Effects of selection harvesting on bark invertebrates and nest provisioning rate in an old forest specialist, the brown creeper (*Certhia americana*)[1]

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Abstract: The brown creeper (*Certhia americana*) is one of the forest bird species most sensitive to partial harvesting in North America. We examined the detailed response of this species and its food (bark-dwelling invertebrates) during the 3rd and 4th year after experimental selection harvesting (30–40% basal area removal) in northern hardwood forest. Relative to control plots, nest densities in treated plots were *ca* 50% lower. Because the density of nesting substrates was not significantly lower in treated plots than in controls, we investigated whether foraging substrates could be the limiting factor. Specifically, we tested for a treatment effect on 1) the abundance and species composition of bark invertebrate assemblages; 2) the biomass of bark invertebrates per unit area; and 3) the frequency of food provisioning. As predicted, treatment had a significant negative effect on food provisioning rate, though not on invertebrate biomass, when accounting for year effects. There was also no evidence for a treatment effect on the structure of bark invertebrate assemblages, which was mainly influenced by cumulative degree days. Selection harvesting thus appeared to reduce the amount of food delivered to brown creeper nestlings, unless greater amounts of food were delivered per feeding trip in treated plots. The lower density of foraging substrates in treated plots (77 *versus* 112 stems·ha^{-1} in controls) may require that adults perform longer foraging trips. Future studies should determine whether this extra effort has short- or long-term consequences for adults and nestlings.
Keywords: bark gleaning, bark invertebrates, northern hardwood forest, parent–offspring conflict, selection harvesting.

Résumé: Le grimpereau brun (*Certhia americana*) est l'une des espèces d'oiseaux forestiers les plus sensibles à la coupe partielle en Amérique du Nord. Nous avons examiné en détail la réponse de cette espèce et de sa nourriture (les invertébrés de l'écorce) durant la 3e et la 4e année après une coupe de jardinage expérimentale (30–40 % de la surface terrière) dans une forêt décidue nordique. La densité des nids était environ 50 % moindre dans les parcelles coupées que dans les témoins. Puisque la densité de substrats de nidification n'était pas significativement plus faible dans les parcelles coupées que dans les témoins, nous avons évalué si la disponibilité des substrats d'alimentation pourrait être le facteur limitatif. Nous avons testé spécifiquement s'il y avait un effet du traitement sur : 1) l'abondance et la composition en espèces des assemblages d'invertébrés de l'écorce; 2) la biomasse d'invertébrés par unité de surface d'écorce; et 3) la fréquence de nourrissage. Comme prévu, le traitement avait un effet négatif significatif sur le taux de nourrissage, mais pas sur la biomasse d'invertébrés une fois la variabilité annuelle prise en compte. Il n'y avait de plus aucune évidence d'un effet du traitement sur la structure des assemblages d'invertébrés de l'écorce, qui était principalement influencée par le cumul des degrés-jours. Ainsi, la coupe de jardinage semble réduire la quantité de nourriture apportée aux oisillons du grimpereau brun, à moins que la quantité apportée par becquée ait été plus élevée dans les parcelles coupées. La plus faible densité de substrats d'alimentation observée dans les parcelles coupées (77 tiges·ha^{-1} contre 112 dans les témoins) peut faire en sorte que les adultes doivent parcourir une plus grande distance pour récolter de la nourriture. De futures études devraient déterminer si cet effort supplémentaire a des conséquences à court ou à long terme pour les adultes et les oisillons.
Mots-clés : conflit parent-progéniture, forêt décidue nordique, alimentation sur l'écorce, invertébrés de l'écorce, récolte sélective.

Nomenclature: Marie-Victorin, 1995; American Ornithologists' Union, online.

Introduction

Habitat loss has a major effect on biodiversity (Wilson, 1988; Pimm & Raven, 2000; Pimm, 2008). In managed forest landscapes, habitat degradation through partial harvesting may also have a significant cumulative impact by reducing bird densities over large spatial scales (*e.g.*, Haché & Villard, 2010). In addition to reducing population densities, habitat degradation associated with negative edge effects may lead to a reduction in the species richness of habitat specialists and an increase in the number of generalist species in fragments (Harrison & Bruna, 1999). Negative edge effects on the distribution or reproductive success of forest birds have rarely been documented in managed forest landscapes, but the sparse evidence available suggests that they can be significant for certain species (Villard, Schmiegelow & Trzcinski, 2007; Poulin & Villard, 2011; but see Falk, Nol & Burke, 2011).

The brown creeper (*Certhia americana*) is one of the bird species most sensitive to partial harvesting in North America (Vanderwel, Malcolm & Mills, 2007). It may act as an umbrella species (Poulin *et al.*, 2008), *i.e.*, its protection could benefit other, sympatric species, especially when

considering its extensive area requirements relative to its body size. However, the processes underlying its sensitivity to harvesting are unclear (Hejl *et al.*, 2002). The preference of this species for large-diameter trees as foraging substrates (Adams & Morrison, 1993) might partly explain its association with old forests. Indeed, in a selection harvesting experiment that maintained similar densities of potential nesting substrates between treatments and controls, Poulin, Villard, and Haché (2010) found a negative treatment effect on nest density, suggesting that foraging substrates may represent a limiting factor. In the Eurasian treecreeper (*Certhia familiaris*), Suorsa *et al.* (2005) concluded that potential food supply was directly linked to mature forest cover, but also to tree diameter: the Eurasian treecreeper also shows a preference for larger trees when foraging (Suhonen & Kuitunen, 1991). Larger trees might support higher invertebrate biomass per unit area of bark (Jackson, 1979). This is specifically the case for spiders, which spend most of their time in the deep furrows of large-diameter trees (Jackson, 1979; Mariani & Manuwal, 1990). Finally, as suggested by Franzreb (1985) and Mariani and Manuwal (1990), energy intake may be higher when foraging on 1 large tree relative to several small ones.

Most studies testing the effect of food abundance on nest provisioning have been conducted using food supplementation experiments (*e.g.*, Grieco, 2001; 2002a,b; Eggers, Griesser & Ekman, 2008). Here, we examine this relationship in an unmanipulated study system where we compare food abundance and provisioning rate by brown creepers at nests located in plots treated through single-tree selection harvesting (30–40% basal area removal) 3 or 4 y earlier and in control plots. As reported for other bird species (Stenger, 1958; Smith & Shugart, 1987; Marshall & Cooper, 2004), creepers might adjust their territory size (or volume) as a function of food abundance. The reduction in density of large-diameter trees in treated plots may force creepers to travel longer distances to feed their nestlings.

The effects of forestry on bark invertebrates are poorly known. Only a few detailed studies have been conducted on the ecology of bark invertebrates (Nicolai, 1986; 1989; Duguay, Wood & Miller, 2000; Majer *et al.*, 2006; Miller, Wagner & Woods, 2007) and on their response to forestry (Duguay, Wood & Miller, 2000; Miller, Wagner & Woods, 2007). The increased light intensity associated with an opening of the canopy can affect epiphytic lichens (Edman, Eriksson & Villard, 2008) and potentially induce a change in microclimatic conditions on tree bark, which in turn may reduce the abundance of arthropods (*e.g.*, Miller, Wagner & Woods, 2007).

This study aimed to test whether there is a treatment effect 1) on the abundance and species composition of bark invertebrate assemblages and 2) on food provisioning rate at brown creeper nests. Although the effects of forest harvesting on ground and foliage invertebrates have been widely studied, tree trunks offer very different microhabitat conditions (Nicolai, 1986; Taylor & Doran, 2001), and it is difficult to speculate from these studies. Assuming that adults deliver a constant amount of food per nest provisioning visit, we predicted that food delivery rate would be significantly higher in control plots than in plots treated

through selection harvesting owing to the longer foraging trips performed by adults in the latter.

Methods

STUDY AREA AND EXPERIMENTAL DESIGN

This study was conducted on private land owned by J. D. Irving Ltd. in northwest New Brunswick (47° 23' N, 67° 40' W) in May–August 2009 and 2010. Study plots (25 ha each) were located in forest stands dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*). Our experimental design consisted of 5 pairs of plots (25 ha each; 1 control plot; 1 treated using single tree selection harvesting). Control plots had been left undisturbed for at least 30 y, and all stands were between 100 and 125 y-old (G. Pelletier, pers. comm.). The selection harvest treatment consisted in removing stems from all diameter classes present to produce a multi-age structure. Density of large-diameter trees (diameter at breast height: dbh > 30 cm) was significantly lower in treated plots than in controls (77 *versus* 112 stems·ha^{-1}), but operators were instructed to protect snags to the extent possible, which explains why their density did not differ between treated plots and controls (see Poulin, Villard & Haché, 2010 for details).

SPOT MAPPING, NEST SEARCHING, AND MONITORING

Each plot was visited at least every 3–4 d to map brown creeper locations and to search for/monitor nests. We mapped brown creeper territories from early May to early July using the standard spot mapping method (Bibby, Burgess & Hill, 1992). We paid particular attention to territorial disputes to separate adjacent territories. Those data gave us relatively precise territory boundaries, especially in 2009 because many males were marked using unique combinations of colour bands. We monitored each nest at least every 3 d to determine laying date, clutch size, hatching date, brood size, and fledging date. To quantify food provisioning, we selected nests where we knew the age of young ± 1 d.

FOOD PROVISIONING

We observed 13 nests in treated plots (2009 = 3; 2010 = 10) and 13 nests in controls (2009 = 8; 2010 = 5), 7–14 d post-hatching, between 0930 and 1200. In many bird species, food provisioning rate tends to be more frequent in the morning (0500 to 1000) and in the evening (1600 to 2000) (Bibby, Burgess & Hill, 2000). However, Kuitunen and Suhonen (1989) found little variation in provisioning rates in a very similar species, the Eurasian treecreeper. Hence, we conducted observations in late morning for logistical reasons. We recorded food provisioning rate from the first feeding trip until the 30-min period had elapsed. To minimize disturbance, observers hid in the vegetation at least 20–30 m away from the nest. We performed two 30-min observation periods at each nest, separated by 1–7 d. Because some nests were depredated or young fledged between observation sessions, provisioning rates had to be calculated on the basis of only 30 min of observation for these. This procedure did not cause a bias since

there was no difference in food provisioning rate at nests with 1 or 2 observation bouts, according to a linear mixed model with plot, context, plot(context), and year as random effects, accounting for repeated measures ($F_{1, 13} = 0.31$, $P = 0.59$).

Invertebrate sampling

We sampled invertebrates around all nests where we had recorded food provisioning rate (13 in treated plots; 13 in controls). Sampling was conducted when nestlings were 7–14-d-old on trees located *ca* 25–30 m away from the nest, *i.e.*, far enough to reduce the risk of prey depletion (Kuitunen, 1989). These trees were selected by walking along a random compass heading. In both control and treated sites, each invertebrate sample consisted of 6 sugar maple trees (dbh: 20–40 cm), the most common tree species in our study plots. Sugar maple was also the only foraging substrate for which brown creepers exhibited a preference (J.-F. Poulin & M.-A. Villard, unpubl. data).

We vacuumed the bark from 0.5–1.5 m above the ground using a 12-V cordless vacuum (method adapted from Kuitunen, 1989; Kuitunen *et al.*, 1996). We only vacuumed the bottom section of trees because previous studies suggest that creepers forage more often between 1 and 9 m than higher, perhaps because bark furrows are deeper (Airola & Barrett, 1985; Franzreb, 1985; Weikel & Hayes, 1999). Harvesting may change arthropod communities on tree bark and treatment effects would be expected to be more pronounced at the bottom of trees because the bark is shadier and more humid than in the upper portion (*e.g.*, Miller, Wagner & Woods, 2007).

Samples were kept in airtight plastic bags in the freezer until invertebrates were sorted and identified. We identified specimens to the family or order, and sometimes to the class or subclass. Abundance (number of specimens) and total dry biomass (mg·m^2 of bark) were determined for each tree. To obtain dry biomass, samples were put in the oven at 80 °C for 48 h and weighed to the nearest 0.0001 g using an electronic scale (Mettler AE 240, Mettler-Toledo, Columbus, Ohio, USA).

Statistical analyses

We used a linear mixed model with polynomial contrasts to determine the potential influence of invertebrate biomass, treatment, year, and their interactions on food provisioning rate. The mixed modelling approach enables the random effects of plot, landscape context, and plot (landscape context) to be taken into account. We also accounted for the potential effect of subsampling (6 trees per nest) in the statistical model.

Independent (bark invertebrate biomass) and dependent (number feeding trips·h^{-1}) variables were log (+1)-transformed to meet assumptions of normality and homogeneity of variance (Zar, 1996). Two candidate covariables (number of nestlings and age at the time of observations) were excluded because of their low variability (*e.g.*, 5 or 6 nestlings per brood) or because their individual effect on food provisioning rate was not significant (age: $F_{1, 8} = 0.26$, $P = 0.62$). This analysis was performed using PROC MIXED in SAS 9.2.0 (SAS Institute, 2008).

We examined the effects of treatment, year, tree dbh, plot, and cumulative degree days (CDD) on the taxonomic composition of invertebrate assemblages (abundance of 14 taxa) using a multivariate regression tree (MRT) (De'ath, 2002). We obtained a CDD value for each sampling day by subtracting 5 °C (threshold value) from the average daily temperature and then adding up those values when they were greater than 0 °C. We determined the size of the multivariate regression tree (X-axis) minimizing the relative error (Y-axis) in the model. We used a total of 150 samples (trees) collected in 2009 ($n = 60$, abundance was not calculated for 1 sample) and 2010 ($n = 90$). This analysis was conducted using the MVPART module in R 2.10.0 (R Development Core Team, online).

Results

Nest provisioning rate

There was a significant treatment effect on nest provisioning rate ($F_{1, 140} = 4.13$; $P < 0.0001$). In treated plots, parents made 18.8 ± 8.2 (mean ± standard deviation) trips·h^{-1}, compared to 22.3 ± 5.2 trips·h^{-1} in controls. Year ($F_{1, 140} = -4.08$; $P < 0.0001$) and treatment × year ($F_{1, 140} = 3.32$; $P = 0.001$) also had significant effects on nest provisioning. Bark invertebrate biomass and all interaction terms that included biomass had no significant effect on nest provisioning (Table I; Figure 1). Finally, treatment had no significant effect on dry biomass of invertebrates; dry biomass available varied widely among trees

TABLE I. Effects of bark invertebrate biomass, year, and treatment (selection harvesting) on brown creeper food provisioning rate, as indicated by a linear mixed model with polynomial contrasts.

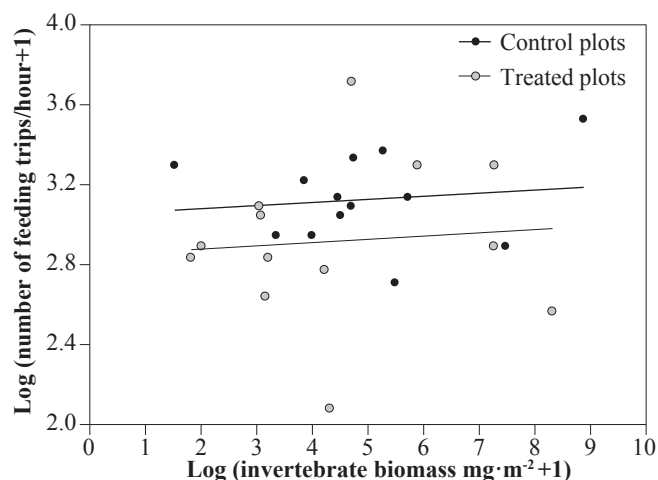| Variables	df	*F* value	*P*
Treatment	140	4.13	< 0.0001
Biomass	140	1.52	0.1300
Year	140	−4.08	< 0.0001
Year × Treatment	140	3.32	0.0011
Biomass × Year	140	0.31	0.7545
Biomass × Treatment	140	−1.61	0.1102
Biomass × Year × Treatment	140	−0.45	0.6528

FIGURE 1. Relationship between dry biomass of bark invertebrates and food provisioning rate at brown creeper nests.

(treated plots: 2.39 ± 4.90 mg·m^{-2} per tree; control plots: 4.42 ± 13.43 mg·m^{-2}; $F_{1, 19} = 0.30$, $P = 0.59$).

Bark invertebrate assemblages

The bark invertebrate assemblage (abundance·m^{-2} of bark) comprised 42.0% Diptera, 19.9% Acarina, 9.9% Araneae, 8.3% Collembola, 5.2% Coleoptera, 4.8% Gastropoda, 4.0% Lepidoptera, and 5.8% other taxa (Hemiptera, Diptera larvae, Hymenoptera, Phalangideae, Psocoptera, Pseudoscorpion, and Coleoptera larvae). In treated plots, the 4 most important groups were Diptera (44.3%), Acarina (25.1%), Collembola (7.6%), and Araneae (7.1%). In control plots, the same 4 groups dominated but with slight differences in order: Diptera (39.7%), Acarina (14.7%), Araneae (12.8%), and Collembola (9.1%).

The best multivariate regression tree included only 2 leaves (Figure 2). No treatment effect was detected, and only cumulative degree days had an effect on the structure of invertebrate assemblages. This factor accounted for 8.3% of the variability in the invertebrate assemblage, and the split corresponded to 213.3 cumulative degree days. Further analysis of the MRT revealed that Diptera, Acarina, Collembola, and Araneae best explained this split (49.8%, 18.6%, 12.0%, and 8.8%, respectively).

Discussion

Previous studies suggest a positive relationship between food abundance and nest provisioning rate by parents (Norberg, 1981; Whittingham & Robertson, 1994; Goodbred & Holmes, 1996; Naef-Daenzer, Naef-Daenzer & Nager, 2000; Kilgo, 2005; but see Rauter, Brodmann & Reyer, 2000). In this study, dry biomass of bark invertebrates per unit area of foraging substrate did not differ between treated and control plots. We still expected a treatment effect on food provisioning rate owing to the lower density of large, live trees. Treatment, year, and their interaction had a significant effect on nest provisioning rate, suggesting that the density of foraging substrates can play an important role in food provisioning of nestlings, depending on the year. However, it should be pointed out that the year effect observed may reflect the departure of the small number of nests sampled in treated plots in 2009 relative to other treatment-year categories.

Snag density did not differ between treated plots and controls 1 y (Poulin, Villard & Haché, 2010) and 4 y post-treatment (É. D'Astous, S. Haché & M.-A. Villard, unpubl. data). Thus, it is unlikely that nesting substrates were a limiting factor in treated plots. Poulin, Villard, and Haché (2010) proposed that the consistently lower density of creeper nests in treated plots was linked to a reduction in the density of foraging substrates. Indeed, the density of large-diameter trees (dbh ≥ 30 cm) was significantly lower in treated plots (see Methods).

In general, the consequences of a shortage in food are shared between young and their parents (*e.g.*, Golet & Irons, 1999; Weimerskirch, Prince & Zimmermann, 2000; Davis, Nager & Robert, 2005). In fact, not only reproductive success but also adult survival could be affected by low food abundance. In our study, treatment had no effect on brood size at fledging (treated plots: 5.5 ± 0.5, $n = 15$; control plots: 5.6 ± 0.5, $n = 14$; mean ± SD). Therefore, adults nesting in treated plots had to adopt strategies to feed the same number of nestlings in spite of a lower density of potential foraging substrates. Potential tradeoffs may include moving over greater distances from the nest to foraging sites (Adams *et al.*, 1994) and increasing the time spent feeding young at the expense of other activities (Cucco & Malacame, 1995). For example, adults could be decreasing their own food intake to benefit their nestlings (Wittenberger, 1982). These strategies could have negative effects on the survival rate of adults (Martin, 1987; Boutin, 1990; Newton, 1998).

Frey-Roos, Brodmann, and Reyer (1995) suggested that birds could increase the amount of food delivered when resources are sparse or located far away from the nest. Grieco (2002a) has shown that prey items brought to the nest by blue tits (*Parus caeruleus*) were larger when feeding rate was lower. An increase in size and selectivity of prey by parents when habitat is food-supplemented has also been suggested (Grieco, 2001; 2002b). However, it is very difficult to estimate the size of brown creeper food carries: the beak of the brown creeper is very small and adults usually enter the nest very quickly.

The negative treatment effect we observed on brown creeper nest density did not reflect food abundance per unit area of bark. Adults appeared to be able to partly compensate for more widely distributed foraging substrates. Even though nest provisioning rate was lower in treated plots, brood sizes near fledging time were similar, as indicated above. Perhaps those adults spent a greater portion of the day feeding their nestlings to compensate for lower nest provisioning rate. Future studies should examine whether brown creepers increase their time allocation to nest provisioning and determine the consequences of the extra energy expenditure by parents in partially harvested plots on their survival rate and the body condition and survival rate of fledglings.

Temperature is a critical factor for the emergence of invertebrates, and the peak abundance of invertebrates is known to be related to temperature in some systems (Visser, Holleman & Gienapp, 2006). In insectivorous bird species, nesting phenology has evolved to reflect temperature (*e.g.*, Visser, Holleman & Caro, 2009) and peaks in invertebrate abundance (Dias & Blondel, 1996; Naef-Daenzer, Naef-Daenzer & Nager, 2000). In our study, cumulative degree-days was the only factor influencing the structure of invertebrate assemblages. The split (213.3 CDD) was reached on 23 June in 2009 and on 12 June in 2010. In both years, the split date corresponded to the second half of the nestling period for first nesting attempts. This suggests that creepers may adjust their nesting phenology according to invertebrate emergence times.

There was no treatment effect on the structure of bark invertebrate assemblages. Nonetheless, it should be noted that identification to the order may have been too coarse to detect such an effect. For example, 2 species or 2 families from the same order can respond differently to harvesting (Cherry, 2003; Miller, Wagner & Woods, 2008; Halaj, Halpern & Yi, 2009). Nonetheless, previous studies testing
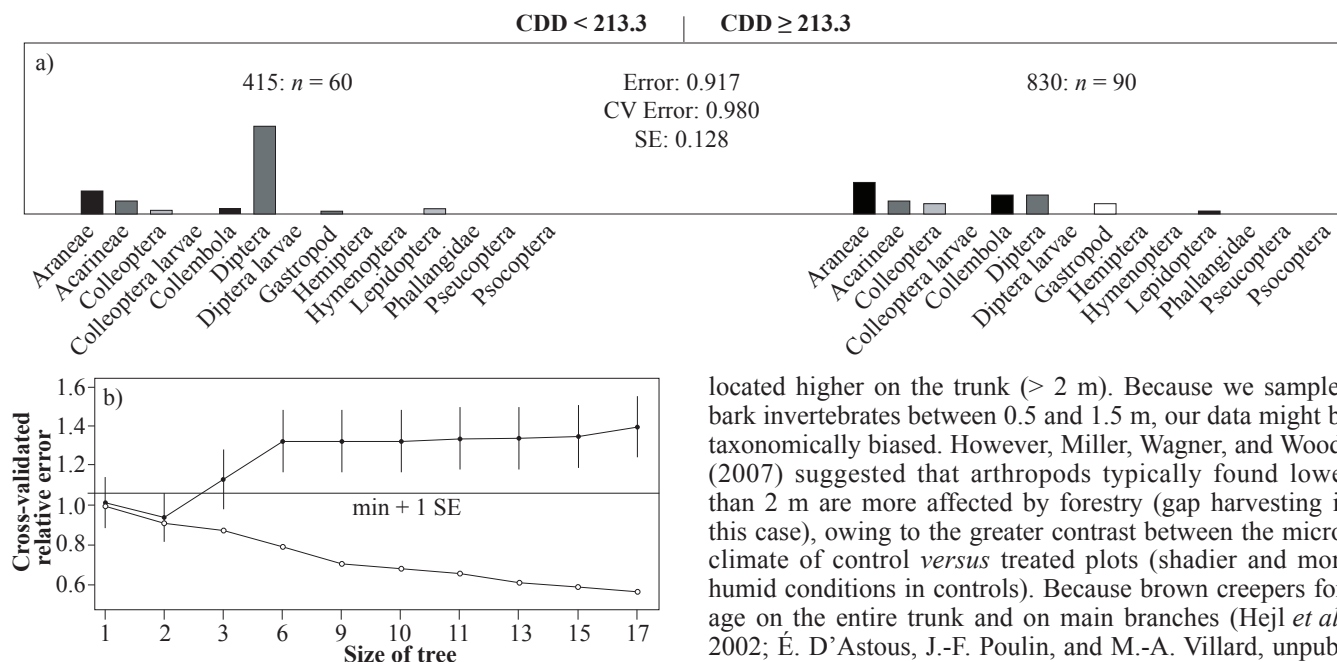
FIGURE 2. Effect of environmental variables on bark invertebrates, as determined from a multivariate regression tree (MRT) (a) relating the abundance of 14 bark invertebrate taxa (shown in histograms from left to right) to 5 environmental variables (treatment, year, tree dbh, site, and cumulative degree days). Cross-validation results (b) are also shown. Relative error (open circles) and cross-validated relative error (filled circles). Vertical bars indicate 1 standard error (SE) for the cross-validated relative error.

for effects of forest harvesting on invertebrate communities using the same level of taxonomic resolution have reported significant differences (*e.g.*, Bellocq, Smith & Doka, 2001; Miller, Wagner & Woods, 2007). Even though the brown creeper seems to exhibit preferences for certain invertebrate taxa (Mariani & Manuwal, 1990; Hejl *et al.*, 2002), stomach contents suggest that this species has a generalist diet (Hejl *et al.*, 2002). In fact, adults feed on a wide variety of insect adults and larvae, spiders and their eggs, and pseudoscorpions (Hejl *et al.*, 2002). However, no data are available on stomach contents of brown creeper nestlings. Stomach contents of Eurasian treecreeper nestlings contained mainly Diptera (40.9% of items identified), but were composed mainly of spiders when measuring food items using dry biomass (Kuitunen & Törmälä, 1983). Hemiptera, Lepidoptera, Coleoptera, cockroaches, and seeds were also found in Eurasian treecreeper stomach contents (Kuitunen & Törmälä, 1983).

Partial harvest treatments such as selection harvesting change light intensity, which has been shown to affect epiphytic lichens (Edman, Eriksson & Villard, 2008), which in turn could affect the abundance of bark invertebrates (Pettersson *et al.*, 1995). In our treated plots, some samples were collected in residual forest and not always at the edge of skid trails, where the incident light is stronger.

In Maine, USA, Miller, Wagner, and Woods (2007) have shown that bark arthropod communities on red maple (*Acer rubrum*) were distributed according to a height gradient. Acarina, spiders, and Collembola were more prevalent at the bottom of trees (< 2 m), whereas Diptera were

located higher on the trunk (> 2 m). Because we sampled bark invertebrates between 0.5 and 1.5 m, our data might be taxonomically biased. However, Miller, Wagner, and Woods (2007) suggested that arthropods typically found lower than 2 m are more affected by forestry (gap harvesting in this case), owing to the greater contrast between the microclimate of control *versus* treated plots (shadier and more humid conditions in controls). Because brown creepers forage on the entire trunk and on main branches (Hejl *et al.*, 2002; É. D'Astous, J.-F. Poulin, and M.-A. Villard, unpubl. data), future studies should sample bark invertebrates over a broader range of heights to better represent food abundance from the perspective of this species.

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