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Beetle diversity in a matrix of old-growth boreal forest: influence of habitat heterogeneity at multiple scales

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The relative contribution of compositional and structural heterogeneity on biodiversity is currently ambiguous because field studies generally integrate these two sources of habitat heterogeneity into a single index. We established the relationship between species richness of ground-dwelling and flying beetles and compositional and structural attributes of forest heterogeneity. The relationship was evaluated at two spatial scales: the scale of forest stand, corresponding to an 11.3 m radius, and the scale of landscape, corresponding to either a 400 or 800 m radius. Seventy stands were sampled in the matrix of old-growth boreal forest of the North Shore region of Québec, Canada, during the summers of 2004 and 2005. A total of 133 ground-dwelling beetle species (range: 4–42 species per site) were captured in pitfall traps and 251 flying species (range 16–58 species per site) in flight-interception traps. We found that the most relevant type of heterogeneity to explain variations in species richness and the significance of landscape scale information varied between groups of beetles. Compositional heterogeneity (i.e. the number of species of forest trees and shrubs) at the stand scale best predicted species richness in ground-dwelling beetles. On the other hand, it was the combined influence of structural and compositional habitat heterogeneity at stand and landscape scales that best explained richness patterns in flying beetles. Our study outlines the significance of considering multiple types and spatial scales of habitat heterogeneity when describing patterns of species richness.

Biological diversity usually relates positively to habitat heterogeneity (MacArthur and MacArthur 1961, Huston 1994). In forest ecosystems, habitat heterogeneity arises when either stand composition or structure varies over space or time (Li and Reynolds 1995, Franklin and Van Pelt 2004). Forest structure has been identified as a key determinant of biodiversity (review by McElhinny et al. 2005). Although some researchers have suggested that “stand structural complexity is essential for biodiversity conservation in all forests” (Lindenmayer et al. 2006), others have noted that indices of habitat structure often include attributes of forest composition (McElhinny et al. 2005). Combining structural and compositional attributes into one index may obscure the relative effect of habitat composition on biodiversity.

Several studies have shown that different components of habitat heterogeneity can have distinct consequences on biodiversity patterns (MacArthur and MacArthur 1961, Bersier and Meyer 1994, Schaffers et al. 2008). Only few studies, however, have examined the separate effects of habitat structure and composition on biodiversity, with mixed results. For example, ground-dwelling beetle richness was influenced by the compositional attributes of heterogeneity in dwarf shrub habitats (González-Megías et al.

2007), whereas carabid beetle richness was more closely associated with structural attributes of heterogeneity in temporary wetlands (Brose 2003). The contrasting results could reflect differences in habitat heterogeneity between study areas, thereby pointing out a need for a closer examination of the effect of habitat composition on biodiversity.

The link between biodiversity and the type of habitat heterogeneity may also vary with spatial scale (Tews et al. 2004). In riparian forests, for example, birds select their breeding habitat on the basis of structural attributes at broad spatial scale and on compositional attributes at a finer scale (Bersier and Meyer 1994). The latter example illustrates the fact that diversity is scale dependent (Magurran 2004), and emphasizes the need to evaluate the relationship between diversity and habitat heterogeneity at multiple scales (Wiens and Milne 1989).

Most studies quantifying the relationship between habitat heterogeneity and species richness have been conducted on vertebrate communities, and have generally focused on habitats under anthropogenic disturbance (review by Tews et al. 2004). Information is thus limited for major taxonomic groups, such as insects, in natural forest stands. A number of studies have outlined the

significance of individual habitat attributes for beetle diversity in boreal forest, particularly in northern Europe forests. Most of these studies have used old-growth forests as benchmarks for estimating the impact of forest management (Martikainen et al. 2000, Similä et al. 2002a), or have concentrated their investigation towards specific groups such as saproxylics (Økland et al. 1996, Franc et al. 2007) or carabids (Niemelä et al. 1996, Martikainen et al. 2006). The only study linking global richness of beetles to attributes of natural boreal forests was conducted along a productivity gradient in northern Finland (Similä et al. 2002b). To our knowledge, however, there has been no multi-scale investigation of the relative contribution of various types of habitat heterogeneity on overall beetle richness in landscapes dominated by old-growth boreal forest. Given the fundamental role that insects play in many ecosystem processes, this gap in knowledge could preclude our ability to develop efficient strategies for sustainable forest management (Wilson 1987).

Our study examines the relationship between species richness of beetles and habitat heterogeneity at multiple spatial scales in boreal landscapes dominated by old-growth forests. Specifically, we investigate 1) whether habitat heterogeneity influences beetle species richness, 2) whether ground-dwelling and flying beetles respond similarly to habitat heterogeneity, 3) which component of habitat heterogeneity (structure or composition) best explains species richness and 4) whether the link between heterogeneity and species richness is scale dependent.

Materials and methods

Study area

The study was carried out in the North Shore 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 2003a). The region is characterized by a humid climate that results in a long fire cycle (Bouchard et al. 2008) and by forest stands irregular in

structure and composition (Boucher et al. 2003). Dominant tree species are black spruce *Picea mariana*, and balsam fir *Abies balsamea*. White spruce *Picea glauca*, white birch *Betula papyrifera*, trembling aspen *Populus tremuloides*, and jack pine *Pinus banksiana*, are also locally abundant.

The study area was characterized by landscapes dominated by old-growth forests, where average stand age was >270 yr old (Bouchard et al. 2008). We sampled 36 sites in 2004 and 34 sites in 2005, for a total of 70 sites over the two years. Selected stands were virgin, under natural disturbance regimes and had never been logged. Stand age was >70 yr old (range: 70 to >500 yr old, with age of the oldest stands being estimated from Bouchard et al. 2008), with nearly 65% of sampled stands being ≥ 120 yr old. Stand selection reflected the range of structure and composition of the boreal forests of the North Shore region. It was based on the 1:20 000 ecoforest maps of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNFQ), updated for cutovers and logging roads by the local forestry companies. Sites were established in >4 ha stands, located >100 m from stand edge, and >2 km from any other sampling site.

Insect sampling

Insects were collected from 2 June to 17 August 2004 at 36 sites and from 7 June to 15 August 2005 at 34 sites. Two types of traps were used at each site: flight-interception traps efficient at capturing flying insects and pitfall traps efficient for ground-dwelling insects. One multidirectional flight-interception trap was placed at the center of each sampling site, 0.5–1 m above the ground to capture flying insects. The trap was built using four 15 × 40 cm panels (two made of Plexiglas and two of mosquito net) mounted into a cross pattern, along a 10-cm diameter black ABS cylinder, with two funnels located above and below the cylinder, and leading to collecting vials (Saint-Germain et al. 2004). Four pitfall traps (MultiPher[®] traps) were buried into the ground, 7 m away from the multidirectional flight-interception trap, and 10 m from each other to capture ground-dwelling insects. Pitfall traps had a diameter of 10 cm and

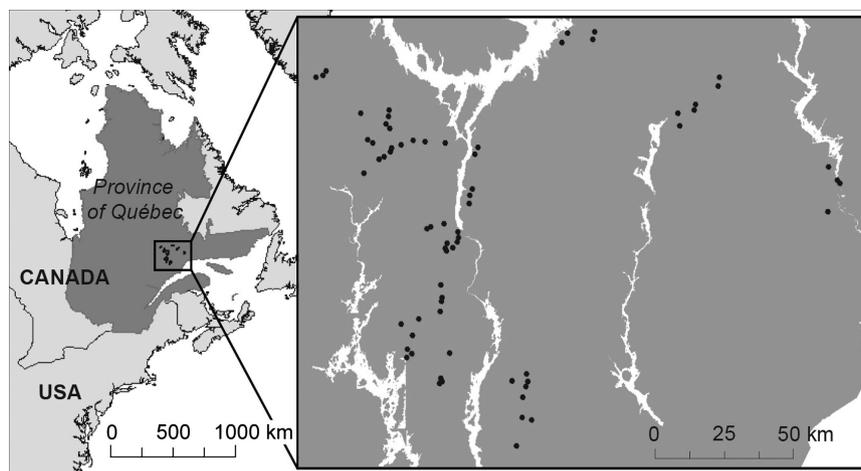


Figure 1. Study area and distribution of sampling sites in a forest matrix dominated by old-growth boreal forests in the North Shore region of Québec, Canada.

were screened with a wire mesh (10 × 10 mm) to limit the captures of vertebrates.

We used a 40% ethanol solution with traces of household vinegar (5% acetic acid) to preserve insects. Trapped insects were collected every two weeks. Most beetles were identified at the species (85%) or genus level (14%), depending on the available information in the literature. Some Aleocharinae sub-family specimens (Staphylinidae) were identified at tribe level (1%). Identifications were verified by experts of the Canadian National Collection (CNC) of Insects, Arachnids and Nematodes (Ottawa, Canada) and cross-checked with insect collections from the CNC or the Insectarium René-Martineau of the Canadian forest service (Québec, Canada).

Characterization of sampling sites

Sampling sites were characterized at the stand and landscape scales. At the stand scale, a 400 m² circular plot (radius: 11.3 m) was established in which the diameter at breast height (DBH) of every living and dead tree ≥ 9 cm was recorded (2 cm classes). The DBH of all living and dead trees < 9 cm was also recorded in two perpendicular subplots of 2 × 20 m. Coarse woody debris with diameter ≥ 9 cm at base and ≥ 1 m in length were inventoried: the diameter at both ends (2 cm classes), the length, and the tree species, whenever possible, were recorded. Only the portion of debris located inside the plots was considered.

At the landscape scale, a Geographic Information System (GIS), managed with ArcGIS 9.1 (Environmental Systems Research Inst., Redlands, CA, USA), was used to characterize the landscape mosaic within 400 and 800 m of each sampling site. We used forest inventory maps, based on MRNFQ ecoforest classification (i.e. Normes de cartographie écoforestière, Ministère des Ressources Naturelles et de la Faune du Québec 2003b), to describe landscape composition and structure within each of the two radii. These maps constitute baseline information for the planning of logging operations by forestry companies. By studying the link between species richness and habitat attributes using information already used by forest managers, our findings should be more readily applicable to the conservation and management of forest ecosystems.

Ecoforest classification uses age classes to define structural classes. Stand age provides a suitable index of forest structure because the two are closely associated in our study area (Boucher et al. 2003). Landscape structure was characterized by 14 mutually exclusive land cover types: young even-aged stands, i.e. basal area of stems dominated by one age class ≤ 80 yr (classes: 0–20, 21–40, 41–60, 61–80 yr old), old even-aged stands, i.e. basal area of stems dominated by one age class > 80 yr (classes: 81–100, ≤ 101 yr old), young uneven-aged stands, i.e. basal area of stems dominated by at least three age classes ≤ 80 yr, old uneven-aged stands, i.e. basal area of stems dominated by at least three age classes > 80 years, multi-storied stands, i.e. basal area of stems distributed in two-stories separated by at least 5 m. Each of these five classes of forest stands were subdivided into two classes based on tree density (A: ground projection of tree canopy ≤ 60%, B: > 60%). The remaining four additional structure classes were: sparse plant cover (combining wet and

dry barrens), cutovers (0–20 yr), water bodies and other features (e.g. anthropogenic infrastructures, burns and windthrows, which covered < 3% of the study sites).

Landscape composition was characterized based on 14 stand composition mutually exclusive classes: stands dominated by spruce or fir species (2 classes: spruce stands, fir stands), stands co-dominated by spruce and fir species (2 classes: spruce-fir stands, fir-spruce stands), stands dominated by spruce or fir species with at least two companion species (2 classes: spruce+spp. stands, fir+spp. stands), other stands dominated by one species with one or more companion species (3 classes: pine+spp. stands, aspen+spp. stands, birch+spp. stands), dry barren lands, wet barren lands, water bodies, cutovers and other features (e.g. anthropogenic infrastructures, burns and windthrows).

Heterogeneity indices and environmental variables

At the stand scale, structural heterogeneity was estimated as the number of diameter classes (2 cm classes) and compositional heterogeneity as the number of tree (e.g. black spruce, jack pine) and shrub (e.g. speckled alder *Alnus rugosa*, American mountain ash *Sorbus americana*) species within the 400 m² circular plot and within the two perpendicular 2 × 20 m subplots. The indices were calculated for standing trees (combining live and dead trees) and for coarse woody debris (Table 1). Also, the basal area (m² ha⁻¹) of standing trees and the volume (m³ ha⁻¹) of coarse woody debris of medium (9–16 cm) and large (≥ 16 cm) diameter were considered as structural attributes. The 16-cm threshold value corresponded to the upper limit of the diameter class (14–16 cm) in which fell the mean diameter recorded in the study area (15 ± 5 cm, n = 70). The basal area (m² ha⁻¹) of standing black spruces and balsam firs and the volume (m³ ha⁻¹) of coarse woody debris of these two species were considered as compositional attributes.

At the landscape scale, structural heterogeneity was measured as the number of landscape structure classes (14 classes) and compositional heterogeneity as the number of landscape composition classes (14 classes), within the 400 m and 800 m radii (Table 1). Also, the area covered by old even-aged stands and the area of old uneven-aged stands were considered as structural attributes, whereas the area covered by spruce dominated stands (combining spruce stands, spruce-fir stands and spruce+spp. stands) and the area covered by fir dominated stands (combining fir stands, fir-spruce stands and fir+spp. stands) were considered as compositional attributes. The areas covered by cutovers and water bodies were considered as influencing landscape composition and structure, and thus appear in both categories of models (Supplementary material, Appendix 1).

Statistical analyses

We used variograms to assess spatial autocorrelation in landscape attributes among sampling sites. Analyses were based on 50 plots of 10 m buffers distanced by 20 m from each other, and laid out in each of the four cardinal directions around each sampling site, in addition to the central buffer (i.e. 201 plots by site). Within these buffers,

Table 1. Description of stand and landscape variables used to model beetle richness in a boreal forest matrix dominated by old-growth stands in the North-Shore region of Québec, Canada.

Variable	Description	Range
latitude	Latitude in UTM coordinates	5532265–5681758
<i>Stand characteristics measured within a 11.28 m radius, leading to a 400 m² plot: variables closely associated to stand structure:</i>		
sstand	Number of diameter classes of standing trees	6–17
mediumba	Basal area of medium size trees (DBH: 9–16 cm)	1.9–42.7 m ² ha ⁻¹
largeba	Basal area of large trees (DBH: >16 cm)	0–41.6 m ² ha ⁻¹
stlog	Number of diameter classes of coarse woody debris	0–13 m ³ ha ⁻¹
mediumvl	Volume of coarse woody debris of medium logs (basal diameter: 9–16 cm)	0–34.1 m ³ ha ⁻¹
largevl	Volume of coarse woody debris of large logs (basal diameter: >16 cm)	0–224.3 m ³ ha ⁻¹
<i>Variables closely associated to stand composition:</i>		
spstand	Species richness of standing trees and shrubs	1–7
spruceba	Basal area of black spruce	2.1–92.3 m ² ha ⁻¹
firba	Basal area of balsam fir	0–88.3 m ² ha ⁻¹
splog	Number of species of coarse woody debris	0–4
sprucevl	Volume of coarse woody debris of black spruce	0–117.6 m ³ ha ⁻¹
firvl	Volume of coarse woody debris of balsam fir	0–126.6 m ³ ha ⁻¹
<i>Landscape characteristics measured within both radius $i=400$ or 800 m, leading to landscapes of 50 and 201 ha, respectively:</i>		
water _i	Area covered by lakes and rivers	0–58.7 ha ⁻¹
cut _i	Area covered by 0–20 yr cutovers	0–135.5 ha ⁻¹
<i>Variables closely associated to landscape structure:</i>		
structure _i	Number of landscape structure classes	2–11
oldeven _i	Area covered by old even-aged stands	0–197.4 ha ⁻¹
olduneven _i	Area covered by old uneven-aged stands	0–125.2 ha ⁻¹
<i>Variables closely associated to landscape composition:</i>		
composition _i	Number of landscape composition classes	1–10
sprucestand _i	Area covered by spruce stands, spruce-fir stands and spruce+spp. stands	0–177.9 ha ⁻¹
firstand _i	Area covered by fir stands, fir-spruce stands and fir+spp. stands	0–197.5 ha ⁻¹

we estimated the area covered by the main landscape component, i.e. old-even aged stands, old-uneven aged stands, spruce dominated stands and fir dominated stands.

Richness-habitat relationships were evaluated based on two dependent variables: 1) species richness of ground-dwelling beetles, measured from captures in pitfall traps and 2) species richness of flying beetles from captures in the multidirectional flight-interception trap. We developed 61 a priori biologically plausible models in order to verify hypothesis statements (Supplementary material, Appendix 1). To avoid statistical issues linked to overdispersion, we used negative binomial regressions to relate richness in beetle species and variables of habitat heterogeneity at the different scales. Some of the candidate models included variables describing forest composition only, some models included forest structure only, and other models included both types of variables. Similarly, some models described habitat heterogeneity at either the stand or landscape scale, whereas other models incorporated both spatial scales. We considered a balanced number of models to avoid biasing estimates toward a particular type of heterogeneity or scale. Candidate models were based on subsets of 29 potential independent variables (Table 1). A square-root transformation was applied to environmental variables with skewness >1 to approximate normal distribution (McCune and Grace 2002). Multicollinearity among explanatory variables was assessed using variance inflation factors. This verification led to the exclusion of volume of coarse woody debris

of black spruce (sprucevl) and of large diameter (largevl) from candidate models. Also, variance inflation factors indicated that effects of sampling year on species richness were already accounted for by latitude. Hence, only latitude was used in candidate models. In the end, we considered only models with variance inflation factor <2.5.

Model performance was evaluated using Akaike's information criterion corrected for small sample sizes (AIC_c, Anderson et al. 2000). AIC_c can identify the most parsimonious regression model, i.e. the one explaining most of the variance with the minimum number of parameters (Burnham and Anderson 2004). We used model averaging (Burnham and Anderson 2004) when the AIC_c weight of the top-ranking model was <0.95. Average parameter estimates and associated unconditional standard errors were calculated from the subset of top ranking models for which the sum of AIC_c weights reached ≥0.95. This subset of models can be viewed as a confidence set on the Kullback-Leibler best model (Burnham and Anderson 2004).

To determine the relative importance of forest composition versus structure on beetle richness, we compared the sum of AIC_c weights for models including compositional or structural variables only, and those including both type of variables (Burnham and Anderson 2004). To identify which spatial scale best explained beetle richness, we compared the sum of AIC_c weights for models including only variables estimated at the stand scale or at a landscape scale (400 or 800 m radius), and models including variables measured at

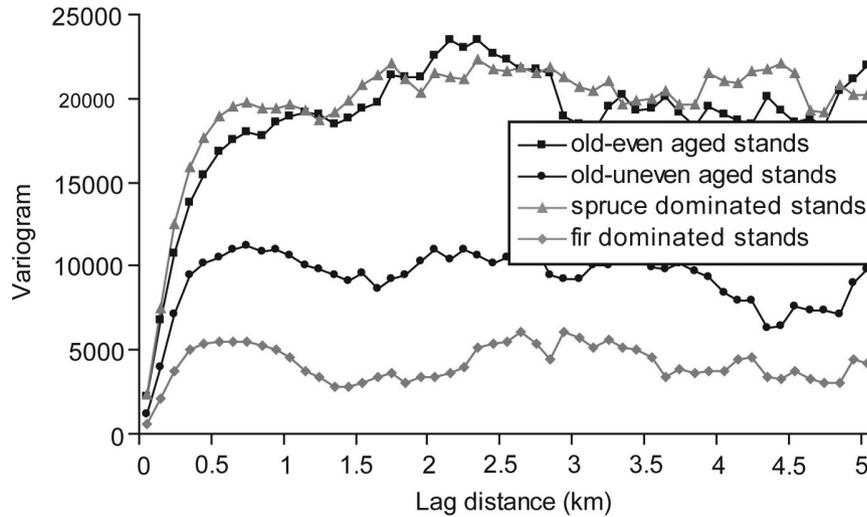


Figure 2. Variogram estimated for four vegetation cover classes in the boreal forest of the North Shore region of Québec, Canada.

both scales. Analyses were performed using SAS ver. 9.1 (Anon. 2003).

Results

Spatial autocorrelation became absent at distances >750 m for the major vegetation classes of the boreal forest of the North-Shore region of Québec, Canada (Fig. 2). Given that sampling sites were >2 km apart (Fig. 1), habitat attributes could be considered as independent among sites.

Beetle richness and habitat heterogeneity

A total of 313 beetle species (14 819 individuals), belonging to 53 families were captured at the 70 sites; 133 species (4236 individuals) from 21 families were caught in pitfall traps and 251 species (10 583 individuals) from 52 families in the multidirectional flight-interception traps. The most abundant species were *Epuraea planulata* (Nitidulidae) and *Rhizophagus dimidiatus* (Monotomidae). Ground-dwelling species richness averaged 16 species per site, with a range of

4–42 species, whereas flying species richness averaged 30 species per site, with a range of 16–58 species.

Species richness of ground-dwelling beetles

The top-ranking model (model 3; $w_3 = 0.31$, $r^2 = 41.8\%$ for the correlation between predicted and observed values) predicting species richness of ground-dwelling beetles only accounted for stand composition (Table 2). Model 3 was at least 2.8 times (i.e. $0.309/0.112$) more likely to explain species richness of ground-dwelling beetles than other models. Its AIC_c weight, however, was relatively low, indicating that other models also received a certain level of support (Burnham and Anderson 2004). We therefore combined the 12 best models ($\sum w = 0.963$) and used model averaging to draw inferences about the variables influencing ground-dwelling beetle richness. The top 10 models are displayed in Table 2. Species richness in ground-dwelling beetles increased with increasing heterogeneity in tree species composition (spstand) and diameter (ststand), as well as with the basal area of balsam fir (firba). In contrast, species richness decreased as the area of cutovers increased within a 400 m (cut_{400}) or an 800 m (cut_{800}) radius. The

Table 2. The 10 top-ranking models among 61 models (Supplementary material, Appendix 1) predicting richness of ground-dwelling beetles in 70 forest stands, as assessed with Akaike's information criterion corrected for small sample size (AIC_c). Number of estimated parameters including the intercept (K), AIC_c , the difference in AIC_c (ΔAIC_c), and AIC_c weight (w) are provided.

No.	Candidate model	K	AIC_c	ΔAIC_c	w
3	latitude spstand firba	4	-4007.2	0.0	0.309
42	latitude spstand ststand firba mediumba	6	-4005.2	2.0	0.112
46	latitude spstand ststand spruceba mediumba composition ₄₀₀ structure ₄₀₀ sprucestand ₄₀₀ oldeven ₄₀₀ cut ₄₀₀	11	-4005.0	2.2	0.105
41	latitude spstand ststand spruceba mediumba	6	-4004.8	2.4	0.094
16	latitude spstand spruceba firba composition ₄₀₀ sprucestand ₄₀₀ firstand ₄₀₀ water ₄₀₀ cut ₄₀₀	10	-4004.3	2.9	0.073
14	latitude spstand firba composition ₈₀₀ firstand ₈₀₀	6	-4004.2	3.0	0.069
13	latitude spstand firba composition ₄₀₀ firstand ₄₀₀	6	-4003.8	3.4	0.056
17	latitude spstand spruceba firba composition ₈₀₀ sprucestand ₈₀₀ firstand ₈₀₀	8	-4003.5	3.7	0.048
6	latitude spstand splog spruceba firba firvl	7	-4002.9	4.3	0.035
15	latitude spstand spruceba firba composition ₄₀₀ sprucestand ₄₀₀ firstand ₄₀₀	8	-4002.4	4.8	0.028

Table 3. The 10 top-ranking models among 61 models (Supplementary material, Appendix 1) predicting richness of flying beetles in 70 forest stands, as assessed with Akaike's information criterion corrected for small sample size (AIC_c). Number of estimated parameters including the intercept (K), AIC_c, the difference in AIC_c (Δ AIC_c), and AIC_c weight (w) are provided.

No.	Candidate model	K	AIC _c	Δ AIC _c	w
48	latitude spstand sstand firba mediumba composition ₄₀₀ structure ₄₀₀ firstand ₄₀₀ olduneven ₄₀₀ cut ₄₀₀	11	-9648.5	0.0	0.368
54	latitude spstand sstand stlog composition ₄₀₀ structure ₄₀₀	7	-9645.6	2.9	0.087
46	latitude spstand sstand spruceba mediumba composition ₄₀₀ structure ₄₀₀ sprucestand ₄₀₀ oldeven ₄₀₀ cut ₄₀₀	11	-9645.3	3.2	0.076
32	latitude stlog mediumvl structure ₄₀₀ oldeven ₄₀₀	6	-9645.1	3.4	0.069
34	latitude sstand mediumba mediumvl structure ₄₀₀ oldeven ₄₀₀ olduneven ₄₀₀	8	-9645.0	3.5	0.065
49	latitude spstand sstand firba mediumba composition ₈₀₀ structure ₈₀₀ firstand ₈₀₀ olduneven ₈₀₀ cut ₈₀₀	11	-9643.5	5.0	0.031
21	latitude mediumba largeba mediumvl	5	-9643.2	5.3	0.026
52	latitude spstand sstand splog composition ₄₀₀ structure ₄₀₀	7	-9643.0	5.4	0.024
43	latitude spstand stlog firvl mediumvl	6	-9643.0	5.4	0.024
40	latitude spstand sstand	4	-9642.9	5.6	0.023

influence of the other habitat attributes appeared less important, given that the 95% confidence interval of their regression coefficient included 0 (Table 4).

Species richness of flying beetles

The top-ranking model (model 48, $r^2 = 49.5\%$) was 4.8 times more likely to explain flying beetle richness than the second best model. However, the AIC_c weight of model 48 was low ($w_{48} = 0.37$). We used the 27 best models ($\Sigma w = 0.951$), the first 10 being displayed in Table 3, for model inference. Species richness of flying beetles increased with the heterogeneity in tree species composition (spstand), the basal area of large size trees (largeba), the volume of medium size woody debris (mediumvl), the area of

old-uneven stand within a 400 m radius (olduneven₄₀₀) and the area of cutovers within 400 or 800 m radii (cut₄₀₀ or cut₈₀₀). Richness of flying beetles decreased with increasing latitude and as the heterogeneity of stand structure within 400 or 800 m radii (structure₄₀₀ or structure₈₀₀) increased. Other habitat attributes appeared to have little influence on flying beetle richness, given that the 95% confidence interval of their regression coefficient included 0 (Table 4).

Beetle richness and types of heterogeneity

The sum of AIC_c weights for models including compositional variables (models 1–20), structural variables (models

Table 4. Average coefficients and confidence intervals (CI) for each variable of the 12 most parsimonious models predicting richness of ground-dwelling beetles (first 10 provided in Table 2) and each variable of the 27 most parsimonious models (first 10 provided in Table 3) predicting richness of flying beetles in a forest matrix dominated by old-growth boreal stands. The 95% confidence interval of coefficients in bold excluded 0.

Variable	Ground-dwelling		Flying	
	Average coeff.	(95% CI)	Average coeff.	(95% CI)
latitude	8.21 _{E-07}	(-6.6 _{E-07} , 2.3 _{E-06})	-2.30_{E-06}	(-3.6_{E-06}, -1.0_{E-06})
spstand	0.0872	(0.024, 0.150)	0.0675	(0.028, 0.107)
sstand	0.0501	(0.008, 0.093)	0.0147	(-0.010, 0.039)
firba	0.0112	(0.006, 0.017)	-0.0007	(-0.004, 0.003)
spruceba	-0.0076	(-0.016, 0.000)	-0.0033	(-0.007, 0.000)
mediumba	0.0134	(-0.006, 0.033)	0.0032	(-0.004, 0.011)
largeba	-	-	0.0057	(0.001, 0.011)
splog	-0.0017	(-0.094, 0.090)	0.0144	(-0.041, 0.070)
stlog	-	-	0.0082	(-0.013, 0.030)
firvl	-0.0020	(-0.006, 0.002)	-0.0004	(-0.003, 0.002)
mediumvl	-	-	0.0103	(0.002, 0.018)
composition ₄₀₀	0.0408	(-0.022, 0.104)	0.0089	(-0.029, 0.047)
structure ₄₀₀	0.0336	(-0.033, 0.101)	-0.0661	(-0.110, -0.022)
firstand ₈₀₀	-0.0045	(-0.021, 0.012)	-0.0015	(-0.008, 0.005)
sprucestand ₈₀₀	-0.0043	(-0.016, 0.008)	0.0041	(-0.002, 0.010)
oldeven ₈₀₀	0.0002	(-0.005, 0.006)	-0.0024	(-0.006, 0.001)
olduneven ₈₀₀	-0.0025	(-0.011, 0.006)	0.0068	(0.001, 0.013)
water ₄₀₀	-0.0181	(-0.052, 0.016)	0.0051	(-0.016, 0.026)
cut ₄₀₀	-0.0172	(-0.029, -0.004)	0.0079	(0.002, 0.014)
composition ₈₀₀	0.0304	(-0.035, 0.096)	0.0171	(-0.031, 0.065)
structure ₈₀₀	0.0391	(-0.002, 0.004)	-0.0342	(-0.067, -0.001)
firstand ₈₀₀	0.0012	(-0.002, 0.004)	-0.0020	(-0.004, 0.001)
sprucestand ₈₀₀	0.0007	(-0.003, 0.004)	0.0006	(-0.002, 0.003)
oldeven ₈₀₀	0.0003	(-0.002, 0.002)	-0.0008	(-0.002, 0.001)
olduneven ₈₀₀	-	-	0.0021	(-0.0005, 0.004)
cut ₈₀₀	-0.0039	(-0.006, -0.001)	0.0022	(0.001, 0.003)

21–39) or both types of variables (models 40–61) (see Supplementary material, Appendix 1 for model descriptions) revealed that the type of habitat heterogeneity influencing species richness differed between ground-dwelling and flying beetles (Fig. 3). Species richness of ground-dwelling beetles was mostly influenced by compositional heterogeneity. Seven of the top 10 models included only attributes of forest composition (Table 2). Cumulative AIC_c weight for all models including only compositional variables was 0.65. In contrast, species richness of flying beetles was influenced by both compositional and structural heterogeneity. The top three models included both types of heterogeneity (Table 3). Also, the cumulative AIC_c weight for models including a combination of compositional and structural variables was 0.70.

Beetle richness and scales of heterogeneity

Species richness of ground-dwelling beetles was a function of multiple scales, although models based only on stand characteristics performed slightly better than those combining both stand and landscape attributes (Fig. 4). Species richness of flying beetles was associated with attributes of both scales (stand and landscape within 400 m, Fig. 4). The weight of evidence favoured models accounting for both scales of attributes 4.88 times (i.e. $0.825/0.169$) more than models based on stand characteristics alone. For the two groups of beetles, models of species richness performed better when landscape variables were measured within a 400 m than an 800 m radius (Fig. 4). However, the six models including only landscape variables (models 56–61) were poor predictors of beetle richness (Fig. 4).

Discussion

Our study shows that the compositional and structural components of forest heterogeneity have distinct consequences on the species richness of ground-dwelling and

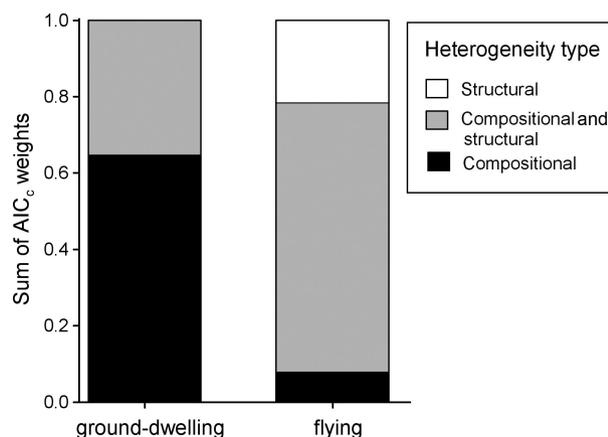


Figure 3. Influence of types of habitat heterogeneity on the richness of ground-dwelling and flying beetles in old-growth boreal forests. Sums of AIC_c weights are provided for models based exclusively on compositional variables, on structural variables or on both types of variables.

flying beetles in boreal landscapes dominated by old-growth forests. Our findings are significant because habitat heterogeneity studies commonly integrated compositional and structural heterogeneity into a single index simply referred to as “structural” heterogeneity or complexity (McElhinny et al. 2005). This has resulted in guidelines for sustainable management that put more emphasis on structural than compositional components of forests (Lindenmayer et al. 2006). The preservation of biodiversity is recognized as a criterion of sustainable management in most countries (Lindenmayer et al. 2000, Kuuluvainen 2002), and our results outline the importance of considering compositional heterogeneity for beetle richness in a forest mosaic dominated by old-growth stands. Schaffers et al. (2008) also reported that plant species composition was a better predictor of arthropod assemblages than vegetation structure in grassland ecosystems. They argue that the importance of vegetation structure is integrated by plant species composition.

Richness of ground-dwelling beetles was influenced primarily by compositional heterogeneity, i.e. the number of tree and shrub species and the basal area of balsam fir. Models that accounted for both compositional and structural heterogeneity also received some support, indicating that stand structure (e.g. the number of diameter classes of standing trees) also appeared to influence the richness of ground-dwelling beetles. Previous studies have reported a positive effect of habitat heterogeneity on biodiversity in this group of beetles (Lassau et al. 2005), but only few studies have investigated the relative contribution of different types of habitat heterogeneity on ground-dwelling beetles (Brose 2003, González-Megías et al. 2007). Higher compositional heterogeneity in old-growth boreal forests might be associated with greater amounts of resources at ground level (e.g. leaf litter), which may have a positive effect on biodiversity.

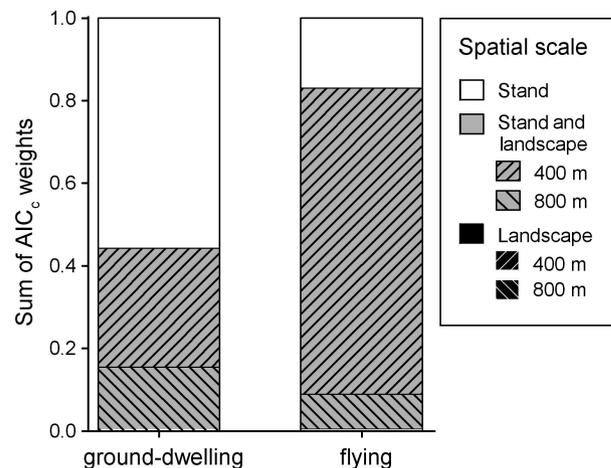


Figure 4. Influence of heterogeneity estimated at different spatial scales on the richness of ground-dwelling and flying beetles in boreal landscapes dominated by old-growth forests. Sum of AIC_c weights are provided for models based exclusively on stand variables, on landscape variables or on variables estimated at both scales. The hatched bar indicates the relative contribution of models including variables measured at 400 m and 800 m radii, within models including stand and landscape variables and models including exclusively landscape variables.

Indeed, amount of leaf-litter has been shown to increase ground-dwelling beetle richness (Lassau et al. 2005) and affect assemblage structure of carabid beetles (Koivula et al. 1999). Similarly, balsam fir may have a positive effect on species richness because its relative abundance generally increases with time since fire (Bouchard et al. 2008). Balsam fir therefore may be related to multiple characteristics of old-growth forest stands, such as large amount and high diversity of dead wood, as well as the presence of deciduous trees or shrubs that colonize forest gaps following fine-scale canopy disturbances. The presence of balsam fir may be indicative of particular habitat conditions that generally support rich ground-dwelling beetle assemblages. In our study, the abundance of the two dominant species of carabid beetles, *Pterostichus punctatissimus* and *Stereocerus haematopus*, and of the two dominant taxa of staphylinid beetles, *Tachinus frigidus* and *Atheta (Dimetrota) sp.*, all predators, increased with the presence and abundance of balsam fir.

Unlike the ground beetles, compositional heterogeneity alone explained poorly the spatial variations in local richness of flying beetles. Instead, species richness of flying beetles was influenced by both structural and compositional attributes of forest heterogeneity. Flying beetles occupying an old-growth forest mosaic display a wide range of diets and use many microhabitats, potentially explaining why both forest composition and structure influenced species richness. Richness decreased with landscape structural heterogeneity (i.e. number of landscape structural classes found within 400 or 800 m, among the 14 possible land cover types). This is contrary to the positive link between richness and heterogeneity usually reported in the literature (Tews et al. 2004). One plausible explanation for our results is that beetle flight is favoured in habitats characterized by simple vertical structures (Lassau et al. 2005). The latter hypothesis could also explain the negative effect of structural heterogeneity on flying beetle richness observed at landscape scales. In contrast, flying beetle richness increased with compositional heterogeneity or the number of tree and shrub species. The presence of deciduous trees in coniferous stands has been reported to increase the richness of non-saproxylid beetles (Martikainen et al. 2000) and saproxylid beetles (Bakke 1999), a trend consistent with our results. The richness of saproxylid species depends on various attributes linked to the quantity and diversity of dead wood (Økland et al. 1996, Franc et al. 2007). In our study, richness of flying beetles increased with the basal area of large trees and the volume of coarse woody debris, two habitat attributes strongly associated with saproxylid beetles (Martikainen et al. 2000). Flight-interception traps are known as efficient tools for catching saproxylid insects (Økland 1996), and such species ended up making ca 70% of the total richness of flying beetles in our study. The most abundant species caught in our study, the predatory *Rhizophagus dimidiatus* was most abundant in oldest stands, where CWD were also more abundant. Other species of *Rhizophagus* have been reported to be more abundant in large felling areas at broad scale (314 ha) after windstorm in French forests (Bouget 2005).

Spatial scale also influenced species richness of beetles. The richness of flying beetles was a function of both stand

and landscape attributes, whereas the richness of ground-dwelling beetles was influenced mostly by stand attributes. The greater mobility of flying beetles may make them more likely than ground dwelling beetles to respond to landscape features measured over broad spatial extents (With and Crist 1995). In agricultural landscape, the richness of most soil macroarthropod taxa was better explained by variables measured at the local scale (i.e. land use and habitat characteristics) than by those measured at landscape scales (i.e. composition of the neighbouring landscape) (Dauber et al. 2005). Fine-scale habitat heterogeneity should be particularly important for species with reduced mobility because it reflects variations in microhabitat and resource availability (Niemelä et al. 1996). In contrast, species richness of saproxylid flying beetles in the Norwegian boreal forest was weakly linked to forest attributes measured at fine scales (0.16 ha) compared to landscape scales of 1 and 4 km² (Økland et al. 1996). Similarly, in temperate mixed forest of southern Sweden, saproxylid beetle richness was more closely associated to oak woodland attributes estimated at regional (within 1 km of sampled sites) rather than local scale (Franc et al. 2007).

Although landscape features had less influence on the richness of ground-dwelling than flying beetles, both groups displayed a certain level of response to landscape attributes. The abundance of cutovers in the surrounding landscape decreased the richness of ground-dwelling beetles in residual forest stands but increased the richness of flying beetles. Cutovers may harbour different animal communities than closed stands (Koivula and Niemelä 2002, Similä et al. 2002a, Martikainen et al. 2006). Adults of flying beetles such as *Emmesa connectans* (Melandryidae) and *Mordellaria borealis* (Mordellidae) are known to be floricolous and, as they are relatively mobile, their probability of being captured in adjacent forest stands is thus likely to be increased by the proximity of flowering plants, which are abundant in cutovers. Certain flying beetles may also be attracted by the warmer conditions found in cutovers and forest edges than under forest canopy. Also, the less mobile ground-dwelling beetles may disperse over relatively small distances, and they may favour movements between relatively similar land cover types (e.g. among forested stands). In fact, the availability and connectivity of mature stands would appear essential to maintain forest-specialist carabid species, and forest gaps exceeding 50–200 m would already act as a barrier (Koivula and Niemelä 2002). Similarly, we found that cutovers had a negative effect on ground-dwelling beetle richness, highlighting the sensitivity of these species to habitat perturbations. In the boreal forest, logging operations may thus induce fragmentation that may be detrimental for less mobile beetle species by constraining their dispersal ability, impeding resource acquisition (Saunders et al. 1991) and impacting on population size (Williamson 1981). This might be true for the carabid *Scaphinotus bilobus*, a snail predator rarely caught in eastern North America and for which we found seven individuals exclusively in forests of > 120 yr, in seven different sites.

Forest practices aiming sustainable management should account for species response to fine-scale heterogeneity and

to forest mosaic characteristics (Niemelä et al. 1996) in managed landscapes dominated by old-growth forest. We suggest that management strategies should consider that forest harvesting impacts species richness at distances reaching 400 m (Fig. 4) inside adjacent forest stands, even for animals as small as insects.

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