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Response of Forest Bird Communities to Managed Landscapes in the Acadian Forest

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Abstract: The loss of mature forests is a known stressor of forest management on biodiversity. Mature forests provide unique habitat for forest birds. Here, we examine the capacity of mature forest stands embedded in an intensively managed landscape to provide habitat for landbird species that are associated with mature, unfragmented habitats. We carry this out by comparing bird communities in forest stands in three landscapes with a gradient of management activity. We examined community-level indicators (richness, diversity, abundance and community structure), and trait-level indicators (species groups associated with cavity nesting, mature forests, interior forests and area sensitivity). We found no obvious negative effects on bird communities, species and trait groups in forest stands in the most intensively managed landscape relative to the less intensively managed landscapes. Our ability to draw inferences about the influence of management intensity is limited due to lack of replication; however, these results do provide evidence that mature forest stands within intensively managed landscapes can provide valuable habitat to mature forest associates. There are often trade-offs between generating wood products from the forest and the provision of mature forest habitats. Research on forest birds can provide some of the necessary information for assessing the size and shape of those trade-offs and help to inform the conversation about the desired structure, function and composition of forests.

Keywords: bird communities; forest management; Acadian Forest; indicators; functional traits; landscape effects; management intensity; mature forest

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1. Introduction

Forest management is often criticized for having negative impacts on forest health, forest biodiversity and forest landbirds in particular. Increasing the intensity of management is often associated with increasing impact, with implications for biodiversity decline worldwide [1,2]. There has been significant debate on the role of managed landscapes in supporting natural forest biodiversity [3–5]. Landscape-scale effects can be large drivers of community change at stand scales [6]. The impact of landscape on local scales in forested landscapes without land conversion is a matter of debate, however [7–9]. Much of the often-cited research on landscape-scale effects was conducted in deforested landscapes where forest patches are embedded in a sea of agriculture or non-forest [10–13]. In this study, we examine the evidence that in managed forested landscapes without significant land use change, local stands can continue to provide habitat for a range of forest birds, including those that are associated with older forests. We examine landbird communities in forested landscapes with limited land use change, but with intensive management, reflected by a high percentage of planted stands.

Sustainability is a widely held goal of forest management in Canada, including respecting the principles of conservation and biodiversity [14,15], and, in some cases, a legislated mandate [16]. Assessing sustainability is an extremely complex task [8], but one common approach is the use of indicators of sustainability, especially biodiversity indicators [17]. Birds have long been suggested as a good indicator of environmental sustainability [18,19] and forest sustainability in particular [18,20,21]. There are well-established standardized methods of measurement of the relative abundance and distribution of birds [22,23]. In particular, habitat specialists can be informative because they can be most sensitive to specific stressors to the system [24,25]. Here we focus on old forest associates.

Autonomous recording technology for collecting auditory data is also facilitating the collection of significantly more bird abundance data [26–29]. Auditory methods permit the collection of data for a large diversity of landbird species at the same time. This diversity provides increased potential to detect change in the bird community due to the large variety of habitats and resource use by distinct species. Forest birds also represent a fairly high trophic level, and, as such, they are integrators of the forest system and respond to multiple changes in the ecosystem. In addition, we know a lot about the life history of forest birds due to a long history of research and interest (Birds of the World online, https://birdsoftheworld.org/bow/home, accessed on 15 October 2023). This knowledge allows us to interpret changes in bird communities based on their functional traits that can link changes directly to potential stressors in the forest. Lastly, there is extensive bird data collection across provinces and territories through the Breeding Bird Atlas program (e.g., [30,31]) and the United States Geological Survey's Breeding Bird Survey (BBS; [32]).

The objective of this study is to compare landbird communities in terms of richness, diversity, abundance, community structure and specific abundance in relation to functional traits in mature forest stands in three landscapes with different levels of management intensity. Bird communities in these landscapes have been studied for many years, and the landscape is known to have a high diversity of forest birds [33–36]. We were interested in understanding the ecological value of mature forests in the context of intensive forest management. This is a landscape-scale investigation in that birds were measured in matched forest stands in all three landscapes that were comparable in terms of ecosystem characteristics but differed in management intensity. We had no a priori expectation for the comparison of richness, diversity and abundance overall, but we hypothesized that if management intensity was impacting mature forest habitat at landscape scales, we would see community composition differences between landscapes. Specifically, we anticipated that cavity nesters, mature and overmature habitat associates, interior habitat associates and area-sensitive species would all be less common in the mature habitat of the most intensively managed landscape. We are aware that our capacity for statistical inference is limited here due to the lack of replication [37], although parsimony allows us to draw some reasonable conclusions about the value of older forest patches in intensively managed landscapes. Landscapes were chosen for their ecological similarity, all within the Acadian Forest. Landscape replication is often prohibitively difficult and expensive, and we must draw conclusions from more limited but still valuable data. An assessment of the ecological value of mature forests in management contexts will improve our ability to manage forests sustainably by allowing us to better understand and map elements of the ecological value of these mature forest stands.

2. Methods

2.1. Study Area

The three landscapes, Black Brook (BBRO), Quisibis (QUIS) and Debouille (DEBU), are all located within 100 km of each other in the province of New Brunswick, Canada, and the state of Maine, United States of America (Figure 1), all within the Acadian Temperate Forest [38], which covers an area including the Maritime provinces of Canada as well as the northeastern United States. Forest canopies are coniferous (e.g., balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), red spruce (*Picea rubens*), black spruce (*Picea mariana*), eastern white cedar (*Thuja occidentalis*), deciduous (e.g., sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), white birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), American beech (*Fagus grandifolia*) or a mixture). Anthropogenic disturbance is widespread in the Acadian Forest and includes forest harvesting, road building, agricultural conversion, rail and utility corridors and urban development. Windthrow, ice loading and insect infestations are the most widespread forms of natural disturbance. Wildfire is generally not a factor in the study areas [38]. In the study areas, the disturbances are primarily due to roads and harvest. Understory structure varies from dense to sparse and includes cold-deciduous broad-leaved shrubs, perennial herbs, tree regeneration and bryophytes.

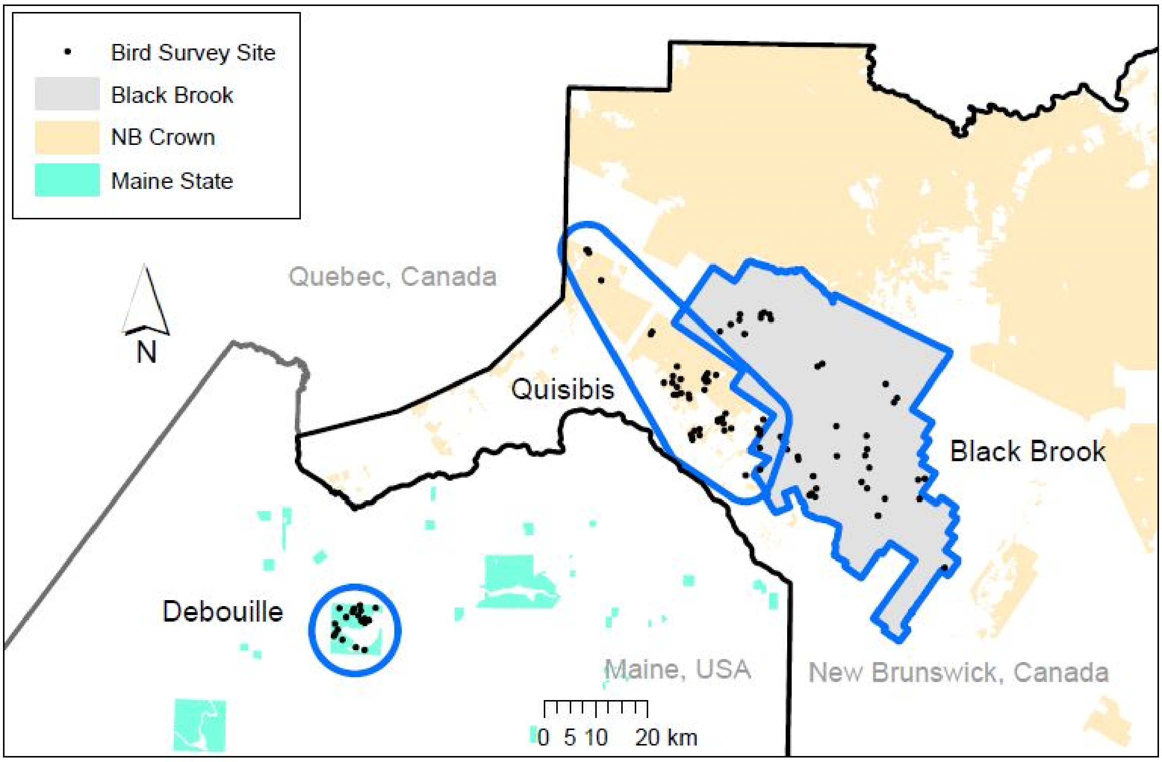

Figure 1. Study areas. The three landscapes, Black Brook (BBRO), Quisibis (QUIS) and Debouille (DEBU), blue polygons, are all located within 100 km of each other in the province of New Brunswick, Canada, and the state of Maine, United States of America. QUIS polygon was drawn using a fixed-width buffer, creating an artificial overlap with BBRO. Bird survey sites located within the BBRO polygon contributed only to the BBRO data.

BBRO (209,679 ha) is land owned and managed by J.D. Irving, Limited since the mid-1940s. The planting of stands began in the late 1950s. Twenty-five-year forest management plans are in place, which are revised on a five-year interval. These plans include multiple strategies and objectives related to sustainable wood supplies to support mills and communities; maintaining environmental quality, including water, site productivity and biological diversity; maintaining forest health; supporting non-timber use; and public accountability through third-party certification. The QUIS forest (37,294 ha) is provincially owned Crown land, also managed under a 25-year management plan according to strategies and objectives of the Province of New Brunswick (Crown Lands and Forests Act) and managed by an industrial licensee (part of Crown License 10, Twin Rivers Paper Company). The DEBU Township Forest (8489 ha) is managed for timber production and was acquired by the State of Maine in 1975. The area was first logged in the 1800s, heavily logged in the 1950s and 1960s and affected by the spruce budworm outbreak in the 1970s and 1980s and includes a nearly 364 ha ecological reserve. Timber management has been ongoing, with harvest levels at half of the calculated sustainable limit. The Deboullie Forest is 33%

softwood, 25% hardwood and 42% mixedwood, with a general lack of stems under 10 m noted in the management plan.

GIS analysis was performed on forest resource inventories from each landowner along with forest management GIS updates to assess 5 landscape indicators of management activity, including area planted, area in softwood regeneration, area thinned in the last 10 years, area operated for hardwood and the amount of mature forest. BBRO had the highest area planted by a large margin (Table 1), the highest area thinned and the highest area of softwood regeneration and the least amount of mature forest and area of hardwood operated. QUIS and DEBU were more similar. Based on these values, we identified the BBRO landscape as the most intensively managed followed by QUIS and then DEBU. Primarily though, the large percentage of area planted in BBRO relative to the other forests is the most significant indicator of the amount of management activity.

Table 1. Landscape-scale measures of management activity taken from aerially interpreted forest resource inventory polygons.

Management	BBRO	QUIS	DEBU
% Area planted to conifer (of total landbase)	41.8	10.2	0
% Area softwood regeneration (of total landbase)	4.4	1.0	3
% Area thinned in last 10 years (of total landbase)	8.3	0.6	0
% Hardwood Area operated (of total hardwood area)	21.1	21.8	32
% Mature forest (of total landbase)	34.0	39.4	45.7

2.2. Bird Sampling

All bird sampling was conducted in 2018. We identified 6 forest types to sample (Table 2) and attempted to sample 7 stands in each forest type for a total of 42 stands per landscape. We struggled to identify enough stands in the DEBU landscape that met size (at least 5 ha) and spatial (at least 100 m to all stand edges from the sampling location and at least 250 m from the next sampling location) requirements but were able to sample at least two stands in each forest type (Table 2). Stands ranged from 5 ha to approximately 100 ha. In each selected forest stand, we placed an autonomous recording unit (Song Meter 2, 3 or 4 from Wildlife Acoustics, Maynard, MA, USA) at a sampling location for a minimum of 20 days between June 1 and June 30 and recorded in stereo each day for 80 min, 10 min each hour from 30 min before sunrise to the 8th hour after sunrise. From the recordings, we chose the first 4 days where the recordings were free from noise (wind, rain and industrial) and interpreted two 5 min recordings from each day, one 20–30 min before sunrise and one within an hour after sunrise. Interpretation of recordings involves listening to the recording while examining a spectrogram and identifying all individuals heard by species. It is possible to identify multiple individuals of the same species on recording through the identification of counter singing with the use of stereo microphones. This gives a total of 8 recordings (40 min) per sampling location in the breeding season. Estimates of bird abundance in samples were generated using the maximum abundance for each species in the 8 recordings in each sampling location.

Table 2. The number of stands sampled in six forest types in this study (classified by stand attributes in GIS).

Forest Type	BBRO	QUIS	DEBU
Cedar Mature/Over Mature [1]	7	7	2
Mixedwood Mature/Over Mature [2]	7	7	3
Spruce Fir (16–45 years old) [3]	7	7	3
Spruce Fir Mature/Over Mature [4]	7	7	2
Tolerant Hardwood Mature–Over Mature–No Recent Harvest [5]	7	6	3
Tolerant Hardwood Mature–Over Mature–Selection Harvest [6]	7	7	2
Total	42	41	15

[1] Cedar Mature/Over Mature: Eastern cedar-dominated stands, greater than 65 years old. Mature and overmature stands may have undergone selection harvest that favours cedar for retention and removes other softwood species unlikely to live another 25 years. [2] Mixedwood Mature/Over Mature: Natural stands with tolerant hardwoods and intolerant hardwoods mixed with softwood species that are older than 65 years and have had no silvicultural interventions. [3] Spruce Fir (16–45 years old): Natural spruce/fir forests that are 16 to 45 years old and have had no silvicultural interventions. [4] Spruce Fir Mature/Over Mature: Natural spruce/fir forests composed of white, red and/or black spruce and/or balsam fir. Stands are older than 45 years and have had no silvicultural interventions. [5] Tolerant Hardwood Mature–Over Mature–No Recent Harvest: Natural stands of tolerant hardwoods (sugar maple, yellow birch, American beech and red maple) that are older than 75 years and have had no silvicultural interventions. [6] Tolerant Hardwood Mature–Over Mature–Selection Harvest: Natural stands of tolerant hardwoods that are older than 75 years. Stands have typically undergone single tree selection or gap harvesting favouring healthy, vigorous stems conducive to selection harvest regimes (i.e., multiple entries in perpetuity).

2.3. Analysis

We performed analyses in R version 4.2.1 (2022-06-23). We compared mean richness, diversity and abundance between landscapes and forest types using a one-way ANOVA and Tukey's multiple comparisons ($\alpha = 0.05$). Richness was estimated using the Margalef richness index [39], which controls for effort (number of samples). Diversity was measured using the Shannon diversity index [40]. We also conducted non-metric multidimensional scaling (metaMDS), PERMANOVA (Adonis II) and comparisons of Beta dispersion (Betadisp), all using the vegan package in R [41], to visually compare landscape types based on bird community structure and to compare bird community centroids and dispersion between landscapes ($\alpha = 0.05$). Lastly, we grouped species by migration strategy, nesting strategy, habitat association, successional stage association, affinity for interior forest and area sensitivity (Table A1) and compared total abundance within groups between landscapes.

3. Results

3.1. Species Presence, Richness, Diversity and Abundance

Excluding rare species with fewer than five total observations, Scarlet Tanager was the only species not found in BBRO samples but present in QUIS (12 times) and DEBU (6 times). There were seven species absent from DEBU samples, excluding rare species (<5), American Bittern, American Crow, American Goldfinch, Bay-breasted Warbler, Evening Grosbeak, Fox Sparrow and White-winged Crossbill (Table A2). There were three species absent from QUIS samples: Alder Flycatcher, Mourning Warbler and Northern Flicker. The 10 most common species of each of the three landscapes had a high degree of overlap and included Ovenbird, Swainson's Thrush, White-throated Sparrow, Ruffed Grouse, Hermit Thrush, Yellow-bellied Sapsucker and Black-throated Green Warbler (Table A2). We observed more individuals and more species in BBRO than QUIS and DEBU (Table 3).

Table 3. Bird richness, abundance and diversity summaries with standard deviation (SD) for 3 landscapes in the Acadian Forest in 2018.

	Total Number of Species	No. of Sampled Stands	Abundance	Mean Margalef Richness Per Sampled Stand (SD)	Mean Abundance Per Sampled Stand (SD)	Mean Shannon Diversity Per Sampled Stand (SD)
All Landscapes	86	99	3193	6.01	31.16	
BBRO	77	42	1456	6.28 (0.84)	34.7 (7.1)	3.03 (0.17)
QUIS	65	41	1278	5.95 (0.86)	31.2 (7.4)	2.96 (0.19)
DEBU	56	16	459	5.48 (0.75)	28.7 (5.8)	2.83 (0.16)

A one-way ANOVA revealed that there was a statistically significant difference in the richness index, Shannon diversity and abundance between the landscapes (Table 4). Tukey's HSD test for multiple comparisons supported that these differences are primarily between the BBRO and DEBU landscapes, with BBRO having higher richness, diversity and abundance (Tables 3 and 4 and Figure 2). The data met the assumptions of normality, homoscedasticity of variance (assessed through visual examination of data) and independence (observations were spaced to maintain independence).

Table 4. Results of one-way ANOVA and Tukey's HSD test of multiple comparisons for the three landscapes. The F statistic is reported with degrees of freedom in brackets.

Comparison	Richness	Shannon Diversity	Abundance
Overall (one-way ANOVA)	F(2, 96) = 5.634, p = 0.0049	F(2, 96) = 6.345, p = 0.0026	F(2, 96) = 5.017, p = 0.0085
BBRO vs. QUIS (Tukey's HSD test for multiple comparisons)	p = 0.17	p = 0.15	p = 0.06
QUIS vs. DEBU (Tukey's HSD test for multiple comparisons)	p = 0.13	p = 0.096	p = 0.45
BBRO vs. DEBU (Tukey's HSD test for multiple comparisons)	p = 0.004	p = 0.002	p = 0.013

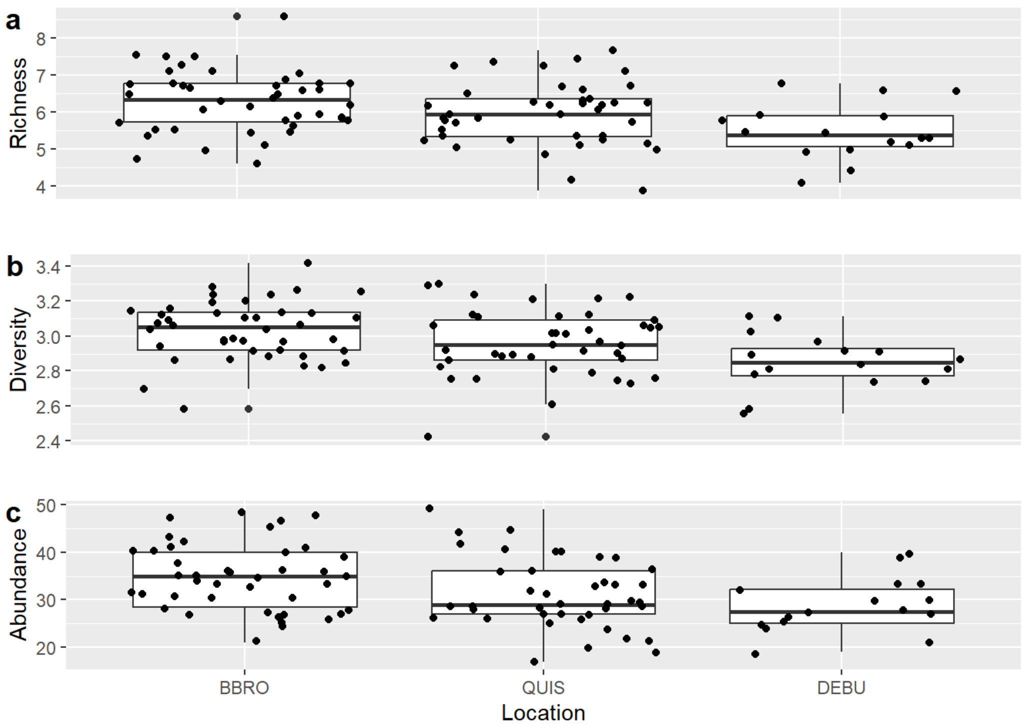

Figure 2. Boxplot comparison of (**a**) Margalef richness index per sampled stand, (**b**) Shannon diversity index and (**c**) abundance for the 3 landscapes (BBRO = Black Brook, QUIS = Quisibis and DEBU = Debouille). Data points are represented by black dots.

3.2. Community Composition

The non-metric multidimensional scaling (NMDS) results point to considerable overlap between landscape polygons, suggesting limited differences in bird community composition between the selected stands of landscapes (Figure 3). The Permanova test showed a significant difference at $p < 0.05$ for the comparison of BBRO with QUIS and DEBU but with very little variance explained. The beta dispersion paired comparisons showed no significant differences in community variance between BBRO and other landscapes (Table 5), suggesting that the variance between landscapes is homogeneous and, therefore, that the comparison of centroids is robust.

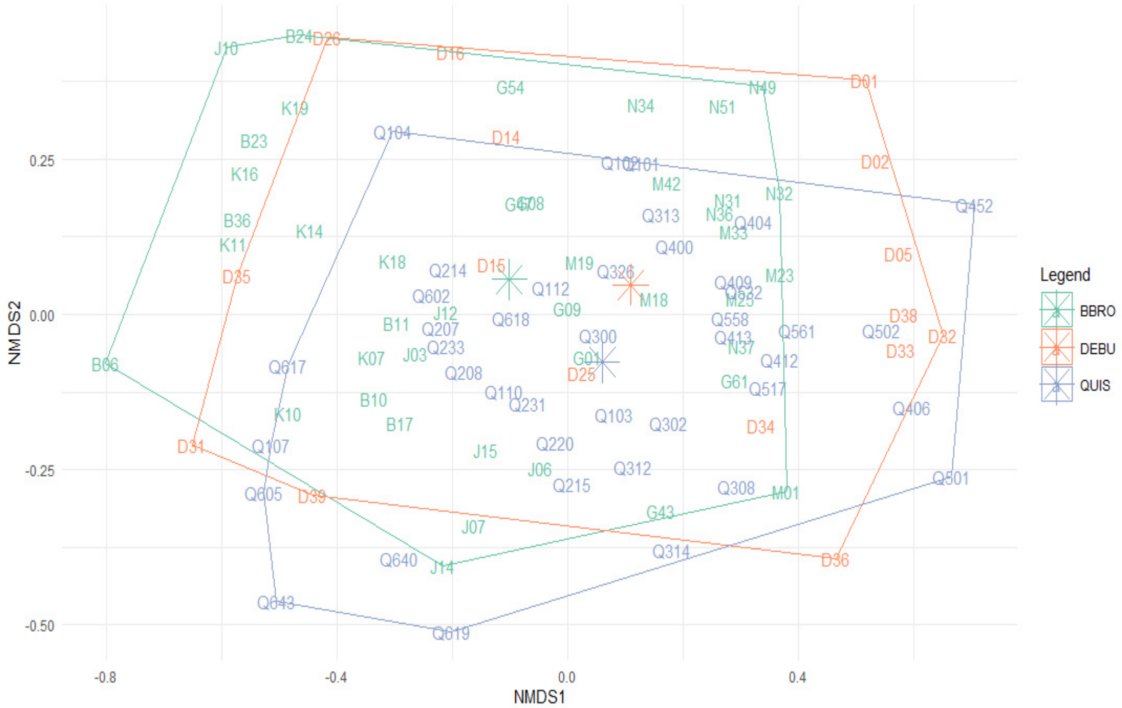

Figure 3. Non-metric multidimensional scaling (NMDS) plot of bird communities in the 3 landscapes. The overall stress value for the NMDS is 0.20. This level of stress suggests that too much reliance should not be placed on the details of the plot but that the overall plot can still correspond to a usable picture [42]. The non-metric R-squared is 0.96. Centroids of polygons are displayed as stars.

Table 5. Pairwise comparisons of centroid and dispersion of the communities from the 3 landscapes.

Comparisons	Df	Permanova F	Permanova *p*	R-Squared	Beta Dispersion F	Beta Dispersion *p*
BBRO: QUIS	1	3.53	0.003	0.041	0.839	0.362
BBRO: DEBU	1	3.46	0.001	0.058	2.97	0.090
QUIS: DEBU	1	1.59	0.1	0.028	4.50	0.038

3.3. Bird Functional Trait Analysis

We saw no evidence of significant differences between the abundance of cavity nesters, mature forest associates, interior species and area-sensitive species in the three landscapes (Figure 4a–d). Overmature forest associates were too infrequent to assess (Figure 4b). In general, none of the classifications demonstrated obvious differences between landscapes and between functional classifications (Figure 4a–f), including habitat association and migration strategy (Figure 4e–f).

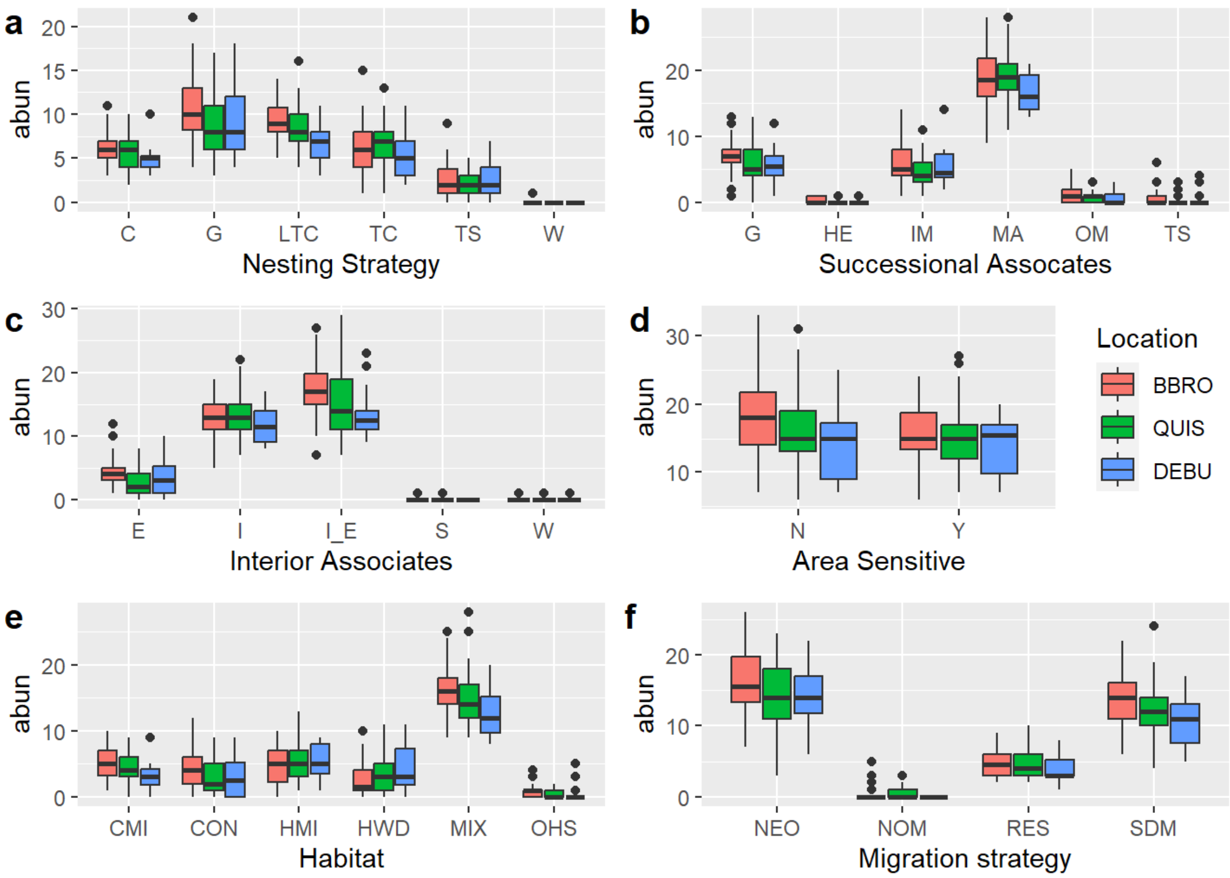

Figure 4. Comparison of landscapes according to functional traits for abundance (abun). Functional classifications include (**a**) nesting strategy: C = cavity, G = ground, LTC = lower tree canopy, TC = tree canopy, TS = tall shrubs and W = wetland; (**b**) successional associates: G = generalist, HE = herbs, IM = immature, MA = mature, OM = overmature and TS = tall shrubs; (**c**) interior associates: E = edge, I = interior, I_E = both, S = shore and W = wetland; (**d**) area sensitive: Y = yes and N = no; (**e**) habitat: CMI = conifer mixedwood, CON = conifer, HMI = hardwood mixedwood, HWD = hardwood, MIX = mixedwood and OHS = open herb and shrub; (**f**) migration strategy: NEO = neotropical migrant, NOM = nomadic, RES = resident and SDM = short-distance migrant. Box and whisker plots display quartiles and median values.

4. Discussion

We saw no obvious negative effects of greater management intensity of the BBRO landscapes at the stand scale. The effect of landscape-level influence on stand-level community composition and species abundance has been hypothesized for a long time. Landscape ecology theory predicts the existence of threshold levels of habitat in landscapes required to maintain species because of decreasing colonization rates and in increasing local extinction rates [43]. This effect has been clearly demonstrated in deforested landscapes, in particular in agricultural contexts [44–46]. The results for landscape-level effects have always been more equivocal in forests within forest management contexts [47–49]. Some studies have shown important landscape-scale effects on richness in one year only to demonstrate stronger stand-scale effects the next year [49]. Local patch size has also been demonstrated to be an important driver of species abundance, which can be both a local and landscape measure [3]. The low sensitivity of many boreal songbirds to harvesting at a landscape scale has been reported in several studies [50–53], and it has been suggested by others [7,19,54]. This may be because birds in boreal forests are adapted to frequent disturbances in natural boreal forest landscapes. In addition, though, it may also be because the context for the fragmentation is still forest, where there are gradients of habitat value, soft edges between patches and good connectivity, unlike agricultural areas with hard edges and habitat loss [55]. This is a more likely explanation for the Acadian Forest. Our results indicate a lack of landscape-scale effect that is consistent with other studies in forest management rather than agricultural contexts.

Significantly, there were no differences in the abundance of mature forest associates. We suggest that this should be the most sensitive indicator of landscape effect. The age class distribution of a forested region is one of the key characteristics that dictate the provision of habitat to wildlife [8]. All forest ages provide habitat, but currently in New Brunswick, forest management is reducing the distribution of the mature forest age classes, which could put stress on the species most associated with older age classes [56]. Mature forests provide unique habitat features for birds and other species [57–60], including larger trees and deadwood, which can support cavity nesters and saproxylics [54,61]. A reduction in the area of older forests can also be associated with shorter rotation planted forests.

There are a few studies on the Acadian Forest that have looked at landscape thresholds in species occurrence, predicting that there may be a threshold of habitat loss at the landscape scale below which ecological processes change abruptly [33,62]. This suggests that landscape-scale effects may not be evident until landscape-level habitat change reaches this threshold. There is some evidence for thresholds at which some species responded to landscape-level habitat change, ranging from 8.6 to 28.7% [33]. These results suggest that effects of landscape context have been identified, although at fairly low levels of landscape habitat. Our results suggest that if a threshold exists, it has not been reached on the BBRO landscape. This result suggests that the relatively high intensity of silviculture in the intensively managed forest landscape is not reducing the ability of mature forests to provide important habitat. This lends confidence to habitat estimates based on the prevalence and distribution of mature forests in ecosystems with forest continuity. Other studies have shown the ecological value of plantations themselves, where they contain diverse avian communities relative to native stands [63] or where they improve connectivity in landscapes [4,64].

The use of indicators that are known to respond to forest management stressors has long been a recommended approach to evaluating forest management practices [18]. This is supported by research that has demonstrated that generalist species are becoming more dominant while specialists are becoming rarer through a process of homogenization in response to human disturbance [24,25]. Our approach examined species with functional traits expected to be most impacted by common hypothesized stressors of intensive forest management. Cavity nesters [65] species that are area-sensitive or, alternatively, species that are associated with interior habitat [11,66] and species associated with mature or overmature habitat are all more likely to be impacted by a landscape-level reduction in older forest through intensive management. One of the key mechanisms that is used to explain this landscape-scale effect is meta-population dynamics [11,67], which suggests that patch occupancy will be higher in landscapes with more habitat or more connectivity [68]. Our results showed no evidence that these indicator groups were responding to the landscape-level management intensity. We speculate that this may be due to very high connectivity in these landscapes that are primarily forested even when mature patches of habitat are dispersed. The data suggest that all of these potentially sensitive specialists can be supported on these highly managed landscapes. This narrowing of the focus to forest birds at the highest risk of turnover or loss in abundance adds additional support to the ecological value of mature forest stands in a planted stand-rich context. We are not suggesting that there are no landscape-scale effects here but only that mature forest stands in BBRO appear to be providing similar habitat quality to mature forests in landscapes with a much smaller area of planted stands.

These results must be interpreted considering several caveats. First, our landscapes represent a gradient in planted stand management intensity (BBRO > QUIS > DEBU), but we do not have replication at the landscape scale, and so the results are confounded with landscape identity and all of the possible differences that might occur between landscapes we did not measure. However, these landscapes occur in a single forest system (the

Acadian Forest) and have considerable overlap in bird communities based on the NMDS, suggesting that they represent a common forest system. In addition, the difference in the area of planted stands in these landscapes is so significant that parsimony would suggest that if management intensity was important, it would be visible here. Second, the sample size in the DEBU landscape was small relative to the other landscapes, and so this comparison should hold less weight but is consistent with the interpretation that high management intensity in BBRO is not compromising bird habitat quality. The third caveat is that perhaps the level of landscape management intensity in QUIS and DEBU is already sufficient to impact bird communities in the oldest forest stands. A comparison with an unmanaged landscape would be ideal but was not available in a comparable forest. It may be possible to use more generalized data from the Breeding Bird Survey and Breeding Bird Atlas to understand the pool of species that is expected as a point of comparison or reference condition, but, in the end, the vast majority of these data will come from managed landscapes. The reality that we have a limited selection of primary, or at least mature, unmanaged forest landscapes to act as reference conditions for sustainability assessments is significant and problematic.

An important implication of these results is that mature stands in these landscapes are able to provide mature forest habitat despite their context. The presence of species in these stands is not proof of the ability to breed here. There is a long-standing debate about the relationship between abundance and productivity [69], where some habitats contain sink populations that rely on immigration from outside of the stand to maintain populations [70]. Research in Ontario has demonstrated that many old forest associates do breed successfully in small patches of mature forest in a forest management context [53]. In contrast, there is evidence from areas fragmented by agriculture that reproductive success can be lowered in habitat fragments such that they become population sinks that cannot be maintained without immigration [71]. The BBRO landscape has been intensively managed for 70 years, and the area planted has been stable for the last 10 years, suggesting that these are persistent populations. Haché et al. [35] used demographic data collected from the BBRO forest to model ovenbird population dynamics under forestry as usual and climate change scenarios. They found that ovenbird populations act as demographic sinks in an intensively managed landscape under climate change but that without climate change (i.e., under current conditions), the number of territorial males would remain relatively constant. Given the inevitability of climate change, however, forest management planning and approaches may need to be altered to conserve old forest associates on these managed landscapes into the future.

5. Conclusions

Old forests provide unique habitat for forest birds, and the loss of that habitat in the Acadian Forest of New Brunswick has been linked directly to the long-term decline in old forest associates [56]. There is an inevitable trade-off between generating wood products from the forest and the provision of older forest habitat, although balance may be achievable through natural disturbance-based silvicultural systems that can better support mature forest birds [72]. Research on forest birds can provide some of the necessary information to assess the size and shape of those trade-offs and help to inform the conversation about the desired structure, function and composition of those forests. Specifically, improving our knowledge of the ecological value of mature forest stands in this managed context is an important step in our ability to assess trade-offs and find balance.

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Data Availability Statement: Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Conflicts of Interest: Greg Adams has retired from his position as science director with JD Irving (owner of the Black Brook landscape). Kevin Porter is a consultant paid by JD Irving. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. The JD Irving had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Appendix A

Table A1. Functional classifications of bird species' functional trait identities include (1) Migration Strategy: NEO = neotropical migrant, NOM = nomadic, RES = resident and SDM = short-distance migrant; (2) nesting strategy: C = cavity, G = ground, LTC = lower tree canopy, TC = tree canopy, TS = tall shrubs and W = wetland; (3) habitat association: CMI = conifer mixedwood, CON = conifer, HMI = hardwood mixedwood, HWD = hardwood, MIX = mixedwood and OHS = open herb and shrub; (4) successional association: G = generalist, HE = herbs, IM = immature, MA = mature, OM = overmature and TS = tall shrubs; (5) area sensitivity: Y = yes and N = no; (6) interior association: E = edge, I = Interior, I_E = both, S = shore and W = wetland.

Specie Code	Common_Name	Migration Strategy	Nesting Strategy	Habitat	Successional Association	Area Sensitive	Interior Association
ALFL	Alder Flycatcher	NEO	Tall Shrubs	OHS	Tall Shrubs	N	E
AMBI	American Bittern	SDM	Ground	OHS	Herbs	N	W
AMCR	American Crow	SDM	Tree Canopy	OHS	Generalist	N	E
AMGO	American Goldfinch	SDM	Lower Tree Canopy	MIX	Tall Shrubs	N	E
AMRE	American Redstart	NEO	Tall Shrubs	HMI	Immature	Y	I_E
AMRO	American Robin	SDM	Lower Tree Canopy	MIX	Generalist	N	E
BAOW	Barred Owl	RES	Cavity	HMI	Mature	Y	I
BAWW	Black-and-white Warbler	NEO	Ground	CMI	Mature	Y	I
BBCU	Black-billed Cuckoo	NEO	Lower Tree Canopy	HWD	Immature	N	I_E
BBWA	Bay-breasted Warbler	NEO	Lower Tree Canopy	CMI	Overmature	N	I_E
BBWO	Black-backed Woodpecker	RES	Cavity	CON	Mature	Y	I_E
BCCH	Black-capped Chickadee	RES	Cavity	MIX	Generalist	N	I_E
BHVI	Blue-headed Vireo	SDM	Lower Tree Canopy	CMI	Mature	Y	I_E
BLBW	Blackburnian Warbler	NEO	Tree Canopy	MIX	Mature	Y	I

Table A1. *Cont.*

Specie Code	Common_Name	Migration Strategy	Nesting Strategy	Habitat	Successional Association	Area Sensitive	Interior Association
BLJA	Blue Jay	SDM	Lower Tree Canopy	CMI	Generalist	N	I_E
BLPW	Blackpoll Warbler	NEO	Lower Tree Canopy	MIX	Overmature	N	I
BOCH	Boreal Chickadee	RES	Cavity	CON	Mature	N	I
BRCR	Brown Creeper	SDM	Cavity	MIX	Mature	Y	I
BTBW	Black-throated Blue Warbler	NEO	Tall Shrubs	HWD	Immature	Y	I
BTNW	Black-throated Green Warbler	NEO	Lower Tree Canopy	MIX	Mature	Y	I
CAWA	Canada Warbler	NEO	Ground	MIX	Immature	Y	I_E
CEDW	Cedar Waxwing	SDM	Lower Tree Canopy	HMI	Immature	N	E
CHSP	Chipping Sparrow	SDM	Tall Shrubs	MIX	Immature	N	E
CMWA	Cape May Warbler	NEO	Tree Canopy	MIX	Mature	N	I_E
CONI	Common Nighthawk	NEO	Ground	OHS	Herbs	N	E
CONW	Connecticut Warbler	NEO	Ground	CON	Overmature	N	I_E
CORA	Common Raven	RES	Tree Canopy	MIX	Generalist	N	I_E
COYE	Common Yellowthroat	NEO	Ground	OHS	Tall Shrubs	N	E
CSWA	Chestnut-sided Warbler	NEO	Tall Shrubs	HWD	Immature	N	E
DEJU	Dark-eyed Junco	SDM	Ground	CON	Immature	N	E
DOWO	Downy Woodpecker	RES	Cavity	HWD	Immature	N	I_E
EAKI	Eastern Kingbird	NEO	Lower Tree Canopy	OHS	Tall Shrubs	N	E
EAWP	Eastern Wood-Pewee	NEO	Tree Canopy	HWD	Mature	N	I_E
EVGR	Evening Grosbeak	NOM	Tree Canopy	CON	Mature	N	I_E
FOSP	Fox Sparrow	SDM	Ground	CON	Immature	N	E
GCFL	GreatCrested Flycatcher	NEO	Cavity	HWD	Immature	N	I_E
GCKI	Golden-crowned Kinglet	SDM	Tree Canopy	CON	Mature	N	I
GHOW	Great Horned Owl	RES	Cavity	HMI	Mature	N	I_E
GRAJ	Canada Jay	RES	Lower Tree Canopy	CMI	Overmature	N	I_E
GRHE	Green Heron	NEO	Tall Shrubs	OHS	Tall Shrubs	N	E
HAWO	Hairy Woodpecker	RES	Cavity	MIX	Mature	Y	I
HETH	Hermit Thrush	SDM	Ground	MIX	Mature	Y	I_E
HOWR	House Wren	SDM	Cavity	HWD	Tall Shrubs	N	E
LEFL	Least Flycatcher	NEO	Tree Canopy	HWD	Immature	Y	E
MAWA	Magnolia Warbler	NEO	Lower Tree Canopy	CON	Immature	Y	I_E

Table A1. *Cont.*

Specie Code	Common_Name	Migration Strategy	Nesting Strategy	Habitat	Successional Association	Area Sensitive	Interior Association
MERL	Merlin	SDM	Tree Canopy	CON	Generalist	N	I_E
MOWA	Mourning Warbler	NEO	Ground	HMI	Immature	N	E
NAWA	Nashville Warbler	NEO	Ground	MIX	Immature	N	E
NOFL	Northern Flicker	SDM	Cavity	MIX	Immature	N	E
NOPA	Northern Parula	NEO	Tree Canopy	MIX	Mature	Y	I
NOWA	Northern Waterthrush	NEO	Ground	CMI	Mature	N	I_E
NSOW	Northern Saw-whet Owl	RES	Cavity	CMI	Mature	N	I_E
OCWA	Orange-crowned Warbler	SDM	Ground	CMI	Tall Shrubs	N	E
OSFL	Olive-sided Flycatcher	NEO	Tree Canopy	CON	Overmature	N	I_E
OVEN	Ovenbird	NEO	Ground	HMI	Mature	Y	I
PAWA	Palm Warbler	SDM	Ground	CON	Tall Shrubs	N	E
PHVI	Philadelphia Vireo	NEO	Tree Canopy	HWD	Immature	N	I_E
PIGR	Pine Grosbeak	NOM	Lower Tree Canopy	MIX	Mature	N	I_E
PIWA	Pine Warbler	SDM	Tree Canopy	CON	Mature	Y	I
PIWO	Pileated Woodpecker	RES	Cavity	MIX	Mature	Y	I
PUFI	Purple Finch	SDM	Tree Canopy	MIX	Mature	N	I_E
RBGR	Rose-breasted Grosbeak	NEO	Lower Tree Canopy	HMI	Immature	N	I_E
RBNU	Red-breasted Nuthatch	RES	Cavity	CMI	Mature	Y	I
RCKI	Ruby-crowned Kinglet	SDM	Tree Canopy	CON	Mature	N	I_E
REVI	Red-eyed Vireo	NEO	Lower Tree Canopy	HWD	Mature	N	I_E
RTHU	Ruby-throated Hummingbird	NEO	Lower Tree Canopy	HWD	Generalist	N	E
RUBL	Rusty Blackbird	SDM	Lower Tree Canopy	MIX	Generalist	N	E
RUGR	Ruffed Grouse	RES	Ground	HMI	Generalist	N	I_E
RWBL	Red-winged Blackbird	SDM	Wetland	OHS	Tall Shrubs	N	W
SCTA	Scarlet Tanager	NEO	Tree Canopy	HWD	Mature	Y	I
SPSA	Spotted Sandpiper	NEO	Ground	OHS	Herbs	N	S
SWTH	Swainson's Thrush	NEO	Lower Tree Canopy	MIX	Mature	N	I
TEWA	Tennessee Warbler	NEO	Ground	HMI	Immature	N	I_E
TRES	Tree Swallow	SDM	Cavity	OHS	Immature	N	E
VEER	Veery	NEO	Tall Shrubs	HMI	Immature	Y	I
WAVI	Warbling Vireo	NEO	Tree Canopy	HWD	Immature	N	E

Table A1. *Cont.*

Specie Code	Common_Name	Migration Strategy	Nesting Strategy	Habitat	Successional Association	Area Sensitive	Interior Association
WBNU	White-breasted Nuthatch	RES	Cavity	HWD	Mature	Y	I
WISN	Wilson's Snipe	SDM	Ground	OHS	Herbs	N	W
WIWA	Wilson's Warbler	NEO	Ground	OHS	Tall Shrubs	N	E
WIWR	Winter Wren	SDM	Cavity	CMI	Mature	Y	I
WOTH	Wood Thrush	NEO	Lower Tree Canopy	MIX	Mature	N	I_E
WTSP	White-throated Sparrow	SDM	Ground	MIX	Generalist	N	I_E
WWCR	White-winged Crossbill	NOM	Tree Canopy	MIX	Mature	N	I_E
YBFL	Yellow-bellied Flycatcher	NEO	Ground	CON	Overmature	N	I_E
YBSA	Yellow-bellied Sapsucker	SDM	Cavity	MIX	Mature	Y	I_E
YEWA	Yellow Warbler	NEO	Tall Shrubs	HWD	Tall Shrubs	N	E
YRWA	Yellow-rumped Warbler	SDM	Tree Canopy	MIX	Mature	N	I_E

Table A2. Bird species lists including common name, scientific name and abundance in each landscape.

Species Code	Common Name	Scientific Name	BBRO	QUIS	DEBU
			Abundance		
ALFL	Alder Flycatcher	*Empidonax alnorum*	11	0	5
AMBI	American Bittern	*Botaurus lentiginosus*	4	3	0
AMCR	American Crow	*Corvus brachyrhynchos*	9	5	0
AMGO	American Goldfinch	*Spinus tristis*	9	11	0
AMRE	American Redstart	*Setophaga ruticilla*	21	7	3
AMRO	American Robin	*Turdus migratorius*	52	41	14
BAOW	Barred Owl	*Strix varia*	2	3	3
BAWW	Black-and-white Warbler	*Mniotilta varia*	6	2	4
BBCU	Black-billed Cuckoo	*Coccyzus erythropthalmus*	2	0	0
BBWA	Bay-breasted Warbler	*Setophaga castanea*	7	5	0
BBWO	Black-backed Woodpecker	*Picoides arcticus*	1	3	1
BCCH	Black-capped Chickadee	*Poecile atricapillus*	46	31	4
BHVI	Blue-headed Vireo	*Vireo solitarius*	40	33	8
BLBW	Blackburnian Warbler	*Setophaga fusca*	30	26	8
BLJA	Blue Jay	*Cyanocitta cristata*	29	26	8
BLPW	Blackpoll Warbler	*Setophaga striata*	2	0	0
BOCH	Boreal Chickadee	*Poecile hudsonicus*	5	5	4
BRCR	Brown Creeper	*Certhia americana*	22	23	10
BTBW	Black-throated Blue Warbler	*Setophaga caerulescens*	42	47	17
BTNW	Black-throated Green Warbler	*Setophaga virens*	56	51	19
CAWA	Canada Warbler	*Cardellina canadensis*	12	5	2
CEDW	Cedar Waxwing	*Bombycilla cedrorum*	0	1	0
CHSP	Chipping Sparrow	*Spizella passerina*	3	5	2
CMWA	Cape May Warbler	*Setophaga tigrina*	7	7	1
CONI	Common Nighthawk	*Chordeiles minor*	3	1	0
CONW	Connecticut Warbler	*Geothlypis agilis*	1	0	0
CORA	Common Raven	*Corvus corax*	8	23	3
COYE	Common Yellowthroat	*Geothlypis trichas*	3	0	2
CSWA	Chestnut-sided Warbler	*Setophaga pensylvanica*	4	2	6
DEJU	Dark-eyed Junco	*Junco hyemalis*	2	7	5

Table A2. *Cont.*

Species Code	Common Name	Scientific Name	BBRO	QUIS	DEBU
			Abundance		
DOWO	Downy Woodpecker	*Dryobates pubescens*	1	0	1
EAKI	Eastern Kingbird	*Tyrannus tyrannus*	0	0	1
EAWP	Eastern Wood-Pewee	*Contopus virens*	12	11	5
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*	6	3	0
FOSP	Fox Sparrow	*Passerella iliaca*	8	1	0
GCFL	Great Crested Flycatcher	*Myiarchus crinitus*	0	0	1
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	37	35	10
GHOW	Great Horned Owl	*Bubo virginianus*	5	0	0
GRAJ	Gray Jay	*Perisoreus canadensis*	10	6	1
GRHE	Green Heron	*Butorides virescens*	1	1	0
HAWO	Hairy Woodpecker	*Dryobates villosus*	2	1	0
HETH	Hermit Thrush	*Catharus guttatus*	67	65	18
HOWR	House Wren	*Troglodytes aedon*	0	1	0
LEFL	Least Flycatcher	*Empidonax minimus*	8	12	9
MAWA	Magnolia Warbler	*Setophaga magnolia*	41	25	12
MERL	Merlin	*Falco columbarius*	2	0	0
MOWA	Mourning Warbler	*Geothlypis philadelphia*	2	0	5
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*	42	21	10
NOFL	Northern Flicker	*Colaptes auratus*	8	0	1
NOPA	Northern Parula	*Setophaga americana*	53	50	14
NOWA	Northern Waterthrush	*Parkesia noveboracensis*	24	2	3
NSOW	Northern Saw-whet Owl	*Aegolius acadicus*	0	1	0
OCWA	Orange-crowned Warbler	*Oreothlypis celata*	1	0	0
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	13	3	4
OVEN	Ovenbird	*Seiurus aurocapilla*	72	85	28
PAWA	Palm Warbler	*Setophaga palmarum*	3	1	0
PHVI	Philadelphia Vireo	*Vireo philadelphicus*	8	10	2
PIGR	Pine Grosbeak	*Pinicola enucleator*	1	0	0
PIWA	Pine Warbler	*Setophaga pinus*	1	0	0
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	1	4	2
PUFI	Purple Finch	*Haemorhous purpureus*	9	18	4
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	20	19	3
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	55	59	12
RCKI	Ruby-crowned Kinglet	*Regulus calendula*	35	24	6
REVI	Red-eyed Vireo	*Vireo olivaceus*	30	46	19
RTHU	Ruby-throated Hummingbird	*Archilochus colubris*	1	0	0
RUBL	Rusty Blackbird	*Euphagus carolinus*	4	0	0
RUGR	Ruffed Grouse	*Bonasa umbellus*	57	61	32
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	1	0	0
SCTA	Scarlet Tanager	*Piranga olivacea*	0	12	6
SPSA	Spotted Sandpiper	*Actitis macularius*	1	1	0
SWTH	Swainson's Thrush	*Catharus ustulatus*	82	78	25
TEWA	Tennessee Warbler	*Oreothlypis peregrina*	5	9	1
TRES	Tree Swallow	*Tachycineta bicolor*	0	1	0
VEER	Veery	*Catharus fuscescens*	21	14	7
WAVI	Warbling Vireo	*Vireo gilvus*	0	0	0
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	0	0	1
WISN	Wilson's Snipe	*Gallinago delicata*	4	1	1
WIWA	Wilson's Warbler	*Cardellina pusilla*	1	0	0
WIWR	Winter Wren	*Troglodytes hiemalis*	49	45	14
WOTH	Wood Thrush	*Hylocichla mustelina*	0	5	0
WTSP	White-throated Sparrow	*Zonotrichia albicollis*	94	61	28
WWCR	White-winged Crossbill	*Loxia leucoptera*	9	12	0
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*	37	19	6
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	59	60	28
YEWA	Yellow Warbler	*Setophaga petechia*	1	0	0
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	13	22	10

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