

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

3
4 **Short title:** Bird functional traits and post-fire salvage logging

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1 **Abstract**

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

21 **Keywords:** Bird communities; boreal forest; disturbance; Fourth-corner analysis; post-fire
22 salvaging; RLQ, trait-habitat links

1 **1. Introduction**

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

19 The present study examines trait-habitat relationships and habitat occupancy patterns of bird
20 assemblages in boreal forest stands following forest fire and salvage logging. In boreal forest
21 ecosystems, forest fire is recognized as key disturbance agent that shapes landscape and
22 temporal dynamics of fauna and flora (Saab & Powell, 2005; Lindenmayer et al., 2008).
23 Episodic fires generate structural and compositional heterogeneity, which is characterized by

1 large numbers of dead trees and other rare and/or ephemeral habitat resources that are critical to
2 long-term regional persistence, particularly, of fire-associated species (Hutto, 2006; Saab et al.,
3 2007b; Kotliar et al., 2007). However, the same critical habitat features and associated species
4 are also being increasingly threatened by post-fire salvage logging, thereby prompting the
5 urgency in developing ecologically based guidelines for sustainable management of burned
6 forests (Hutto, 2006; Lindenmayer et al., 2008).

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

17 Identifying the specific traits linked to burn-severity and other fire-generated habitat
18 attributes is important to understand the biological consequence of salvage-logging and for
19 setting guidelines to minimize their effects (e.g., snag-retention guidelines; Hutto, 2006). For
20 example, a few large trees may be sufficient for nesting (Spiering & Knight, 2005), but not for
21 foraging (Brawn & Balda, 1988). In addition, habitat selection in birds is a multi-scale process,
22 in which nesting and foraging habitat requirements are not selected at the same spatial scales.
23 Given such differences between trait requirements, management focus on single trait-habitat

1 link (e.g., cavity-nesting alone) could be inadequate (Hutto, 2006). Thus, it is important to
2 consider the trait-habitat link of several traits simultaneously. Recently, inferences about trait-
3 habitat links in post-fire environments have been done only “indirectly” or a posteriori (e.g.,
4 Kotliar et al., 2002; Morissette et al., 2002).

5 We have two major objectives: 1) to determine trait-habitat relationships and identify the
6 differential response of bird species traits (related to nesting, foraging and residence) to forest
7 landscapes characterized by ecological conditions following post-fire salvage-logging; 2) to
8 model species habitat occupancy probabilities and examine how trait-habitat relationships
9 pertain to species occupancy probabilities. Our study sites cover gradients of burn-severity (low
10 to high severity), age structure (20 to 120 years) and tree composition, amount of residual
11 retention (20 -100%), and landscape context of burns (e.g., distance from closest burned forest).
12 These factors all have known effect on bird communities (e.g., Kotliar et al., 2002; Saab et al
13 2007b). We applied two complementary multivariate statistical methods, the fourth-corner
14 (Legendre et al., 1997; Dray & Legendre, 2008) and RLQ analyses (Dolédec et al., 1996) that
15 allow a direct assessment of the link between species traits and habitat attributes by way of
16 species distribution data. While the Fourth-corner analysis performs a detailed test of the
17 significance of each trait and environment combination, the RLQ analysis provides an
18 ordination depicting the generalized trait-habitat relationships. We expected that abundant
19 nesting substrates and greater numbers of insects associated with high amount of residual trees
20 should favor traits characteristic of fire-associated species (e.g., bark-insectivores, cavity-
21 nesters) over other traits, e.g., omnivores or shrub nesters. It is also plausible, however, that
22 their cavity-nesting and foraging traits may respond differently to burn severity and amount of
23 residual trees (see above). For example, while severe burns might increase availability of snags

1 for cavity-nesting or generate conducive conditions for ground-feeding species, bark- and
2 foliage-insectivores may respond negatively to such burns. In addition, trait responses to habitat
3 attributes could be scale dependent, for example, the link of nesting guilds to burn severity may
4 be more prominent at small than at large scale. Because burned forests are potential source
5 populations for fire-associated species (e.g., Nappi & Drapeau, 2009) and their influence is
6 related to age-since-fire (Smucker et al., 2005), we expected that recent burns in the landscape
7 could promote occupancy of fire-associated species on focal burns. Identifying which
8 ecological variable depicted in trait-habitat relationships would also be selected in species
9 habitat occupancy models have valuable conservation implications, particularly when a species
10 possesses traits that have opposite trait-habitat relationships.

11 **2. Methods**

12 **2.1 Study area description**

13 The study was conducted in 55 study sites within four forest burns totaling more than 65100 ha
14 (Fig. 1, burned in 2005). The forest burns were located within the western spruce–moss
15 bioclimatic subdomain of northwestern Quebec, Canada (49° 15'–50° 40'N and 75° 00'W–
16 73° 45'W). This subdomain is dominated typically by black spruce *Picea mariana*, with jack
17 pine *Pinus banksiana* and balsam fir *Abies balsamia*. The forest landscapes also contain some
18 deciduous trees such as trembling aspen *Populus tremuloides* and paper birch *Betula*
19 *papyrifera*. Due to relatively short fire cycles (120–180 years), landscapes of this ecoregion are
20 dominated by even-aged forest stands (Bergeron et al., 2004).

21 We selected sampling sites using systematic random sampling to represent a gradient of pre-
22 fire composition and age structure (20–120 years), post-fire burn severity (low to high severity)
23 and salvage logging intensities (0–80%) observed within the forest burns (Table 1). The sites

1 also incorporated a range of landscape-level habitat contexts, namely distance from previously
2 burned and unburned (green) forest. These habitat variables were selected as they have been
3 shown to differentially influence the community structure and life-history traits (most
4 significantly the foraging and nesting guilds) of bird assemblages in burned forests (see reviews
5 in Kotliar et al., 2002; Saab et al., 2007b). Immediate post-fire environments are typically
6 characterized by abundance of dead and dying trees and associated insect outbreaks; and bark-
7 insectivores and cavity-nesters are known to capitalize on such resource availability. Variation
8 in snag size, burn characteristics (severity and heterogeneity) and salvage-logging intensity can
9 affect the availability of these resources and other habitat conditions, whose influence on bird
10 distribution may differ depending on their traits. For instance, increasing burn severity and
11 salvage logging intensity (often targeting larger trees) may decrease available insect prey for
12 bark- and foliage-insectivores. These conditions, however, can create conducive conditions for
13 species that are adapted to open-canopies, such as ground-insectivores and omnivores. Also, the
14 proximity to unburned forest and/or remnants within burn forests associated with riparian areas
15 (which might limit burn severity) could be important habitats for species not adapted to post-
16 fire environments (Kotliar et al. 2002). Similarly, the proximity to previous burns (and their
17 time since fire) might increase the flow or colonization of focal burns by species possessing
18 fire-adapted traits (e.g., bark-insectivores).

19 We thus measured the amount of residual tree basal area (by species and size classes), burn
20 characteristics (mean severity and heterogeneity), and edge-length (aquatic and salvage) at
21 stand-level within 100 m and 500 m circular buffers centered on bird survey centre points
22 (Table 1). We characterized residual tree retention using information about age structure, stand
23 composition, and post-fire forest logging intensity (expressed as a percentage) in ecoforest

1 classification maps and a database inventory (Stock data) of basal area (by species and diameter
2 class) (*Ministère des Ressources naturelles de la Faune du Québec*, MRNFQ). Because pre-
3 salvage basal area varied between stands, we focused on the amount of residual retention rather
4 than intensity of salvage logging which was carried between August 2005 and June 2006. We
5 characterized the basal area of young residual ($\text{dbh} \leq 9 \text{ cm}$) and merchantable ($\text{dbh} > 9 \text{ cm}$)
6 trees, which are the main target of post-fire salvage. The stand-level buffers were all included in
7 studied burns, and consequently, most trees were dead, although a few live trees might be found
8 at the 500 m scale (J. Boucher, *personal observation*).

9 Following Key and Benson (2006), we quantified burn severity using the Difference (delta)
10 Normalized Burn Ratio (dNBR) index. The dNBR was computed from differences between
11 pre- and post-fire in reflectance of bands 4 and 7 (that respond most to burning) of satellite
12 images taken before salvage logging was carried. We computed dNBR values for each pixel
13 (30 m) within the four burns, these ranged from 93 to 1341; thus covering to the whole range
14 of fire severity (low – high) according to Key and Benson (2006). We extracted dNBR values
15 for each pixel within 100 m and 500 m buffer, and considered the mean and standard deviation
16 at respective scales as a measure of burn severity (Brn.Sev) and heterogeneity (Brn.het),
17 respectively. We measured also landscape-level variables, namely the distance of focal burn
18 from the closest burned forest (Dis.BF) and its age (Age.BF) together with isolation from
19 neighboring unburned, green forest (Dis.GF). All habitat variables were extracted using Arc
20 MAP 9.2 (ESRI, 2006).

21 **2.2 Bird Sampling**

22 Birds were surveyed in 55 stands using the fixed-radius point count method (Hutto et al., 1986)
23 twice in 2006, and three times in 2007 approximately every week from early June to early July.

1 Birds that were heard or seen within a 100 m radius were recorded. To minimize observation
2 overlap and ensure statistical independence, sites were at least 1 km apart. Surveys were
3 conducted during morning hours when field conditions were conducive, i.e., no rain and light
4 winds. To counteract observer (total of four observers) and time biases, we alternated sampling
5 and surveyors order visiting each site (three observers per site).

6 **2.3 Data Analysis**

7 *2.3.1 Trait-habitat relationship*

8 We selected a set of four species traits, namely nesting (site location and type), foraging, and
9 migratory behavior (Table 2), that have been shown as proximate mechanisms to explain
10 response patterns of birds to post-fire habitat legacies and salvage logging (e.g., review in Saab
11 et al 2007b; also see section 2.1). These traits also have applicability in formulating post-fire
12 salvage logging management strategies, e.g., nesting requirements of cavity-nesting species has
13 been recognized as one of key component in formulating snag-retention guidelines (Kotliar et
14 al. 2002; Hutto, 2006). We compiled the information of these traits of bird species from Poole
15 (2008).

16 We examined trait-habitat relationships by means of two complementary multivariate
17 analyses: the Fourth-corner (Legendre et al., 1997; Dray & Legendre, 2008) and RLQ analyses
18 (Dolédec et al. 1996). Both methods are three-table analyses that allow a direct assessment of
19 relationships between habitats (Matrix R: habitat by sites) and species traits (Matrix Q: species
20 by traits) by way of species distribution data (Matrix L: Species by sites). The Fourth-corner
21 primarily focuses on tests of the significance of the links between each trait and environment
22 combination in a correlation-type analysis (Legendre et al., 1997). The RLQ analysis proceeds
23 with eigenvalue decomposition of product matrices, thereby providing a common ordination

1 axes of species traits and environment of sites (onto which species and sites are projected, an
2 option not available in the Fourth-corner analysis) and, thus, focuses more on interpretation of
3 their links.

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

18 We also tested trait-habitat link using the “two-step approach,” which combines results of
19 two permutation models, viz., Model 2 and Model 4, as proposed by Dray & Legendre (2008).
20 The critical value of the “two-step approach” is taken by adjusting for the simultaneous test,
21 i.e., square root of 0.05 ($p = 0.24$), which, however, could be regarded as too liberal (for details
22 see Dray & Legendre, 2008). In our study, even considering a more conservative level

1 ($p < 0.10$) indicated a general support for the results obtained by fixed-fixed null model (results
2 presented in Appendix A in the electronic Supplementary material).

3 We performed RLQ analysis (Dolédec et al., 1996) to ordinate the joint structure of the
4 three tables (R, L and Q). RLQ analysis was performed using the `ade4` package for R (Dray &
5 Dufour 2007). We conducted two separate RLQ analyses, using habitat variables at 100 m and
6 500 m scales, by also considering landscape-level variables.

7 *2.3.2 Species habitat occupancy models*

8 Our study focus was to understand how site-specific habitats relate to species traits and species
9 occupancy patterns rather than survey-specific or year specific relationships. Therefore, we
10 pooled the five survey data for each site to construct a single species by site presence/absence
11 matrix of bird occurrences. This pooled data across multiple surveys (over two years) should
12 increase the number of detection (i.e., minimize false absences) of species in each site (see also
13 Toms et al., 2006). We performed multiple logistic regression analysis (Hosmer & Lemeshow,
14 2000) to model the occurrence of each species (presence /absence) at each study site based on
15 habitat predictor variables (Table 1) and then we examined how trait-habitat relationships
16 pertain to these species occupancy probabilities. In all analyses, we considered only species
17 recorded in at least three sites (5% of stations), thereby including 33 bird species (Table 2) that
18 constituted 98% of the total presence-distribution. For three widespread species (Dark-eyed
19 Junco, White-throated Sparrow and Black-backed Woodpecker) that were recorded 95-98% of
20 the sites, fitting logistic model was not informative. Therefore, instead of omitting them
21 altogether, we modelled variation in their abundance pattern by using the maximum number of
22 individuals recorded in each site among the five surveys as “abundance” index.

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

1 to obtain cumulative detection probability estimates for each species (formula as provided in
2 MacKenzie & Royle, 2005).

3 **3 Results**

4 *3.1 Species trait-habitat relationship*

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

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

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

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

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

16 Some apparent trait-habitat relationships in the RLQ analysis were non-significant
17 according to the Fourth-corner analysis. For example, in the RLQ ordination (100 m scale),
18 both burn heterogeneity (Brn.het) and balsam fir had similar scores, and the trait foliage
19 insectivore appeared to fall on same axis (Fig. 2a). Yet, only balsam fir had a significant link to
20 foliage insectivores according to Fourth-corner (Table 3). Similarly, the apparent relationships
21 of aerial insectivores and omnivores to burn severity in RLQ (500 m scale) were not significant
22 in the Fourth-corner analysis. However, RLQ distinguished which specific habitat (among
23 correlated habitat factors) could be more related to a given trait. For example, Fourth-corner

1 analysis indicated that ground nesters were associated positively with burn severity and aquatic
2 edge (100m scale, Table 3). Although RLQ supported both relationships (axis 1, Fig. 2a),
3 ground nesters were related mainly to aquatic edge-length (axis 2, Fig. 2a).

4 *3.2 Species habitat occupancy models*

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

20 Habitat occupancy models also indicated which of the opposing trait-habitat relationships
21 were important for occupancy. High occupancy probabilities of species such as Black-backed
22 Woodpecker, Tree Swallow, and Eastern Bluebird in severe burns (100 m, Table 5) were in
23 concordance to their cavity-nesting trait rather than to being canopy nesters (Table 3). The latter

1 relationship could be due to open-cup nesters, with which they share the canopy nesting trait.
2 Some species having the same trait responded differently to the same variable. Both Lincoln
3 Sparrow and Common Nighthawk are open-cup, ground nesters, but they responded negatively
4 and positively, respectively, to burn severity. Note that the open-cup (type) and ground-nesting
5 (location) traits had contrasting link to burn severity. Some habitat occupancy relationships
6 could not be explained by trait-habitat relationships (e.g., Northern flicker and Red-breasted
7 nuthatch had negative coefficient with balsam fir, BAF.C) or were opposite to that trait-habitat
8 relationship (e.g., White-throated Sparrow with deciduous trees, DEC.Y).

9 Our analysis using the colonization-extinction model [data pooled per primary sampling
10 year or by considering each of the five secondary survey independently] indicated that the
11 cumulative detection probability estimates for most species were fairly good (0.74-1.00, mean
12 0.94). However, the estimated cumulative detection probability was relatively low (0.15-0.64)
13 for six species (Magnolia Warbler, Wilson's Warbler, Least Flycatcher, White-winged
14 Crossbill, Common Yellowthroat and Hairy Woodpecker, Scientific names in Table 2).

15

16 **4. Discussion**

17 We addressed the differential response of bird functional traits to post-fire habitat conditions
18 and salvage-logging and their bearing to species habitat occupancy probabilities. Regardless of
19 whether or not salvaging was affecting merchantable or young trees, higher amount of residual
20 tree basal area was important for canopy-nesters, and foliage- and bark-insectivores than guilds
21 such as omnivores, ground- and shrub-nesters, that seem to thrive better in salvaged areas and
22 associated edges. Moreover, we found differential response to tree composition between foliage
23 insectivores (e.g. for balsam fir) and bark insectivores (e.g. for black spruce). These findings

1 were consistent with studies showing guild response to levels of salvaging or the amount of
2 residuals (e.g., Morissette et al., 2002) and its composition (Koivula & Schmiegelow, 2007).

3 Degree of burn severity is an important habitat attribute in post-fire disturbance, especially
4 for fire-associated species (Smucker et al., 2005). Our results suggest that bark-insectivores
5 (also foliage insectivores) preferred low- to moderate-severity burns (Kotliar et al., 2002;
6 Smucker et al., 2005), where there is probably greater insect availability than in severe burns
7 (Nappi et al., 2003; Smucker et al. 2005). Thus, we found no support for suggestions that strong
8 affinity of fire-associated species with severe-burns was for foraging (e.g., Koivula &
9 Schmiegelow, 2007). Our finding rather suggests that their affinity for severe-burns could be
10 related to being cavity-nesters, perhaps a condition particularly important for secondary cavity-
11 nesters. Also, in notable contrast to foraging (see above), the amount of residual basal area was
12 less critical for cavity-nesting (also see, Spiering & Knight, 2005). Our results add support to
13 the finding highlighted in the synthesis by Kotliar et al. (2002) that fire-associated species
14 might have a contrasting preference for foraging and nesting. Species may meet such
15 contrasting resource requirement, for example, by using alternative habitats in the landscape
16 (i.e., habitat complementation, sensu Dunning et al. 1992).

17 Severe burns, however, enhanced the foraging conditions for ground feeders (insectivores or
18 for other prey), perhaps by exposing insects or seeds or by increasing availability of deadwood-
19 associated insects (e.g., Northern Flicker, Koivula & Schmiegelow, 2007). Also, 'vegetation'
20 remnants along aquatic edges within severe burns appear to be conducive for ground and shrub
21 nesters (Fig. 2a,b). Such remnants could form important habitats also for species that would
22 otherwise avoid severe burns, such as the Lincoln Sparrow and Northern Waterthrush (Table 5).
23 It is noteworthy that nesting guilds' positive (e.g., ground nesters) and negative (open-cup,

1 canopy nesters) associations with burn severity were particularly evident at a smaller scale
2 (100 m buffer), perhaps closer to the nest-site selection scale by birds, than at the larger scale
3 (500 m buffer). Taken together, our findings suggest that mosaics of severely burned and
4 unburned remnants in focal burned forests could yield habitat attributes attuned to the different
5 requirements of bird traits (Saab et al., 2007a).

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

17 The birds' habitat-occupancy probabilities were consistent with known ecology of the
18 species and, more importantly, with the trait-habitat relationships revealed in this study, thus,
19 providing a mechanistic explanation for species habitat occupancy patterns. The interpretation
20 is more straightforward when a significant number of traits for a given species have similar
21 associations with habitat factors. For example, the foraging and nesting traits could have
22 simultaneously determined the lower probability of Black-backed Woodpecker with increased

1 salvage edge, of Yellow-rumped warbler with severe burns or higher occupancy probability of
2 Northern Waterthrush with aquatic edge (see also Table 5).

3 However, there were several exceptions, perhaps more crucial findings, where a species
4 might have traits that exhibit simultaneous and contrasting associations with a given habitat
5 attribute. For example, some cavity nesters (e.g., Tree swallow, Table 5) were more likely to
6 occupy severe burns at least at fine-scale (100 m) in concordance to nest type (cavity-nesting)
7 than to location (canopy) or foraging (some were bark-insectivores) depiction of trait-habitat
8 relationship. This relationship of the cavity-nesters with burn severity, however, was not
9 evident at 500 m scale; which suggests scale-specific influence of traits on species' habitat-
10 occupancy. Also the heterogeneity of species that are categorized into constraining
11 classifications might cause such divergent relationships, e.g., cavity-nesters share the canopy
12 nesting trait with open-cup nesters that had a negative association with burn severity. There
13 were also cases where habitat occupancy patterns could not be explained or were opposite to
14 those depicted by trait-habitat relationships. For example, Northern flickers were less likely to
15 occupy stands containing balsam fir (BAF.C) (also see Koivula & Schmiegelow, 2007);
16 however, this relationship was not evident in its trait-habitat relationship. This lack of
17 concordance may reflect flexibility of trait responses, interdependence of traits, or a mismatch
18 of responses that is imposed by the environmental stochasticity caused by fire and salvaging. In
19 addition, there were some subtle differences in results from Fourth-corner and RLQ analyses,
20 which may reflect more of their complementary in establishing trait-habitat links. For instance,
21 while the Fourth-corner revealed the significance of the trait links to each of the habitats, albeit
22 weak and correlated they are, the RLQ ordination could help to visualize which of the
23 correlated habitats can have the strongest contribution to their cumulative effect on the specific

1 trait response. Regardless of these exceptions, trait-habitat relationships allowed significant and
2 ecological meaningful mechanistic inferences about underlying species responses to habitat
3 conditions. Furthermore, the value of such integrated and concise information regarding
4 relationships between traits of communities and environment can not be underestimated, given
5 that disturbance by fire can disrupt taxonomic-level community patterns; for example, fire
6 disrupts the co-occurrence patterns of species (Sara et al., 2006), a situation that was evident
7 also in our study (*unpublished results*). Indeed, the concept of functional trait-environment
8 relationship is increasingly being emphasized in understanding varied response of ecological
9 communities in other disturbance agents such as those caused by forest fragmentation and
10 logging (e.g., Hausner et al., 2003; Cleary et al., 2007; Barbaro & van Halder 2009).

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

21 Our findings emphasize that management guidelines such as those directed towards snag-
22 retention should be comprehensive and pay due attention to the requirements of multiple traits
23 (Hutto, 2006). For example, cavity-nesting (a frequently targeted trait) was positively linked to

1 severe burns, but it showed no association with the amount of residual trees. Snag retention
2 recommendations based only on such a notion, e.g., leaving aside a few severely burned trees,
3 could be simplistic and dangerous. In fact, our study indicated that cavity nesters, which were
4 also bark-insectivores (5 of 12 cavity-nesting species in our study), would require abundant and
5 less-severely burned trees for foraging. Also, the greater importance of recent burned forests
6 and lesser importance of old burned forests in the landscape for focal burns suggest that
7 delaying salvage logging may be crucial for maintaining productivity pulses in fire-associated
8 bird species (Nappi & Drapeau, 2009), although this would inevitably decrease the economic
9 value of the trees (Sessions et al., 2004). The trait-habitat relationships, thus, could provide an
10 integrated framework to understand the complex responses of biological communities to post-
11 fire and salvage conditions and, consequently, could provide critical information in formulating
12 sound management actions to alleviate the impact of salvage logging.

13

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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 \leq 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 (<i>Picea mariana</i>) of dbh \leq 9 cm [m ² /0.1 ha]	0-68.33	0.26-38.34
[£] BSP.M	Basal area of Black spruce (<i>Picea mariana</i>) of dbh > 10cm [m ² /0.1 ha]	0-184.83	0.53-85.31
[§] JPL.Y	Basal area of Jack pine (<i>Pinus banksiana</i>) of dbh \leq 9 cm [m ² /0.1 ha]	0-4.23	0-1.82
[§] JPL.M	Basal area of Jack pine (<i>Pinus banksiana</i>) with dbh > 9 cm [m ² /0.1 ha]	0-109.78	0.06-37.94
[§] BFI.Y	Basal area of Balsam fir (<i>Abies balsamea</i>) of dbh \leq 9 cm [m ² /0.1 ha]	0-48.54	0-23.68
[§] BFI.M	Basal area of Balsam fir (<i>Abies balsamea</i>) 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	

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

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	-	.	+	-
	JPL.Y	.	.	+	.	.	.	+	+	.
	JPL.M	-	.	+	+	.	.	-	.	.	.
	BFL.Y	+	.	.	.	-	.	.	.
	BFL.M	+	.	.	.	-	.	.	.
	Brn.Sev	+	+	-	+	-	+	-	-	.	.	.	+	.	.
	Brn.Het	.	.	.	-
	SalEdge	+	+	-	-	.	.	.	-	.	.
	AquEdge	+	.	-	-	.	.	.	+	.	+
	Stand scale 500 m	DEC.Y	+	.	.	-	.	.	.
DEC.M		+	+	.	-
BSP.Y		-	-	+	+
BSP.M		-	.	+	+	.	.	.	+	.	-
JPL.Y		-	.	+
JPL.M		-	-	+	+	-
BFL.Y		.	.	.	-	.	.	+	.	.	-	.	.	-	+
BFL.M		+	.	.	-	.	.	-	+
Brn.Sev		.	.	.	+	.	+	-	+	.	.
Brn.Het	
SalEdge		.	+	-	-
AquEdge		+	.	-	-	.	.	.	-	.	+
Landscape		Dis.BF	-	+
	Age.BF	+	.	-	-	+	.	.	-	.	.	.	-	.	.
	Dis.GF	-	.	.	+

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

A) RLQ analysis						
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
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 %)						
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
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

10 *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% (15 **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.

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	JPL.Y	BFLM	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

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⁻)

Table 5 Continued

CODE	AUC	Habitat variables (Stand scale 500 m)						Landscape-level variables		
		DECE.Y	BSP.M	JPL.Y	BFL.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: CEDW, WIWR and WWCR fitted only intercept.. There was no strong support for burn characteristics (**Brn.Sev** and **Brn.Het**) effect at 500m scale.

FIGURE CAPTIONS

Figure 1 Map of study area showing study sites, represented by black triangles, within the four forest fire-blocks burned in 2005 (Total area 65100 ha).

Figure 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.

Figure 1

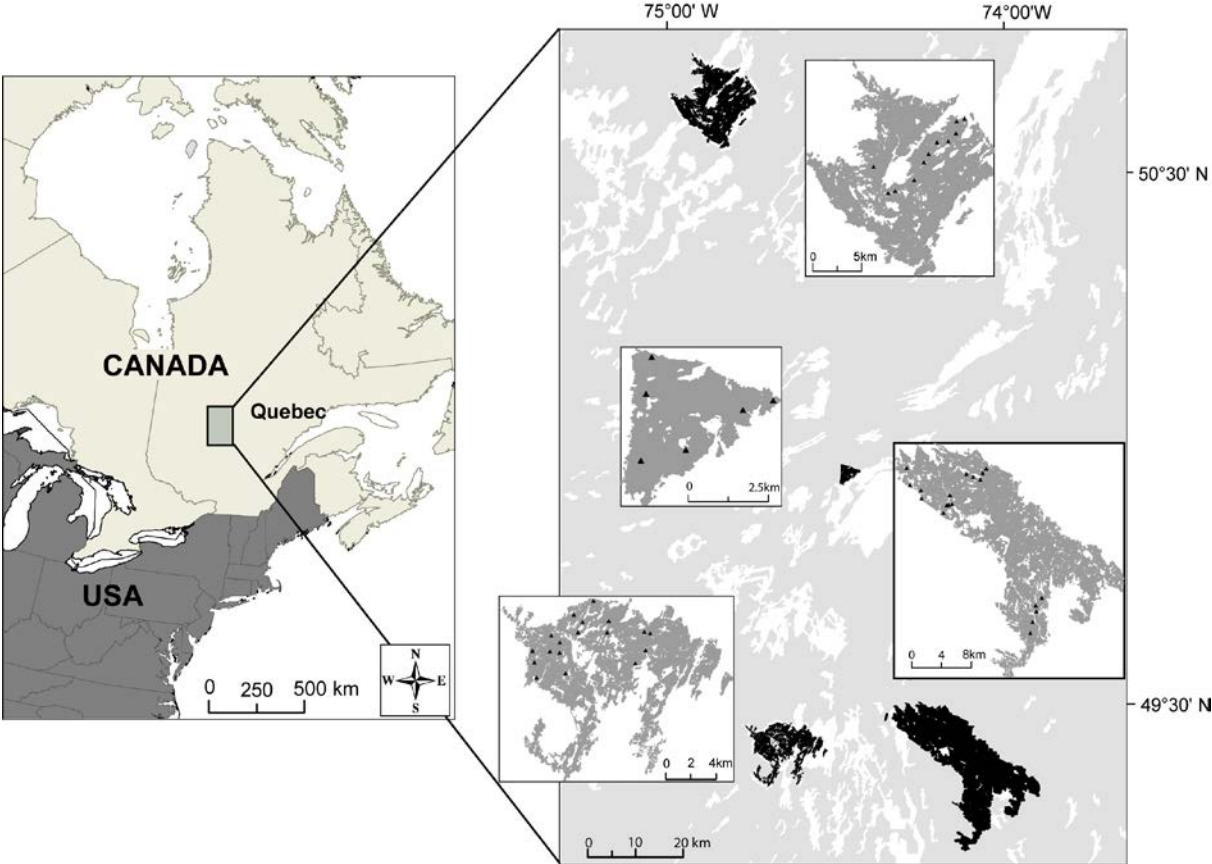
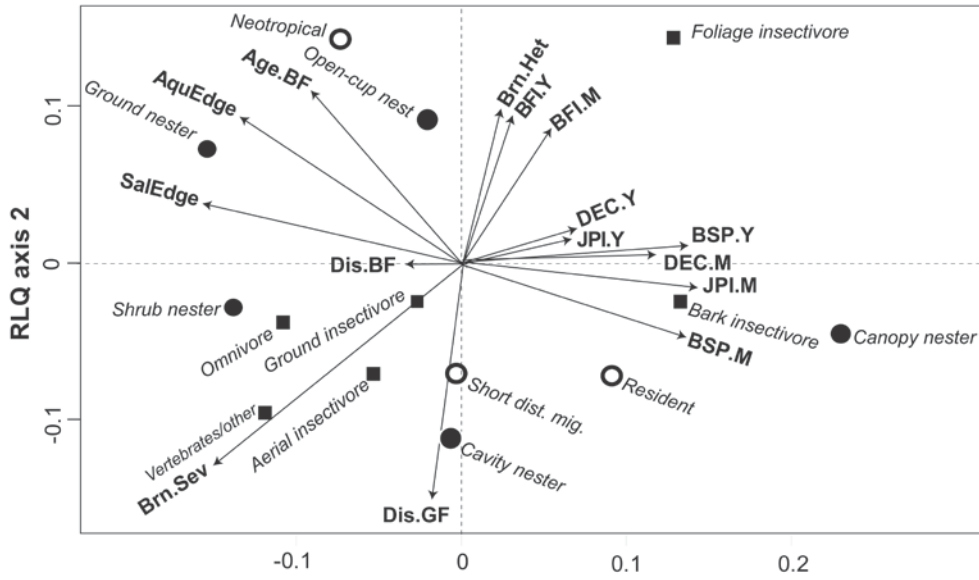


Figure 2

(a) Scale 100m



(b) Scale 500 m

