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Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem

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ABSTRACT

The concept of functional trait-environment relationship posits that species in a local community should possess similar traits that match the selective environment. The present study examines species trait-habitat (using Fourth-corner and RLQ analyses) and habitat occupancy patterns (logistic regression models) of bird assemblages in boreal forest stands following disturbances by forest fire and salvage logging. The stands differed in the amount and composition of residual tree retention, salvage- and aquatic-edges, degree of burn severity (all measured at 100 and 500 m buffers), as well as landscape-level variables such as distance to previously burned forests. Tests of trait-habitat relationships showed that canopy-nesters and bark- and foliage- insectivores required high levels of residual trees of low burn severity, with the feeding guilds showing affinity for different stand composition. In contrast, ground-nesters and omnivores thrived in salvaged areas and associated edges. In addition, cavity-nesting and ground-foragers were associated with severely burned stands. The species' habitat occupancy patterns were commensurate with trait requirements, which also appeared to be scale-dependent. For example, some fire-associated species had high occupancy probability in severely burned stands at small-scale (100 m buffer), which was consistent with their cavity-nesting trait. This pattern, however, was not evident at large-scale, where their feeding requirement (bark-insectivores) for low-severity burns dominated. Our study suggests that trait-habitat relationships can provide critical information to the complex ways species' relate to key habitat factors following natural and anthropogenic disturbances.

1. Introduction

The concept of functional trait-environment relationship posits that environmental filters select species, from a regional pool, to a community possessing similar traits that match the selective environment (Simberloff and Dayan, 1991). Deciphering the link between species' traits and their environment is thought to provide a mechanistic explanation to species' occupancy and community patterns across local and landscape variables (e.g., Thuiller et al., 2006; Cleary et al., 2007; Dray and Legendre, 2008). Also, by reducing the responses of multiple species to a few functional traits, empirical trait-environment relationships could provide an integrated and concise framework for linking responses of assemblages, regardless of species identity, to environmental changes (Petchey et al., 2007; Dray and Legendre, 2008). Such relationships would be particularly valuable in ecosystems subjected to disturbances, which may disrupt aggregate assemblage patterns (e.g., random species co-occurrence patterns of vertebrates following fire, Sara et al., 2006). Yet, if post-disturbance environmental conditions indeed select traits deterministically, then repeated trait-environment links may emerge across assemblages, thus informing about biotic response to disturbances, which may be less evident when considering only species' identity. Examination of trait-habitat relationships, indeed, has been stressed as one of key research area in the context of fire management and biodiversity conservation in a recent review (Driscoll et al., 2010).

The present study examines trait-habitat relationships and habitat occupancy patterns of bird assemblages in boreal forest stands following forest fire and salvage logging. In boreal forest ecosystems, forest fire is recognized as key disturbance agent that

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shapes landscape and temporal dynamics of fauna and flora (Saab and Powell, 2005; Lindenmayer et al., 2008). Episodic fires generate structural and compositional heterogeneity, which is characterized by large numbers of dead trees and other rare and/or ephemeral habitat resources that are critical to long-term regional persistence, particularly, of fire-associated species (Hutto, 2006; Saab et al., 2007b; Kotliar et al., 2007). However, the same critical habitat features and associated species are also being increasingly threatened by post-fire salvage logging, thereby prompting the urgency in developing ecologically based guidelines for sustainable management of burned forests (Hutto, 2006; Lindenmayer et al., 2008).

In this context, birds have been the subjects of many studies to understand biotic response to post-fire ecological conditions, including salvage logging (Kotliar et al., 2002; Morissette et al., 2002; Hutto, 2006), because they are considered as good indicators of ecological "integrity" of forest habitats (e.g., Woodpeckers (Piciformes: Picidae), Mikusiński et al., 2001). Despite the availability of extensive information, our understanding of the life-history traits underlying their response patterns remains far from complete (Kotliar et al., 2002). For example, many fire-associated species (e.g., the Black-backed Woodpecker, *Picoides arcticus*) are known to have strong affinity for severely burned forest stands (e.g., Nappi and Drapeau, 2009); yet, it is not clear whether their affinity for severe burns is primarily for nesting (cavity-nesting), foraging (bark insectivores), or for both activities (e.g., Koivula and Schmiegelow, 2007).

Identifying the specific traits linked to burn-severity and other fire-generated habitat attributes is important to understand the biological consequence of salvage-logging and for setting guidelines to minimize their effects (e.g., snag-retention guidelines; Hutto, 2006). For example, a few large trees may be sufficient for nesting (Spiering and Knight, 2005), but not for foraging (Brawn and Balda, 1988). In addition, habitat selection in birds is a multi-scale process, in which nesting and foraging habitat requirements are not selected at the same spatial scales. Given such differences between trait requirements, management focus on single trait-habitat link (e.g., cavity-nesting alone) could be inadequate (Hutto, 2006). Thus, it is important to consider the trait-habitat link of several traits simultaneously. Recently, inferences about trait-habitat links in post-fire environments have been done only "indirectly" or a posteriori (e.g., Kotliar et al., 2002; Morissette et al., 2002).

We have two major objectives: 1) to determine trait-habitat relationships and identify the differential response of bird species traits (related to nesting, foraging and residence) to forest landscapes characterized by ecological conditions following post-fire salvage-logging; 2) to model species habitat occupancy probabilities and examine how trait-habitat relationships pertain to species occupancy probabilities. Our study sites cover gradients of burn-severity (low to high severity), age structure (20 to 120 years) and tree composition, amount of residual retention (20–100%), and landscape context of burns (e.g., distance from closest burned forest). These factors all have known effect on bird communities (e.g., Kotliar et al., 2002; Saab et al., 2007b). We applied two complementary multivariate statistical methods, the fourth-corner (Legendre et al., 1997; Dray and Legendre, 2008) and RLQ analyses (Dolédec et al., 1996) that allow a direct assessment of the link between species traits and habitat attributes by way of species distribution data. While the Fourth-corner analysis performs a detailed test of the significance of each trait and environment combination, the RLQ analysis provides an ordination depicting the generalized trait-habitat relationships. We expected that abundant nesting substrates and greater numbers of insects associated with high amount of residual trees should favor traits characteristic of fire-associated species (e.g., bark-insectivores, cavity-nesters) over other traits, e.g., omnivores or shrub nesters. It is also plausible, however, that their cavity-nesting and foraging traits may respond differently to burn severity and amount of residual trees (see above). For example, while severe burns might increase availability of snags for cavity-nesting or generate conducive conditions for ground-feeding species, bark- and foliage-insectivores may respond negatively to such burns. In addition, trait reponses to habitat attributes could be scale dependent, for example, the link of nesting guilds to burn severity may be more prominent at small than at large scale. Because burned forests are potential source populations for fire-associated species (e.g., Nappi and Drapeau, 2009) and their influence is related to age-since-fire (Smucker et al., 2005), we expected that recent burns in the landscape could promote occupancy of fire-associated species on focal burns. Identifying which ecological variable depicted in trait-habitat relationships would also be selected in species habitat occupancy models have valuable conservation implications, particularly when a species possesses traits that have opposite trait-habitat relationships.

2. Methods

2.1. Study area description

The study was conducted in 55 study sites within four forest burns totaling more than 65,100 ha (Fig. 1, burned in 2005). The forest burns were located within the western spruce–moss bioclimatic subdomain of northwestern Quebec, Canada (49°15′-50°40′N and 75°00′W–73°45′W). This subdomain is dominated typically by black spruce *Picea mariana*, with jack pine *Pinus banksiana* and balsam fir *Abies balsamia*. The forest landscapes also contain some deciduous trees such as trembling aspen *Populus tremuloides* and paper birch *Betula papyrifera*. Due to relatively short fire cycles (120–180 years), landscapes of this ecoregion are dominated by even-aged forest stands (Bergeron et al., 2004).

We selected sampling sites using systematic random sampling to represent a gradient of pre-fire composition and age structure (20–120 years), post-fire burn severity (low to high severity) and salvage logging intensities (0–80%) observed within the forest burns (Table 1). The sites also incorporated a range of landscape-level habitat contexts, namely distance from previously burned and unburned (green) forest. These habitat variables were selected as they have been shown to differentially influence the community structure and life-history traits (most significantly the foraging and nesting guilds) of bird assemblages in burned forests (see reviews in Kotliar et al., 2002; Saab et al., 2007b). Immediate post-fire environments are typically characterized by abundance of dead and dying trees and associated insect outbreaks; and bark-insectivores and cavity-nesters are known to capitalize on such resource availability. Variation in snag size, burn characteristics (severity and heterogeneity) and salvage-logging intensity can affect the availability of these resources and other habitat conditions, whose influence on bird distribution may differ depending on their traits. For instance, increasing burn severity and salvage logging intensity (often targeting larger trees) may decrease available insect prey for bark- and foliage-insectivores. These conditions, however, can create conducive conditions for species that are adapted to open-canopies, such as ground-insectivores and omnivores. Also, the proximity to unburned forest and/or remnants within burn forests associated with riparian areas (which might limit burn severity) could be important habitats for species not adapted to post-fire environments (Kotliar et al., 2002). Similarly, the proximity to previous burns (and their time since fire) might increase the flow or colonization of focal burns by species possessing fire-adapted traits (e.g., bark-insectivores).

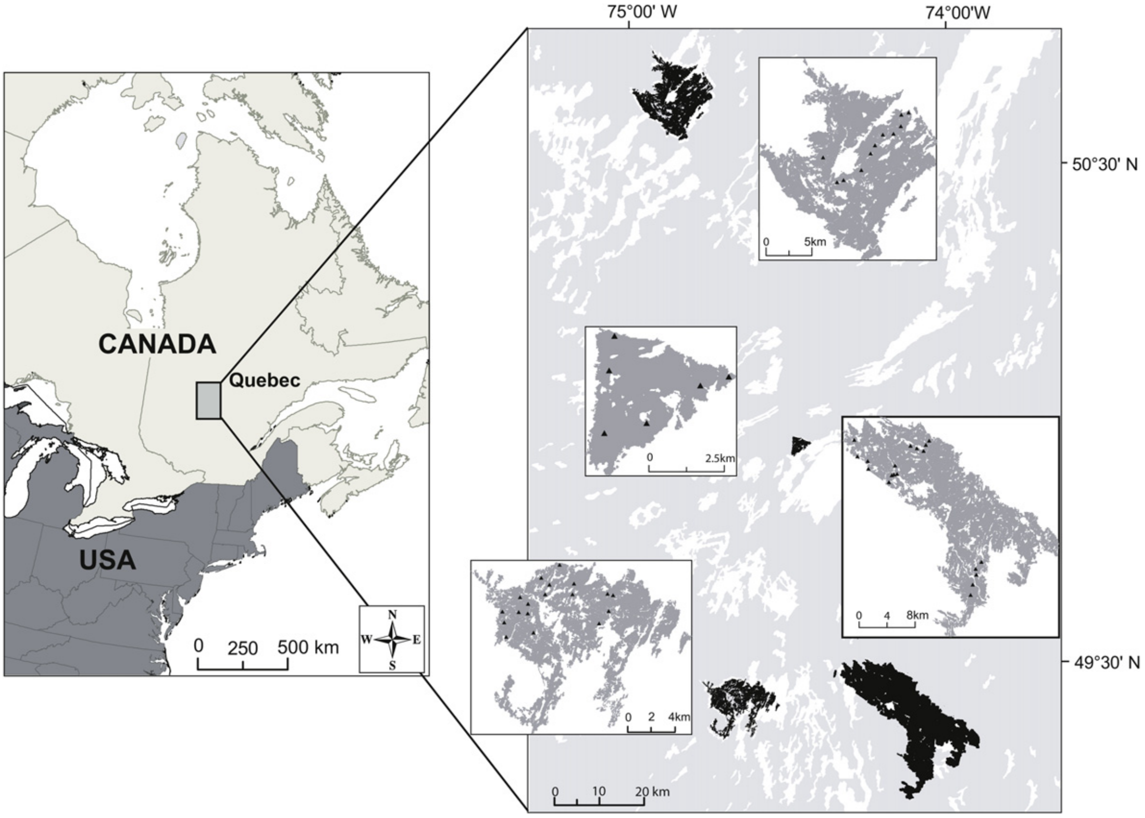

Fig. 1. Map of study area showing study sites, represented by black triangles, within the four forest fire-blocks burned in 2005 (Total area 65,100 ha).

We thus measured the amount of residual tree basal area (by species and size classes), burn characteristics (mean severity and heterogeneity), and edge-length (aquatic and salvage) at stand-level within 100 m and 500 m circular buffers centered on bird survey centre points (Table 1). We characterized residual tree retention using information about age structure, stand composition, and post-fire forest logging intensity (expressed as a percentage) in ecoforest classification maps and a database inventory (Stock data) of basal area (by species and diameter class) (*Ministère des Ressources naturelles de la Faune du Québec*, MRNFQ). Because pre-salvage basal area varied between stands, we focused on the amount of residual retention rather than intensity of salvage logging, which was carried between August 2005 and June 2006. We characterized the basal area of young residual (dbh ≤ 9 cm) and merchantable (dbh > 9 cm) trees, which are the main target of post-fire salvage. The stand-level buffers were all included in studied burns, and consequently, most trees were dead, although a few live trees might be found at the 500 m scale (J. Boucher, *personal observation*).

Table 1
Code, description and range of habitat variables measured at two scales (100 m and 500 m buffer) from the centre of bird census station. Variables indicated by [£] and [§] were square-root and double square-root transformed, respectively, in the species trait-habitat and species habitat occupancy analyses. Dbh stands for tree diameter at breast height.

Habitat variables		Variable range by scale	
Code	Description	Scale 100 m	Scale 500 m
[§]DEC.Y	Basal area deciduous trees (Birch and trembling aspen) of dbh ≤ 9 cm [m^2/0.1 ha]	0–7.11	0–4.93
[§]DEC.M	Basal area deciduous trees with dbh > 9 cm [m^2/0.1 ha]	0–26.81	0.01–20.06
[£]BSP.Y	Basal area of Black spruce (*Picea mariana*) of dbh ≤ 9 cm [m^2/0.1 ha]	0–68.33	0.26–38.34
[£]BSP.M	Basal area of Black spruce (*Picea mariana*) of dbh > 10 cm [m^2/0.1 ha]	0–184.83	0.53–85.31
[§]JPI.Y	Basal area of Jack pine (*Pinus banksiana*) of dbh ≤ 9 cm [m^2/0.1 ha]	0–4.23	0–1.82
[§]JPI.M	Basal area of Jack pine (*Pinus banksiana*) with dbh > 9 cm [m^2/0.1 ha]	0–109.78	0.06–37.94
[§]BFI.Y	Basal area of Balsam fir (*Abies balsamea*) of dbh ≤ 9 cm [m^2/0.1 ha]	0–48.54	0–23.68
[§]BFI.M	Basal area of Balsam fir (*Abies balsamea*) of dbh > 9 cm [m^2/0.1 ha]	0–83.52	0.02–43.64
Brn.Sev	Index of burn severity (mean) quantified as difference in Normalized Burn Ratio (scaled from 0 to 1)	0.21–0.62	0.17–0.59
Brn.Het	Index of burn heterogeneity (sd) computed from difference in Normalized Burn Ratio (scaled from 0 to 1)	0.04–0.19	0.11–0.32
SalEdge	Salvage edge (km)	0–0.59	0–7.3
AquEdge	Aquatic edge (lakes, rivers) within buffer (km)	0–0.31	0.24–4.79
Dis.BF	Distance (km) to burned forest in the landscape	20.15–76.58	
Age.BF	Number of years since fire (Age) of neighboring burned forest	3–6 (yrs)	
[£]Dis.GF	Shortest distance (km) to unburned forest	0.07–5.47	

Following Key and Benson (2006), we quantified burn severity using the Difference (delta) Normalized Burn Ratio (dNBR) index. The dNBR was computed from differences between pre- and post-fire in reflectance of bands 4 and 7 (that respond most to burning) of satellite images taken before salvage logging was carried. We computed dNBR values for each pixel (30 m) within the four burns, these ranged from 93 to 1341; thus covering to the whole range of fire severity (low–high) according to Key and Benson (2006). We extracted dNBR values for each pixel within 100 m and 500 m buffer, and considered the mean and standard deviation at respective scales as a measure of burn severity (Brn.Sev) and heterogeneity (Brn.het), respectively. We measured also landscape-level variables, namely the distance of focal burn from the closest burned forest (Dis.BF) and its age (Age.BF) together with isolation from neighboring unburned, green forest (Dis.GF). All habitat variables were extracted using Arc MAP 9.2 (ESRI, 2006).

2.2. *Bird sampling*

Birds were surveyed in 55 stands using the fixed-radius point count method (Hutto et al., 1986) twice in 2006, and three times in 2007 approximately every week from early June to early July. Birds that were heard or seen within a 100 m radius were recorded. To minimize observation overlap and ensure statistical independence, sites were at least 1 km apart. Surveys were conducted during morning hours when field conditions were conducive, i.e., no rain and light winds. To counteract observer (total of four observers) and time biases, we alternated sampling and surveyors order visiting each site (three observers per site).

2.3. *Data analysis*

2.3.1. *Trait-habitat relationship*

We selected a set of four species traits, namely nesting (site location and type), foraging, and migratory behavior (Table 2), that have been shown as proximate mechanisms to explain response patterns of birds to post-fire habitat legacies and salvage logging (e.g., review in Saab et al., 2007b; also see section 2.1). These traits also have applicability in formulating post-fire salvage logging management strategies, e.g., nesting requirements of cavity-nesting species has been recognized as one of key component in formulating snag-retention guidelines (Kotliar et al., 2002; Hutto, 2006). We compiled the information of these traits of bird species from Poole (2008).

We examined trait-habitat relationships by means of two complementary multivariate analyses: the Fourth-corner (Legendre et al., 1997; Dray and Legendre, 2008) and RLQ analyses (Dolédec et al., 1996). Both methods are three-table analyses that allow a direct assessment of relationships between habitats (Matrix R: habitat by sites) and species traits (Matrix Q: species by traits) by way of species distribution data (Matrix L: Species by sites). The Fourth-corner primarily focuses on tests of the significance of the links between each trait and environment combination in a correlation-type analysis (Legendre et al., 1997). The RLQ analysis

Table 2
Bird species percentage of occurrence (Frequency in %) and their respective traits used to examine trait-habitat relationships.

Code	Common name	Latin name	Frequency	Life history attributes			
				Forage	Nest location	Nest type	Migration
DEJU	Dark-eyed Junco	*Junco hyemalis*	98.2	OM	GN	OC	SDM
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	96.4	OM	GN	OC	SDM
BBWO	Black-backed Woodpecker	*Picoides arcticus*	94.5	BI	CN	CV	RES
HETH	Hermit Thrush	*Catharus guttatus*	70.9	OM	GN	OC	SDM
AMRO	American Robin	*Turdus migratorius*	69.1	OM	CN	OC	SDM
TRES	Tree Swallow	*Tachycineta bicolor*	63.6	AI	CN	CV	SDM
WIWR	Winter Wren	*Troglodytes troglodytes*	45.5	GI	CN	CV	SDM
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	43.6	FI	CN	OC	NEO
EABL	Eastern Bluebird	*Sialia sialis*	41.8	GI	CN	CV	SDM
YRWA	Yellow-rumped Warbler	*Dendroica coronata*	41.8	FI	CN	OC	SDM
LISP	Lincoln's Sparrow	*Melospiza lincolnii*	40	OM	GN	OC	NEO
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	34.5	OM	CN	OC	SDM
NOFL	Northern Flicker	*Colaptes auratus*	27.3	GI	CN	CV	SDM
COYE	Common Yellowthroat	*Geothlypis trichas*	25.5	FI	GN	OC	NEO
TTWO	Three-toed Woodpecker	*Picoides tridactylus*	25.5	BI	CN	CV	RES
BRCR	Brown Creeper	*Certhia americana*	21.8	BI	CN	CV	SDM
MOWA	Mourning Warbler	*Oporornis philadelphia*	21.8	FI	GN	OC	NEO
WWCR	White-winged Crossbill	*Loxia leucoptera*	20	SF	CN	OC	SDM
ALFL	Alder Flycatcher	*Empidonax alnorum*	16.4	AI	SN	OC	NEO
NAWA	Nashville Warbler	*Vermivora ruficapilla*	14.5	FI	GN	OC	NEO
NOWA	Northern Waterthrush	*Seiurus noveboracensis*	14.5	GI	GN	CV	NEO
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	14.5	BI	CN	CV	RES
SWTH	Swainson's Thrush	*Catharus ustulatus*	12.7	FI	SN	OC	NEO
OSFL	Olive-sided Flycatcher	*Contopus borealis*	10.9	AI	CN	OC	NEO
NOHO	Northern Hawk Owl	*Surnia ulula*	9.1	GV	CN	CV	RES
RUBL	Rusty Blackbird	*Euphagus carolinus*	9.1	OM	SN	OC	SDM
BEKI	Belted Kingfisher	*Megaceryle alcyon*	7.3	GV	GN	CV	SDM
CONI	Common Nighthawk	*Chordeiles minor*	7.3	AI	GN	OC	NEO
MAWA	Magnolia Warbler	*Dendroica magnolia*	7.3	FI	SN	OC	NEO
WIWA	Wilson's Warbler	*Wilsonia pusilla*	7.3	FI	GN	OC	NEO
COGR	Common Grackle	*Quiscalus quiscula*	5.5	OM	CN	OC	SDM
HAWO	Hairy Woodpecker	*Picoides villosus*	5.5	BI	CN	CV	RES
LEFL	Least Flycatcher	*Empidonax minimus*	5.5	AI	CN	OC	NEO

Codes for bird species traits are as follows. Nest location: CN = Canopy/trees; GN = Ground; SN = Shrubs. Nest type: CV = cavity nester; OC = Open-Cup. Foraging strategy: AI = Aerial Insectivore; BI = Bark insectivore; FI = Foliage Insectivore; GI = Ground insectivore; GV = Vertebrates; SF = Seeds/fruits; OM = Omnivore. Note that the OM feeding guild may feed exclusively on insects during breeding season, and include fruits and seeds during non-breeding. No analysis was carried for SF, which had only a single species. Migration strategy: RES = permanent resident; SDM = short distance migrant; NEO = Neotropical/long distance migrant.

proceeds with eigenvalue decomposition of product matrices, thereby providing a common ordination axes of species traits and environment of sites (onto which species and sites are projected, an option not available in the Fourth-corner analysis) and, thus, focuses more on interpretation of their links.

In the Fourth-corner analysis the significance of trait-habitat links is tested by a permutation procedure. When a random distribution is assumed, the recommended method is permutation Model 1, which assigns species randomly among sites (Legendre et al., 1997). However, this permutation may result in sites with no species and cause "false" positives, which are not desirable (Legendre et al., 1997). Here we used a slightly modified permutation or null model, whereby species are assigned randomly, but with the constraints that species frequency and richness of sites are maintained, i.e., the fixed-fixed null model. Thus, species niche breadth and site capacities are maintained in the random matrices. For this study, we generated 1000 random matrices by a quasi-swap algorithm (Miklós and Podani, 2004) using the function commsimulator in the vegan package (Oksanen et al., 2009) implemented in R (R-Development Team, 2009; Oksanen et al., 2009). We used a routine custom code in R to upload each of the random matrices to the ade4 package for R (Dray and Dufour, 2007) to compute (and store) trait-habitat statistics for each null matrix (Dray and Legendre, 2008; Dray and Dufour, 2007). Results from fixed-fixed null models will be our preference in this paper.

We also tested trait-habitat link using the "two-step approach," which combines results of two permutation models, viz., Model 2 and Model 4, as proposed by Dray and Legendre (2008). The critical value of the "two-step approach" is taken by adjusting for the simultaneous test, i.e., square root of 0.05 ($p = 0.24$), which, however, could be regarded as too liberal (for details see Dray and Legendre, 2008). In our study, even considering a more conservative level ($p < 0.10$) indicated a general support for the results obtained by fixed-fixed null model (results presented in Appendix A in the electronic Supplementary material).

We performed RLQ analysis (Dolédec et al., 1996) to ordinate the joint structure of the three tables (R, L and Q). RLQ analysis was performed using the ade4 package for R (Dray and Dufour, 2007). We conducted two separate RLQ analyses, using habitat variables at 100 m and 500 m scales, by also considering landscape-level variables.

2.3.2. *Species habitat occupancy models*

Our study focus was to understand how site-specific habitats relate to species traits and species occupancy patterns rather than survey-specific or year specific relationships. Therefore, we pooled the five survey data for each site to construct a single species by site presence/absence matrix of bird occurrences. This pooled data across multiple surveys (over two years) should increase the number of detection (i.e., minimize false absences) of species in each site (see also Toms et al., 2006). We performed multiple logistic regression analysis (Hosmer and Lemeshow, 2000) to model the occurrence of each species (presence/absence) at each study site based on habitat predictor variables (Table 1) and then we examined how trait-habitat relationships pertain to these species occupancy probabilities. In all analyses, we considered only species recorded in at least three sites (5% of stations), thereby including 33 bird species (Table 2) that constituted 98% of the total presence-distribution. For three widespread species (Dark-eyed Junco, White-throated Sparrow and Black-backed Woodpecker) that were recorded 95–98% of the sites, fitting logistic model was not informative. Therefore, instead of omitting them altogether, we modelled variation in their abundance pattern by using the maximum number of individuals recorded in each site among the five surveys as "abundance" index.

To eliminate model misspecification due to multicollinearity, correlations between variables were examined. There was a strong correlation between basal area of young and merchantable trees; therefore, we used the merchantable residual for black spruce (BSP.M) and balsam fir (BFI.M), while the young for jack pine (JPI.Y) and deciduous trees (DEC.Y). This action minimized the correlations between composition types. Although merchantable trees contributed a greater proportion to basal area retention, young trees had higher density (%). We then built two separate habitat-models for 100 m and 500 m buffers, by also considering landscape-level variables (e.g., distance to the closest burned forest). For each scale, we estimated useful predictor variables using the Akaike Information Criterion (AIC) for best subset model as our selection procedure. We performed analyses using the bestglm-package for R (McLeod and Xu, 2009), which implements the complete enumeration algorithm to examine all possible regression models (Morgan and Tatar, 1972). Such an exhaustive search could be ideal for exploratory purposes, and has been shown to yield useful predictor models comparable to alternative modeling approaches (Murtaugh, 2009). Accuracy of the "best" logistic regression model to predict presence or absence was assessed using the area under Receiver Operating Characteristic (ROC) curve, also known AUC (Pearce and Ferrier, 2000). A reasonably accurate model will have an AUC value of at least 0.7, and models with $\text{AUC} > 0.8$ are regarded as good ones (Pearce and Ferrier, 2000). Finally, in order to estimate the importance of detection probability as a source of bias in previous analyses (MacKenzie and Royle, 2005), we performed detection analysis using the package unmarked for R (Fiske et al., 2010). More specifically, we used the colonization-extinction model of MacKenzie et al. (2003) [data pooled per primary sampling year or by considering each of the five secondary survey independently] to obtain cumulative detection probability estimates for each species (formula as provided in MacKenzie and Royle, 2005).

3. Results

3.1. *Species trait-habitat relationship*

We recorded 1481 individuals of 42 bird species during the five surveys across the 55 study sites. In each site, the total number of species detected during the five surveys was between 6 and 17 (mean ± sd: 10.5 ± 2.5). There was differential association of traits with the amount and composition of residuals (Table 3, Appendix A in the electronic Supplementary material). For example, bark insectivores were positively associated with large amount of black spruce and jack pine, and foliage insectivores with balsam fir and deciduous residuals (Table 3). Canopy nesters had similar patterns as that of bark-insectivores, and both were negatively affected by salvage edge. In contrast, ground and shrub nesters had the opposite relationship. Also, omnivores (and those feeding on vertebrates) were negatively associated with amount of balsam fir and deciduous tree residual basal area (scale of 500 m). There was also a contrasting preference (scale of 500 m) between neotropical migrants that were positively associated to balsam fir and deciduous residuals, and residents and short-distance migrants that preferred black spruce, jack pine or both.

Most traits exhibited significant link with burn severity (particularly at the 100 m scale) (Table 3). Foliage- and bark-insectivores, as well as open-cup nesting on canopies had affinity for low burn severity. In contrast, cavity-, ground- and shrub-nesters, as well as ground- foragers (insectivores or vertebrates) were associated with high burn severity.

Aquatic edge was positively associated with ground-nesters and Neotropical migrants, and negatively associated with canopy-nesters, bark-insectivores, and residents.

Table 3
Relationships between traits (columns) and habitats (rows) according to Fourth-corner analysis. The "+"and "−" signs indicate, respectively, positive and negative trait-habitat links that are significant ($P < 0.05$) according to fixed-fixed null model tests. Details of statistics provided in Appendix A in the electronic Supplementary material. Codes for habitats and species-traits are shown in Tables 1 and 2, respectively.

Habitats		Nesting location and type					Foraging guilds						Migration status		
		GN	SN	CN	CV	OC	GI	FI	BI	AI	OM	GV	RES	SDM	NEO
Stand scale 100 m	DEC.Y	.	.	.	.	.	.	.	.	.	−	.	.	.	.
	DEC.M	.	.	+	.	.	.	+	+	.	−	.	.	.	.
	BSP.Y	−	.	+	.	.	.	+	.	.	.	−	.	.	.
	BSP.M	−	.	+	.	.	.	.	.	.	−	.	.	.	.
	JPI.Y	.	.	+	.	.	.	+	.	.	.	.	.	+	.
	JPI.M	−	.	+	.	.	.	.	+	.	.	−	.	.	.
	BFI.Y	.	.	.	.	.	.	+	.	.	−	.	.	.	.
	BFI.M	.	.	.	.	.	.	+	.	.	−	.	.	.	.
	Brn.Sev	+	+	−	+	−	+	−	−	.	.	+	.	.	.
	Brn.Het	.	.	.	−	.	.	.	.	.	.	.	.	.	.
	SalEdge	+	+	−	.	.	.	.	−	.	.	.	−	.	.
	AquEdge	+	.	−	.	.	.	.	−	.	.	+	−	.	+
Stand scale 500 m	DEC.Y	.	.	.	.	.	.	+	.	.	−	.	.	.	+
	DEC.M	.	.	.	.	.	.	+	+	.	−	.	.	.	.
	BSP.Y	−	−	+	.	.	.	.	+	.	.	.	.	.	.
	BSP.M	−	.	+	.	.	.	.	+	.	.	.	+	.	−
	JPI.Y	−	.	+	.	.	.	.	.	.	.	.	.	.	.
	JPI.M	−	−	+	.	.	.	.	+	.	.	.	.	.	−
	BFI.Y	.	.	.	−	.	.	+	.	.	−	.	.	−	+
	BFI.M	.	.	.	.	.	.	+	.	.	−	.	.	−	+
	Brn.Sev	.	.	.	+	.	+	−	.	.	.	+	.	.	.
	Brn.Het	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	SalEdge	.	+	−	.	.	.	.	−	.	.	.	.	.	.
	AquEdge	+	.	−	.	.	.	.	−	.	.	.	−	.	+
Landscape	Dis.BF	.	.	.	.	.	.	.	−	+	.	.	.	.	.
	Age.BF	+	.	−	−	+	.	.	−	.	.	.	−	.	.
	Dis.GF	−	.	.	+	.	.	.	.	.	.	+	.	.	.

At the landscape scale, cavity-nesters, bark-insectivores and residents preferred adjacent burned forests of recent fire (Age.BF). In contrast, ground and open-cup nesters were positively associated with time-since-fire of the neighboring forest, and in fact, preferred green/unburned forests close to focal-burn. Bark and aerial insectivores had negative and positive correlation with distance to burned forest, respectively (Table 3, Appendix A in the electronic Supplementary material).

The results from RLQ analysis summarized the aforementioned trait-habitat relationships (Table 4, Fig. 2). For both examined scales, the first three RLQ axes extracted 87.8% (100 m scale) and 91.7% (500-m scale) of the covariation between species traits and habitat attributes (Table 4, Fig. 2a,b). The first RLQ axis correlated positively with amount of black spruce and jack pine, canopy nesters, bark-insectivores and residents, but negatively with salvage edge, shrub nesters, ground nesters, and omnivores. On the second axis, the most prominent trends were positive scores for balsam-fir and deciduous trees (500 m), foliage insectivores, and Neotropical migrants. Burn severity and isolation from green forest, cavity nesters, and vertebrate-feeders were arrayed in the opposite direction along same axis.

Some apparent trait-habitat relationships in the RLQ analysis were non-significant according to the Fourth-corner analysis. For example, in the RLQ ordination (100 m scale), both burn heterogeneity (Brn.het) and balsam fir had similar scores, and the trait foliage insectivore appeared to fall on same axis (Fig. 2a). Yet, only

Table 4
Results of RLQ analyses and comparison with the separate ordination analyses (R, L and Q alone) at two spatial scales.

Analysis	Scale 100 m			Scale 500 m		
	RLQ axis 1	RLQ-axis 2	RLQ axis 3	RLQ axis 1	RLQ axis 2	RLQ axis 3
A) RLQ analysis						
R/RLQ (Var)	3.770	1.854	1.481	2.918	3.718	1.425
Q/RLQ (Var)	2.352	2.721	2.389	2.727	2.035	2.366
Eigenvalue	0.173	0.096	0.049	0.172	0.125	0.038
Covariance	0.415	0.310	0.222	0.414	0.353	0.195
Correlation	0.140	0.138	0.118	0.147	0.128	0.106
B) RLQ summary (Explained variance in %)						
R/RLQ	74.2	75.0	77.3	64.6	88.2	83.7
L/RLQ	31.7	33.1	31.0	33.4	30.8	27.9
Q/RLQ	52.2	74.2	83.9	60.6	69.7	80.1
Inertia (trace)	47.7	26.5	13.6	47.1	34.2	10.4

Notes: In Panel (A), the **R**/RLQ (Var) and **Q**/RLQ (Var) are the variances of habitat variables and species traits, respectively, that were computed for the first three RLQ axes, as well as the covariance and correlation between them resulting from the RLQ analysis. The RLQ summary in Panel (B) shows the percentage each RLQ axis accounts for the variance of the habitat attributes (**R**/RLQ), species composition (**L**/RLQ) and species-trait (**Q**/RLQ) tables when they were analysed separately (not shown). For instance, the first axis in the RLQ analysis at 100 m scale accounted for 74.2% (**R**/RLQ) of the variance obtained in the first axis by the separate correspondence analysis of the habitat attributes (R-table). The values associated with inertia are the percentage variance total variance explained by each of the RLQ axis.

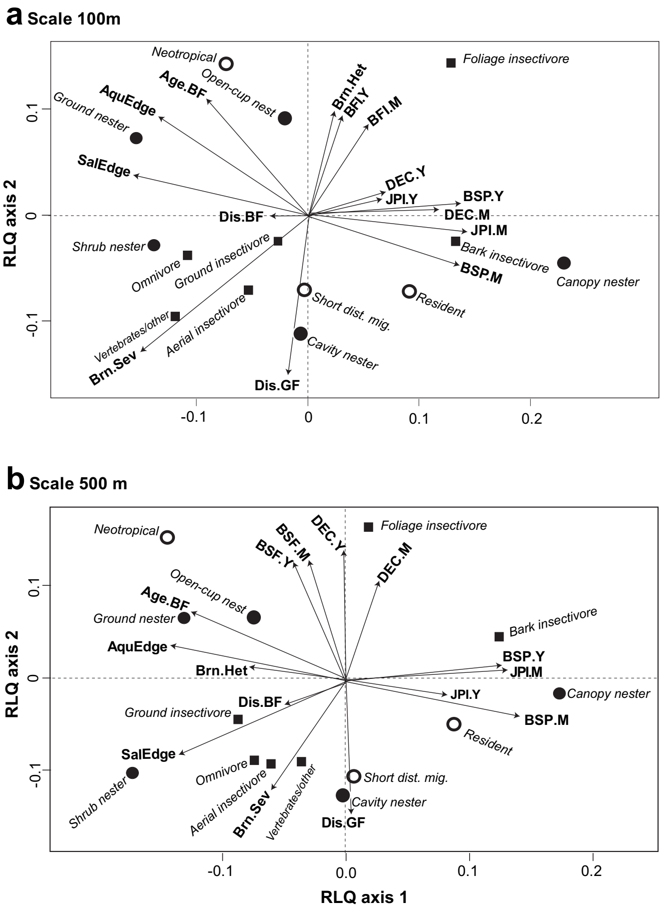

Fig. 2. RLQ scores of habitat variables (arrows) and bird species traits (symbols and italicized) along the first two RLQ axes. The RLQ analysis considered habitat variables measured at (a) 100 m buffer and (b) 500 m buffer distances from the centre of the bird census point. Codes for habitats are shown in Table 1.

balsam fir had a significant link to foliage insectivores according to Fourth-corner (Table 3). Similarly, the apparent relationships of aerial insectivores and omnivores to burn severity in RLQ (500 m scale) were not significant in the Fourth-corner analysis. However, RLQ distinguished which specific habitat (among correlated habitat factors) could be more related to a given trait. For example, Fourth-corner analysis indicated that ground nesters were associated positively with burn severity and aquatic edge (100 m scale, Table 3). Although RLQ supported both relationships (axis 1, Fig. 2a), ground nesters were related mainly to aquatic edge-length (axis 2, Fig. 2a).

3.2. Species habitat occupancy models

We developed reasonably accurate (internal validation) habitat-occupancy models (AUC > 0.7) for 25 (83%) species (Table 5, Appendix B in the electronic Supplementary material). In addition, 'abundance' models for three widespread species (Dark-eyed Junco, White-throated Sparrow and Black-backed Woodpecker) explained 10–38% of their abundance variation. The habitat-occupancy models were in good concordance with trait-habitat relationships, particularly when different traits of a species had similar associations with a given habitat. For example, low occupancy probability with salvage edge was shown for Black-backed Woodpecker, American Three-toed Woodpecker, Red-breasted Nuthatch, and Brown Creeper (Table 5); these species posses trait-combinations (canopy-nesting, bark insectivores and resident; Table 3 and Fig. 2) that were negatively associated with salvage edge. Similarly, species such as Ruby-crowned Kinglet and Yellow-rumped Warbler were less likely to occupy severely burned stands, as would be expected from their traits (foliage insectivores, open-cup nesters, in canopy). Occupancy models for most ground nesters, such as White-throated Sparrow, Lincoln Sparrow, Northern Waterthrush, and Wilson's Warbler, indicated positive relationships with aquatic edge, as also shown by the Fourth-corner analysis (500 m scale).

Habitat occupancy models also indicated which of the opposing trait-habitat relationships were important for occupancy. High occupancy probabilities of species such as Black-backed Woodpecker, Tree Swallow, and Eastern Bluebird in severe burns (100 m, Table 5) were in concordance to their cavity-nesting trait rather than to being canopy nesters (Table 3). The latter relationship could be due to open-cup nesters, with which they share the canopy nesting trait. Some species having the same trait responded differently to the same variable. Both Lincoln Sparrow and Common Nighthawk are open-cup, ground nesters, but they responded negatively and positively, respectively, to burn severity. Note that the open-cup (type) and ground-nesting (location) traits had contrasting link to burn severity. Some habitat occupancy relationships could not be explained by trait-habitat relationships (e.g., Northern flicker and Red-breasted nuthatch had negative coefficient with balsam fir, BAF.C) or were opposite to that trait-habitat relationship (e.g., White-throated Sparrow with deciduous trees, DEC.Y).

Our analysis using the colonization-extinction model [data pooled per primary sampling year or by considering each of the five secondary survey independently] indicated that the cumulative detection probability estimates for most species were fairly good (0.74–1.00, mean 0.94). However, the estimated cumulative detection probability was relatively low (0.15–0.64) for six species (Magnolia Warbler, Wilson's Warbler, Least Flycatcher, White-winged Crossbill, Common Yellowthroat and Hairy Woodpecker, Scientific names in Table 2).

4. Discussion

We addressed the differential response of bird functional traits to post-fire habitat conditions and salvage-logging and their bearing to species habitat occupancy probabilities. Regardless of whether or not salvaging was affecting merchantable or young trees, higher amount of residual tree basal area was important for canopy-nesters, and foliage- and bark-insectivores than guilds such as omnivores, ground- and shrub-nesters, that seem to thrive better in salvaged areas and associated edges. Moreover, we found differential response to tree composition between foliage insectivores (e.g. for balsam fir) and bark insectivores (e.g. for black spruce). These findings were consistent with studies showing guild response to levels of salvaging or the amount of residuals (e.g., Morissette et al., 2002) and its composition (Koivula and Schmiegelow, 2007).

Degree of burn severity is an important habitat attribute in post-fire disturbance, especially for fire-associated species (Smucker et al., 2005). Our results suggest that bark-insectivores (also foliage insectivores) preferred low- to moderate-severity burns (Kotliar et al., 2002; Smucker et al., 2005), where there is probably greater insect availability than in severe burns (Nappi et al., 2003; Smucker et al., 2005). Thus, we found no support for suggestions that strong affinity of fire-associated species with severe-burns was for foraging (e.g., Koivula and Schmiegelow, 2007). Our finding rather suggests that their affinity for severe-burns could be related to being cavity-nesters, perhaps a condition particularly important for secondary cavity-nesters. Also, in notable contrast to foraging (see above), the amount of residual basal area was less critical for cavity-nesting (also

Table 5

The direction (−: negative; +: positive) of habitat variable influence on species occupancy probability (model details in Appendix B) and the respective species traits linked similarly (unless indicated otherwise) to that variable according to Fourth-corner analysis (Table 3, and Appendix A in the electronic Supplementary material). Code for traits and species (in *Notes*) are provided in Table 2, and for habitats are as in Table 1. AUC = Area under ROC curve. For species indicated by (§), "abundance" model were fitted.

Species common name	AUC	Habitat variables (Stand scale 100 m)							Landscape-level variables		
		DEC.Y	BSP.M	JPI.Y	BFI.M	Brn.Sev	SalEdge	AquEdge	Age.BF	Dis.BF	Dis.GF
Dark-eyed Junco §	0.15	.	.	.	.	.	+, GN	.	.	+	.
White-throated Sparrow §	0.373	+, **OM**$^-$	.	−, **SDM**$^+$	−, OM	.	.	+, GN	+, GN/OC	.	.
Black-backed Woodpecker §	0.276	.	.	.	+	+, CV/**CN**$^-$/**BI**$^-$	−, CN/BI/RES	.	−, CN/CV/BI/RES	+, **BI**$^-$	.
Hermit Thrush	0.798	.	.	.	.	+, GN/**OC**$^-$	.	.	−, **GN**$^+$/**OC**$^+$	−	−, GN
American Robin	0.697	+, **OM**$^-$	.	.	−, OM	.	.	.	.	.	.
Tree Swallow	0.757	.	.	.	.	+, CV/**CN**$^-$	.	.	−, CN/CV	+, AI	−, **CV**$^+$
Winter Wren	0.643	.	+, CN	.	.	.	.	+, **CN**$^-$	.	.	.
Ruby-crowned Kinglet	0.808	.	.	.	.	−, CN/OC/FI	−, CN	+, NEO/**CN**$^-$	.	.	.
Eastern Bluebird	0.767	.	.	+, CN/FI/SDM	.	−, CN/OC/FI	.	.	.	.	.
Yellow-rumped Warbler	0.8	−	+, CN	.	.	+, CV/GI/**CN**$^-$	+, **CN**$^-$	.	.	.	+, CV
Lincoln's Sparrow	0.791	.	−, GN/OM	.	.	−, OC/**GN**$^+$	.	+, GN/NEO	.	.	.
Northern Flicker	0.813	.	.	.	−	.	.	−, CN	+, **CN**$^-$/**CV**$^-$	−	.
Three-toed Woodpecker	0.784	.	.	−, **CN**$^+$	.	.	.	−, CN/BI/RES	−, CN/CV/BI/RES	.	.
Brown Creeper	0.721	.	.	.	.	.	−, CN/BI	.	.	−, BI	.
Mourning Warbler	0.872	.	.	−, **FI**$^+$	.	.	.	.	.	.	−, GN
White-winged Crossbill	0.781	−, OM	.	−, **CN**$^+$/**SDM**$^+$	.	.	.	−, CN	.	.	.
Alder Flycatcher	0.748	.	−	.	.	.	+, SN	.	.	.	.
Northern Waterthrush	0.766	.	+, **GN**$^-$	.	.	.	.	+, GN/NEO	.	−	.
Red-breasted Nuthatch	0.862	.	.	.	−	.	−, CN/BI/RES	−, CN/BI/RES	.	.	.
Nashville Warbler	0.761	.	.	.	.	−,OC/FI/**GN**$^+$	+, GN	.	.	.	.
Olive-sided Flycatcher	0.905	.	+, CN	.	.	.	.	+, NEO/**CN**$^-$	−, CN/**OC**$^+$	.	.
Swainson's Thrush	0.743	−	.	.	+, FI	.	−, **SN**$^+$	.	.	.	.
Magnolia Warbler	0.683	.	.	.	.	.	−, **SN**$^+$	.	.	.	−
Belted Kingfisher	0.729	+	.	.	.	.	.	+, GN/GV	.	.	.
Common Nighthawk	0.76	.	.	.	.	+, GN/**OC**$^-$	.	.	.	.	.
Wilson's Warbler	0.892	.	.	+, FI	.	.	.	+ .G/NEO	.	−	.
Least Flycatcher	0.808	.	.	.	.	.	−, CN	.	.	.	.

Code	AUC	Habitat variables (Stand scale 500 m)						Landscape-level variables		
		DECE.Y	BSP.M	JPI.Y	BFI.M	SalEdge	AquEdge	Age.BF	Dis.BF	Dis.GF
Dark-eyed Junco §	0.231	.	.	+, GN$^-$	.	.	+, GN	.	.	.
White-throated Sparrow §	0.379	.	.	.	−, OM/SDM	.	+, GN	+, GN/OC	−	.
Black-backed Woodpecker §	0.106	.	.	.	+	.	.	−, CN/CV/BI/RES	.	.
Hermit Thrush	0.748	.	.	.	.	.	.	−, **GN**$^+$/**OC**$^+$	−	.
American Robin	0.746	.	.	.	−, OM/SDM	.	.	+, OC/**CN**$^-$	.	.
Tree Swallow	0.764	−	.	.	.	.	.	.	+, AI	.
Ruby-crowned Kinglet	0.757	.	.	.	+, FI/NEO	.	.	−, CN/**OC**$^+$	.	.
Eastern Bluebird	0.74	.	.	.	.	+, **CN**$^-$	.	.	.	+, CV
Yellow-rumped Warbler	0.615	.	+, CN	.	.	.	.	.	.	.
Lincoln's Sparrow	0.787	.	−, GN/NEO	.	.	.	+, GN/NEO	.	.	.
Northern Flicker	0.748	.	−, **CN**$^+$	.	.	.	.	.	−	−, **CV**$^+$
Three-toed Woodpecker	0.768	.	.	.	.	.	−, CN/BI/RES	−, C/NCV/BI/RES	.	.
Brown Creeper	0.816	+	.	.	.	.	.	−, CN/CV/BI	−, BI	.
Mourning Warbler	0.895	+, FI/NEO	.	−, GN	−, **FI**$^+$/**NEO**$^+$	.	.	.	.	−, GN
Alder Flycatcher	0.749	.	−, NEO	.	.	+, SN	.	.	.	.
Northern Waterthrush	0.742	.	.	.	−, **NEO**$^+$	.	+, GN/NEO	.	−	.
Red-breasted Nuthatch	0.758	.	.	−, **CN**$^+$	−	−, CN/BI	.	.	.	.
Nashville Warbler	0.691	+, FI/NEO	−, GN/NEO	.	.	.	.	.	.	.
Swainson's Thrush	0.703	.	.	.	+,FI/NEO	.	.	.	.	.
Olive-sided Flycatcher	0.908	.	+, CN	.	.	.	+, NEO/**CN**$^-$	−, CN/**OC**$^+$	.	.
Northern Hawk Owl	0.814	.	.	.	.	.	.	−, CN/CV/RES	.	.
Rusty Blackbird	0.791	−, OM	.	.	.	.	.	.	+	.
Magnolia Warbler	0.877	.	−, NEO	.	.	−, **SN**$^+$	−, **NEO**$^+$	.	.	.
Belted Kingfisher	0.86	+	.	.	−, SDM	.	+, GN	.	.	.
Common Nighthawk	0.908	−, NEO$^+$	.	.	+, NEO	+	.	.	+, AI	.
Wilson's Warbler	0.745	.	.	.	.	+	.	.	.	.
Hairy Woodpecker	0.789	.	.	−, **CN**$^+$	+	.	.	.	.	.
Least Flycatcher	0.971	+, NEO	.	.	.	−, CN	.	.	.	.
Common Grackle	0.732	.	.	.	.	.	+, **CN**$^-$	.	.	.

Notes: NOHO (0.814), RUBL (0.746), and HAWO (0.701) fitted only Age. BF or Dis.BF. No model fit for CEDW & COGR. **Brn.Het** was important only for BBWO (**+, CV**$^-$).
Notes: CEDW, WIWR and WWCR fitted only intercept.. There was no strong support for burn characteristics (**Brn.Sev** and **Brn.Het**) effect at 500 m scale.

see, Spiering and Knight, 2005). Our results add support to the finding highlighted in the synthesis by Kotliar et al. (2002) that fire-associated species might have a contrasting preference for foraging and nesting. Species may meet such contrasting resource requirement, for example, by using alternative habitats in the landscape (i.e., habitat complementation, sensu Dunning et al., 1992).

Severe burns, however, enhanced the foraging conditions for ground feeders (insectivores or for other prey), perhaps by exposing insects or seeds or by increasing availability of deadwood-associated insects (e.g., Northern Flicker, Koivula and Schmiegelow, 2007). Also, 'vegetation' remnants along aquatic edges within severe burns appear to be conducive for ground and shrub nesters

(Fig. 2a,b). Such remnants could form important habitats also for species that would otherwise avoid severe burns, such as the Lincoln Sparrow and Northern Waterthrush (Table 5). It is noteworthy that nesting guilds' positive (e.g., ground nesters) and negative (open-cup, canopy nesters) associations with burn severity were particularly evident at a smaller scale (100 m buffer), perhaps closer to the nest-site selection scale by birds, than at the larger scale (500 m buffer). Taken together, our findings suggest that mosaics of severely burned and unburned remnants in focal burned forests could yield habitat attributes attuned to the different requirements of bird traits (Saab et al., 2007a).

Moreover, we found that some traits also responded to the landscape context of burned forests. More specifically, cavity-nesting, bark insectivores and residents (typical of fire-associated species) occupied focal burns adjacent to burned forests (landscape) of recent rather than old fires. Early post-fire environments are characterized by abundant nesting substrates and greater insect availability (Nappi et al., 2003); this may increase breeding success of fire-associated species in focal burns, which in turn, may act as source populations at a regional scale (e.g., Black-backed Woodpecker, Nappi and Drapeau, 2009). Our results support this notion of regional dynamics (for insular systems, see Azeria et al., 2006) by illustrating that early post-fire forests at a landscape scale may provide potential colonizers for focal burns (also in occupancy models), similar to what has been demonstrated also in post-fire colonization pattern of birds in Mediterranean landscapes (Brotons et al., 2005).

The birds' habitat-occupancy probabilities were consistent with known ecology of the species and, more importantly, with the trait-habitat relationships revealed in this study, thus, providing a mechanistic explanation for species habitat occupancy patterns. The interpretation is more straightforward when a significant number of traits for a given species have similar associations with habitat factors. For example, the foraging and nesting traits could have simultaneously determined the lower probability of Black-backed Woodpecker with increased salvage edge, of Yellow-rumped warbler with severe burns or higher occupancy probability of Northern Waterthrush with aquatic edge (see also Table 5).

However, there were several exceptions, perhaps more crucial findings, where a species might have traits that exhibit simultaneous and contrasting associations with a given habitat attribute. For example, some cavity nesters (e.g., Tree swallow, Table 5) were more likely to occupy severe burns at least at fine-scale (100 m) in concordance to nest type (cavity-nesting) than to location (canopy) or foraging (some were bark-insectivores) depiction of trait-habitat relationship. This relationship of the cavity-nesters with burn severity, however, was not evident at 500 m scale; which suggests scale-specific influence of traits on species' habitat-occupancy. Also the heterogeneity of species that are categorized into constraining classifications might cause such divergent relationships, e.g., cavity-nesters share the canopy nesting trait with open-cup nesters that had a negative association with burn severity. There were also cases where habitat occupancy patterns could not be explained or were opposite to those depicted by trait-habitat relationships. For example, Northern flickers were less likely to occupy stands containing balsam fir (BAF.C) (also see Koivula and Schmiegelow, 2007); however, this relationship was not evident in its trait-habitat relationship. This lack of concordance may reflect flexibility of trait responses, interdependence of traits, or a mismatch of responses that is imposed by the environmental stochasticity caused by fire and salvaging. In addition, there were some subtle differences in results from Fourth-corner and RLQ analyses, which may reflect more of their complementary in establishing trait-habitat links. For instance, while the Fourth-corner revealed the significance of the trait links to each of the habitats, albeit weak and correlated they are, the RLQ ordination could help to visualize which of the correlated habitats can have the strongest contribution to their cumulative effect on the specific trait response. Regardless of these exceptions, trait-habitat relationships allowed significant and ecological meaningful mechanistic inferences about underlying species responses to habitat conditions. Furthermore, the value of such integrated and concise information regarding relationships between traits of communities and environment can not be underestimated, given that disturbance by fire can disrupt taxonomic-level community patterns; for example, fire disrupts the co-occurrence patterns of species (Sara et al., 2006), a situation that was evident also in our study (*unpublished results*). Indeed, the concept of functional trait-environment relationship is increasingly being emphasized in understanding varied response of ecological communities in other disturbance agents such as those caused by forest fragmentation and logging (e.g., Hausner et al., 2003; Cleary et al., 2007; Barbaro and van Halder, 2009).

As most of our plots were within burned and salvaged forests, they were less likely to be obstructed by vegetation, which probably contributed to generally high detection probabilities of most sampled bird species. Thus, we did not consider that overall detection issues are likely to have significant effects for most species on trait-habitat relationships presented, or on habitat occupancy models. The low detection estimation obtained for six species can be, however, due to the species being genuinely rare and/or vagrant rather than the species being elusive. For example, the Magnolia Warbler is primarily associated with mature forests and may have low occupancy within burned forests. The White-winged Crossbill tend to flock, and is usually easily detected when present. Thus, low detection for such species can not be attributed simply due to sampling artifacts.

Our findings emphasize that management guidelines such as those directed towards snag-retention should be comprehensive and pay due attention to the requirements of multiple traits (Hutto, 2006). For example, cavity-nesting (a frequently targeted trait) was positively linked to severe burns, but it showed no association with the amount of residual trees. Snag retention recommendations based only on such a notion, e.g., leaving aside a few severely burned trees, could be simplistic and dangerous. In fact, our study indicated that cavity nesters, which were also bark-insectivores (5 of 12 cavity-nesting species in our study), would require abundant and less-severely burned trees for foraging. Also, the greater importance of recent burned forests and lesser importance of old burned forests in the landscape for focal burns suggest that delaying salvage logging may be crucial for maintaining productivity pulses in fire-associated bird species (Nappi and Drapeau, 2009), although this would inevitably decrease the economic value of the trees (Sessions et al., 2004). The trait-habitat relationships, thus, could provide an integrated framework to understand the complex responses of biological communities to post-fire and salvage conditions and, consequently, could provide critical information in formulating sound management actions to alleviate the impact of salvage logging.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.actao.2011.02.005.

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