variance homogeneity was verified using Levene's test. We averaged body mass per sampling period considering only adult males because body mass of growing juvenile males was likely to vary during the sampling period and because gestating and non-gestating females could not be differentiated. We square-root transformed male body mass and confirmed the normal distribution of the model residuals using a Shapiro–Wilk test. Variance homogeneity was verified using Levene's test. We fitted each model using the maximum likelihood method (Pinheiro & Bates, 2000). Considering significant effects at α = 0.05, we compared the nested models using deviance statistics (LRT; Crawley, 2007).

We performed additional analyses to verify that differences in mice abundance between habitat types or deer densities were not caused by differences in age structure or the proportion of reproducing individuals. We conducted ANOVAs on the following parameters: age structure by calculating juvenile/adult and male juvenile/adult ratios; adult sex ratio (adult females/adult males); and reproductive output (juveniles/adult females ratio).

Results

We captured only deer mice and no other small mammal species. We made 1344 captures over 2 y (685 in 2007 and 659 in 2008), of which 330 mice were recaptured (1.77 ± 0.08 recaptures per individual). We captured on average 6.3 ± 0.6 mice per 100 trap-nights. Twenty mice (1.5%) were found dead inside the traps. Sex could not be identified in 34 and 0 cases in 2007 and 2008, respectively. We recorded 603 trap malfunctions (10%), of which 385 corresponded to triggered traps without a mouse but with bait, 189 to non-triggered traps from which the bait had disappeared, and 29 to other types of problems (*e.g.*, disappearance of the traps).

Deer mice showed high fidelity for habitat type. Among all individuals caught more than once, 64% of the individuals that were originally captured in forest were also recaptured in forest (compared to 15% in the edge and 21% in cutblocks). Likewise, 83% of the individuals that were originally captured in cutblocks were also recaptured in this habitat (7% of recaptures in the edge and 10% in forest).

Mice relative abundance only varied according to habitat type (G^2 = 25.47, df = 2, P = 0.02), being higher in cutblocks than in forest (G^2 = 18.05, df = 1, P < 0.001) and edges (G^2 = 14.81, df = 1, P < 0.001, Figure 2a), with no significant difference between edges and forest (G^2 = 0.18, df = 1, P = 0.67). Contrary to our expectations, mice relative abundance was not significantly related to deer density (Figure 2b, G^2 = 7.07, df = 3, P = 0.07; nor in interaction with habitat type: G^2 = 5.02, df = 6, P = 0.54). The mean body mass of adult male mice (n = 380) was 19.7 ± 0.2 g. Contrary to our hypotheses, neither habitat type (G^2 = 1.29, df = 2, P = 0.68) nor deer density (G^2 = 6.22, df = 3, P = 0.10; interaction: G^2 = 4.33, df = 6, P = 0.63) was related to adult male body mass (Figures 2c, 2d).

We found no impact of habitat type and deer density on population age and sex structure or reproductive output (results presented in Appendix I).

Discussion

Although we expected deer density to affect deer mice, we observed no impact on abundance, body mass, or population sex and age composition. However, habitat type affected mice abundance, which was higher in cutblocks than in forest or edges, but had no influence on any of the other tested parameters. While deer mice may use a wide range of habitat types, multiple studies reported an increase in abundance in disturbed habitats, such as those experiencing early environmental succession following fire or logging (Kaufman, Kaufman & Finck, 1988; Pearce & Venier, 2005; Zwolak, 2009). The higher number of recaptures in cutblocks compared to forests is in line with these studies. Mice may benefit from habitat opening in cutblocks because it increases habitat heterogeneity by favouring the growth of various shade-intolerant grasses and woody species. However, although deer mice benefited from logging, they were not influenced by deer density, suggesting that the benefits of cutblocks may be independent of deer browsing.

In a similar study of small mammal–deer interactions from Wytham Woods (United Kingdom), Buesching *et al.* (2011) found no differences in sex ratio, age structure, body weight, or reproductive status for bank voles and wood mice (*Apodemus sylvaticus*) between woodlands and deer exclosures. However, they did find evidence that wood mice were more numerous in open woodlands than in deer exclosures, whereas bank voles represented a greater proportion of the small mammal population in deer exclosures relative to other areas, suggesting that bank voles benefit from deer exclusion. In our study, no deer mouse parameters were influenced by deer density, despite high browsing pressure having clear impacts on the environment, often resulting in more open and homogeneous habitats (Russell, Zippin & Fowler, 2001; on Anticosti Island: Potvin, Boots & Dempster, 2003; Tremblay, Huot & Potvin, 2006). Deer mice may benefit from the vertical vegetation complexity available in cutblocks regardless of deer density, favoured either by the regeneration of browse-sensitive species at reduced deer densities or by browse-resistant species at ambient deer density. Mice may also benefit from other advantages afforded by logged areas. The opening of cutblocks may help mice to better track seeds on the ground (Kaufman, Kaufman & Finck, 1988), and it could improve
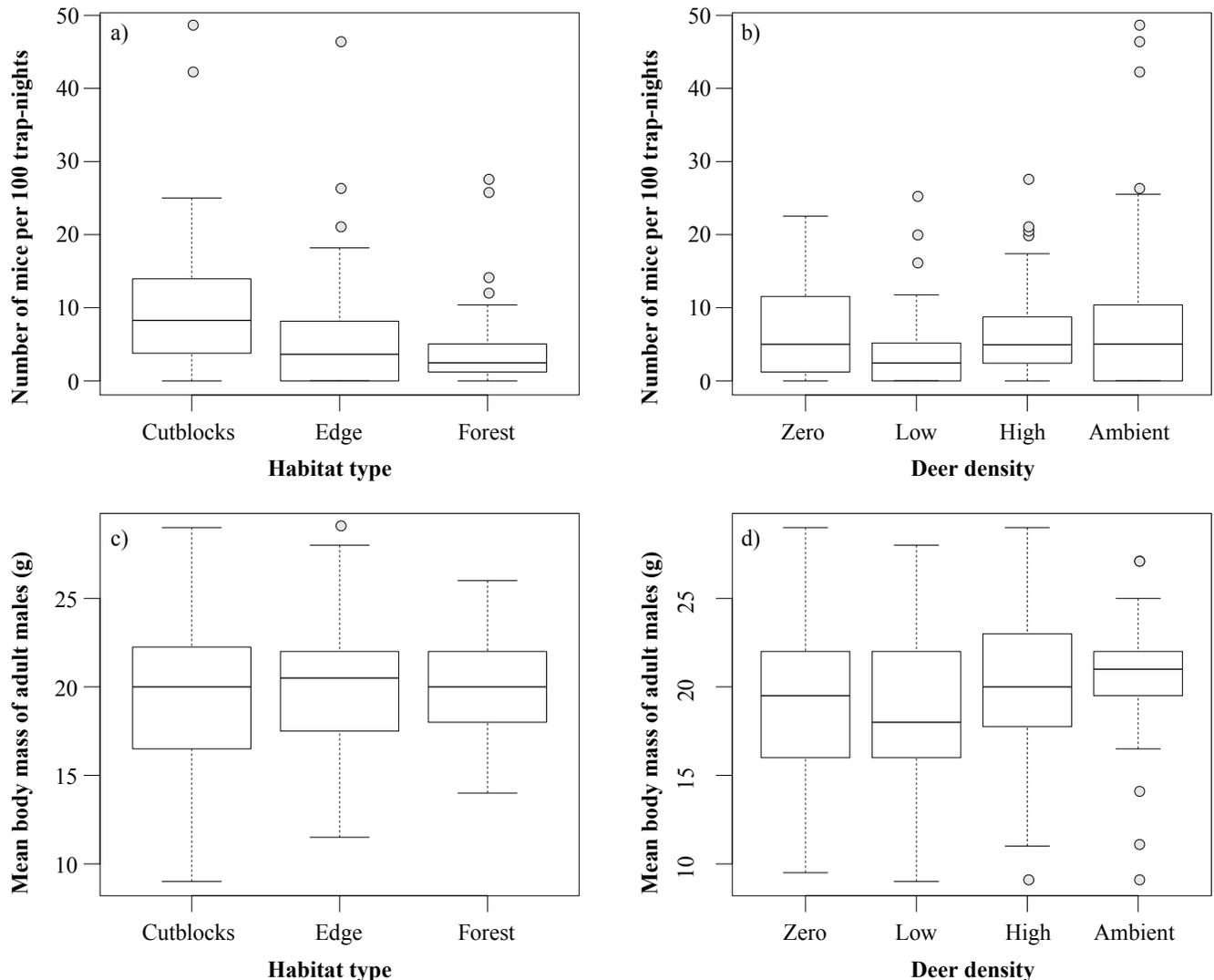
FIGURE 2. Deer mice relative abundance was significantly higher in cutblocks compared to edge and forest (a), but was not influenced by deer density (b). Neither habitat type (c) nor deer density (d) influenced the body mass of adult males. (Boxplots represent mean, 1st, and 3rd quartiles.)

their ability to anticipate attacks and escape from their aerial predators. The woody debris left on site following logging and the greater height of the grass layer in these open areas could also benefit mice by providing shelter for thermoregulation and refuge from predators (Tallmon & Mills, 1994; Fauteux *et al.*, 2012).

The time elapsed since the appearance of the habitat disturbance may be of major importance in the observed response of animal guilds. After 4–5 y of deer exclusion in their Wytham Woods experiment, Buesching *et al.* (2011) observed significant differences in rodent abundance between exclosures and open woodlands, but these differences became insignificant after an additional 8–9 y of deer exclusion, 13 y after the initial establishment of the exclosures (Bush *et al.*, 2012). It is therefore possible that the response of small mammals to habitat disturbances from logging or high deer density varies over time with forest regeneration. Pearce and Venier (2005) noted that, while deer mice abundance increases in logged areas, it declines sharply in 5- to 15-y-old stands. In our study,

deer mice may certainly benefit from the seed bank available 6 y after logging, but this advantage may be progressively lost with stand regeneration (Pearson, 1999; de Bellefeuille *et al.*, 2001; Pearce & Venier, 2005; Zwolak, 2009). On Anticosti Island, >100 y of browsing pressure by white-tailed deer has greatly decreased the complexity of the vegetation vertical structure, leading to open habitats dominated by white spruce interspersed with graminoids, a landscape that has been classified as spruce savanna (Tremblay *et al.*, 2005). Hence, by maintaining open stands and favouring the regeneration of browse-tolerant plant species that provide vertical micro-heterogeneity, deer browsing may benefit deer mice in later stages of forest succession in the logged areas.

Responses of rodent communities to large herbivore densities have been regularly reported (*e.g.*, Smit *et al.*, 2001; Steen, Mysterud & Austrheim, 2005; Bakker, Olff & Gleichman, 2009; Buesching *et al.*, 2011). Unlike deer mice, other small mammal species may be negatively impacted by habitat disturbance from logging or

deer browsing. The negative response of red-backed voles (*Myodes gapperi*) to clear cutting (Pearce & Venier, 2005; Zwolak, 2009) suggests they may be sensitive to high browsing pressure that impedes forest regeneration. In pastures, the response of small mammals to grazing pressure also varies among species. Common voles (*Microtus arvalis*) have been shown to avoid areas grazed by cattle (Bakker, Olff & Gleichman, 2009). Steen, Mysterud, and Austrheim (2005) noted a negative response of field voles to sheep (*Ovis aries*) density, while bank voles were unaffected. The type of consumption (grazing/browsing) (Bakker, Olff & Gleichman, 2009; Bueno *et al.*, 2012) and the joint effects of large and small herbivores on vegetation (Austrheim *et al.*, 2007) may influence plant availability to animals and thus may influence interactions between species within communities.

Trophic effects induced by deer browsing have already been demonstrated in previous work. On Anticosti Island, using the same deer density control experiment, it was shown that a reduction in densities to 7.5–15 deer·km^{-2} may favour the regeneration of tree species such as balsam fir and paper birch and of herbaceous species such as fireweed (*Chamerion angustifolium*) and bunchberry (*Cornus canadensis*). Above 15 deer·km^{-2}, plant succession leads to the dominance of white spruce and grasses (Tremblay, Huot & Potvin, 2006; Cardinal *et al.*, 2012; Hidding, Tremblay & Côté, 2013). In parallel, censuses performed on birds have demonstrated that certain species that previously were negatively impacted at high deer density recovered at reduced deer densities (Cardinal *et al.*, 2012). In insects, Brousseau *et al.* (2013) showed that abundance varies according to taxa and the degree of association of species with plants. However, while plant and insect community composition changes at high deer density, the availability and the quality of food may possibly remain constant and sufficiently high to satisfy the requirements of deer mice.

Animal species that strongly depend on plant species and strata directly or indirectly influenced by deer browsing are naturally more likely to be impacted by deer browsing pressure, but these impacts may be positive or negative depending on the animal species (*e.g.*, positive response of some insectivorous bird species [Loe *et al.*, 2007], but negative response of bird species nesting in understory vegetation [Allombert, Gaston & Martin, 2005; Cardinal *et al.*, 2012]). Furthermore, species directly associated with the forest litter layer are also likely to be affected (Brousseau *et al.*, 2013). It has been suggested that the severity of large herbivore impacts may decline with increasing trophic levels; indeed, Wardle *et al.* (2001) found that the magnitude of the response of microflora and nematodes to browsing was rather limited in comparison with the magnitude of the vegetation response. In contrast, Lessard *et al.* (2012) suggested that the magnitude of the browsing impact remains equivalent among trophic levels, from plants to animal species relying on leaf-litter and soil arthropod communities. The consequences for insects, and to a lesser extent for birds, seem to vary mainly depending on the ecological niche of the species. Species that rely on leaf-litter or shrub layers are likely to be impacted the most by deer browsing pressure (Cardinal *et al.*, 2012; Brousseau *et al.*, 2013).

Our findings suggest that the indirect effects of browsing on generalist omnivorous species such as deer mouse may be weak, possibly due to the feeding habits of omnivores and their ability to adapt to changing conditions. The magnitude of large herbivore impacts on small mammals is likely to be strongest for leaf-litter and shrub specialists, for species that decrease in abundance after disturbances, such as the red-backed vole after logging (Martell, 1983b), and for species relying on complex vertical vegetation structure, such as the white-footed mouse (*Peromyscus leucopus*) (Kaufman *et al.*, 1983; Swihart & Slade, 1990). The severity of the natural disturbance resulting from browsing (Pickett & White, 1985) may depend on the population density of large herbivores (van Wieren, 1998). However, the indirect impact of browsing on other animal species is also likely to be determined by their range of ecological requirements (*i.e.*, specialized *versus* generalist species).

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Appendix I

APPENDIX I, TABLE I. Analyses of variance testing the influence of habitat type and deer density on parameters characterizing sex and population age structure of deer mice (mean ± SD shown under each factor).

Parameter	Habitat type										Deer density										
	Cutblocks		Edge		Forest		F (df=2)	P			Zero		Low		High		Ambient		F (df=3)	P	
	Mean	SD	Mean	SD	Mean	SD					Mean	SD	Mean	SD	Mean	SD	Mean	SD			
Ratio juveniles/adults	0.75	0.69	0.71	0.56	1.04	0.86	0.89	0.41			0.85	0.80	1.01	0.79	0.98	0.98	0.60	0.34	0.99	0.40	
Ratio male juveniles/adults	0.85	0.71	1.00	0	1.07	0.95	0.27	0.76			0.74	0.37	1.35	0.88	1.03	0.94	0.32	0.24	2.63	0.07	
Sex ratio (females/males)	1.55	1.56	0.90	0.83	1.25	1.14	1.18	0.31			1.12	0.74	1.58	1.66	1.36	1.12	1.46	1.81	0.33	0.80	
Ratio juveniles/adult females	1.49	1.60	1.17	0.56	2.00	1.69	0.82	0.44			1.43	1.52	1.32	1.52	1.56	1.66	1.79	1.49	0.21	0.89	