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Ermias T Azeria, Daniel Fortin, Jérôme Lemaître, Philippe Janssen, Christian Hébert, et al.. Fine-scale structure and cross-taxon congruence of bird and beetle assemblages in an old-growth boreal forest mosaic. *Global Ecology and Biogeography*, 2009, 18 (3), pp.333-345. 10.1111/j.1466-8238.2009.00454.x . hal-04145505

HAL Id: hal-04145505

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Fine-scale structure and cross-taxon congruence of bird and beetle assemblages in an old-growth boreal forest mosaic

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ABSTRACT

Aim Nestedness occurs when species present in depauperate sites are subsets of those found in species-rich sites. The degree of congruence of site nestedness among different assemblages can inform commonalities of mechanisms structuring the assemblages. Well-nested assemblages may still contain idiosyncratic species and sites that notably depart from the typical assemblage pattern. Idiosyncrasy can arise from multiple processes, including interspecific interactions and habitat preferences, which entail different consequences for species co-occurrences. We investigate the influence of fine-scale habitat variation on nestedness and idiosyncrasy patterns of beetle and bird assemblages. We examine community-level and pairwise species co-occurrence patterns, and highlight the potential influence of interspecific interactions for assemblage structure.

Location Côte-Nord region of Québec, Canada.

Methods We sampled occurrences of ground-dwelling beetles, flying beetles and birds at sites within old-growth boreal forest. We examined the nestedness and idiosyncrasy of sites and sought relationships to habitat attributes. We analysed non-random species co-occurrence patterns at pairwise and community levels, using null model analysis and five 'association' indices.

Results All three assemblages were significantly nested. There was limited congruence only between birds and flying beetles whose nestedness was related to canopy openness. For ground-dwelling beetles, nestedness was related to high stand heterogeneity and sapling density, whereas site idiosyncrasy was inversely related to structural heterogeneity. For birds, site idiosyncrasy increased with canopy cover, and most idiosyncratic species were closed-canopy specialists. In all assemblages, species idiosyncrasy was positively correlated with the frequency of negative pairwise associations. Species co-occurrence patterns were non-random, and for flying beetles and birds positive species pairwise associations dominated. Community-level co-occurrence summaries may not, however, always reflect these patterns.

Main conclusions Nestedness patterns of different assemblages may not correlate, even when sampled at common locations, because of different responses to local habitat attributes. We found idiosyncrasy patterns indicating opposing habitat preferences, consistent with antagonistic interactions among species within assemblages. Analysis of such patterns can thus suggest the mechanisms generating assemblage structures, with implications for biodiversity conservation.

Keywords

Association indices, community structure, diversity, habitat heterogeneity, idiosyncrasy, irregular forest, nestedness, Québec, species co-occurrence.

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INTRODUCTION

Quantifying assemblage structure and revealing causal mechanisms are central to the discipline of biogeography and, increasingly, of conservation biology (Ricklefs, 2004). Another fundamental question is also whether different assemblages that are spatially congruent are structured similarly. Such similarities may help to identify surrogate groups for total regional biodiversity, with applications to conservation planning (Hansson, 1998; Fleishman *et al.*, 2002; Pinto *et al.*, 2008). Species richness is often used to describe and evaluate the congruence of distributional patterns across assemblages, but richness is uninformative about the patterns of species composition within and between assemblages. In contrast, quantitative measures such as patterns of nestedness and complementarities provide additional mechanistic insight into composition pattern (Azeria, 2004a; Pinto *et al.*, 2008).

Nestedness measures the degree to which the communities in species-poor sites are subsets of those found in species-rich sites (Patterson & Atmar, 1986). Nestedness thus provides a more comprehensive framework for species assemblage by considering both richness and composition. Several mechanisms have been proposed to explain observed patterns of nestedness, such as differential extinction or colonization rates, nested distributions of habitats, niche structure and passive sampling (Wright *et al.*, 1998; Hylander *et al.*, 2005; Azeria & Kolasa, 2008). When different assemblages exhibit highly congruent nestedness patterns, one may infer that they were structured by common, or correlated, causal factors.

An important, but rarely addressed, feature of many well-nested assemblages is that they may still contain *idiosyncratic* species and sites (communities) that notably depart from the typical assemblage nestedness (Atmar & Patterson, 1993; McAbendroth *et al.*, 2005; Azeria *et al.*, 2006). Idiosyncratic species may have biased distributions towards species-poor sites (e.g. Azeria *et al.*, 2006), or exhibit characteristically segregated co-occurrence patterns with other species (Simberloff & Martin, 1991). Species idiosyncrasy may be explained by limited overlap in habitat selection relative to the majority of species in an assemblage (McAbendroth *et al.*, 2005; Azeria *et al.*, 2006) or by antagonistic interspecific interactions such as competition (Patterson & Atmar, 2000). Biased immigration from source pools (Azeria 2004a) and other biogeographical processes, such as allopatric speciation, may give rise to idiosyncrasies over biogeographical and macroecological scales (Atmar & Patterson, 1993; Patterson & Atmar, 2000). Similarly, idiosyncratic sites may depart from regional nestedness patterns, presumably because they contain some unique features such as rare habitats critical for the existence of many idiosyncratic species (Azeria *et al.*, 2006). In summary, idiosyncratic species and sites may reflect ecological and biogeographical processes that are distinct from the process organizing the majority of the assemblage structure (Simberloff & Martin, 1991). Thus, patterns of idiosyncrasy may provide insight into assemblage structure-generating mechanisms, independent of overall patterns of nestedness.

The specific mechanisms of species- and site-specific idiosyncrasy have rarely been addressed (McAbendroth *et al.*, 2005; Azeria *et al.*, 2006). In particular, to our knowledge, no study has explicitly investigated the relationship between species idiosyncrasy and the frequency of exclusive distributions. We contend that null model analyses of pairwise species associations (e.g. Sanderson, 2000) can clarify whether idiosyncratic species have more frequent exclusive distributions than species conforming to overall assemblage nestedness.

The present study investigates patterns of nestedness and idiosyncrasy of birds, ground-dwelling beetles and flying beetles within an old-growth boreal forest mosaic in the Côte-Nord region of Québec, Canada. In this region, small-scale gap dynamics driven by windthrow, insects and forest pathogens, and other causes of individual or small-group tree mortality have created a complex forest structure (Pham *et al.*, 2004). This heterogeneity, in turn, influences the distributions of fauna (e.g. Hannon, 2005; Lassau *et al.*, 2005). We investigated: (1) whether species distributions are nested and congruent amongst three assemblages; (2) whether stand-level habitat attributes influence the nestedness and idiosyncrasies of communities and if they are similar amongst the assemblages; (3) whether pairwise species and community-level co-occurrence patterns are non-random; and (4) whether the incidence of significant pairwise associations, especially negative associations, is related to species idiosyncrasy. Finally, for a subset of species occurring in both the ground-dwelling and flying beetle assemblages, we tested (5) whether their pairwise association is consistent in both assemblages.

METHODS

Study area and data collection

The study was conducted in the boreal forest of the Côte-Nord region of Québec, Canada (Fig. 1). The study area is characterized by a humid climate, with annual precipitation from 1000 to 1400 mm and mean annual temperature from -2.5 to 0.0 °C (Pham *et al.*, 2004). The region is characterized by a dominance of old-growth forest stands (> 120 years old). Major 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 frequently observed. We sampled faunal distribution and vegetation structure at 108 forest 'stands', or polygons of relatively 'homogeneous' structure as mapped by forest inventories. The stands were between 50 and over 120 years old and at least 5 ha in size. The stands were typically embedded within a continuous forest matrix, at a minimum distance of 2 km (range 2–194 km) from each other.

Beetle assemblages

Beetles were sampled at 87 sites over 2 years: 2 June to 17 August 2004 (44 sites) and 7 June to 15 August 2005 (43 sites). Flying-beetles were sampled using a multidirectional flight-intercept trap (Janssen, 2008), suspended 1 m above the centre of a plot on

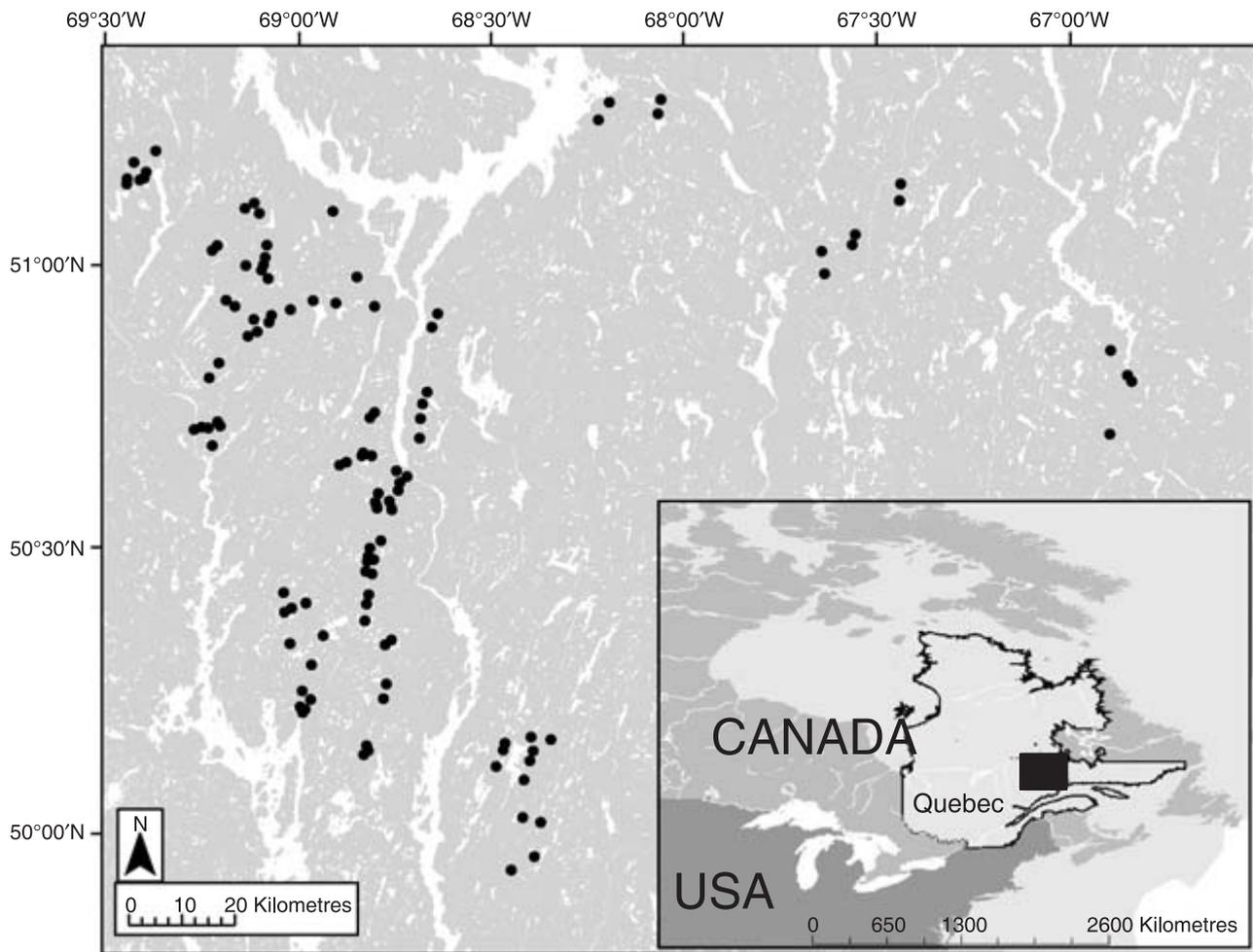


Figure 1 Map showing site locations and (inset) general location of the study area in Québec, Canada.

a rope between two live trees. Ground-dwelling beetles were sampled with four pitfall traps (Janssen, 2008) placed in cardinal directions, 7 m from the centre of the plot. All beetles caught were identified to species whenever published keys or other literature permitted. The exception was members of the group Aleocharinae (Staphylinidae) which could not be classified below genus level. Vouchers were deposited at the Insectarium René-Martineau, Laurentian Forestry Centre, Canadian Forest Service and at the Université Laval insect collection. Identifications were validated by specialists or cross-checked at the Canadian National Collection of insects, arachnids and nematodes in Ottawa, Ontario, Canada.

Bird assemblages

Breeding birds were sampled at 104 sites using 10' point count surveys (Verner, 1985). Sampling was conducted between 11 June and 8 July 2004 (52 sites) and 1 June and 25 June 2005 (52 sites). A single point-count station was located at the centre of each stand. Each station was sampled twice (2 weeks apart) between 04:00 h and 10:00 h. Observers recorded the species of

all individuals heard or seen within 100 m. In total, 74 stands were sampled for both beetles and birds.

Vegetation structure

We sampled stand characteristics known or expected to influence species distributions of boreal beetles (e.g. Niemelä, 1997) and birds (e.g. Imbeau *et al.*, 1999; Hannon, 2005). Three 400-m² circular plots were established in each stand, one at the centre and the other two at 60 m from the centre in opposite directions. In each plot, we recorded the species and diameter at breast height (d.b.h.) for each tree and snag with d.b.h. \geq 9 cm. Canopy heights were measured from clinometer readings of two dominant trees within each plot. We counted all saplings (d.b.h. < 9 cm) in two 2 \times 20 m perpendicular subplots (six per stand). We sampled coarse woody debris (minimum diameter \geq 10 cm) within the central plot by measuring end diameters and lengths for each log. The thickness of ground lichens was estimated in four 1 \times 1 m quadrats placed in cardinal directions, 4 m from the centre of each plot. Canopy closure was estimated from five measurements taken at plot centres and their midpoints using a densiometer.

We used principal components analysis to reduce the dimensionality of the measured habitat variables. Principal components (PCs) were extracted using a correlation matrix on the stand-level variables, standardized to mean 0 and variance 1. Variables were first log-transformed or arcsine square root-transformed, as necessary, to approximate multivariate normal distributions. We retained important and interpretable axes by evaluating a scree plot, i.e. by inspecting the inflection of eigenvalue magnitudes. We determined the significance of variable loading into each axis using a broken-stick bootstrap test (Peres-Neto *et al.*, 2003).

DATA ANALYSES

Nestedness analysis of species assemblages

We examined the nestedness pattern of ground beetle, flying beetle and bird assemblages using the Binary Matrix Nestedness Temperature Calculator (BINMATNEST, Rodríguez-Gironés & Santamaría, 2006). This metric is based on Atmar and Patterson (1995) – with improvements to maximally pack the species-by-site matrix and estimate the distance from the isocline (see below). The method calculates a metric ‘temperature’ (T) – a measure of deviation of the observed data distribution from perfect nestedness (Atmar & Patterson, 1993; Rodríguez-Gironés & Santamaría 2006). The temperature will be zero in a perfectly nested species-by-site matrix with all presences occurring in the upper-left corner of a theoretical isocline, which defines the maximum packing given the matrix size and fill (Atmar & Patterson, 1993). The matrix temperature increases with unexpected empty cells above the isocline (holes) and unexpected filled cells (outliers) below the line. The ‘unexpectedness’ of cells further from the isocline is given a higher weight than cells near the isocline. In other words, the unexpectedness of the absence of the most common species from the most species-rich site is given a higher weight than its absence from a moderately species-rich site (for details see Atmar & Patterson, 1993). The degree of unexpectedness of cells is used to calculate the indices of matrix temperature (assemblage-level departure from nestedness), and the idiosyncratic temperatures for each species (species-specific idiosyncrasy) and for each site (site-specific idiosyncrasy).

BINMATNEST packs the matrix elements to minimize matrix temperature (i.e. maximum nestedness), and then tests its statistical significance by comparing the metric value with that of null communities ($n = 1000$) generated by randomizing the original matrix (Rodríguez-Gironés & Santamaría, 2006). In this study, we employ the null model recommended by Rodríguez-Gironés and Santamaría (2006), where the probability of each cell in the species-by-site matrix being occupied is the average of its row and column occupancy probabilities. Recently, Ulrich and Gotelli (2007a) recommended the use of a fixed–fixed (FF) null model (i.e. a null model that holds both row and column total fixed) to evaluate nestedness, suggesting that the method was less vulnerable to type I errors than other null models. The FF null model, however, leads to a high risk of type II error, i.e. of

falsely accepting the null hypothesis that assemblages are not nested (risk as high as 98%, see Table 2 in Ulrich & Gotelli, 2007a). The FF model could also incorporate the mechanisms responsible for site and species nestedness in the null communities by keeping occupancy probabilities fixed (Jonsson, 2001). The debate over the choice of null models has yet to be resolved (see Jonsson, 2001; Ulrich & Gotelli, 2007a).

The absolute metric value is potentially dependent on matrix dimension (see also Wright *et al.*, 1998; Rodríguez-Gironés & Santamaría, 2006; Ulrich & Gotelli 2007a) or may ‘overestimate’ nestedness (Almeida-Neto *et al.* 2008). The latter criticisms only limit the use of the absolute metric value to comparing the degree of nestedness across different assemblages. The size and fill of the matrix does not influence the test for nestedness because both are the same in observed and ‘null’ matrices (Rodríguez-Gironés & Santamaría, 2006; Greve & Chown 2006). The BINMATNEST algorithm should alleviate such size dependency (Rodríguez-Gironés & Santamaría, 2006). We also examined the nestedness of assemblages using the various nestedness metrics in the program NESTEDNESS (Ulrich 2006) and the metric NODF recently proposed by Almeida-Neto *et al.* (2008). The results were qualitatively similar regardless of the choice of metric, so here we only report the results using the BINMATNEST method.

Habitat correlates of stand nestedness, idiosyncrasy and their congruence across assemblages

To examine potential effect of habitat on nestedness we calculated Spearman’s rank correlations between stands nestedness ranks and habitat PC scores (e.g. Patterson & Atmar, 2000). Similarly, we assessed whether the departure of site communities from nestedness was related to habitat characteristics based on correlations between site idiosyncrasy and PC scores. We also tested for congruence of nestedness among the three assemblages by calculating pairwise Spearman’s rank correlations between nested ranks of sites according to each assemblage.

Species-specific idiosyncrasy and its relationship to pairwise species associations

We assessed the relationship between species-specific idiosyncrasy temperature (score) and the frequency of a species’ negative pairwise associations, which may indicate interspecific competition (Rejmánek & Lepš, 1996). We determined the sign and significance of pairwise species associations using null model analysis (Sanderson, 2000). We measured mutual exclusivity of species pairs with the checkerboard units (CU) index (Stone & Roberts, 1990). This is expressed as $CU = B \times C$, where B is the number of sites where species 1 is present but species 2 is absent and C is the converse. The community average of the checkerboard units, designated as the C -score, may not reveal whether mutually exclusive distributions dominate (Sfenthourakis *et al.*, 2006). We suspect this is because the CU is not standardized by species incidence so that the community average (C -score) may be inflated in cases where a few common species

are highly mutually exclusive or vice versa. We therefore standardized the CU index by applying the following equation: $SCU = (B \times C) / (N_1 \times N_2)$. The community-level summary of SCU or the average of all SCU for pairs of species is referred to as the StC-score. For species pairwise analysis, we employed also an index of association based on the number of common presence or shared sites (SS), i.e. $SS = A$ (Sfenthourakis *et al.*, 2006; Roberts & Stone, 1990). However, SS is not amenable to community-level tests as the mean number of shared sites across all possible pairs of species cannot change in the randomized matrices generated by the fixed-fixed null model (for details see Roberts & Stone, 1990) employed in this study. Therefore, we also calculated two standardized forms of the SS: the Sorensen index, $SOR = 2A / (2A + B + C)$ (Dice, 1945), and the Jaccard index, $JAC = A / (A + B + C)$ (Krebs, 1999), where A is the number of sites where both species are present and B and C are as above.

We assessed species co-occurrences using the FF null model that randomizes species co-occurrences independently, constrained by observed species incidences (fixed row totals) and site richness (fixed column totals). This null model is believed to be robust against type I and II statistical errors in a species co-occurrence analysis (Gotelli, 2000). Its sensitivity (and slight bias) towards detecting negative associations (Azeria, 2004b; Ulrich & Gotelli, 2007b) also makes FF null models desirable when studying relationships of species-specific idiosyncrasy and exclusive distributions. The FF null model, however, may implicitly incorporate species and site properties that determine interspecific interactions (and their outcome) into the null communities (Gilpin & Diamond, 1982; Sfenthourakis *et al.*, 2006), resulting in a conservative estimate of co-occurrence patterns (Jackson *et al.*, 1992). We generated 1000 random matrices by the sequential swap algorithm using EcoSim (Gotelli & Entsminger, 2006). We used a custom code to upload the EcoSim output matrices into R version 2.5.0 (R Development Core Team, 2007) and tested pairwise species association indices.

If the observed CU and SCU is larger than in the random matrices, it indicates negative association, and vice versa. The opposite is true when using the SS, SOR and JAC indices. For pairwise species-association tests, we report mainly results for species with an incidence of at least 5%, which included 89–92% of the species occurrences. A subset of beetle species was recorded in both the flying and ground-dwelling assemblages.

We extracted their pairwise associations in each assemblage to assess association consistency over space.

Finally, we tested the significance of community-level species co-occurrences by computing standardized effect size, SES (e.g. Gotelli, 2000) for each association index. $SES = (I_{Obs} - I_{Sim}) / \sigma_{Sim}$, where I_{Obs} is the mean index value between all species pairs in the observation matrix, and I_{Sim} and σ_{Sim} are, respectively, the mean and standard deviations of the index value in the simulated matrices. SES values greater than 1.98 ($P < 0.05$) indicate a segregated distribution using the index C-score and StC-score and aggregated distribution using the SOR or JAC indices, and vice versa when SES values are less than -1.98.

RESULTS

Nestedness of assemblages

We recorded 156 ground-dwelling beetle species, 286 flying beetle species and 64 bird species (Table 1; see Appendix S2 in the Supporting Information for summaries of beetle species by family). In total 350 species (7325 specimens) of ground-dwelling and flying beetles were recorded, of which 92 species were recorded in both assemblages. If we consider only species recorded in more than 5% of the stands, only 24 species were common to both assemblages. Thus, the two assemblages were largely distinct in terms of species composition.

Nestedness temperatures for all three assemblages were significantly lower than the simulated mean under the null model, which indicates that the species found in species-poor stands were generally a subset of those found in species-rich stands (Table 1). However, each assemblage contained idiosyncratic species and stands (communities) having a higher 'temperature' (hereafter idiosyncrasy score) than the matrix as a whole (Table 1 and Fig. 2; for species lists and a breakdown by families see Appendices S1 and S2).

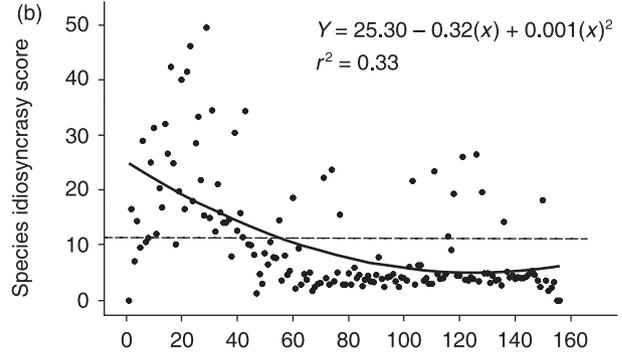
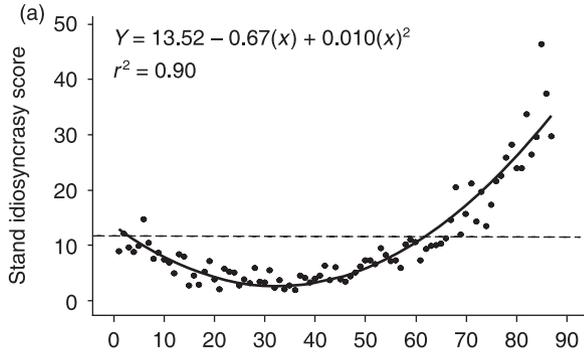
Habitat correlates of stand nestedness, idiosyncrasy and their congruence across assemblages

We retained three PCs that explained 69% of the variance in composition and structure of forest stands (Table 2). Ten of the 13 variables loaded into the first principal component (PC1) accounted for 42.3% of the variance. PC1 represented the 'structural complexity' of stands including the mean and

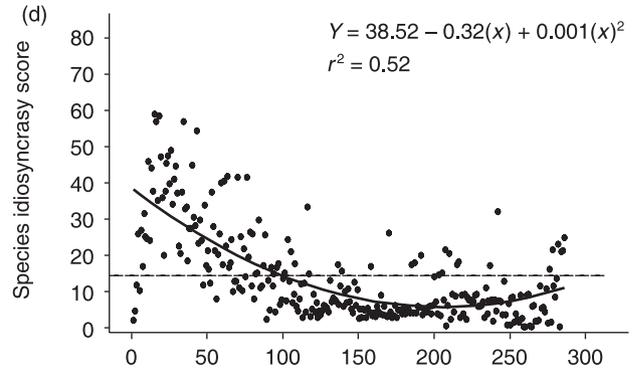
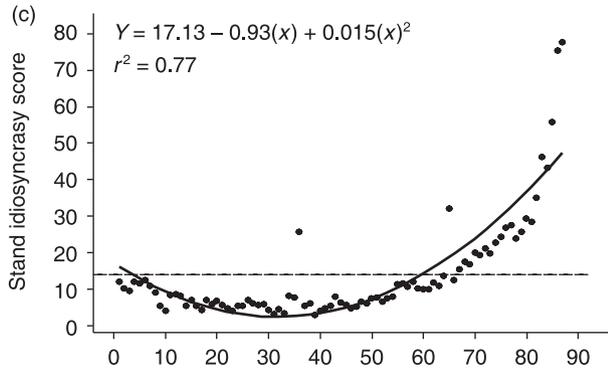
Table 1 Number of sampled stands for bird and beetle species and total number of species detected (percentages of idiosyncratic sites and species in parenthesis). T_{OBS} is the observed temperature and T_{Null} (SD) is the mean and standard deviation of assemblage temperatures generated under null model. P indicates the significance level that the observed assemblages are more nested than null communities.

	Number of stands	Number of species	T_{OBS}	T_{Null} (SD)	$P(T_{Null} \leq T_{OBS})$
Ground beetles	87 (27.6%)	156 (32.7%)	10.51	25.74 (1.40)	< 0.001
Flying beetles	87 (26.4%)	286 (36.0%)	13.87	29.85 (0.90)	< 0.001
Birds	104 (36.5%)	64 (31.3%)	13.92	31.86 (1.62)	< 0.001

Ground-dwelling beetles



Flying beetles



Birds

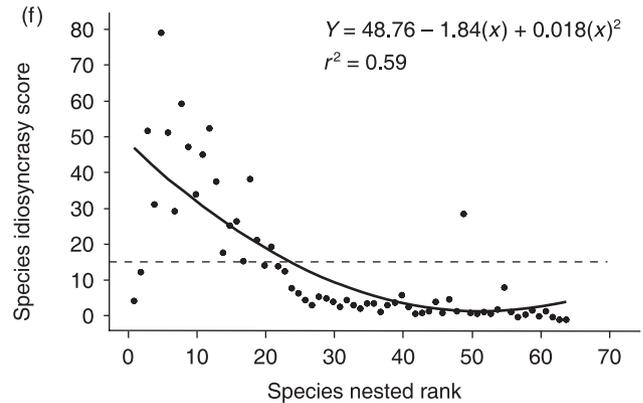
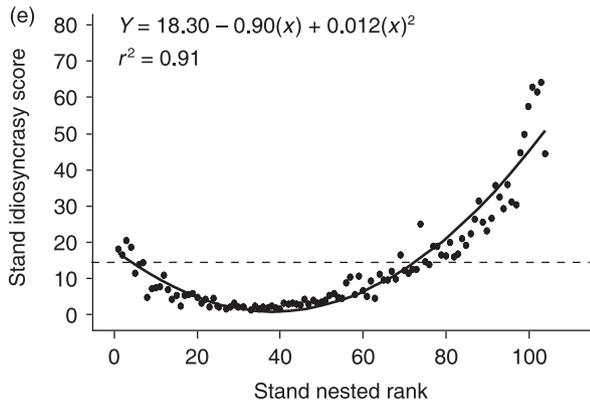


Figure 2 The relationship between stand- and species-specific idiosyncrasy score and the respective nested rank of stands and species. The broken line is mean matrix temperature of the observation data.

variability of the d.b.h. of trees and snags, volume of coarse woody debris and tree height. Moreover, PC1 contrasted stands with a relatively high proportion of balsam fir from those dominated by black spruce. In addition, PC1 was negatively correlated with the thickness of ground lichens. The second principal component (PC2) exhibited positive loading of live tree density and canopy closure representing variation in ‘canopy cover’. The third principal component (PC3) was positively correlated with sapling density.

In a maximally nested matrix, sites are largely ranked by decreasing order of species richness, such that species-rich sites

rank high (small digits) and species-poor sites rank low (large digits). For ground-dwelling beetles, stand nestedness rank was negatively correlated with PC1 and PC3 (Table 3), indicating that species found in stands with low structural complexity and sapling density were a subset of stands with high structural complexity and sapling density. Nestedness ranks of flying beetle and bird assemblages, however, were correlated only with PC2 (an index of canopy cover), such that stands with high nestedness ranking tended to have low canopy cover and live tree density. Thus, nestedness of bird and flying beetle assemblages appear to be influenced, albeit weakly, by similar habitat factors. The latter

Table 2 Summary and factor loadings of the first three principal components of measured stand attributes within the irregular forest of the North Shore region, Québec, Canada.

	Principal components		
	PC1	PC2	PC3
Eigenvalue	5.50	2.01	1.46
Variance explained	0.423	0.155	0.112
Cumulative variance explained	0.423	0.578	0.690
Relative proportion of balsam fir	0.817	0.032	0.310
Snag mean d.b.h.	0.779	-0.277	0.101
Snag d.b.h. variance	0.753	-0.254	0.136
Snag density	0.750	0.179	0.069
Live tree mean d.b.h.	0.746	0.002	-0.561
Live tree d.b.h. variance	0.736	-0.017	-0.514
Tree height	0.720	0.329	-0.346
Coarse woody debris volume	0.710	-0.165	0.095
Relative proportion of snags	0.604	-0.461	0.188
Thickness of ground lichens	-0.561	0.071	-0.207
Live tree density	0.038	0.887	0.069
Percentage canopy cover	0.443	0.807	0.070
Sapling density	0.315	0.200	0.730

Variables with significant loadings (as assessed by broken-stick bootstrap) on a given principal component axis are shown in bold typeface. d.b.h., diameter at breast height.

is exemplified by the correlation between their nestedness ranks ($n = 74$, $r_s = 0.36$, $P < 0.01$). Nestedness of ground-dwelling beetle assemblages was not correlated with the nestedness of assemblages of flying beetles ($n = 87$, $r_s = 0.16$, $P = 0.15$) or birds ($n = 74$, $r_s = 0.10$, $P = 0.38$).

Stand-specific idiosyncrasy scores and nestedness rank had contrasting relationships with attributes of the forest habitat. Stand-specific idiosyncrasy of ground-dwelling beetles increased with decreasing structural complexity of the stand (PC1) (Table 3). Stand-specific idiosyncrasy scores for birds increased with increasing canopy cover (PC2). No relationship was found for the assemblages of flying beetles. The stand-specific idiosyncrasy was more common, with a higher score among the low nestedness ranking, species-poor stands (Fig. 2a,c,e). This

Table 3 The relationships of nestedness and of stand-specific idiosyncrasy score (i.e. measure of departure of communities from nestedness) of animals in forest stands with fine-scale forest attributes (summarized in principal component (PC) scores). PC1, PC2 and PC3 represent 'structural complexity', canopy cover and sapling density of stands, respectively. Values are coefficients of Spearman's rank correlation for nested rank and Pearson's correlation for idiosyncratic temperatures.

Stand-specific:	Principal components	Ground-dwelling beetles	Flying beetles	Birds
Nested rank†	PC1	-0.405***	-0.088	-0.065
	PC2	-0.059	0.332**	0.304**
	PC3	-0.223*	-0.081	0.039
Idiosyncrasy score	PC1	-0.282*	-0.148	-0.110
	PC2	-0.020	0.102	0.277**
	PC3	-0.152	-0.189	0.022

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

†In a maximally nested matrix, stands that rank high are denoted by small values while stands that rank low have large values. Significant results are indicated by bold typeface.

indicates that species-poor stands may contain different sets of the common species that frequently appear as idiosyncratic (Fig. 2b,d,f).

Species-specific idiosyncrasy score and its relationship to pairwise species associations

In general, idiosyncrasy scores were higher for relatively high-rank, common species, which indicates that they were more likely to depart from assemblage nestedness than rare species (Fig. 2b,d,f). There were exceptions, however, in that the most high-ranking ubiquitous species conformed to the nested pattern and, conversely, some relatively low-ranking (rare) species, especially amongst beetles, had a higher idiosyncrasy score than the mean matrix temperature (Fig. 2b,d,f).

Under the FF null model, the proportion of significant pairwise associations (positive or negative) were: ground-dwelling beetles (24.7%), flying beetles (28.7%) and birds (22.2%) (Table 4). These proportions were higher than the 5% expected by chance. The proportion of positive associations

Table 4 The number of negative (-) and positive (+) pairwise species associations among species that conform (i.e. nested, NST) and depart (i.e. idiosyncratic, IDY) from the assemblage-level nested pattern. Species identified as idiosyncratic have temperature values larger than the mean (+ SE) of the matrix value.

Taxa (number of IDY or NST species)	Pairwise species associations		
	IDY versus IDY	IDY versus NST	NST versus NST
Ground-dwelling beetles (IDY = 38; NST = 25)	178- (56+)	100- (120+)	13- (66+)
Flying beetles (IDY = 79; NST = 40)	514- (458+)	406- (434+)	55- (146+)
Birds (IDY = 17; NST = 11)	23- (19+)	15- (16+)	2- (9+)

was slightly higher than negative associations for flying beetles (51.6%) and birds (52.4%). For ground-dwelling beetles, the negative associations were more frequent (54.6%) (Table 4). However, the results shown are primarily for high-ranking, relatively common species (> 5%) that were predominantly idiosyncratic species (Fig. 2b,d,f; Table 4, 61–69% of the species were idiosyncratic). When considering all species, 66–69% of the significant pairwise species associations were positive. The results of pairwise species associations were invariant to the choice of association index (CU, SCU, SS, SOR or JAC).

Species-specific idiosyncrasy scores and the frequency of significant negative pairwise associations were positively correlated in all assemblages (Fig. 3). We identified species as ‘strongly’ idiosyncratic if they had temperature values larger than the mean (\pm SE) of matrix value. Most negative associations involved at least one idiosyncratic species (Table 4). Negative associations were more frequent than positive associations among pairs of idiosyncratic species, especially among ground-dwelling beetles. Conversely, associations among pairs of nested species were mostly positive (Table 4).

The contrasting pattern between idiosyncratic and nested species (and related association patterns) appeared to be related to habitat preferences. Many of our idiosyncratic bird species (Appendix S1) prefer closed-canopy forest with high tree density, e.g. golden-crowned kinglet *Regulus satrapa*, boreal chickadee, *Parus hudsonicus*, red-breasted nuthatch, *Sitta canadensis*, magnolia warbler, *Dendroica magnolia*, brown creeper, *Certhia americana*, and black-backed woodpecker, *Picoides arcticus* (e.g. Hannon, 2005). Most species considered to be generalists or associated with open habitats conformed to a nested pattern, e.g. the ruby-crowned kinglet, *Regulus calendula*, pine siskin, *Carduelis pinus*, white-throated sparrow, *Zonotrichia albicollis*, chipping sparrow, *Spizella passerina*, Lincoln’s sparrow, *Melospiza lincolni*, and alder flycatcher, *Empidonax alnorum*. This is consistent with the contrasting correlations between stand nestedness and idiosyncrasy with canopy cover (PC3), i.e. stands with high canopy cover had a low nestedness rank and a high idiosyncrasy score (Table 3). However, there were few exceptions among open-forest or generalists species which appeared as idiosyncratic, e.g. the dark-eye junco, *Junco hyemalis*, and the hermit thrush, *Catharus guttatus*. These species tended to have frequent negative associations with other species such as the red-breasted nuthatch and boreal chickadee (Appendix S1).

We had little prior information about the habitat choice of beetle species to compare differences between idiosyncrasy and nested species. For ground-dwelling beetles, site idiosyncrasy scores increased with declining forest complexity (PC1) (Table 3). Some families with many idiosyncratic species (e.g. the families Elateridae and Cryptophagidae; Appendix S2) are linked to early successional forest stages (e.g. after severe fire) rather than to structural complexity (e.g. Saint-Germain *et al.*, 2004). The same families also had many idiosyncratic species in flying assemblage (e.g. Elateridae, Cryptophagidae and Ptiliidae; Appendix S2). In addition, idiosyncratic species were often negatively associated with each other, notably in ground-dwelling

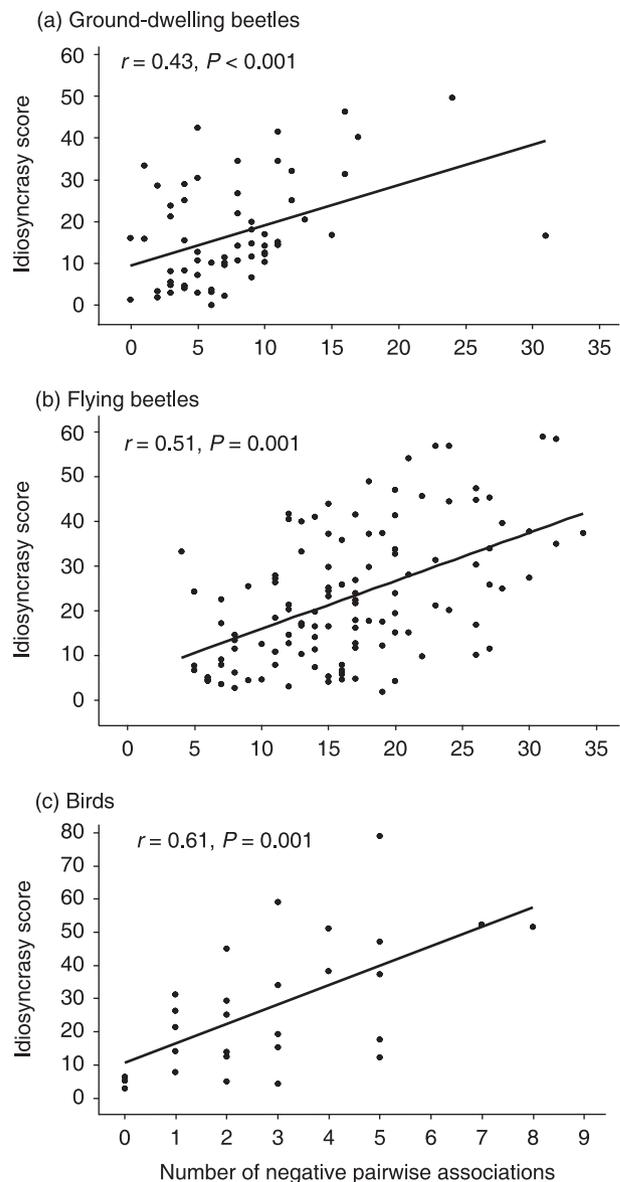


Figure 3 The relationship between species-specific idiosyncrasy score and the number of negative pairwise associations of each species.

beetles (Table 4), which may indicate the existence of some form of antagonistic interspecific interactions.

Among the 24 beetle species common to flying and ground-dwelling assemblages, only 20.3% of the significant pairwise associations had the same sign in both assemblages. Most (66.2%) significant associations appeared in only one assemblage, and 13.5% showed a change in sign (Appendix S3). Thus, pairwise species associations may not always be consistent in space, or may be dependent on habitat context.

Patterns of co-occurrence at the community level

At the community-level, the directions and significance of co-occurrence patterns varied depending on the association

Table 5 Community-level co-occurrence pattern of faunal assemblages in the irregular forest stands using different indices. Significance (indicated by bold type) was tested using the same null matrices generated by the fixed–fixed null model algorithm. Values are standard effect size (SES, see Methods). SES values larger than 1.98 ($P < 0.05$, one-tailed test) indicate segregated (S) distribution using the indices *C*-score and St*C*-score and aggregated (A) distribution using the Sorensen (SOR) or Jaccard (JAC) indices (and vice versa for SES values smaller than -1.98).

	Association indices			
	<i>C</i> -score	St <i>C</i> -score	SOR	JAC
Ground-dwelling beetles	0.95	3.50***(S)	-1.22	-0.64
Flying beetles	8.37***(S)	-4.52***(A)	9.33***(A)	10.01***(A)
Birds	4.70***(S)	-2.43*(A)	4.26***(A)	4.12***(A)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

index used, even though we used the same random matrices (Table 5). Assemblages of birds and flying beetles were aggregated according to the standardized *C*-score (St*C*-score) and Sorensen (SOR) and Jaccard (JAC) indices, but segregated according to the *C*-score index (Table 5). The results using St*C*-score, SOR and JAC indices are in line with the finding that more of the species pairwise associations were positive than negative (Table 4). However, all indices except the St*C*-score denoted ground-dwelling beetles as randomly distributed (Table 5), although there were both significant negative (dominating and correctly identified by St*C*-score) and positive species pairwise associations (Table 4).

DISCUSSION

Fine-scale distributions of bird and beetle assemblages in irregular boreal forest were significantly nested, as in many insular and non-insular study systems (Wright *et al.*, 1998; Azeria & Kolasa, 2008). Co-occurrence patterns were generally non-random, and positive species pairwise associations dominated for flying beetles and birds, as expected for nested assemblages (e.g. Leibold & Mikkelson, 2002; Azeria, 2004b). This was also supported by our community-level co-occurrence summaries using pairwise association indices that are standardized by species incidence, whether computed using number of checkerboard units (i.e. the St*C*-score) or the shared sites (i.e. SOR and JAC).

Our results indicate, however, that the *C*-score index summarized at the community level may not reflect the dominance of segregated or aggregated associations (see also Sfenthourakis *et al.*, 2006). Using the *C*-score index, both flying assemblages were characterized as being predominantly segregated. Using the *C*-score index, Ulrich and Gotelli (2007b) recently concluded that assemblages might be simultaneously nested and segregated. The community-level summary using *C*-score, SOR and JAC denoted co-occurrence pattern ground-dwelling beetles as ‘random’

despite both positive and negative species pairwise associations. Therefore, we suggest cautious interpretations of community-level summaries, and particularly of the *C*-score index. Interestingly, using the *standardized C*-score (St*C*-score), proposed in this study, ground-dwelling beetles were denoted as predominantly segregated. Indeed, negative associations were more frequent among ground-dwelling beetles (Table 4). Further assessment of the properties of association indices would be of value. Note, however, that species pairwise associations were the same for all association indices (CU, SCU, SS, SOR, JAC) as far as species incidence in the null matrices is fixed.

Nestedness may be partially explained by differences in ‘habitat quality’ among sites (Hylander *et al.*, 2005) and our study supports this hypothesis. Our fine-scale measurement of habitat attributes is likely to be commensurate with the scale of habitat selection for the species, particularly for ground-dwelling beetles (e.g. Niemelä, 1997). At the same time, however, the particular fine-scale forest attributes that influence nestedness of the three assemblages are not necessarily identical (Table 3). For ground-dwelling beetles, species found in stands with a low forest structural complexity (PC1) were a subset of stands with high forest structural complexity (e.g. large and heterogeneous diameter of trees and snags and large quantity of coarse woody debris). Forest attributes similar to those reflected by PC1 are known to influence species richness patterns of ground-dwelling beetle assemblages in other systems (e.g. Lassau *et al.*, 2005). However, habitat structural complexity (PC1) had no detectable influence on nestedness patterns of the bird and flying beetle assemblages. For these two assemblages, high nestedness ranking was associated with relatively low canopy cover and density of live trees (summarized by PC2). This may reflect the dominance of both assemblages by species associated with open habitats. Our bird assemblages were dominated by migratory species, many of which are open-habitat generalists (Imbeau *et al.*, 1999). Many species of flying beetles prefer sun-exposed habitats and probably require relatively open, dry conditions, i.e. they are open-habitat specialists (Martikainen, 2001). In addition, individuals of both species assemblages are more mobile than ground-dwelling beetles; hence, they should be influenced by habitat attributes characterizing the landscape matrix in addition to local forest stands (Lassau *et al.*, 2005; Janssen 2008). Our results provide evidence that congruence of nestedness among taxa may be weak because of differences in the way taxa interact with the abiotic and biotic environment (e.g. Hansson, 1998; Fleishman *et al.*, 2002). Moreover, our results suggest that nestedness may differ even among assemblages within taxa having different traits or life histories (e.g. among ground-dwelling versus flying beetles), as reported for species richness patterns in other systems (Lassau *et al.*, 2005).

Each of the three studied assemblages contained idiosyncratic species and site communities that departed notably from the significant assemblage-level nestedness. Idiosyncratic species have been predicted to have mutually exclusive distributions or to occur frequently in species-poor sites (Simberloff & Martin, 1991; Atmar & Patterson, 1993; Azeria *et al.*, 2006). Our study is the first to present results that support this prediction. In each

assemblage, species that most departed from nestedness were the species with the most mutually exclusive distributions. Moreover, site idiosyncrasy was notably higher among species-poor stands. This observation suggests that idiosyncratic species are preferentially distributed towards species-poor sites, although not always evenly shared amongst them.

Idiosyncratic species distributions suggest that there is an influence of ecological attributes distinct from the processes organizing the majority species of an assemblage. We found a tendency to opposing habitat preferences between idiosyncratic and nested species. Bird species identified as idiosyncratic (e.g. boreal chickadee, red-breasted nuthatch, black-backed woodpecker) prefer dense, closed-canopy forest. In contrast, the majority of bird species conforming to assemblage-level nestedness were open-habitat generalists (e.g. ruby-crowned kinglet, pine siskin and white-throated sparrow; see Hannon, 2005). This offers a plausible explanation of the negative pairwise associations between individual species from the two groups (e.g. boreal chickadee and red-breasted nuthatch versus white-throated sparrow; see Appendix S1). It is also consistent with other studies illustrating differential habitat selection and limited site overlap between idiosyncratic and nested species (Azeria, 2004b; McAbendroth *et al.*, 2005). Stand-specific avian idiosyncrasy increased with canopy cover, evidently as a consequence of these sites being selected by the few closed-canopy specialists. We emphasize that although idiosyncratic sites were often species-poor, they may have distinct habitat attributes necessary to sustain the habitat-specialist, idiosyncratic species (Azeria *et al.*, 2006).

Prior information about habitat preference of beetle species is scarce. Therefore, only limited inferences could be made about causal factors for idiosyncrasy and nested species distributions or the related pairwise associations. For ground-dwelling beetles, stand-specific idiosyncrasy scores increased as forest complexity (PC1) declined, opposite to the pattern of nestedness. Thus, it appears that many idiosyncratic species (e.g. members of the Elateridae and Cryptophagidae) are associated with simply structured and/or recently disturbed forests (e.g. Saint-Germain *et al.*, 2004). The majority of nested species (e.g. the Carabidae) are associated with forests of greater structural and compositional complexity (e.g. Lassau *et al.*, 2005). For flying beetle assemblages, there was no significant relationship between stand-specific idiosyncrasy and forest habitat attributes.

Interspecific interactions have been shown to influence the assemblage structure of bird (Gilpin & Diamond, 1982) and beetle communities (Rejmánek & Lepš, 1996; Lassau *et al.*, 2005). We found that negative pairwise associations were more frequent among idiosyncratic than nested species, for both birds and beetles. The predominantly negative associations between pairs of idiosyncratic species of ground-dwelling beetles suggest that interspecific competition may structure these communities. The same may also apply among flying beetles (e.g. between Elateridae and the scavengers Lathridiidae) and for some open-forest or generalist idiosyncratic bird species (e.g. the dark-eye junco and hermit thrush). Given that our study was conducted at a fine-spatial scale commensurate with the breeding territory

sizes of these avian species, negative interspecific interactions are more likely to be detectable, and consequently to be correlated with species-specific and stand-specific departure from nestedness.

We also detected positive pairwise associations within all three assemblages, even though our strict null model was biased against their detection. Positive associations might indicate similar habitat requirements (Jackson *et al.*, 1992), as evident here among highly nested avian species. Positive pairwise associations might also indicate some beneficial relationships. For example, migrants can use other resident species to select breeding sites (heterospecific attraction: Thomson *et al.*, 2003). The distribution of predatory beetle functional groups can also be influenced more by the availability of potential prey species than by habitat specialization of the predators (Lassau *et al.*, 2005). Among predacious beetles, we observed both nested species (e.g. *Nudobius cephalus* (Say), *Reichenbachia spatulifer* (Casey) *Phloeostiba lapponica* (Zetterstedt)) and idiosyncratic species (e.g. *Brachycephus pubipennis* (Casey) and *Parascydms corpusculus* (Casey)).

The nature of interspecific interactions and their influence on community assemblages may be dependent on habitat context and spatially variable (Rejmánek & Lepš 1996; Mönkkönen *et al.*, 2004; Hughes & Grabowski, 2006). Amongst beetle species common to flying and ground-dwelling assemblages, only 20% of those that revealed significant associations had constant signs in both assemblages. Such inconsistency may arise when generalist predators are associated with different prey species, depending on critical habitat for the prey. It is noteworthy that most of the species associations switched from significantly positive or negative to neutral. Switches from negative to positive, or vice versa, were not common. The majority of significant pairwise species associations, especially negative ones, occurred between rather than within families. For example within the ground-dwelling beetle assemblage, species of family Staphylinidae were often positively associated with each other, but were negatively associated with species of Cryptophagidae, Curculionidae, Nitidulidae and Scydmanidae. Thus, co-occurrence analysis that focuses on single families or related groups (e.g. only Carabidae; Niemelä 1993) may not detect negative associations that may indicate competition and its influence on community assembly (see also Stone & Roberts 1992; Sfenthourakis *et al.*, 2006). The few studies based on nestedness analyses of beetle assemblages have focused on relatively limited species groups, such as dung beetles (Avendaño-Mendoza *et al.*, 2005). To our knowledge, we provide the first evaluation of nestedness and co-occurrence patterns of encompassing multiple taxonomic families and functional groups.

In conclusion, we found that patterns in the fine-scale structure of three spatially congruent species assemblages were dependent on between-site variation in habitat structure. However, their responses to particular habitat features differed, rendering the nestedness pattern of the three assemblages less congruent. Differential responses to habitat features were also prevalent within assemblages, between nested and idiosyncratic species. The abundance of negative pairwise associations within

groups of idiosyncratic species was consistent with expectations under antagonistic interspecific interactions such as competition. Finally, interspecific interaction may be dependent on habitat context and spatially variable. Our study addresses fundamental questions about the relative role of habitat selection and interspecific interactions in determining assemblage structure (Gilpin & Diamond, 1982; Connor & Simberloff, 1983; Lassau *et al.*, 2005; Azeria & Kolasa, 2008). How these processes manifest in assemblage structures over other spatial and temporal scales (e.g. Mönkkönen *et al.*, 2004; Azeria & Kolasa, 2008) cannot be resolved without more detailed studies. However, we have demonstrated that combining nestedness and species pairwise co-occurrence analyses can reveal features of assemblage structure and identify potential underlying mechanisms.

Although this study was not intended to comprehensively address the problem of selecting and evaluating surrogate measures of biodiversity, our results have some general implications for developing such measures to aid biological conservation strategies. First, the three assemblages displayed limited congruence; hence, any of the groups may not be reliable surrogates of biodiversity patterns of the others. Secondly, each of the three assemblages included multiple idiosyncratic species. This implies that a single-species, e.g. a nested bird species associated with open-canopy forest, will be an inadequate surrogate for idiosyncratic bird species linked to closed-canopy forests, and vice versa. Comprehensive biodiversity management strategies are thus likely to entail a multi-taxa and multi-species approach (Hansson, 1998; Fleishman *et al.*, 2002). Conservation of species assemblages that have limited congruence and sometimes contrasting distribution patterns will probably require forest management plans that maintain different and contrasting suites of habitat structures at the stand and landscape scales, and that incorporate to some extent natural stand composition and structure (Niemelä, 1997).

ACKNOWLEDGEMENTS

This research was funded by the NSERC–Université Laval Industrial Research Chair in Silviculture and Wildlife and the Canada Foundation for Innovation. We thank our numerous industrial partners who facilitated field work and provided access to management areas. We thank C. Germain, L. Côté and Y. Dubuc for technical assistance. We also thank G. Pelletier, P. Bouchard, Y. Bousquet, A. Davies, S. Laplante, L. Lesage and A. Smetana for taxonomic help on beetles. W. Atmar provided additional information on Nestedness Temperature Calculator, while S. Sharma, K. Lefevre, C. Johnson, J. Hodson and two anonymous referees provided valuable comments on this paper.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Fine-scale pairwise species association among bird species in the old-growth boreal forest mosaic of Côte-Nord.

Appendix S2 The number of species in each beetle family that conformed (i.e. nested) and notably departed (i.e. idiosyncratic), from the assemblage-level nested pattern.

Appendix S3 Variation in fine-scale pairwise species association among beetle species found in both aerial and ground assemblages.

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Editor: José Alexandre F. Diniz-Filho