

# Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity?

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Received: 24 April 2013 / Accepted: 13 September 2013 / Published online: 8 October 2013  
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**Abstract** Harvest impact on forest biodiversity has been widely studied, but for managers confronted with a need for integrated cross-taxa assessment, application remains a significant challenge. Using post-harvest boreal forest succession as a model system, we investigate the usefulness of a trait-based multi-taxa approach to improve our understanding of the community dynamics after disturbance. We assess the strength of response to forest harvesting and recovery patterns of four taxa with contrasting attributes (vegetation, carabids, spiders and birds) along a post-harvest chronosequence of jack pine stands in the boreal forests of Canada. We used a complementary set of functional and taxonomic diversity metrics to identify commonalities and dissimilarities in the community assembly processes and sensitivities to harvesting among taxa. Despite the overall similarity of community response for most pairs of taxa and metrics, the strength of cross-taxa congruency varied greatly among metrics, illustrating the complexity of taxa response to harvest as well as the necessity of including a variety of biodiversity metrics in impact assessments. Of the four selected taxa, spiders were found the most sensitive to harvesting,

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**Electronic supplementary material** The online version of this article (doi:[10.1007/s10531-013-0565-6](https://doi.org/10.1007/s10531-013-0565-6)) contains supplementary material, which is available to authorized users.

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with a strong response to environmental changes after harvest and a slow community recovery process. Birds and carabids showed highly congruent response patterns, with a strong response to harvest followed by a marked recovery process. Ground vegetation was the most resilient to harvesting. We discuss the management implications of these contrasting recovery processes, outline the current limitations of this method and suggest steps toward the implementation of effective integrated multi-taxa monitoring programs.

**Keywords** Birds · Carabids · Forest harvesting · Ground vegetation · Recovery process · Spiders

## Introduction

Numerous biodiversity indicators have been developed in the last decades and are now widely used (Lamb et al. 2009; de Bello et al. 2010; Mouchet et al. 2010). Nevertheless, assessing forest harvest impacts on biodiversity is one of the core elements of contemporary forest management practices which remain a significant challenge for managers. The intrinsic complexity of biodiversity requires multiple metrics for its accurate quantification (Sattler et al. 2013; de Bello et al. 2010), creating needs for response integration across a wide range of taxa and trophic levels (Lindenmayer and Laurance 2012).

From the many available biodiversity metrics, trait-based approaches focusing on the functional aspects of biodiversity have been singled-out as promising complements to the traditional taxonomic approach (Cadotte et al. 2011; McGill et al. 2006; de Bello et al. 2010). Initially developed to study plant communities in open grasslands (e.g. Lavorel et al. 1998), the trait-based approach has since been used to characterize human impacts on a wide range of vegetation communities (Mouillot et al. 2013; Diaz et al. 2004) and their effects on ecosystem processes (Lavorel and Garnier 2002). Following this success in vegetation ecology, there has recently been significant interest in adapting this approach to animal ecology (e.g. Vandewalle et al. 2010; Wellstein et al. 2011; Langlands et al. 2011).

The trait-based approach characterizes organisms in terms of multiple biological attributes (Violle et al. 2007) that determine the organisms' functional response to its abiotic and biotic environment (Wellstein et al. 2011). Through the simplification of species diversity to a diversity of functions and attributes (Gitay and Noble 1997), this integrative approach provides a synthetic view of plant community (Lavorel et al. 1997). This approach has recently been used in a multi-taxa framework, i.e. linking the responses of multiple taxa to a given environmental change across different processes and ecosystems (Gobbi et al. 2010; Barbaro and Halder 2009; Le Viol et al. 2008). The universality of traits breaks down vastly differing taxa to their lowest common denominator, permitting an integrative impact assessment and making possible the delineation of functional syndromes underlying community-wide ecological processes such as pollination, leaf litter decomposition and nutrient cycling (Moretti and Legg 2009).

Because it streamlines the identification of similarities across regions and taxa, a trait-based multi-taxa approach presents opportunities for managers to extend their assessment of disturbance impacts to a broader range of organisms and/or spatial scales (de Bello et al. 2010). For example, this approach could help identify traits sensitive to a stressor of interest, irrespective of taxon and thus serve as a broad scale indicator of species and ecosystems sensitivity at the functional level (Mouillot et al. 2013). Although having clear

potential, this approach is still in its exploratory phase and immediate applicability to forest management and monitoring will remain limited until tools and knowledge are further developed and adapted.

Using post-harvest boreal forest as a model system, we examine the response of four taxa (vegetation, carabid beetles, ground spiders and birds) to successional changes using a combination of taxonomic and trait based indicators. These datasets have been collected as part of a biomonitoring program led by the Canadian Forest Service to evaluate the use of these bioindicators for forest sustainability (Pearce and Venier 2004). The selected taxa are known to be good indicators of ecosystem response to disturbance (Work et al. 2008; Moffatt and McLachlan 2004; Pearce and Venier 2006; Venier and Pearce 2004) and present contrasting resource use and mobility, making them suitable model groups to assess a range of ecological and functional patterns of succession after harvesting.

Boreal forests are characterized by large-scale natural disturbances, with agents such as fire and insect outbreaks creating a mosaic of stands at various developmental stages (Bonan and Shugart 1989); however, in many regions of the boreal forest, harvesting has now replaced fire as primary disturbance agent (McRae et al. 2001). In this role, forest harvesting is known to contrast with fire in a variety of ways, such as increased fragmentation, truncated age structure and decreased amount of coarse woody debris left on site (Cyr et al. 2009; McRae et al. 2001). Multiple studies have demonstrated the influence of these factors on biodiversity (Paillet et al. 2010; Drapeau et al. 2000; Paquin and Coderre 1997). Whether the biodiversity traditionally generated by the post-fire successional stages will be maintained in managed boreal forests remains an open question (Drapeau et al. 2000). A partial answer to this question is linked to the recovery process after harvesting which must be given a sufficiently long rotation period for managed and naturally disturbed areas to converge. A few studies have examined recovery processes in boreal forest (e.g. Buddle et al. 2000) but rarely has a broad range of taxa across distinct trophic levels been considered, limiting the possibility to improve our mechanistic understanding of observed processes.

The goal of our study is to investigate whether a trait-based multi-taxa approach can improve our understanding of processes involved in boreal forest community responses to harvesting. With the knowledge and tools currently available, what information can we gain by analysing taxa together, and combining taxonomic and functional metrics? Specifically, we asked the following questions: (1) How do taxonomic and functional diversity respond to time since harvest? (2) What are the effects of post-harvest stand age on the community trait composition of plants and animals? (3) Are there common patterns of response to forest harvesting across taxa? Overall, we expect that analysing traits across different taxonomic groups of known sensitivity to harvesting will reveal inter and intra-taxon patterns that could not have been detected by stand-alone analyses.

For each taxon, we analyse changes along a forest succession gradient using a series of taxonomic and functional metrics to provide information on the different dimensions of community response to harvest. To better understand harvest impact on biodiversity, we synthesize the functional response patterns of each taxonomic community into syndromes of co-occurring trait attributes (McIntyre et al. 1999). For each taxon, we focus on two elements of the community response: the magnitude of community change post-harvest and the recovery rate of communities toward the attributes of mature stands. We then compare the patterns of response across taxa to identify commonalities and dissimilarities in the community assembly processes and sensitivities to harvesting from both taxonomic and functional perspectives. In light of our results, we outline steps toward the development of an integrated multi-taxa monitoring program.

## Methodology

### Study area and sampling design

The study area is located near White River, Ontario, Canada (85°47'N, 48°31'W, Appendix S1). It is a boreal forest landscape with undulating hills of low to moderate relief, and an elevation ranging from 300 to 600 m. The underlying terrain is dominated by bedrock, often with a thin veneer of glacial till. The mean annual temperature is 1 °C with approximately 167 days above 5 °C and a mean annual precipitation of approximately 850 mm, half of it as snow (Pearce and Venier 2005). Extensive commercial logging in the area first began in the 1970s on a matrix of original unmanaged forest. At that time, approximately 83 % of the study area was mature closed-canopy forest, of which 42 % was conifer dominated. Between 1980 and 2000, approximately 21 % of the study area was clear-cut and replanted. Sites have been harvested at different times providing us today with a mosaic of clear-cut areas at different successional stages. The main tree species in the study area are currently jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*), balsam fir (*Abies balsamifera*), and white birch (*Betula papyrifera*). In 2001, 64 study sites were selected according to their age since last harvest (space-for-time substitution, Pickett and McDonnell 1989). Sites were at least 500 m apart and located within jack pine stands identified by the forest resource inventory of Ontario (Gillis and Leckie 1993). Study sites were classified in stand age classes following time elapsed since harvesting at the time of site selection (2001): ≤1, 5, 10, 15, 20, and 40 to 100 years, with the last category having never been clear-cut and corresponding to the original unmanaged forest (hereafter called >40). Four taxa, occupying different trophic levels and with contrasting life-forms, mobility and resource use were selected to monitor the impact of harvesting and the recovery pattern during the post-harvest succession: ground vegetation (primary producer, sessile, large proportion of clonal propagation, relatively low disperser), carabid beetles (mainly carnivores with few granivores, ground-dwellers, distinct dispersion ability with some species able to actively fly), ground spiders (carnivores, ground- and grass-dwellers, distinct dispersion ability with some species able to balloon), and birds (different trophic guilds, using distinct vegetation structures, good dispersers).

### Vegetation sampling

Floristic composition of the ground vegetation (i.e. all vascular species under 1 m in height; Gilliam and Roberts 2003) was determined using photoplots (sensu Elzinga et al. 1998). Vegetation above 1 m in height was considered too closely related to stand stage (particularly in young stands) to be included in the survey. Three photoplots per site were taken in July 2001 (i.e. the time of maximum vegetation activity) along the arthropod sampling transect (see below). Each photoplot was taken from a height of 1 m, parallel to the ground. In the laboratory, all species (including woody species <1 m in height) present in each photoplot were evaluated for percent cover following the nomenclature of Gleason and Cronquist (1991). This was undertaken by a single botanist (the first author) to ensure consistency. Species representing less than 2 % cover were not recorded. Grasses, sedges and *Amelanchier* spp. were identified to genus only. Percent cover by species per site was calculated as the average of a given species' cover across the three photoplots.

## Bird survey

Forest birds were sampled during the breeding season, i.e. from early June to early July in 2001, 2002, and 2003 using a point count method (Howe et al. 1997). In each study site, an observation point was established at least 100 m from the edge of the stand. Each site was visited twice each year and all birds heard or seen from the observation point during a 10-min period were recorded. Only birds counted within 100 m radius were used in the analysis. Counts were performed between dawn and 9:30 a.m. EDT. Point counts were not conducted under windy conditions or during precipitation. Annual abundance was calculated as the maximum count for the species in two visits. Mean abundance over the 3 years was used in the analysis (see Venier and Pearce 2005 for more details).

## Arthropod sampling

At each study site, carabid beetles (carabids hereafter) and ground spiders (spiders hereafter) were collected using nine 1 l pitfall traps with 10.6 cm diameter opening, installed at 20 m intervals along a 160 m transect located at least 100 m from the edge of the stand. Traps were filled with a 200 ml 50:50 mixture of propylene glycol and water as a preservative. A plastic cover placed above the traps provided protection from rain. Traps were established in May 2001, and emptied every 2 weeks from June 6 to August 28, 2001 and from May 7 to July 9, 2002. In each year, samples were pooled over the nine traps to generate one sample per study site per year. Samples were standardized to 500 trap days and averaged over 2 years to create an abundance index. Carabids and spiders were identified to species, with voucher collections housed at the Canadian Forest Service, Sault Ste. Marie and the National Insect Collection in Ottawa. For spiders, only adults were identified and included in the analyses. In total, 39,106 spider individuals and 12,010 carabid individuals were recorded over a total of 38,040 trap days. Carabid species were identified according to Lindroth (1961–1969), following the nomenclature of Bousquet and Laroche (1993). Spiders were identified to species according to standard literature; nomenclature followed Paquin and Buckle (2001).

## Species traits

For each taxon, we selected a set of species traits considered to be sensitive to environmental changes following harvest (see Appendix S2). Species trait data were available from literature and mainly related to major components of individual performance and fitness (Violle et al. 2007) and to species physiology, resource acquisition, and mobility (Flynn et al. 2009). We recognize that some of the selected ecological traits might not be strictly considered functional traits but rather as a response of multiple traits to environmental factors (Violle et al. 2007), nevertheless they can help improve our understanding of niche use/occupation and ecological processes (Doledec et al. 1996; Knapp et al. 2008; Ernst et al. 2012). For vegetation, we obtained trait information from the TOPIC database (Traits of Plants in Canada, Aubin et al. 2012), but to our knowledge no such database existed for animal species in Canada. We thus created a first Canadian animal trait database from a compilation of literature sources (Multi-Traits database; see Appendix S3 for a full description of sources).

## Data analyses

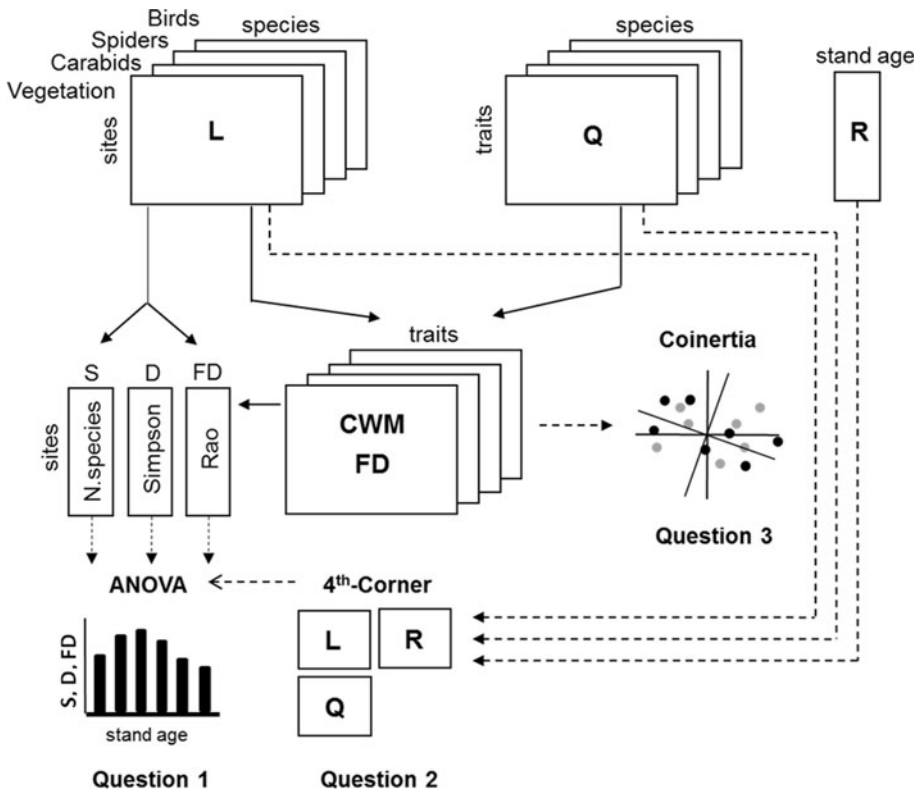
Analyses were designed to find relationships between post-harvest stand age and various taxonomic and functional metrics of biodiversity and to outline similarities of response between taxa. We based the analyses on three distinct matrices for each taxon: (1) matrix Q (traits by species) containing mixed species traits data, (2) matrix L (sites by species) containing quantitative species abundance data (except for vegetation where we used percentage cover), and (3) matrix R (sites by stand age classes) comprising one ordinal variable representing five age classes ( $\leq 1$ , 5, 10, 20,  $>40$  years) as a post-harvest chronosequence of stands. To reduce the effect of sporadic and erratic species in the communities, single observations (i.e. only one individual of a given species observed in the whole dataset) were removed from matrix L prior to analysis. Figure 1 shows a diagram of the different datasets and analytical steps with respect to the three questions of our study.

### *Question 1: How do taxonomic and functional diversity respond to time since harvest?*

Taxonomic and functional diversity indices were calculated and compared along the chronosequence of stands for each taxon. Biodiversity was measured as taxonomic diversity using species richness (S; i.e. the number of species per site) and Simpson diversity index (D; Simpson 1949) computed on matrix L. Rao's quadratic entropy index (FD; Rao 1982) was chosen as functional diversity index for its widespread use, allowing comparisons with other studies (de Bello et al. 2007). Rao's index has been shown to have all the necessary properties of a functional diversity index (Botta-Dukát 2005) and to successfully identify habitat filtering patterns (Moretti et al. 2009; Mouchet et al. 2010). Rao's index is the sum of pairwise distances between species weighted by their relative abundances and describes the variation of species trait composition within the community. Using matrices L and Q, FD was computed for each individual trait ( $FD_{\text{trait}}$ ) as a multivariate index. Within each taxon, single  $FD_{\text{trait}}$  varied in similar patterns with successional stages (Appendix S4), we therefore computed a univariate index ( $FD_{\text{global}}$ , i.e. the mean value of the single  $FD_{\text{trait}}$ ) without obscuring traits specific patterns. Differences in diversity indices among stand age classes (alpha diversity) were assessed for each taxon using one-way permutation ANOVAs and Monte Carlo tests with 9,999 permutations, followed by a Bonferroni post hoc test for multiple tests when significant effects of stand age were detected.

### *Question 2: What are the effects of post-harvest stand age on the community trait composition of plants and animals?*

We investigated relationships between species traits and succession processes for each taxon, examining the shift in mean trait values along the chronosequence of stands using the fourth-corner analysis described by Dray and Legendre (2008). This method allows the simultaneous analysis of three matrices (L, Q and R), and therefore tests for significant relationships among all species traits and all environmental variables in a single step. To reduce the dominant species effects, the L matrices of animal taxa were log transformed prior to analysis. This transformation was not performed on the % cover data of the vegetation L matrix. Each L matrix was then transformed into relative frequencies to adjust for the possible effect of abundance patterns along stand age. Permutation model 1 (where the cell values are permuted within the columns of L) was chosen. This model tests the null hypothesis that species are randomly distributed relative to site characteristics, and best



**Fig. 1** The different datasets needed for this study and their role in the analytical steps followed with respect to the three studied questions

represents our dataset, with matrix L as a random component and the R and Q matrices as fixed components (Dray and Legendre 2008). The probabilities resulting from the significance tests of global statistics were adjusted for multiple testing using Holm's procedure (1979) to reduce the risk of a Type II error (ter Braak et al. 2012).

### Question 3: Are there common patterns of response to forest harvesting across taxa?

Co-inertia analysis (Dray et al. 2003) was used to explore the degree of association between community responses to harvesting for each taxon pair. Three aspects of beta biodiversity were compared: (a) species abundance, (b) weighted mean values of each trait in the community (CWM, Garnier et al. 2004), and (c) functional diversity of single traits ( $FD_{\text{trait}}$ ). First, a PCA was performed for each matrix pair and in each case the principal axes were selected to reduce dimensionality; the concordance between the pair of datasets was then maximized by the rotation of the multidimensional space, thus generating new axes. To interpret the relationships between matrix pairs across the different taxa, we used RV coefficients, where the RV coefficient is a measure of global similarity between the datasets (between 0 and 1, with values closer to 1 indicating greater global similarity between the two datasets). We finally tested the strength of these similarities using a Monte-Carlo permutation test (9,999 permutations).



All analyses were carried out using the R 2.15.1 package (R Development Core Team 2012) with the libraries ‘ade4’ (Dray and Dufour 2007), ‘vegan’ (Oksanen et al. 2013) and ‘FD’ (Laliberté and Legendre 2010). CWM and FD Rao’s quadratic entropy were calculated using the library ‘FD’ (Laliberté and Legendre 2010). For computational details and definition of CWM and FD, see Ricotta and Moretti (2011).

## Results

### Diversity response to time since harvest (question 1)

None of the diversity indices computed for the 61 plant species inventoried in the 64 study sites (Appendix S5) showed a significant pattern with post-harvest stand age (Fig. 2). This is in direct contrast with the results obtained for the 63 carabid species identified at these sites (Appendix S5) and for which all diversity indices showed similarly significant patterns i.e. decreasing values with stand age and reached lowest values 15–20 years after harvest (Fig. 2). Similar pattern was found for the spiders Species richness (S), totalling 155 species in all (Appendix S5; Fig. 2). Departing from this trend, spider Simpson diversity index (D) showed no significant pattern with stand age (Fig. 2). Spider functional diversity index (FD<sub>global</sub>) decreased with time since harvest, with mature stands hosting communities with significantly less diverse trait assemblages than  $\leq 5$  years old stands (Fig. 2). A different trend was observed for the 74 bird species recorded at our study sites (Appendix S5) with all diversity indices showing similarly significant patterns of increase along succession, with highest values in mature stands (Fig. 2).

### Trait succession after harvesting (question 2)

The fourth-corner analyses showed significant positive and negative relationships between species traits and post-harvest stand age for the four selected taxonomic groups. The results are summarized in Table 1.

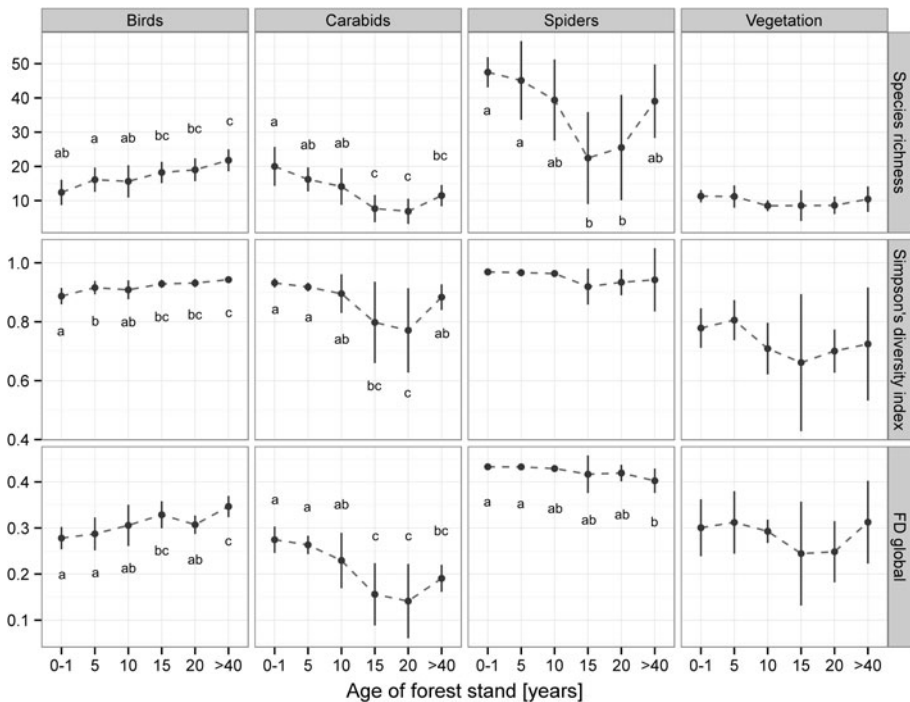
### *Vegetation*

Shortly after harvest (<1 year), ground vegetation communities were characterized by short-lived, shade intolerant, primarily obligate seeders with non-persistent foliage. Fifteen years after harvest, the community shifted toward a higher proportion of species with persistent foliage, and a lower proportion of obligate seeders, particularly those dispersed by wind. The ground vegetation communities of mature stands were dominated by chamaephyte tree seedlings and shade tolerant species while hemicryptophytes and obligate seeders were less represented in these communities.

### *Carabids*

In young stands ( $\leq 5$  years), carabid communities were characterized by diurnal granivore and omnivore species with a marked preference for dry habitats. Generalist carnivores and species with a dimorphic wing condition were significantly less prevalent. Trait community composition shifted 15–20 years after harvest with an increase in generalist carnivores preferring mesic conditions. Carabid communities in mature stands (>40 years) were





**Fig. 2** Diversity indices for the four taxa: species richness, Simpson diversity and functional diversity as Rao univariate index ( $FD_{global}$ ). A different letter indicates a significant differences at  $P < 0.05$  (one-way permutation ANOVAs followed by a multiple comparison Bonferroni post-hoc test). Lines are drawn for readability only and do not indicate interpolation

dominated by nocturnal, short winged specialist carnivores and omnivores preferring shady and moist habitats.

### Spiders

Spider communities in young stands ( $\leq 5$  years) showed a high prevalence of large, night hunting species that prefer open habitats, and of ballooning spiders. These characteristics remained dominant until 15–20 years after harvest, although habitat preference shifted to intermediate light conditions by 15 years. Mature stands ( $>40$  years) were characterised by small, aerial web builders with diurnal habits and low mobility (no ballooning), as well as a preference for shady environments.

### Birds

In young stands ( $\leq 5$  years old), bird communities were mainly characterized by nomadic or short distance migrants, omnivore species foraging and nesting on the ground, and species with low clutch size. Fifteen years after harvest, a significantly higher proportion of year-round residents, upper canopy foragers with higher nesting height (1 to  $<5$  m) was observed. Bird communities in mature stands were dominated by neotropical migrants and year-round resident, insectivore species, with bark or upper canopy foraging habits; cavity nesting was prevalent, as well as high nesting height and clutch size.

**Table 1** Synthesis of the results of the fourth-corner analysis for all four taxonomic groups (vegetation, carabids, spiders and birds), in which stand age classes are related to species traits (see Supporting Information, Table S6 for details)

Taxonomic groups	Traits	Categories	Stand age in years					
			≤1	5	10	15	20	>40
Vegetation	Raunkier life	mega or meso-phanerophyte						
		micro or nano-phanerophyte						
		chamaephyte						
		hemicryptophyte						
	Reproduction strategy	geophyte						
		therophyte						
		vegetative						
		mostly by seeds						
	Foliage persistence	seeds						
		no						
	Seed dispersal by wind	yes						
		no						
	Shade tolerance	yes						
		intolerant						
Carabids	Feeding guild	mid tolerant						
		tolerant						
		specialist carnivore						
		generalist carnivore						
	Diel activity	omnivore						
		granivore						
		nocturnal						
		diurnal						
	Wing condition	brachypterous						
		dimorphic						
	Light requirement	macropterous						
		low						
	Moisture requirement	moderate						
		high						
Spiders	Body size*	moist						
		mesic						
		dry						
	Prey capture strategy	hunting						
		web building						
	Vertical stratification	ground						
		aerial and ground						
	Diel activity	aerial						
		nocturnal						
	Ballooning	diurnal						
		no						
	Light requirement	yes						
		low						
Birds	Migration	low to moderate						
		moderate						
		moderate to high						
		high						
	Primary food	sedentary						
		nomadic						
		neotropical migrant						
		omnivore						
	Foraging	insectivore						
		upper canopy						
		midair						
		bark						
	Nest height in m	ground						
		lower canopy						
		< 1						
		1 to < 2.5						
	Cavity nester	2.5 to < 5						
		≥ 5						
		no						
		yes						
	Clutch size*							

\* Numerical data

Only significant relationships at the 5 % significance level after Holm correction are shown. Color indicates if the statistic is above (black) or below (white) the expected value (mean of the permutation results), thus showing positive or negative link between traits and stand age. The shaded background indicates non-significant results

### Patterns of response to forest harvesting across taxa (question 3)

Patterns of community response to time elapsed since harvest were investigated between pairs of taxa based on three distinct matrices of taxonomic and functional community composition: species abundance of animals or plant cover, community weighted mean trait values (CWM) and overall functional diversity (FD<sub>global</sub>). All pairs of taxa showed

significant similarity, except for the vegetation and birds  $FD_{global}$  (co-inertia analysis  $P \leq 0.05$ ; Table 2). Species abundance had the highest pattern similarity, particularly between carabids and spiders ( $RV = 0.6356$ ), while birds and carabids were least similar ( $RV = 0.3999$ ). For CWM, the highest similarity was between bird and carabid communities ( $RV = 0.4321$ ), while vegetation and bird communities were least similar ( $RV = 0.1235$ ). Of the three metrics,  $FD_{global}$  showed the lowest congruence; the highest similarity for this metric was between birds and spiders ( $RV = 0.1920$ ).

## Discussion

Our study comes in response to the call by scientists and practitioners for the development of integrative tools for the assessment of forest management impacts covering both a comprehensive range of organisms and aspects of diversity (Lindenmayer and Laurance 2012; Mouchet et al. 2010; Moretti and Legg 2009). Community dynamics were analysed under a multi-taxa approach, using a set of complementary taxonomic and functional diversity metrics. Diversity indices were first used to provide a global understanding of the different aspects of alpha diversity along post-harvest succession. The fourth-corner analysis then allowed us to identify trait syndromes pointing to mechanisms which determine the strength of each taxon's functional response and recovery rate along post-harvest succession. Finally, the co-inertia analysis provided a quantitative assessment of the overall congruence in response patterns between pairs of taxa for different metrics of beta biodiversity.

### Patterns of community response to forest harvesting across taxa

The significant similarity of community response patterns for most pairs of taxa and metrics suggests that disturbance by harvest induces an overall convergent response across taxa. Our results are consistent with the investigations by Moretti and Legg (2009) and Moretti et al. (2009) of post-fire succession in southern Switzerland. The taxonomical groups included in our study do not have strong trophic ties, therefore the similarity of patterns observed between taxa should be interpreted as a correlative similarity in response to harvesting rather than cause-effect trophic interactions.

Despite an overall convergent response, the strength of the cross-taxon congruency varied greatly among metrics, illustrating the complexity of taxa response to harvesting as well as the necessity of considering different aspects of biodiversity to obtain a representative impact assessment. As shown by Ricketts et al. (2002) and by Lovell et al. (2007), divergence in response patterns between taxa may be caused by contrasting community assembly processes, resource use, and dispersal ability. However, in our study, while we observed a high similarity in taxonomic response between the two epigeic taxa community (i.e. spider and carabid), we found relatively low similarity in their functional responses, suggesting divergent trait selection following harvest. This contrasts with the similarity we found between bird and carabid response, two taxa with distinct resource use and dispersal abilities.

Despite the dissimilarity in their ecology, birds and carabids had the strongest congruence in response patterns of community trait composition with similarly strong response to harvest followed by a gradual recovery in older stands. While high mobility enabled bird communities to respond rapidly to changes in habitat and foraging conditions by moving to more suitable forest habitats, the less mobile carabid communities (Driscoll and Weir

**Table 2** RV-coefficient and *P*-value of co-inertia analyses on three distinct matrices of taxonomic and functional community composition (*Sp. abundance* species abundance of animals and plant % cover; *CWM* community weighted mean trait values; *FD<sub>global</sub>* overall functional diversity) for six pairs of taxa considered in our study

Pairs of taxa	Sp. abundance		CWM		FD <sub>trait</sub>	
	RV	<i>P</i> -value	RV	<i>P</i> -value	RV	<i>P</i> -value
Vegetation–birds	0.4449	0.0030**	0.1235	0.0105*	0.0817	0.2187 n.s.
Vegetation–carabids	0.5198	0.0041**	0.1409	0.0038**	0.1230	0.0090**
Vegetation–spiders	0.5613	0.0011**	0.1766	0.0005***	0.1412	0.0043**
Birds–carabids	0.3999	0.0300*	0.4321	0.0001***	0.1616	0.0006***
Birds–spiders	0.5912	0.0001***	0.2905	0.0007***	0.1920	0.0002***
Carabids–spiders	0.6356	0.0001***	0.1712	0.0001***	0.0909	0.0430*

With the co-inertia analysis we aimed to test the degree of congruence of pairwise response patterns using Monte Carlo test with 9,999 permutations. The higher the RV-coefficient (a generalization of the squared Pearson correlation coefficient), the more congruent are the responses

2005) responded more slowly, with young stand communities exhibiting trait syndrome characteristic of both pioneers and pre-harvest, mature communities. The recovery of both the bird and the carabid community was heavily influenced by canopy closure (around 15 years), with birds being sensitive to stand structure (Venier and Pearce 2007) and carabids to epigeaic microclimatic conditions (Ober and DeGroot 2011). Bird and carabid traits found to be associated with undisturbed habitat (related to nesting and foraging strategies for birds and to mobility and resource use for carabids) were still underrepresented at 20 years, indicating that the recovery process was not yet complete. Similar recovery rates have been described in the literature for birds (e.g. Schieck and Song 2006) and carabids (e.g. Buddle et al. 2006).

Spider communities showed a strong response to harvesting with contrasting trait syndromes between pioneer and mature stands. However, this response was not captured by diversity indices, which showed similarly high *S* and *D* between young and mature stands and a lower *FD* with stand stage. *S* reached its lowest value after canopy closure (15 years after harvesting), suggesting a filtering process removing pioneer species during intermediate successional stages. Nevertheless, spider communities in 20 year-old stands remained closer to pioneer than to mature stands in terms of functional composition, suggesting a slower recovery process than for other taxa in this study. This is consistent with other studies which have shown slower recovery for spiders in comparison to carabid communities (Niemelä et al. 1996; Buddle et al. 2000).

Vegetation had the lowest congruence in response pattern; in contrast with other taxa, ground vegetation showed a weak response to harvesting. One possible explanation may reside in the high resilience of boreal understory to disturbance; species display a wide variety of regeneration mechanisms to cope with their disturbance-prone boreal forest ecosystem (Haeussler et al. 2002; Bartemucci et al. 2005). In boreal forests, vegetation response to disturbance is better reflected by structural rather than diversity and compositional changes (Bartemucci et al. 2005), with the upper understory developing quickly, leading to a rapid return to pre-disturbance abiotic conditions (Constabel and Lieffers 1996; Aubin et al. 2000).

## Indicators of biodiversity and management implications

Differences observed in response and recovery processes among taxa and biodiversity metrics highlight the challenges of selecting relevant biodiversity indicators (taxa and metrics) for future post-harvest monitoring. A crucial aspect of bioindicator suitability is how well they represent the response of other taxa (Caro 2010; Ricketts et al. 2002). Our study showed high variation in response pattern and recovery process among taxa, and different conclusions might have been drawn had any one of these taxa been considered independently. The contrasting recovery processes presented here have serious implications for management and demonstrate the importance of multi-taxa based monitoring. Of the four groups included in our study, spiders were the most sensitive to harvesting in boreal forests. Being notably one of the most important pest controlling guilds in forest ecosystems (Bianchi et al. 2013), adequate recovery periods should be ensured by any sustainable management plan. In some cases, as in this study, frequently monitored taxa such as ground vegetation may have only low congruence with more rarely monitored taxa such as spiders (Andelman and Fagan 2000; Lovell et al. 2007). A multi-taxa approach succeeds in capturing the spatio-temporal extent of the community response, including taxa with both high and low resilience, thus providing a more accurate evaluation of ecosystem recovery.

Besides choice of taxa, choice of indices used to monitor biodiversity is also critical (Lamb et al. 2009). Indeed, degree of similarity between taxa varied according to the different biodiversity metrics included in our study. Based on the assumption that they co-vary, taxonomic diversity indices have traditionally been used in monitoring programs as surrogates for functional diversity. However, recent studies (Srivastava and Vellend 2005; Flynn et al. 2009; Mayfield et al. 2010) have produced empirical evidence that this is not always the case. In our study, with the exception of spider communities, taxonomic and functional diversity indices along the post-harvest successional gradient responded similarly for distinct taxa. In the case of spider communities however, the exclusive use of taxonomic indices would have overlooked the strong functional response of this taxa to forest harvesting.

Multi-taxa monitoring represents a large resource investment, and it might be difficult to implement it in a nation-wide monitoring program within the real world of limited resources. Intensive a priori multi-taxa monitoring could be performed in a core of well-coordinated set of research trials covering key forest ecotypes and/or land-use intensity gradient (including the least disturbed available forest areas) in order to define sensitive taxa as well as congruence and interaction in response patterns across taxa (Gardner 2012). The community-wide mechanistic understanding of harvesting response we would gain could subsequently be used in support of the development of a cost-effective sampling strategy applicable in a broad-scale effectiveness monitoring program. With more multi-taxa studies being undertaken (e.g. Pedley et al. 2013; Braaker et al. 2013), guidelines should emerge to inform the choice of taxa and metrics to be monitored. However, taxa and traits selection will remain highly context dependent, in particular on the type of ecosystem, processes and spatial scale under study.

## Toward a multi-trophic approach in applied ecology

In echo of theoretical advances, there is growing interest in bringing the trait-based approach a step further, from multi-taxa assessment toward integration of biotic interactions at community level and into a multi-trophic framework (Lavorel et al. 2013; Reiss

et al. 2009; Brooks et al. 2012). However, only few empirical studies have been performed (but see: Schmitz 2008; Frenette-Dussault et al. 2013; Moretti et al. 2013), and further theoretical development is needed before they can be applied in forest management.

Our understanding of the link between traits and ecosystem processes is just beginning for plants, with substantial advances in the last decade (e.g. Garnier et al. 2004; Freschet et al. 2012), but we still only have a minimal understanding of interactions across traditional taxonomic barriers (Ings et al. 2009; Brooks et al. 2012; Lavorel et al. 2013). Cases in which we can claim to have a good understanding of the trophic networks are primarily simple systems in isolated experimental units (Duffy et al. 2007); overall, trophic interactions remain poorly understood and need to be further explored (Lavorel et al. 2013; Thébault and Loreau 2006). The trait-based approach was developed by and for vegetation ecology and its application to animal taxa is not as straightforward as may be intuitively predicted (Blaum et al. 2011). Several elements of plant functional ecology do not have parallels in animal ecology and vice versa, such as sociality (degree of interactive behaviour with other members of the same species) and ontogenetic functional displacement where different development stages (larvae, pupa and imago) shift their trophic level and interaction networks. There is an urgent need to outline the limits of the trait approach in animal ecology. A necessary first step would be a thorough evaluation of the relationships between traits, fitness and ecosystem processes in animal ecology.

Data availability is another crucial issue impeding quantitative multi-trophic assessment (Lavorel et al. 2013; Scholes et al. 2013). For traits data, there are large disparities in availability between animal taxa. While birds have traditionally been well documented (e.g. Cleary et al. 2007; Cormont et al. 2011; Fischer et al. 2007), traits for terrestrial invertebrate groups have only recently begun to be documented (e.g. carabids in Ribera et al. 2001; Gobbi et al. 2010; and spiders in Langlands et al. 2011), and most other taxa remain virtually undocumented. Because the physiological traits of animals are difficult to measure, most animal trait data are derived from the literature or expert opinion. Very few studies are specifically designed to measure animal traits, which reduces both the explicative power of specific functional mechanisms and the capacity of prediction of key ecosystem processes (Ibanéz et al. 2013). In other cases, the data is inferred from the habitats where the species was found; this creates a circularity problem in the analysis of response to an environmental gradient. Formal experiments on key animal traits (e.g. cafeteria experiments for feeding preference) should be carried-out to address knowledge gaps systematically (Ibanéz et al. 2013). Additionally, such species-specific experiments could help us address the question of intraspecific variability. This is an area that has been shown to be critical in vegetation studies (Albert et al. 2011) but remains thus far unexplored in animal taxa.

The use of the trait-based approach in vegetation ecology has been strongly supported by the development of standardized definitions and measurement protocols (e.g. Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013), terminologies (e.g. Madin et al. 2008) and ecoinformatics (e.g. Kattge et al. 2010). This type of foundation is required to apply the trait approach to animal taxa (Blaum et al. 2011; Vandewalle et al. 2010). Standardisation is furthermore needed at various scales: from standardized terminologies and protocols to ease trait data integration across regions and researchers, up to cross-discipline standardisation. Only then will the trait-based approach become a truly powerful tool, enabling researchers to make valid cross-taxa comparisons.

In the last decade, numerous statistical procedures and indices have emerged as a result of the unprecedented collaboration between ecologists and statisticians willing to approach complex systems and interactions together. New statistical analyses dedicated to an

integrative analysis of multi-taxa datasets such as the co-inertia analysis used in this paper, but also structural equation modelling (Shipley 2000), multiple factor analysis (Kleyer et al. 2012), trophic network interaction analyses (Ings et al. 2009), and Bayesian based approaches (Ibanéz 2012) have been developed. These procedures must be further tested and adapted to permit crossing the frontier between animal and plant ecology.

## Conclusion

The data used in this paper were originally collected for individual analyses by species group in order to assess harvest impacts on key biodiversity components. Using a trait-based multi-taxa approach, we went one step further, in an attempt to integrate impact assessment. For now, we cannot go beyond the search for common patterns of behaviour among taxa. However, supported by a growing body of literature in theoretical ecology, and as frameworks, knowledge and tools develop, we hope it will soon be possible for applied ecologists to use a trait-based approach in a truly multi-trophic perspective. The integration of biotic interactions is a key challenge and a necessary step toward a holistic understanding of the impact of human induced changes on ecosystems.

**Acknowledgments** Thanks to all field assistants for their time and efforts in the field and in the laboratory. Thanks to F. de Bello for statistical advice. Thanks to F. Cardou and K. Chapman who improved earlier versions of the manuscript. We gratefully acknowledge the statistical and graphical support provided by D. Charbonneau, G. B. Pezzatti and J. L. Payeur-Poirier and the feedback provided by D. Morris. Financial support was provided by the Living Legacy Trust.

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