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Biodiversity conservation in old-growth boreal forest: black spruce and balsam fir snags harbour distinct assemblages of saproxylic beetles

P. Janssen · C. Hébert · D. Fortin

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Abstract Biodiversity conservation of forest ecosystems strongly relies on effective dead wood management. However, the responses of saproxylic communities to variations in dead wood characteristics remains poorly documented, a lack of knowledge that may impede the development of efficient management strategies. We established the relationship between saproxylic beetles—at the species and community levels—and attributes of black spruce and balsam fir in old-growth boreal forests. The relationship was first evaluated for individual snag bole segments, and then for forest stands. A total of 168 bole sections were collected in summer 2006 along a compositional gradient ranging from black spruce-dominated stands to balsam fir-dominated ones, in a boreal forest dominated by >90-year-old stands. A total of 16,804 beetles belonging to 47 species emerged from bole segments, with 21% of the species being found exclusively in black spruce snags and 36% exclusively in balsam fir snags. Black spruce and balsam fir snags thus contributed differently to forest biodiversity by being inhabited by different saproxylic communities. Wood density was an important attribute in the host-use patterns for several species of saproxylic beetles, but no relationship was found between snag availability within stands and abundance of beetles strongly linked to either black spruce or balsam fir. Our study outlines the relative contribution of tree compositional diversity to saproxylic species, while highlighting the contribution of black spruce and balsam fir to animal diversity in old-growth boreal forests.

Keywords Biodiversity conservation · Dead wood · Saproxylic beetles · Balsam fir · Black spruce · Boreal forest

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Introduction

Dead wood is recognized as one of the most important components of forest ecosystems for sustaining biodiversity (Jonsson et al. 2005; Siitonen 2001). Saproxylic species represent a rich group of organisms that depend on dead wood for at least part of their life cycle (Speight 1989). This group is represented by plants, fungi and animals (Harmon et al. 1986; Berg et al. 1994; Esseen et al. 1997), all of which play a fundamental role in wood decomposition and nutrient cycling in forest ecosystems (Hammond et al. 2001; Speight 1989). Saproxylic organisms are sensitive to forest management (e.g., Martikainen et al. 2000; Similä et al. 2002; Hilszczański et al. 2005), and their conservation should be central to the development of forest management practices aimed at maintaining biodiversity (Siitonen 2001).

Saproxylic beetles are among the first organisms to colonize dying trees and, as such, they often initiate the process of decomposition (Speight 1989; Esseen et al. 1997; Siitonen 2001). Previous work has outlined that the diversity of saproxylic beetles is closely linked to certain attributes of dead trees, such as diameter and species (Økland et al. 1996; Franc et al. 2007). Nevertheless, knowledge on the use of host trees by insects and their responses to variation in dead wood availability is still lacking at both the species and community levels (Müller and Büttler 2010). This information is needed, however, to insure that dead wood management practices can fulfill the objective of biodiversity conservation (Langor and Spence 2006).

Dead wood dynamics of forest ecosystems are mostly driven by disturbance regimes (Karjalainen and Kuuluvainen 2002). For example, the dynamics of old-growth forests are largely driven by tree mortality caused by senescence and damage by secondary insects or pathogens. Tree mortality leads to small canopy gaps that influence a variety of organisms and ecosystem processes (Bouget 2005; Hodson et al. 2010). Compared with stands that have been brought to an early-successional stage by logging or broad-scale natural disturbance, old-growth stands offer more diversified stocks of dead wood and better ecological continuity (Siitonen 2001). Old-growth stands are therefore of particular interest for maintaining biodiversity in managed forests because they are important pools of saproxylic species (e.g., Siitonen and Saaristo 2000).

The eastern Canadian boreal forest is mostly composed of old-growth stands (Pham et al. 2004; Bouchard et al. 2008) dominated by black spruce (*Picea mariana* BSP) and balsam fir (*Abies balsamea*) (Rowe 1972). Balsam fir is a late-successional species that often comes to dominate over black spruce as time elapses (De Grandpré et al. 2000; Gauthier et al. 2000). Balsam fir is highly vulnerable to insect defoliators, decay and windthrow (Blais 1983; MacLean and Ebert 1999; Ruel 2000); it thus appears to be an important generator of dead wood, and we hypothesized that it should play a central role in maintaining saproxylic beetle communities in eastern Canadian boreal forests.

We evaluated host-use patterns of black spruce and balsam fir snags by saproxylic beetles in old-growth boreal forests of the Côte-Nord region of Québec, in eastern Canada. Our intent was to quantify the relative contribution of black spruce and balsam fir to biodiversity of saproxylic species in old-growth boreal forests. More specifically, we examined how log volume, snag basal area and dead wood diversity varied with the relative basal area of living black spruce and balsam fir. This assessment revealed the distinct contribution of both tree species to resource availability for saproxylic species at local scale. We then examined (1) whether the richness and abundance of saproxylic beetles varied between black spruce and balsam fir snags and as a function of wood density, (2) whether saproxylic communities differed between snag species, and

(3) whether beetle species strongly linked to black spruce or balsam fir snags were influenced by the availability of dead wood, at the stand level.

Materials and methods

Study area and sampling design

The study area was located in the Côte-Nord region of Québec, Canada, between the 49th and 51st parallels (Fig. 1). The area belongs to the eastern spruce–moss subdomain of the boreal forest (Ministère des Ressources naturelles et de la Faune du Québec 2003). The region is characterized by a humid climate that results in a long fire cycle and in a landscape dominated by a matrix of old-growth forests with irregular stand structure (Bouchard et al. 2008). Dominant tree species are black spruce and balsam fir, but white spruce (*Picea glauca*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) are also abundant.

In the first week of June 2006, 28 sites were selected across a gradient ranging from black spruce- to balsam fir-dominated stands (i.e. >10% of their basal area made up of black spruce and >10% of balsam fir). Sites were selected among those ($n = 103$) previously considered by Côté et al. (2010) when they developed a forest typology specific to the boreal forest of eastern Canada. Each sampling site was located in >4 ha stands, >100 m from stand edge, and >2 km from any other site. Selected stands were >90 years old, and had never been logged.

In order to characterize communities of primary saproxylic beetles, the first species to colonize recently dead trees, we cut six of those trees (decay class 3; Hunter 1990) at each site: three black spruce and three balsam fir, with a diameter at breast height (DBH) ranging from 15 to 20 cm (mean DBH was 15 cm over the study area; Janssen et al. 2009). Then, a 50-cm bole section was collected from each dead tree at a height of 2.0–2.5 m, and brought back to the laboratory.

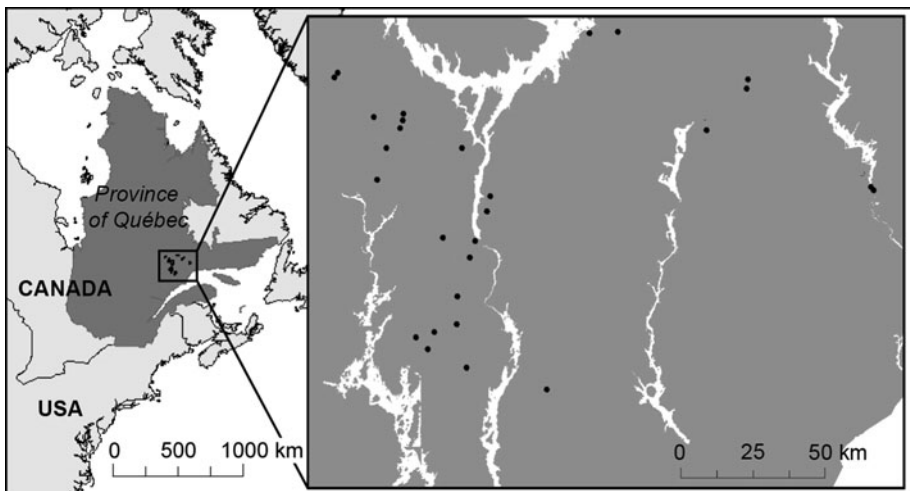


Fig. 1 Map of site distribution within the study area in the Côte-Nord region of Québec, Canada

Characterization of sampling sites

We surveyed three 400-m² circular plots, one located at the centre of the sampling site and two located 60 m away, in opposite directions. The diameter at breast height (DBH; 2-cm classes) and species of each living tree (i.e., ≥ 9 cm at DBH) were recorded in the three 400-m² circular plots. An inventory of coarse woody debris (CWD), considering logs (fallen CWD) and snags (standing CWD), was also conducted. Logs (≥ 9 cm in diameter at the base and ≥ 1 m in length) were inventoried in the central plot of each site. The diameter at both ends and the length of each log were measured. Tree species was determined whenever possible and the Hunter (1990) decay class was recorded. Five decay classes of logs were recognized: (I) bark and texture intact and twigs still present; (II) loose bark, texture beginning to soften and twigs no longer present; (III) only traces of bark present and logs made of large pieces with hard texture; (IV) bark absent and log disassembled into small pieces with a soft texture; and (V) log texture soft and powdery. Snags (≥ 9 cm at DBH) were inventoried in the three 400-m² circular plots of each site. The diameter at breast height (DBH; 2-cm classes), species and decay class were also determined. Nine decay classes were recognized: (I) live; (II) declining; (III) dead with bark intact and small twigs present; (IV) loose bark with no small twigs; (V) bark absent; (VI) broken; (VII) decomposed into small blocky pieces with a soft texture; (VIII) down material; (IX) stump. For saplings (DBH < 9 cm), the DBH, species and state (live, dead or decaying) were determined within two perpendicular subplots of 2 × 20 m in each of the three plots.

Insect collecting and snag characterization

We waxed both ends of each bole segment collected to prevent excessive drying. The bole segments were then suspended in emergence cages, while respecting their natural vertical orientation. Cages were built using white plastic pails (30 × 50 cm) on which holes were pierced and covered with a fine-mesh net to allow ventilation and avoid overheating. A collecting vial was placed under a black funnel fixed under the pail. A 40% ethanol solution with traces of household vinegar (5% acetic acid) was used as preservative. Emerging insects were collected bi-weekly from 1 July to 25 August 2006, and then monthly until 1 November 2006. In a previous study, we found that 84% of all coleoptera and 95% of Scolytinae emerged during the 1st season after being encaged (unpublished data). Menard (1982) also reported that up to 80% of insects inhabiting dead wood had emerged by the end of July. Beetles were identified at the species or genus level, except for the Aleocharinae (Staphylinidae) subfamily, by authors and by taxonomists of the Laurentian Forestry Centre using Arnett and Thomas (2001) and Arnett et al. (2002) nomenclatures. Identifications were cross-checked at the Canadian National Collection of insects, arachnids and nematodes in Ottawa and vouchers are conserved in the insect collection of the Laurentian Forestry Centre.

We estimated wood density (dry weight/volume) for each bole segment at the end of the insect emergence period. This assessment provided a quantitative evaluation of the variability within Hunter's (1990) decay class 3 (i.e. among the collected bole segments) for black spruce and balsam fir. A 2-cm thick wood disk was cut at the base of each bole segment. The volume was measured by water displacement and the disks were weighed using an electronic balance after being dried to constant mass.

Statistical analyses

Linear regressions were used to relate the basal area and the proportion of living black spruce or balsam fir in stands to (1) the volume of logs, (2) the basal area of snags, and (3) dead wood heterogeneity. Because there was only weak variation in the total basal area of living trees among sampled stands ($94 \pm 14 \text{ m}^2/\text{ha}$; $\text{CV} = 15\%$), the proportion of black spruce and of balsam fir was used. This measure was calculated using a ratio between their respective basal areas and the combined basal area of both tree species in a given stand. Dead wood heterogeneity was estimated, for black spruce and balsam fir, as the number of combinations formed by position (standing snag versus lying log), decay classes (Hunter's (1990) classes 3–9 for snags and classes 1–5 for logs), and 2-cm DBH classes for snags and logs ≥ 9 cm. A square-root transformation was applied to the volume of logs because this variable was not normally distributed. Relationships were studied for the total amount of CWD, as well as for black spruce and balsam fir CWD separately. Also, because the amount and heterogeneity of CWD are usually correlated (Müller and Büttler 2010), we used Estimates S (Colwell 2009) to build sample-based rarefaction curves that compared the accumulation of the number of dead wood combinations as a function of the number of dead wood objects for black spruce and balsam fir (see Djupström et al. 2008).

An ANOVA was used to compare the average wood density of balsam fir and black spruce at Hunter's (1990) decay class 3. Because the bole segments collected at a given site were not real replicated samples, we used mixed-effects negative binomial regressions (with "site" as random effect) to relate total abundance and richness of saproxylic beetles to wood density. We also used mixed-effects logistic regressions (with "site" as random effect) to relate the probability of occurrence of individual saproxylic beetle species to snag wood density. Only species that were present in at least three bole sections of either black spruce or balsam fir were considered (22 species in total), and abundance was log-transformed ($\log x + 1$) to linearize the relationship. These analyses were performed using SAS version 9.1 (SAS Institute Inc. 2004).

We contrasted saproxylic beetle communities between tree species using Nonmetric Multidimensional Scaling (NMS) with Bray-Curtis distance, which is a suitable measure of species dissimilarity (see Magurran 2004). Prior to the analysis, data were pooled by snag species for each site and beetle species found in fewer than three sites were discarded. We used NMS because this method avoids the assumption of a linear relationship among variables (Clarke 1993) and is considered the most effective method for analysing ecological community data (McCune and Grace 2002). NMS is an iterative ordination method that uses a stress measure to reflect how well the ordination summarises the Bray-Curtis distances observed among the samples. We ran a "slow and thorough" automated search and then re-ran the best ordination with a three-dimensional configuration, as recommended (see autopilot run in McCune and Mefford 1999). Dissimilarity in community composition among black spruce and balsam fir snags was tested from the NMS ordination with Multi-Response Permutation Procedures (MRPP) based on the Bray-Curtis distance (Mielke and Berry 2001). MRPP is a non-parametric method that has the advantage of not requiring assumptions such as multivariate normality and homogeneity of variances (McCune and Grace 2002). MRPP test the differences between black spruce and balsam fir saproxylic communities by comparing the average distance of observed data within groups to randomised permutations of group members. Within-group homogeneity is measured as the chance-corrected within-group agreement (A), which varies between 0 (no association between sample units and defined groups) and 1 (perfect association) (McCune and Grace 2002). Finally, we tested the affinity of individual saproxylic species with a particular tree

species by running an indicator species analysis (Dufrêne and Legendre 1997). Indicator values (IndVal) varied between 0 (no indication) and 100 (perfect indication), and were evaluated based on a Monte Carlo test of significance, with 9,999 permutations. NMS, MRPP and IndVal were conducted using PC-ORD 5.0 (McCune and Mefford 1999).

Mixed-effects Poisson regressions were used to investigate the relationship between the abundance of species retained by the IndVal analysis and the basal area of black spruce or balsam fir snags. We accounted for the fact that multiple bole segments were taken at each site by considering “site” as a random effect. Species abundance data were log-transformed ($\log x + 1$) to linearize the relationship. We tested all combinations of models based on subsets of two independent variables: balsam fir (BFba3) and black spruce (BSba3) snag basal area of Hunter’s (1990) decay class 3. Regressions were performed using SAS version 9.1 (SAS Institute Inc. 2004).

Results

A total of 16,804 beetles belonging to 20 families and 47 taxa emerged from the 168 bole segments: 11,249 beetles from 30 taxa emerged from black spruce boles, and 5,555 beetles from 37 taxa emerged from balsam fir boles. The most abundant beetles, *Crypturgus borealis* Swaine and *Dryocoetes* prob. *affaber* Hopkins, accounted for 79% and 10% of all collected beetles, respectively. The latter species was found almost exclusively in black spruce (only two individuals emerged from balsam fir), whereas *C. borealis* was twice as abundant in black spruce as in balsam fir. Eighteen additional taxa emerged from both black spruce and balsam fir snags, whereas 10 were exclusive to black spruce snags and 17 to balsam fir snags. Forty-five individuals belonging to 26 species occurred in fewer than 3 boles; 15 of these rare species emerged only from balsam fir, 9 only from black spruce and 2 from both tree species.

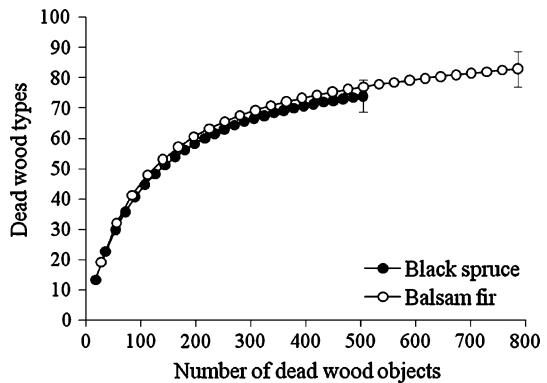
Dead wood abundance and heterogeneity

Snag basal area, log volume and CWD heterogeneity varied largely among sampling sites for both black spruce and balsam fir, as well as when considering both tree species (Table 1). No relationships were detected between the amount of black spruce logs and the proportion ($F_{1,27} = 1.8$; $P = 0.18$) or the basal area ($F_{1,27} = 0.7$; $P = 0.40$) of living black spruce in stands. Likewise, no relationship was found between the basal area of black spruce snags and the proportion ($F_{1,27} = 0.0$; $P = 0.96$) or the basal area ($F_{1,27} = 0.2$; $P = 0.64$) of living black spruce. In contrast, the amount of balsam fir logs increased with the proportion ($F_{1,27} = 10.3$; $P = 0.003$; $r^2 = 0.28$) and the basal area ($F_{1,27} = 4.3$; $P = 0.04$; $r^2 = 0.14$) of living balsam fir in stands. The basal area of balsam fir snags also increased with both the proportion ($F_{1,27} = 10.6$; $P = 0.003$; $r^2 = 0.29$) and the basal area ($F_{1,27} = 4.3$; $P = 0.04$; $r^2 = 0.14$) of living balsam fir in stands. The heterogeneity of black spruce dead wood, estimated as the total number of combinations formed by tree diameter, position and decay classes, was not influenced by the proportion ($F_{1,27} = 2.7$; $P = 0.11$) or the basal area ($F_{1,27} = 0.3$; $P = 0.59$) of living black spruce in stands, whereas the heterogeneity of balsam fir dead wood increased with the proportion ($F_{1,27} = 10.9$; $P = 0.002$; $r^2 = 0.29$) or the basal area ($F_{1,27} = 3.9$; $P = 0.05$; $r^2 = 0.13$) of living balsam fir. Rarefaction curves revealed that the heterogeneity of dead wood increases with the number of dead wood objects following the same pattern for black spruce and balsam fir (Fig. 2).

Table 1 Averages and ranges of snags basal area, log volume and CWD heterogeneity (i.e. number of combinations formed by tree diameter, position and decay classes) for both black spruce and balsam fir, as well as for total tree species

	Mean (\pm SD)	Range
Snags basal area ($\text{m}^2 \text{ha}^{-1}$)		
Total	7.5 (\pm 2.7)	2.0–13.9
Black spruce	2.5 (\pm 1.2)	0.3–4.5
Balsam fir	3.9 (\pm 1.6)	1.0–8.0
Logs volume ($\text{m}^3 \text{ha}^{-1}$)		
Total	63.7 (\pm 47.4)	0.0–225.9
Black spruce	20.5 (\pm 19.1)	0.0–72.2
Balsam fir	30.5 (\pm 35.0)	0.0–135.9
CWD heterogeneity		
Total	39.6 (\pm 10.7)	14.0–63.0
Black spruce	13.3 (\pm 5.6)	4.0–26.0
Balsam fir	19.3 (\pm 7.2)	5.0–35.0

Fig. 2 Sample-based rarefaction curves for comparing dead wood heterogeneity, between black spruce and balsam fir. Error bars indicate 95% confidence intervals



Saproxyltic beetles and the characteristics of individual snags

Average wood density (\pm SD) was significantly higher ($F_{27,139} = 298.06$; $P < 0.0001$) for black spruce ($0.53 \pm 0.04 \text{ g/cm}^3$; $\text{CV} = 7.7\%$) than for balsam fir snags ($0.41 \pm 0.05 \text{ g/cm}^3$; $\text{CV} = 10.9\%$). No relationship was detected between either species richness ($F_{1,139} = 1.30$; $P = 0.25$) or abundance ($F_{1,139} = 1.63$; $P = 0.20$) of saproxyltic beetles and the wood density of snags for all tree species combined. Instead, when considering tree species separately, beetle species richness ($F_{27,55} = 4.48$; $P = 0.04$) and abundance ($F_{27,55} = 8.23$; $P = 0.006$) increased significantly with balsam fir wood density, but not with black spruce wood density ($F_{1,55} < 0.15$; $P > 0.70$ for either relationship).

Among the 22 species tested, the probability of occurrence of five species was significantly associated with wood density (Fig. 3). Four species became more likely to be found as the wood density of snags increased: *C. borealis* was associated with wood density of both tree species, *Pityophthorus* sp. was associated only with black spruce, and *Pityokteines sparsus* (LeConte) and *Serropalpus substriatus* Haldeman were associated only with balsam fir. *Dolichocis manitoba* Dury was the only species less likely to be found in snags of high wood density (Fig. 3).

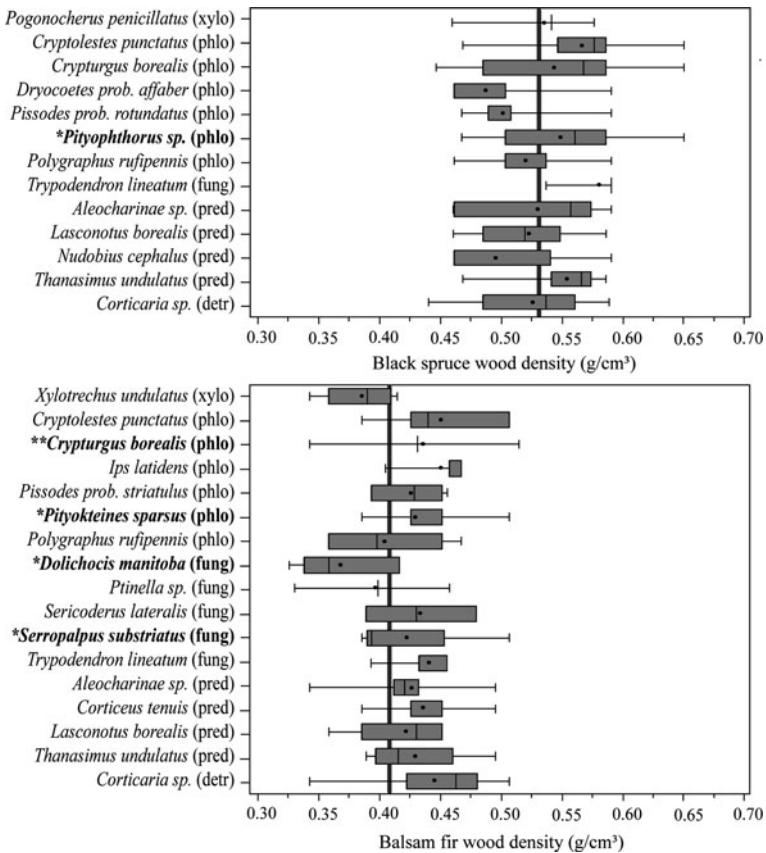


Fig. 3 Boxplot displaying the interquartile range and outliers around the mean (dot) and median (central vertical bar) wood density of black spruce or balsam fir snags in which saproxylic species occurred in at least three bole segments. Species are sorted according to trophic groups: *xylo* xylophagous, *phlo* phloeophagous, *fung* fungivorous, *pred* predaceous and *detr* detritivorous. The bold vertical line going across all species represents the mean density of black spruce or balsam fir bole segments. Bold text indicates a significant effect of snag wood density on the probability of occurrence of saproxylic species (* $P < 0.05$; ** $P < 0.001$) in old-growth boreal forests, as determined from mixed-effects logistic regression

Saproxylic beetle communities vs tree species

NMS ordination showed that different saproxylic beetle communities use black spruce and balsam fir snags (Fig. 4). Axes 1 and 2 explained 33.2% and 25.7% of the overall variance, respectively. The observed stress level of 16.4 fell within the 10–20 limit, which indicates a good representation of the original data structure (Clarke 1993). MRPP indicated that dissimilarity in community composition was significant ($A = 0.04$, $P < 0.001$), confirming that saproxylic species assemblages differed between black spruce and balsam fir snags. According to the indicator species analysis (Duf rene and Legendre 1997), six out of the 22 taxa tested were closely associated with black spruce snags, whereas four were more closely linked to balsam fir snags (Fig. 5).

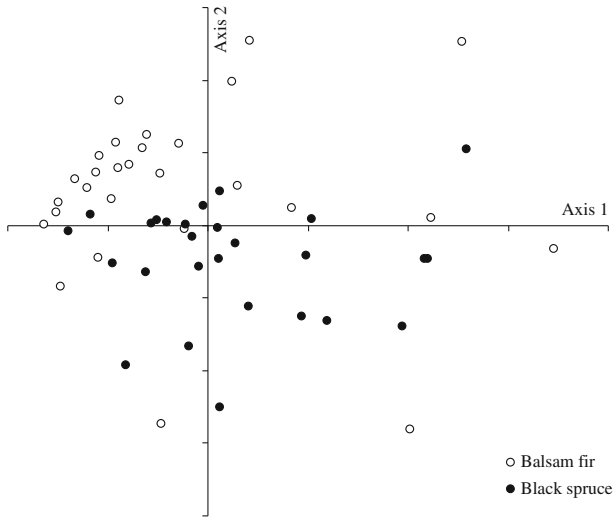
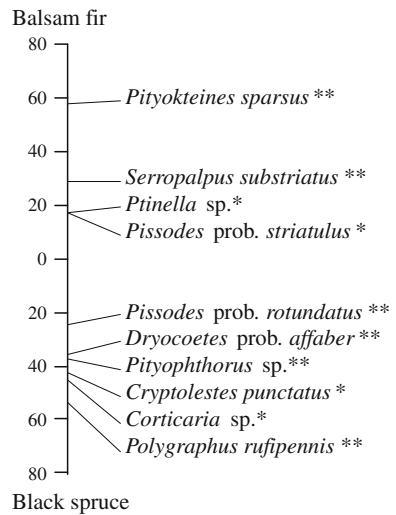


Fig. 4 Nonmetric Multidimensional Scaling ordination of 22 species and 55 sample units of black spruce ($N = 27$) and balsam fir ($N = 28$) snags (each point represents the combined beetles collected from the three black spruce snags per site and the three balsam fir snags per site) (Stress = 16.4, r^2 axis 1 = 0.33, r^2 axis 2 = 0.26)

Fig. 5 Ordination of species based on indicator species analysis, contrasting the association with black spruce and balsam fir snags ($*P < 0.05$; $**P < 0.001$)



Influence of snag availability on the abundance of saproxylic beetles

The abundance of *Pissodes prob. rotundatus* tended ($P = 0.06$) to decrease with the basal area of black spruce snags of Hunter’s (1990) decay class 3. In contrast, the abundance of any of the other nine saproxylic species was not influenced by the basal area of balsam fir or black spruce snags of Hunter’s (1990) decay class 3 (see Table 2).

Table 2 Mixed-effects Poisson regressions between the abundance of saproxylic species in black spruce or in balsam fir snags in old-growth boreal forests and the basal area of balsam fir snags (BFba3) and black spruce snags (BSba3) associated with Hunter's decay class 3, together with the interaction between BFba3 and BSba3

Dependent variable	Predictors	Estimate	SE	<i>t</i>	<i>P</i>
Black spruce snags associated species					
<i>Polygraphus rufipennis</i>	Intercept	-1.78	0.99	-1.79	0.08
	BSba3	-0.64	0.79	-0.81	0.42
	BFba3	-0.51	0.93	-0.54	0.59
	BSba3 × BFba3	0.52	0.62	0.83	0.41
<i>Corticaria</i> sp.	Intercept	-3.10	1.29	-2.39	0.02
	BSba3	0.44	0.96	0.48	0.63
	BFba3	0.01	1.17	0.01	0.99
	BSba3 × BFba3	-0.01	0.78	-0.01	0.99
<i>Cryptolestes punctatus</i>	Intercept	-3.13	1.30	-2.40	0.02
	BSba3	0.93	0.93	1.00	0.32
	BFba3	-0.11	1.23	-0.09	0.92
	BSba3 × BFba3	-0.18	0.85	-0.21	0.83
<i>Pityophthorus</i> sp.	Intercept	-3.54	1.42	-2.49	0.02
	BSba3	0.41	0.98	0.42	0.67
	BFba3	0.22	1.21	0.19	0.85
	BSba3 × BFba3	0.02	0.79	0.03	0.97
<i>Dryocoetes</i> prob. <i>affaber</i>	Intercept	-2.31	1.37	-1.69	0.10
	BSba3	-0.02	1.07	-0.02	0.98
	BFba3	-0.14	1.31	-0.11	0.91
	BSba3 × BFba3	0.06	0.92	0.07	0.94
<i>Pissodes</i> prob. <i>rotundatus</i>	Intercept	-1.17	1.49	-0.78	0.44
	BSba3	-3.29	1.79	-1.84	0.06
	BFba3	-1.50	1.51	-1.00	0.32
	BSba3 × BFba3	1.68	1.06	1.58	0.11
Balsam fir snags associated species					
<i>Pityokteines sparsus</i>	Intercept	-3.21	1.15	-2.77	0.01
	BSba3	1.22	0.93	1.31	0.19
	BFba3	0.98	1.01	0.97	0.33
	BSba3 × BFba3	-0.96	0.79	-1.21	0.22
<i>Serropalpus substriatus</i>	Intercept	-4.32	2.33	-1.85	0.07
	BSba3	0.99	1.62	0.61	0.54
	BFba3	-0.27	2.22	-0.12	0.90
	BSba3 × BFba3	-0.06	1.48	-0.04	0.96
<i>Ptinella</i> sp.	Intercept	-3.91	2.75	-1.42	0.17
	BSba3	3.23	3.52	0.92	0.36
	BFba3	0.18	3.41	0.05	0.96
	BSba3 × BFba3	-4.37	4.75	-0.92	0.36

Table 2 continued

Dependent variable	Predictors	Estimate	SE	<i>t</i>	<i>P</i>
<i>Pissodes prob. striatulus</i>	Intercept	−9.53	5.43	−1.76	0.09
	BSba3	4.44	4.23	1.05	0.29
	BFba3	4.44	4.10	1.08	0.28
	BSba3 × BFba3	−3.72	3.52	−1.06	0.29

Discussion

We showed that balsam fir and black spruce support different saproxylic beetle communities. Several taxa of saproxylic beetles largely specialized on one of the two tree species. Our results demonstrate the importance of maintaining compositional representativeness at the stand level and the necessity to preserve a representative range of stands in the landscape for the conservation of biodiversity in old-growth boreal forests.

Dead wood compartment

Snag basal area was higher and dead wood was more diversified in stands dominated by balsam fir than in those dominated by black spruce, suggesting that balsam fir plays an essential role in the dead wood compartment of old-growth boreal forests of the Cote-Nord region. As a late-successional species (Ali et al. 2008), balsam fir increases in abundance with stand age (De Grandpré et al. 2000; Gauthier et al. 2000). Older stands are particularly susceptible to insect defoliators, and these largely determine the abundance, heterogeneity and turnover rate of dead wood in old-growth boreal forests (Sturtevant et al. 1997). The shorter life expectancy of balsam fir compared with black spruce (Farrar 1995) can explain why the dead wood attributes of fir tend to include a broader range of decay stages. Also, the lower wood density of balsam fir makes this tree species more vulnerable to windthrow than black spruce (Ruel 2000). However, dead wood heterogeneity was strongly related to the amount of CWD and rarefaction curves showed that black spruce heterogeneity follow the same trend as balsam fir (Fig. 2). These results may indicate that, in stands dominated by balsam fir, dead wood amount and heterogeneity are not only provided by this tree species. As a late-successional species, the abundance of balsam fir may be related to multiple characteristics of old-growth forest stands, such as the presence of deciduous trees or shrubs that colonize forest gaps after fine-scale canopy disturbances. Fast growing deciduous trees produce large amounts of dead wood and increase its diversity. Because of the ecological function of dead wood in forest ecosystems and its importance for biodiversity conservation (Harmon et al. 1986), our results underscore the relative contribution of both black spruce and balsam fir to dead wood compartment in North American old-growth boreal forests.

Diversity and assemblage patterns of saproxylic beetles

As for the amount and heterogeneity of dead wood, beetle diversity patterns differed between black spruce and balsam fir snags. Saproxylic beetles emerged in greater numbers from black spruce snags but were less diversified than those emerging from balsam fir snags. These differences may be related to tree species, wood density or, more probably, to

a combination of both factors. Recent dead wood, such as that of decay stage 3 (Hunter 1990) snags, tends to be a less diversified resource than dead wood at older decay stages (Tikkanen et al. 2006; Langor et al. 2008). Balsam fir bole segments were associated with a broader variability of wood density than black spruce boles, which may have provided a larger range of wood microhabitats. The greater richness of saproxylic species that emerged from balsam fir boles might reflect this higher niche diversity. For example, the presence of *D. manitoba*, a species associated with advanced decay wood (Arnett et al. 2002), was only found in balsam fir boles of low wood density. In contrast, fresh dead wood provides abundant resources for many specialized organisms that colonize recently dead trees in large numbers (Langor et al. 2008). For example, the ambrosia beetle *C. borealis* (Arnett et al. 2002) is a *Scolytinae* well represented in balsam fir, but nonetheless twice as abundant in black spruce. Within the decay class 3 of Hunter (1990), we found a larger variability of wood density in balsam fir snags than in black spruce ones. Hunter's classification of dead wood may therefore be insufficient to segregate fresh dead wood from more advanced one in a way that reflects habitat heterogeneity for all tree species. According to the high turnover rate of saproxylic species in the first years after tree death (Siitonen 2001), Hunter's decay class 3 may therefore include beetles of different successional stages. Indeed, Hunter's classification is exclusively based on external characteristics, such as the presence of bark and small twigs. Nevertheless, CWD is a structurally and chemically heterogeneous material that differs in decay rates between tree species (Harmon et al. 1986). For example, bark loss is highly variable between species (Harmon et al. 1986). A given decay class of CWD may therefore provide a broad range of wood microhabitats (Pyle and Brown 1999). To improve dead wood classification, it could be useful to measure the depth of penetration of a pointed metal rod (Lambert et al. 1980).

At the tree species level, we found that assemblages of saproxylic beetles differed between black spruce and balsam fir snags. These results support the idea that tree species has a fundamental influence on saproxylic beetle assemblages in dead wood (Jonsell et al. 1998; Siitonen 2001; Similä et al. 2003; Tikkanen et al. 2006). However, knowledge on single beetle species response to tree species is still rather poor (Müller and Bütler 2010). Host-use information is nevertheless useful to understand diversity patterns and, thus, to develop strategies for the conservation of saproxylic species. Most studies relating saproxylic beetle richness or communities to dead wood attributes have used window traps (Sverdrup-Thygeson and Ims 2002; Similä et al. 2003; Franc et al. 2007; Jacobs et al. 2007). Window traps are useful to collect large amounts of beetles but it is difficult, however, to identify close relationships between beetles collected in these traps and the type of dead wood in a stand (Wikars et al. 2005; Alinvi et al. 2007). For example, distinct patterns of diversity and species occurrence were highlighted by comparing saproxylic assemblages of deciduous and coniferous trees (Lindhe and Lindelöw 2004; Jonsell et al. 2007; Saint-Germain et al. 2007). Our results show that distinct saproxylic assemblages use different coniferous species, i.e. balsam fir and black spruce, which are dominant tree species in North America boreal forest (De Grandpré et al. 2000).

Resource availability and implications for conservation

At the stand level, the abundance of individual saproxylic beetle species closely associated with balsam fir or black spruce snags was not influenced by the amount of these resources in old-growth boreal forests of the Côte-Nord region of Québec, in eastern Canada. Likewise, many have failed to detect a direct relationship between abundance of individual saproxylic species and dead wood availability at a fine scale. For example, in mature

eastern Canadian pine-dominated forests, no relationship was found between the abundance of insects that emerged from decaying logs and the volume of surrounding CWD, at two spatial scales (20 and 79 ha) (Vanderwel et al. 2006). In the same way, Laaksonen et al. (2008) did not find significant relationships between the density of spruce logs measured at three combined decay classes ($DBH \geq 10$ cm) and the incidence of saproxylic species in the boreal spruce-swamp forests of Finland and Russia. They suggested that the range of variation in habitat quality variables was probably not large enough to make it possible to detect potential effects (Laaksonen et al. 2008). Moreover, in Swedish boreal forests, CWD volume measured at the stand level has rarely been found to be related to the abundance of species collected from Elector traps, while landscape composition, at 1 and 10 km scales, was closely linked to the abundance of saproxylic beetles (Gibb et al. 2006). As shown by Økland et al. (1996) and Franc et al. (2007), relationship between saproxylic beetles and CWD is more likely to be scale dependent. At the stand scale, our study suggests that the amount of CWD remained sufficient for maintaining saproxylic beetle diversity. Our study was conducted in a matrix of old-growth forests, where the amount of dead wood is obviously not a limiting factor. Habitat selection of individual saproxylic beetle species may be related to landscape composition (Gibb et al. 2006), whereas the abundance of species associated with specific dead wood types should be more closely related to dead wood features, such as phloem volume, wood humidity, sun exposure or bark cover.

Clearcutting is the main forestry practice in the boreal forest (Bergeron et al. 2007; Rosenvald and Löhmus 2008). This practice threatens old-growth stands (Bergeron et al. 2002) and, thereby, reduces dead tree recruitment and increases landscape heterogeneity (Siitonen 2001). Our findings underscore the significant role played by individual dead trees within old-growth forest stands. The preservation of saproxylic species would benefit from implementing dead tree retention strategies. However, the conservation of individual dead trees in harvested areas may not have the same ecological value because they are fully exposed to the sun and wind, which differs from old-growth forest conditions. Because tree species shape beetle communities, silvicultural practices (e.g., partial and selection cutting) that maintain patches of dead wood of various tree species should be designed to improve conservation of mature forest species. Even for large patches, however, tree retention cannot maintain the structures and the microclimate that are characteristic of old-growth forests (Gustafsson et al. 2010). Saproxylic species conservation would thus benefit from strategies that could ensure stand maintenance and connectivity, at larger scale, from early- to late-successional species.

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