

DESCRIBING THE SIMILARITIES AND DIFFERENCES IN SONGBIRD
COMMUNITIES BETWEEN HARVESTED AND WILDFIRE-ORIGIN STANDS IN
NORTHWESTERN ONTARIO, CANADA.

By

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FACULTY OF NATURAL RESOURCE MANAGEMENT
LAKEHEAD UNIVERSITY

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ABSTRACT

In Ontario, sustainable forest management is mandated by the CFSA. Natural disturbance emulation is viewed as method that improves sustainability in managed forests. However, few studies have attempted to measure the effectiveness of natural disturbance emulation with respect to maintaining ecological integrity. Using songbird data that was collected in 2021 through the deployment of 96 Acoustic Recording Devices on 157 sample plots in the Dog River-Matawin Forest Management Unit, an analysis was conducted to investigate the similarities and differences in song communities between wildfire-origin ($n = 90$) and harvest-origin ($n = 67$) stands. Community-level indices (richness, abundance, and Shannon's diversity index) were calculated for multiple age classes representing different stand development stages for five different forest species compositional groupings. It was found that in natural stands, regardless of forest type, there was an increase in bird species richness, abundance, and diversity as the forest matured. Managed stands supported a similar richness, abundance, and diversity as natural stands. Where compared, natural and managed stands had different community assemblages. Downy woodpecker (*Dryobates pubescens*) was entirely absent from management stands but was present in natural stands, suggesting that there may be functional differences between the two origin types. Managed stands may have a lower density of standing deadwood with specific dimensions preferable to the downy woodpecker. The retention of size-specific standing deadwood during harvesting may benefit the downy woodpecker in managed forests.

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INTRODUCTION

The boreal forest covers large areas of North America and Eurasia, and represents 29% of the global forest area, making it one of the largest biomes in the world (Kayes and Mallik 2020). Because these forests occur at high-latitudes, extreme cold temperatures have a profound influence on the forest by limiting soil nutrients and tree species diversity (McLaren and Turkington 2013). Given these conditions, tree species diversity is relatively low and is predominately represented by coniferous species, although a few deciduous species occur to a lesser extent (Kayes and Mallik 2020). Intermixed with the forested landscape is a substantial amount of lakes and rivers, and especially wetlands in the form of peatlands, which represent 20% of the Canadian boreal forest region total area (National Wetlands Working Group 1988). The boreal forest supports wildlife (Kayes and Mallik 2020) such as birds, mammals, reptiles and amphibians, fish, and insects. Approximately one to three billion birds use the North American boreal forest for breeding (Bird Studies Canada 2003). It is also a place of cultural and spiritual significance for indigenous peoples (Burton *et al* 2010). Furthermore, forest products harvested from boreal forests are integral to Canada's economy, with the forest sector contributing to 1.7% of the country's total GDP in 2021 (Statistics Canada 2022).

In Ontario, nearly 90% of the province's forests are Crown land, of which approximately half is managed (approximately 27 million hectares) (MNRF 2023). As mandated in the Crown Forest Sustainability Act (CFSA) (1994), large, healthy, and productive forests must be conserved using forest practices that emulate natural disturbance and landscape patterns. To achieve the objectives laid out by the CFSA,

several guides have been developed to aid forest managers in planning operations (MNRF 2023). The boreal landscape guide focuses primarily on forest structure, composition, and age class distributions to provide guidance to forest managers in the conservation these factors (e.g., maintain level within the Simulated Range of Natural Variation – SNRV) at the landscape level (MNRF 2014). The stand and site guide is used by forest managers to identify important features and habitats at the stand and site scales, and provides approaches to adjust their forest operations to conserve these factors (MNRF 2010). Both guides utilize the coarse and fine filters approach to managing habitat for conservation purposes. Coarse filters can be viewed as broader scale practices that promote the conservation for many species, whereas the fine filters address the special requirements for certain species.

Given the sustainability and biodiversity conservation objectives outlined by the CFSA, it is important to measure the effectiveness of forest management practices to determine if they are meeting the desired objectives/outcomes. Ecological integrity (i.e., the combination of ecosystem structure, composition, and function) is an important concept for measuring effectiveness when comparing the similarity of biodiversity or species community assemblages between natural versus managed forested ecosystems or landscapes (Parrish *et al* 2003). Because ecosystems are complex and often have a high number of species, it is not realistic or feasible to assess ecological integrity by measuring the biodiversity of an entire ecosystem (Wiens *et al* 2008). Instead, biological indicator taxa have been used to describe changes in ecosystem function (Venier and Pearce 2004) and used to detect changes in biodiversity that occur as result of forest management actions (McLaren *et al* 1998). Birds are considered good

indicators (Jarvinen and Vaisanen 1979, Furness *et al* 1993, McLaren *et al* 1998, Niemi *et al* 1998). The rationale for their use being that they occupy a diverse array of habitats and niches (Jarvinen and Vaisanen 1979), and the degradation of these ecological components can therefore be detected through population changes (McLaren *et al* 1998, Niemi *et al* 1998, Venier and Pearce 2004). Moreover, they account for the majority of terrestrial vertebrates in the boreal forest (Niemi *et al* 1998). Venier and Pearce (2004) highlighted the importance of using indicators not just for broad-scale, long-term monitoring, but for local-scale assessments in order to more precisely understand important stressors driving population changes.

OBJECTIVES

The first objective of this study is to use songbird point count data collected in natural (i.e., wildfire-origin) forests to develop a natural disturbance baseline of the bird community assemblages. The second objective is to compare bird communities in managed (i.e., harvested) stands by examining the similarities between these communities and thereby provide an evaluation of the effectiveness of current forest management practices with respect to maintaining ecological integrity.

HYPOTHESES

H1: Community-level indices (e.g., richness, abundance, and Shannon's index) will be similar between managed (i.e., harvest-origin) and natural (i.e., wildfire-origin), and will generally increase as forest stands mature.

H2: For forest types and specific age classes where sample size is adequate to make comparisons (3+ plots), the bird community assemblages will be similar between managed and natural stands.

H3: For forest types and specific age classes where sample size is adequate to make comparisons (3+ plots), managed stands will have a lower abundance and diversity of woodpeckers compared to natural stands.

LITERATURE REVIEW

DISTURBANCES AND MANAGEMENT IN THE BOREAL FOREST

Natural Disturbances

Stand-replacing wildfire disturbance is the most common natural disturbance in the boreal forest and plays an integral role in shaping the landscape and its ecosystems (Natural Resources Canada 2020). Although there is considerable annual variability in the amount of forest burned, depending on weather conditions, an average of 2.3 million hectares has burned annually since 1990 (Natural Resources Canada 2020). The boreal forest is a disturbance-dependant ecosystem with many plant and animal species that rely on reoccurring disturbances (Stocks *et al* 2001). For example, the black-backed woodpecker (*Picoides arcicus*) utilizes previously burnt forests to forage for beetles (Tremblay *et al* 2020). Economically important tree species, such as black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), depend on fire to create conditions favorable for their regeneration (Natural Resources Canada 2020). Fire influences the structure and species composition of the boreal forest (Natural Resources Canada 2020), and therefore has important implications for sustainable forest management.

Forest Management and Emulating Natural Disturbance Paradigms

It is mandated in Ontario to manage forested landscapes to ensure the sustainable use of forests and their many ecosystem services (CFSA 1994). This mandate is reflected in several forest management guidelines that describe silviculture methods that are economically viable but also maintain biodiversity. Clearcutting in

Canada's boreal forest has been applied in 83% of the total area harvested in Canadian forests, making it the primary harvest method used in the boreal forest (Canadian Council of Forest Ministers 2018). In addition to the economic benefits of clearcutting, it is used in the boreal forest because it is viewed as the harvesting system that most closely emulates stand-replacing natural disturbances from fire (Giron *et al* 2023). To emulate natural disturbance in managed forests one must attempt to maintain structural and compositional components that are similar to natural forests following harvesting, which is assumed will maintain function that, collectively, support ecological integrity (Kuuluvainen and Grenfell 2012, Rempel *et al* 2016). In this context, evaluation of managed forests need to, comparatively, emulate naturally-disturbed forests.

Conceptually, natural disturbance emulation represents an obvious way to evaluate forest sustainability, but the effectiveness of current policy/guidelines needs to be evaluated within an adaptive management framework.

BIRDS AS INDICATORS OF FOREST SUSTAINABILITY

There are a number of reasons birds are considered ideal indicators of forest sustainability, and, therefore, can be used to measuring the sustainability of forest management practices (Venier and Pearce 2004). For example, birds occupy many different forested habitats and utilize various structural components of forests. For this reason, changes in these ecosystems resulting from management practices could influence the presence or absence of forest birds (Jarvinen and Vaisanen 1979). These changes in indicators represent a potential change in ecosystem function that can be directly linked to forest management activities (Venier and Pearce 2004). Given that there are many bird species that use forests, using sampling methods such as point

counts provides the opportunity to assess the impacts of forest management at both the species (e.g., indicator or niche-specific) and community level. (Venier and Pearce 2004). Venier and Pearce (2004) emphasized that the use of bird community assemblages as indicators in local-scale monitoring programs are ideally suited to evaluate the effects of targeted forest management activities on bird occupancy at the stand level, to better isolate the key stressors driving community change.

THE EFFECTIVENESS OF SUSTAINABLE FOREST MANAGEMENT PRACTICES

Comparison of Bird Communities in Managed and Natural Forests

In their meta-analysis Akresh *et al* (2023) found that partial harvesting (e.g., shelterwood) in second growth forests in eastern North America was beneficial to some bird species. In particular, the increased density of understory shrubs resulting from shelterwood harvesting, provided new foraging and nesting opportunities (Akresh *et al* 2023). They also found that more complete harvest removals such as clearcutting, can create a more open landscape with a dense shrub layer that benefit shrubland bird species (Akresh *et al* 2023). Akresh *et al* (2023) did highlight that although disturbance can be beneficial to some birds, undisturbed mature forests also provide unique features important to a variety of forest bird species (Haney 1999, Kirk *et al* 2012). As such, Akresh *et al* (2023) recommend that their findings be used to understand how disturbance influences bird communities, and to guide management in achieving balance between managed and natural forests.

When studying the relationship between birds and habitat in boreal jack pine forests, Kirk and Hobson (2001) found that different assemblages of birds occurred in

different jack pine stands. Under natural circumstances, succession in jack pine forests creates a mixed forest where spruce and fir become important components that, in turn, resulted in higher bird diversity (Kirk and Hobson 2001). As such, pure jack pine stands managed exclusively for commercial purposes are not adequate for maintaining bird diversity in these forest types, suggesting a management strategy to promote these mixed stands (Kirk and Hobson 2001). Moreover, shortened rotations (i.e., 40-70 years) limit the ability of these jack pine-dominated stands to succeed into mixed conifer stand conditions (Kirk and Hobson 2001).

In Quebec's boreal forest, Imbeau *et al* (1999) compared bird assemblages in different aged black spruce stands that originated either from logging or fire. Species richness was constant regardless of forest age; however, birds were more abundant in recent clearcuts (Imbeau *et al* 1999). Specifically, the alder flycatcher (*Empidonax alnorum*), Nashville warbler (*Leiothlypis ruficapilla*), magnolia warbler (*Setophaga magnolia*), common yellowthroat (*Geothlypis trichas*), Lincoln's sparrow (*Melospiza lincolnii*), and white-throated sparrows (*Zonotrichia albicollis*) were described as early- to mid-successional species that would likely benefit from short logging rotations (Imbeau *et al* 1999). Similar results were observed in Ontario (McLaren 1987) and New York State (Peterson 1988) that showed disturbance resulting from forestry operations benefited Nashville warblers. Titterton *et al* (1979) also reported that magnolia warblers, common yellowthroats, and white-throated sparrows were also commonly found in recently logged areas.

Commonly occurring forest bird communities tend to re-establish once regenerating trees reach the sapling stages (Imbeau *et al* 1999). As specific examples,

species such as ruby-crowned kinglet (*Corthylio calendula*) and yellow-rumped warbler (*Setophaga coronate*) increased in abundance after being temporarily decreased (Imbeau *et al* 1999). Imbeau *et al* (1999) also suggested that when the forest is young, whether it originating from fire or logging, does not have a strong influence on bird community composition. For example, irruptive finches such as the white-winged crossbill (*Loxia leucoptera*) and pine siskin (*Spinus pinus*) were not restricted to mature forests and were actually more abundant in younger forests (Imbeau *et al* 1999). Importantly, cavity-nesting birds were absent from recently cut forests, but instead were occupying recently burned or mature forests (Imbeau *et al* 1999). Spytz (1993) made similar observations in northeastern Ontario where cavity-nesting birds were more abundant in mature black spruce forests compared to younger forests. Imbeau *et al* (1999) raised concern about the implications of forest management on the black-backed woodpecker, American three-toed woodpecker (*Picoides dorsalis*), and brown creeper (*Certhia americana*), since they tend to be primarily found in mature forests. Hagan *et al* (1997) suggested that the American three-toed woodpecker was one of the species most impacted by forest operations in Maine. Additionally, it has been argued that resident species with large home ranges are likely to be affected by clearcutting (Hunter 1992, Wiens 1994).

METHODS

STUDY AREA

The study area was in the Dog River-Matawin Forest Management Unit (FMU) in northwestern Ontario, Canada (Figure 1). Representing an area of slightly over a million hectares, the Dog River-Matawin FMU has characteristics of both the Boreal Forest Region and the Great Lakes – St. Lawrence Forest Regions (MNR 2021). The FMU is composed of two different ecoregions: the Pigeon River Ecoregion (4W) and Lake Nipigon Ecoregion (3W).

The Pigeon River Ecoregion covers the southern portion of the Dog River-Matawin FMU, and is influenced by modifying effects of Lake Superior, especially towards the southeast (Crins *et al* 2009). The climate in this ecoregion is cool and dry, with annual precipitation ranging from 674 to 838 mm, a mean annual temperature of 0.2 to 2.7°C (Crins *et al* 2009), and a mean growing season length of 168 to 188 days (Crins *et al* 2009). Mixed forest is extensive, representing 33.2% of the landcover, while coniferous forest represent 11.5% (Crins *et al* 2009).

Covering the northern section of the FMU is the Lake Nipigon Ecoregion, with moister and cooler conditions prevailing (Crins *et al* 2009). This ecoregion is also strongly influenced by the modifying effects of Lake Superior, but these effects vanish rapidly as northward distance from the lake increases (Crins *et al* 2009). Annual precipitation ranges from 654 to 879 mm with a mean annual temperature of -1.7 to 2.1°C (Crins *et al* 2009), and a mean growing season length of 161 to 182 days (Crins

et al 2009). Mixed forest and coniferous forest are almost equal in their extent covering 23.5% and 23%, respectively (Crins *et al* 2009).

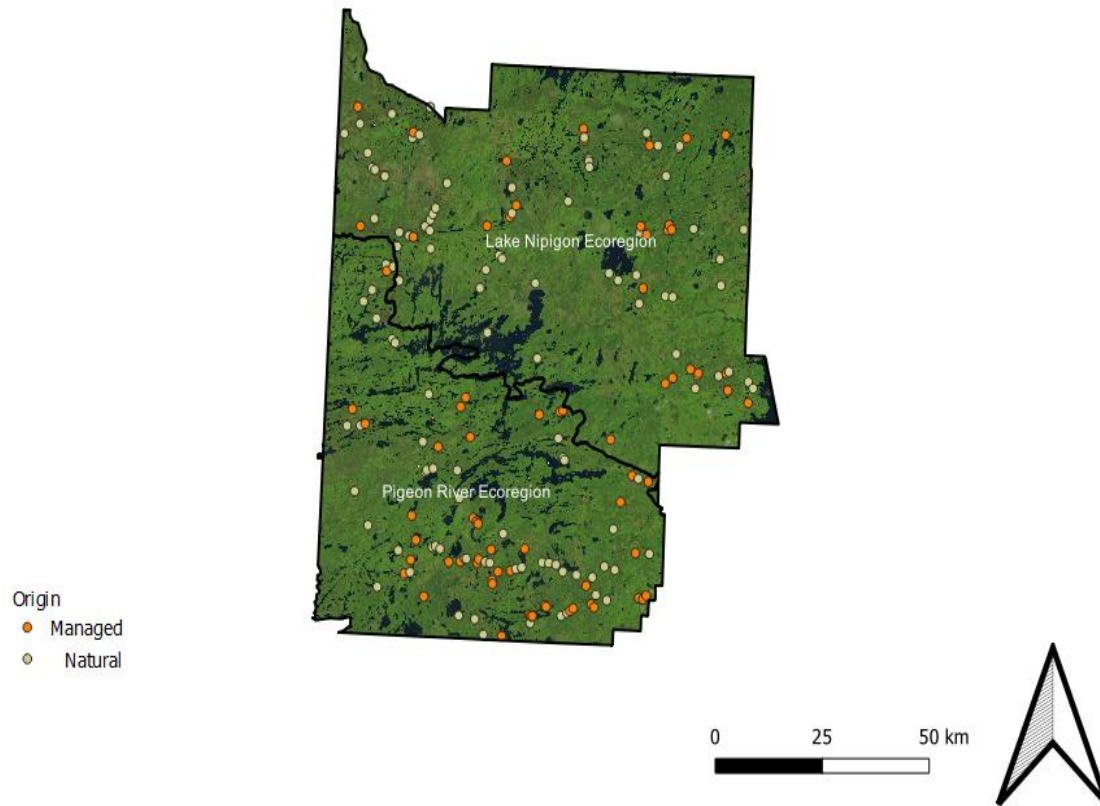


Figure 1. A map of the study area (Dog River-Matawin FMU) showing the location of VSN plots where ARUs were deployed to record songbird data in 2021.

DATA COLLECTION

Study Site Selection

Ontario's Vegetation Sampling Network (VSN) is comprised of a series of fixed area plots (circular, 11.28m radius plots representing 400m²). These plots provided information on the structural and compositional characteristics of the forests within a given FMU that help to derive Forest resource Inventory used in Forest Management

Planning, and include attributes species composition, age class (time since disturbance), and origin (managed or natural). For the Dog River-Matawin FMU, VSN plots were established and measured in 2020. Song bird assessment plots were selected as a subset of the full set of VSN plots by stratifying the plots by origin, and then randomly selecting plots that represented different forest compositions and age classes.

Of the total number of VSN plots sampled for birds ($n = 157$), they were slightly weighted to natural origin stands ($n = 90$) predominately represented by stands in the older age classes (Table 1). Managed origin stands ($n = 67$) were predominately represented by stands in the age classes 21-40 and 41-60, but, understandably, had little representation of stands beyond the age of 80 (Table 1).

Table 1. The number of VSN plots sampled for birds categorized by age class* and species composition** in natural (Nat) and managed (Man) stands in the Dog River-Matawin FMU.

Age class	Pj pure		Sbup		ConMx		HwdMx		Hwd pure		Total
	Nat	Man	Nat	Man	Nat	Man	Nat	Man	Nat	Man	
0-10	0	0	1	0	0	0	0	2	0	1	4
11-20	1	7	1	2	0	0	0	0	0	0	11
21-40	2	9	3	10	3	4	1	1	2	0	35
41-60	5	5	3	1	5	7	4	1	8	4	43
61-80	0	0	4	2	4	2	11	2	5	4	34
81-100	5	0	3	0	5	0	2	2	4	1	22
101+	3	0	1	0	1	0	0	0	3	0	8
Total	16	21	16	15	18	13	18	8	22	10	-

* Age classes represent different stand development stages.

** Pj pure represents pure jack pine stands (>70%); Sbup represents black spruce upland stands (>70%); ConMx represents conifer-dominated mixed stands (51-70%), HwdMx represents hardwood-dominated mixed stands (51-70%); Hwd pure represents pure hardwood stands (>70%).

Songbird Assessments using Acoustic Recording Units (ARUs)

In the spring of 2021, ARUs were deployed in the pre-selected VSN plots in two deployment periods to maximize the number of sampled plots with the available ARUs (96). Deployment 1 occurred during the last week of May through to the end of the first week in June. ARUs were left in the plots for at least two weeks to ensure sufficient (minimum of four) “good weather” days (e.g., no rain, high winds, mechanical noise, etc.) were included in the full set of recordings. At that time, the ARUs were retrieved, SD cards switched out, and placed in the second set of VSN plots and left to record for an additional two weeks (mid-June to first week in July). The ARUs were programmed to record each day at: 30 minutes before sunrise (3 minute recording), at sunrise (5 minute recording), 30 minutes after sunrise (3 minute recording), 30 minutes before sunset, at sunset, and 30 minutes after sunset.

The full set of recordings at each plot was pre-screened for good quality days, then four individual days were randomly selected, and uploaded to Wildtrax. Wildtrax administered the song bird interpretations contracts for all the VSN plot work, using qualified interpreters familiar with the bird species for this region of Canada.

DATA ANALYSIS

The Dog River-Matawin VSN data and the corresponding Wildtrax data were organized in Microsoft Excel and then imported into R studio where the files were merged by plot name to create a joint dataset. The data were then filtered into groups based on their species composition and new data frames were created for each group (ConMx, HwdMx, Hwd pure, Pj pure, Sbu). Following this, the species richness,

abundance, and Shannon's diversity index were calculated for each species composition group individually.

Species Richness

Richness provides a snapshot of the number of species present in a given location. It was calculated by counting the total number of species per site. To calculate richness in R studio, a new data frame using the "group_by" function to group the data plot name, origin, and age class. The "summarize" function was then applied to count the number of distinct species per group, since the number of species were not in numerical form. Another data frame was created to show the sample size and calculate the mean number of species and standard error for each group. This was done by using the "group_by" function to group the data by origin and age class, and summarize function to calculate the mean, standard error, and sample size. The data frame was then plotted using the "ggplot" function to create boxplots.

Abundance

Abundance measures the total number individual birds present in a given location. It was calculated by counting the total number of individuals per site. To calculate abundance in R studio, a new data frame was created by using the "group_by" function to group the data by plot name, origin, and age class. The summarize function was then used to count the maximum number of each species for each group. With the maximum number of each species calculated, a new data frame was created to sum the number of species per group to get the abundance. Using this data frame, the "ggplot" function was used to create boxplots for each group.

Shannon's Diversity Index

Similar to richness, Shannon's diversity index provides a measure of diversity, however it also take into account the abundance of species in a community (Shannon 1948). It was calculated using the following formula:

$$H = - \sum [(p_i) \times \log(p_i)]$$

To calculate Shannon's diversity index in R studio, a new data frame was created by using the "group_by" function to group the data by plot name, origin, and age class. Using the vegan package, the summarize function was then used to calculate Shannon's diversity index. Using this data frame, the "ggplot" function was used to create boxplots for each group.

RESULTS

Over the 157 sampling locations (VSN plots), a total of 70 bird species were recorded during the 2021 breeding season on the Dog-River – Matawin FMU. A total of 66 species (0.73/plot) and 1733 (19.2/plot) individuals were recorded on the wildfire-origin stands (90 plots), compared to 68 species (1.01/plot) and 1357 (20.3/plot) individuals on managed stands (67 plots) (Appendix I). White-throated sparrow, Nashville warbler, and ovenbird (*Seiurus aurocapilla*) were the most abundant species in both wildfire-origin and managed stands, occurring in every forest type and age class. Some other species were highly abundant but showed a preference to particular forest types and age classes. For example, in conifer dominant stands Magnolia warbler, Swainson's thrush (*Catharus ustulatus*), and hermit thrush (*Catharus guttatus*) were more common. Although not as abundant overall, yellow-rumped warbler, yellow-bellied flycatcher (*Empidonax flaviventris*), Cape May warbler (*Setophaga tigrina*), and bay-breasted warbler (*Setophaga castanea*) occurred in increased numbers in conifer dominant stands. Conversely, least flycatcher (*Empidonax minimus*) and red-eyed/Philadelphia vireo (*Vireo olivaceus/V. philadelphicus*) were dominant species in pure and mixed hardwood stands. In younger age classes, as chestnut-sided warbler (*Setophaga pensylvanica*), Lincoln's sparrow (*Melospiza lincolni*), and mourning warbler were more prevalent. With increasing age there was a notable increase in forest-dwelling birds including brown creepers and golden-crowned kinglet (*Regulus satrapa*). There were some species that were only recorded on either wildfire-origin stands or managed stands but not both. Species that were only recorded on managed stands were Eastern kingbird (*Tyrannus tyrannus*), scarlet tanager (*Piranga olivacea*),

white-breasted nuthatch (*Sitta carolinensis*), and yellow-billed cuckoo (*Coccyzus americanus*). Natural stands had fewer unique species, which include downy woodpecker, and Wilson's warbler (*Cardellina pusilla*).

In hardwood pure (>70%) stands, species richness and diversity in natural stands increased consistently as they reached more mature age classes, peaking in the most mature age class (101+) (Figure 2). Abundance in natural stands also showed a general increase as they matured; however, peak abundance (not including 0-10, 11-20 age classes) was reached in the 61-80 age class. For natural stands, all three indices showed the largest increase between the 41-60 and 61-80 age classes, only increasing slightly (richness) or remaining relatively constant (abundance and diversity) in the older age classes.

Managed hardwood pure stands showed similar patterns to natural stands, with all indices increasing in older age classes. In the 41-60 age class, all indices were nearly identical between managed and natural stands, with least flycatcher, ovenbird, and red-eyed/Philadelphia vireo being most the most abundant species in both stand origin types. However, the community assemblages did differ between managed and natural in this age class. Natural stands had 11 unique species, with the managed stands having three. Species unique to natural stands in the 41-60 age class include American redstart (*Setophaga ruticilla*), American robin (*Turdus migratorius*), black-billed cuckoo (*Coccyzus erythrophthalmus*), blue jay (*Cyanocitta cristata*), black-throated green warbler (*Setophaga virens*), Canada warbler (*Cardellina Canadensis*), eastern wood-pewee (*Contopus virens*), northern flicker (*Colaptes auratus*), pileated woodpecker (*Dryocopus pileatus*), Wilson's warbler, and yellow-bellied sapsucker

(*Sphyrapicus varius*). Species unique to managed stands include bay-breasted warbler, Canada jay (*Perisoreus Canadensis*), and ruffed grouse (*Bonasa umbellus*). It is noteworthy to mention that woodpeckers were completely absent from managed stands in the 41-60 age class, while six individuals of three species were present in natural stands. Indices were also very similar between managed and natural stands in the 61-80 age class, with the three most abundant species being identical to the previous age class. The natural and managed community assemblages had fewer differences than in the previous age class, with only four unique species in natural stand, but six in the managed stands. Species unique to natural stands in the 61-80 age class include bay-breasted warbler, blue jay, blackburnian warbler (*Setophaga fusca*), and yellow warbler (*Setophaga petechial*). Species unique to managed stands include American redstart, rose-breasted grosbeak (*Pheucticus ludovicianus*), yellow-bellied flycatcher, yellow-bellied sapsucker, yellow-rumped warbler, and ruffed grouse. Unlike the previous age class, woodpeckers were also present in managed stands in the 61-80 age class, which is likely a function of the advancing self-thinning process and presence of standing dead trees.

The hardwood mixed group (51-70%) showed a trend similar to the hardwood pure group, with natural stands showing a general increase across all three indices as they matured and peaking in the oldest age class (101+) (Figure 3). However, unlike the hardwood pure group, the largest increase in all indices for natural stands in the hardwood mixed group occurred between 21-40 and 41-60 age classes. However, there was only one sample for each managed and natural stands in the 21-40 age class). Following this increase the indices remained relatively constant across the older age

classes. In contrast, there was a peak in diversity in managed hardwood mixed stands in the 0-10 age class, which remained high in the 21-40 age class before decreasing in older stands. Managed hardwood mixed stands had higher indices compared to natural stands in the 21-40 age class, but this may simply be attributed to a low sample size. Beyond the 21-40 age class, richness was very similar between managed and natural stands. Managed stands in the 81-100 age class appear to have a lower abundance and diversity, however there was a wide variation between the two sampled sites, with one site yielding comparably low indices.

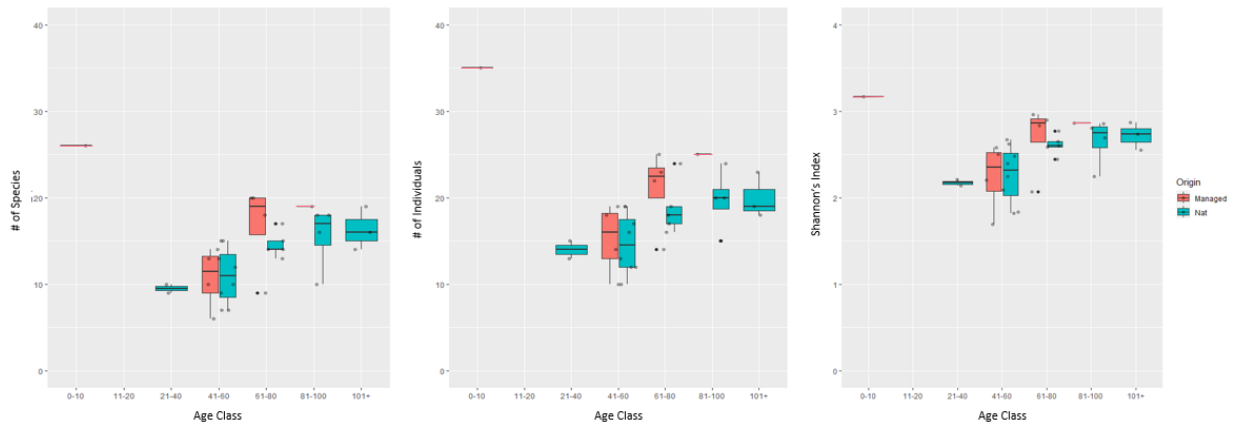


Figure 2. Recorded song species richness (left), abundance (middle), and Shannon's diversity (right) indices for hardwood pure stands comparing wildfire-origin versus harvest-origin stands along a 100+ year age sequence.

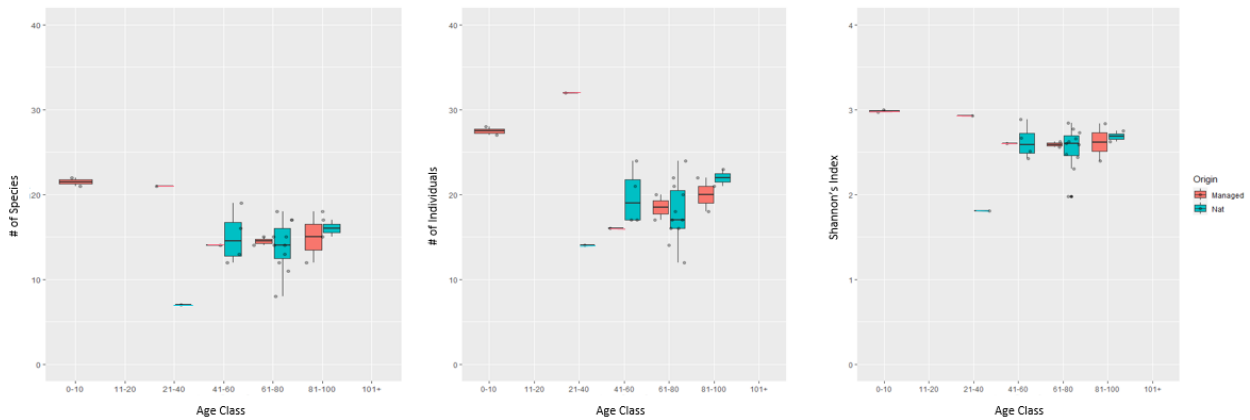


Figure 3. Recorded song species richness (left), abundance (middle), and Shannon's diversity (right) indices for hardwood mixed stands comparing wildfire-origin versus harvest-origin stands along a 100+ year age sequence.

Natural stands in the conifer mixed group (51-70%) generally showed an increasing trend for all indices as they matured, although there was a notable decrease in the 61-80 age class that was not consistent with this generalized trend (Figure 4). Interestingly, the natural stands in the hardwood mixed group (Figure 3) had a similar decrease (albeit smaller) in indices during the same age class. There was also a noticeable decrease in indices in the oldest age class (101+), but this may very well be due to only having one site in this age class. In the three age classes that represent managed stands in the conifer mixed group, there was a consistent increasing pattern across all indices. Unlike the natural stands that showed decreases in the 61-80 age class for all indices, the managed stands in this age class continued along an increasing trend.

The indices are relatively similar between managed and natural stands in the 21-40 age class, and some dominant species such as ovenbird and magnolia warbler showed a similar abundance. There were some differences in community assemblages, with natural stands having eight unique species compared to four in managed stands, although these species were only represented by single individuals. In the 41-60 age class, natural stands had higher indices than managed stands. Besides Nashville warbler, which was a dominant species in both managed and natural stands in this age class, other dominant species differed depending on stand origin type. For example, golden-crowned kinglet and ovenbird were dominant species in managed stands compared to natural stands, however this could be due to managed stands having two additional sample plots. Similar to the previous age class, natural stands in the 41-60 age class had more unique species than managed stands. Species unique to natural

stands include American robin, Canada warbler, Lincoln's sparrow, northern flicker, northern waterthrush (*Parkesia noveboracensis*), veery (*Catharus fuscescens*), and winter wren (*Troglodytes hiemalis*). Species unique to managed stands include boreal chickadee (*Poecile hudsonicus*), black-throated blue warbler (*Setophaga caerulescens*), eastern wood-pewee, and Tennessee warbler (*Leiothlypis peregrine*). Three unique species in natural stands were represented by multiple individuals (two to three), whereas unique species in managed stands were only represented by single individuals. In the 61-80 age class, managed stands showed higher indices than natural stands, unlike all previous age classes.

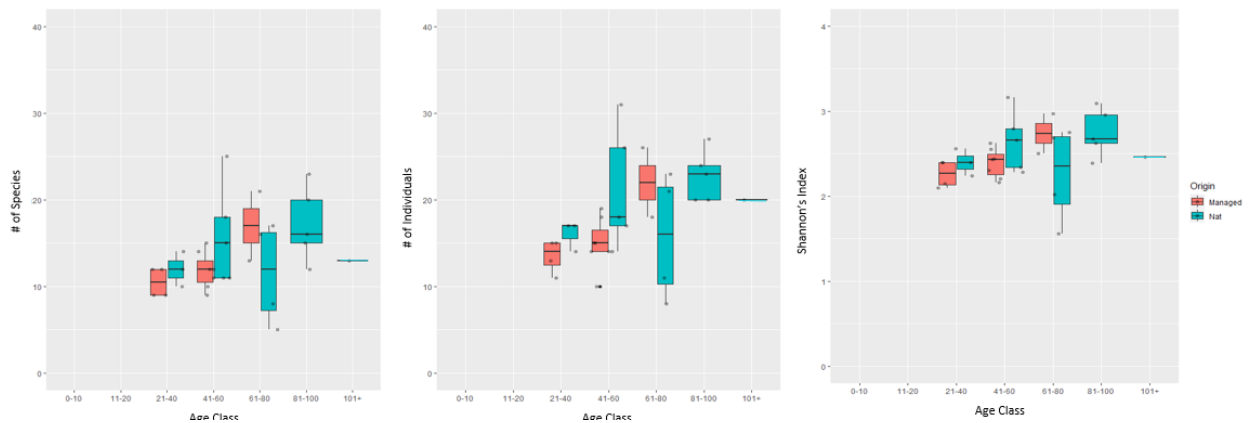


Figure 4. Recorded song species richness (left), abundance (middle), and Shannon's diversity (right) indices for conifer mixed stands comparing wildfire-origin versus harvest-origin stands along a 100+ year age sequence.

All indices peak in the 11-20 age class for natural stands in the jack pine pure group before decreasing in the next age class, although only represented by one sample site (Figure 5). For the most part, the indices increase slightly between 21-40 and 41-60, and continued to increase in older age classes. The exception here was Shannon's diversity, which decreased slightly in the oldest age class surveyed. Where

managed jack pine pure stands were represented, they showed a similar trend to natural stands, with a peak in indices in the 11-20 age classes before decreasing in the 21-40 and 41-60 age classes. The indices showed some differences between natural and managed stands; whereby in the 11-20 age class, natural stands had higher indices, whereas in the 21-40 and 41-60 age classes managed stands had a higher indices. There were comparable sample sizes in both managed and natural stands in the 41-60 age class. Both managed and natural stands in this age class had several unique species, indicating that the community assemblages did differ between the two. Species unique to managed stands include alder flycatcher, cedar waxwing (*Bombycilla cedrorum*), dark-eyed junco (*Junco hyemalis*), Lincoln's sparrow, olive-sided flycatcher (*Contopus cooperi*), purple finch (*Haemorhus purpureus*), ruby-crowned kinglet, and white-winged crossbill. Species unique to natural stands include black-capped chickadee (*Poecile atricapillus*), blackburnian warbler, blue jay, pine siskin, Tennessee warbler, and veery. The majority of these unique species occurred in very small numbers, mostly only represented by one individual, but some did occur in higher numbers. Species that occurred in higher numbers include dark-eyed junco with a total of four individuals recorded on managed stands compared to none on natural stands, and blue jay with a total of four individuals recorded on natural stands compared to none on managed stands. Some species in the 41-60 age class showed some notable variation in abundance between natural and managed stands. For example, there were 11 Nashville warblers in managed stands and only six in natural stands. Similarly, there were six golden-crowned kinglets in managed stands and only two in natural stands.

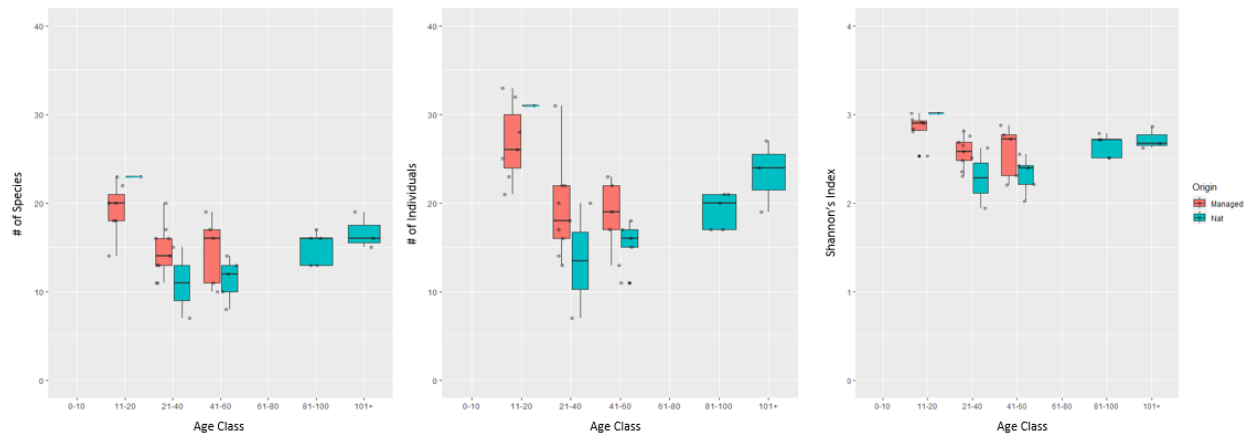


Figure 5. Recorded song species richness (left), abundance (middle), and Shannon's diversity (right) indices for jack pine pure stands comparing wildfire-origin versus harvest-origin stands along a 100+ year age sequence.

Black spruce-dominated upland sites was the only trees species compositional group that had a natural stand represented in the 0-10 age class, albeit only one stand (Figure 6). Hardwood pure and hardwood mixed groups both had managed stands representing the 0-10 age class (Figure 2; Figure 3). Unlike the hardwood dominant groups where the 0-10 age class had the highest indices, they were comparatively low in the black spruce upland group, although there was only one sample site. Black spruce upland natural stands showed a consistent and gradual increase in indices with each successive age class, excluding the spike in the 11-20 age class. It is noteworthy to mention that the black spruce upland group had consistently high indices across all age classes and stand origin types, unlike other species compositional groupings that showed greater differences between origin types. Indices for managed black spruce upland stands were very similar to those calculated for natural stands, with the exception of the 11-20 age class. The black spruce upland group and conifer mixed group (Figure 5) showed the least amount of difference in all indices when comparing managed versus natural stands.

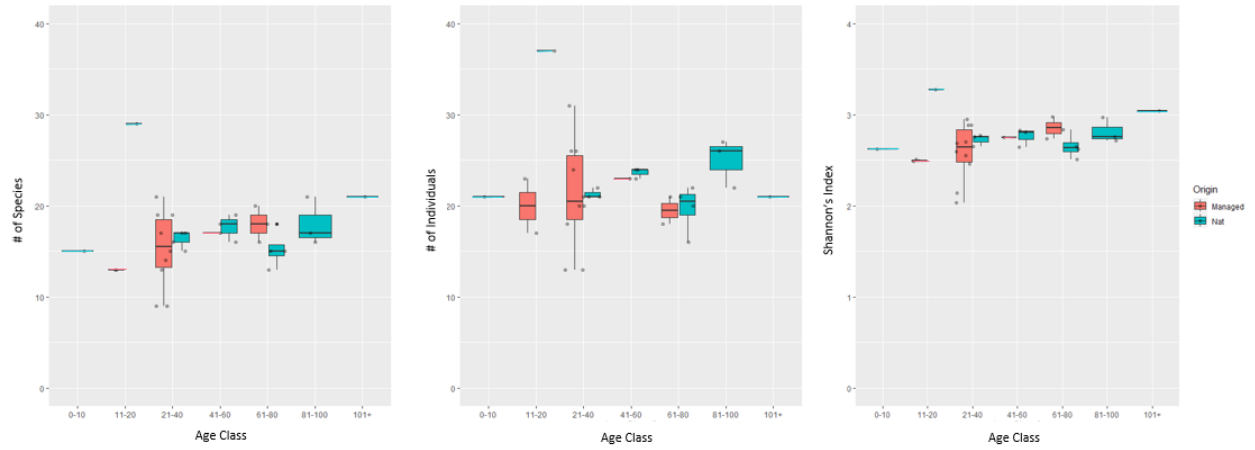


Figure 6. Recorded song species richness (left), abundance (middle), and Shannon's diversity (right) indices for black spruce upland stands comparing wildfire-origin versus harvest-origin stands along a 100+ year age sequence.

DISCUSSION

The first objective of this study was to develop a set of community-level indices that would represent a baseline for bird communities in naturally disturbed forests, and observe the changes in indices (i.e., species richness, abundance, Shannon's diversity index) over a sequence of different stand development stages. This baseline, in turn, set the stage for comparing these indices between managed and natural stands, and describing the differences and similarities in community assemblages, through stand development stages following stand-replacing disturbances (objective 2).

A total of 68 species were recorded in managed stands and 66 in natural stands. Despite an additional 23 sample plots in natural stands, a relatively similar total species richness was observed between the two origin types. This result suggests that nearly all forest songbird species expected to be found were recorded. This similarity is important when determining the differences in community assemblages between managed and natural stands, because it is presumed that nearly all expected species have been detected.

Both managed and natural stands had species that were unique to each origin type. For most species this did not appear to indicate a specific preference to managed or natural stands, and was likely influenced by other factors, such as sample size or rarity effects. For example, in managed stands the unique species were eastern kingbird, scarlet tanager, white-breasted nuthatch, and yellow-billed cuckoo. These species primarily have a more southern distribution, and are at their range edge locally in the Dog River-Matawin FMU. Additionally, these species were only represented by single individuals. Therefore, their presence only in managed stands is probably due to

these species being locally uncommon, and not necessarily related to specific conditions created in managed forests.

The ecological importance of standing deadwood has been well documented (Harmon *et al* 1986), and woodpeckers can act as indicators of forest health with respect to standing deadwood abundance (Drapeau *et al* 2009). Additionally, in Ontario the retention of standing deadwood (i.e., wildlife trees) in managed forests is a target for improving sustainability (MNRF 2010). A total of seven downy woodpeckers were detected in natural stands, with none being detected in managed stands. It should be noted that other woodpecker and cavity-nesting species were present in managed stands. However, compared to the closely related hairy woodpecker, the downy woodpecker has shown a preference (in Iowa) for shorter trees with a smaller diameter (Stauffer and Best 1982, Conner *et al* 1975). The slight differences in nest site selection may explain why hairy woodpecker was present in managed stands and downy woodpecker was not. This result may suggest that there is an inadequate abundance of smaller-sized standing deadwood in managed forests, resulting in low suitability for the downy woodpecker. It is possible that historical management practices that resulted in a smaller amount of standing deadwood in managed forest is responsible for this difference (Goodburn and Lorimer 1998). The majority of downy woodpeckers in natural stands were recorded in stands aged 61-80, 81-100, and 101+. Few to no managed forests typically reach these older age classes due to the shortened harvest rotation cycles (approximately 60 years), which could also explain the absence of downy woodpecker in managed stands.

The pattern of increasing indices from younger to older forests was true for all of the forest types measured in this study, regardless of stands being natural or managed. Keller *et al* (2003) highlighted a peak in richness during the first few years after harvesting, followed by sharp decline that continued over the next 15 years. Then, at about the 25 years of age, species richness began to increase gradually from younger to older forests (Keller *et al* 2003). Younger age classes for both natural and managed stands were not well represented in this study. However, starting in the 21-40 age class, there was a gradual increase in richness from younger to older forests, which is consistent with the pattern observed by Keller *et al* (2003). Other studies (e.g., Owen *et al* 2020) have also shown similar trends of increasing richness with forest maturity. In contrast, the results presented by Imbeau *et al* (1999) that examined bird assemblages in different aged black spruce stands that originated either from logging or fire, were inconsistent with the results of this study. In their case, Imbeau *et al* (1999) found that species richness did not differ depending on forest age in upland black spruce stands. However, in this study, richness in black spruce stands showed a small but steady increase from younger to old stands.

In hardwood dominated stands, there were marginal differences in indices between natural and managed stands. Although the indices were similar between managed and natural stands, the bird community assemblages did differ greatly. One of the more important differences was that woodpeckers were absent in managed stand in the 41-60 age class, despite being present in natural stands. A number studies have observed that following a stand-replacing disturbance, there is an increase in accumulated standing deadwood as the forest matures to a certain age (Nash *et al*

2023, Bormann and Likens 1979). Although recent management practices aim to retain a certain amount of standing deadwood (MNR 2010), studies have shown that some managed forests tend to have less standing deadwood than natural stands (Goodburn and Lorimer 1998). Given the relationship between woodpeckers and standing deadwood, their presence or absence may indicate differences in the amount of standing deadwood accumulated in a stand. The absence of woodpeckers from managed hardwood pure stands in the 41-60 age class would suggest that there are lower amounts of standing deadwood compared to natural stands. In the next age class (61-80) woodpeckers were present again in managed stands, suggesting there may have been an increase in the accumulation of standing deadwood during this age class through the self-thinning process.

Conifer-dominated stands were similar to hardwood stands in that they had minimal differences in indices between natural and managed stands, and had different community assemblages comprised of some unique species. In the conifer mixed group in age class 41-60, there were three species unique to natural stands: American robin, Canada warbler, and winter wren. Unlike the species unique to managed stands that were only represented by single individuals, these three species were represented by two to three individuals. This suggests that natural stands in the conifer mixed group in the 41-60 age class may have habitat features that are preferable to these species, specifically Canada warbler and winter wren. However, both of these species show a strong association to water and riparian areas (Hejl *et al* 2020, Reitsma *et al* 2020). Therefore, a small stream or a low lying wet area in close proximity to some of the natural-origin sample plots may explain their presence in natural stands. Alternatively,

natural stands may have a greater abundance of deadwood (both fallen and standing), which is an important habitat component for the winter wren (Ellison 1994).

For jack pine pure stands in the 41-60 age class, community assemblages in both managed and natural stands showed noticeable differences. In general, managed stands had unique species that tend to be more associated with conifer forests (i.e., dark-eyed junco, ruby-crowned kinglet, white-winged crossbill, purple finch) whereas natural stands had some species that show preference to deciduous undergrowth (i.e., Tennessee warbler, veery). Kirk and Hobson (2007) highlighted that bird diversity was higher in natural jack pine stands compared to managed stands due to natural succession, which created more of a mixed stand comprised of additional tree species. However, this was not the case in this study, where managed jack pine stands showed a slightly higher diversity than natural stands. Therefore, the difference in community assemblage may be primarily influenced by slight differences in understory development.

The main limitation encountered throughout this study was the limited sample size across stand types, origins, and age classes. This limitation lowered the confidence in evaluating some of the community-level indices and patterns observed, and limited community assemblage comparisons to only one or two age classes for a few forest types. More specifically, sample plots in early successional age classes were mostly absent from the study in both natural and managed plots

Replicating the methods of this study in future research could be beneficial if larger samples sizes were used. This would allow for stronger confidence in the truth of the indices and their patterns. Future research should focus specifically on

presence/absence of downy woodpecker, as well as other cavity nesting species, in managed stands. A more comprehensive community analysis, including composition for the whole community using ordination and associated approaches, would also provide more detailed information about the similarities and differences between songbird communities in managed and natural stands.

CONCLUSION

There are limited studies that attempt to measure the effectiveness of natural disturbance emulation in maintaining ecological integrity in managed forest. This study has shown (where sample size was adequate) that natural stands, regardless of forest type, generally increase in bird richness, abundance, and diversity as the forest matures. The indices were very similar between natural and managed stands, which indicates that managed stands support a similar richness, abundance, and diversity as natural stands. These findings are consistent with the first hypothesis (H1). However, most community assemblages did differ greatly between managed and natural stands, which is inconsistent with the second hypothesis (H2). Downy woodpecker was absent from managed stands, which could be due to a difference in standing deadwood characteristics, or because managed stands do not reach a maturity preferable to this species. Additionally, woodpeckers were entirely absent for hardwood pure stands in the 41-60 age class, but were present in natural stands. These findings are consistent with the third hypothesis (H3). Based on the findings of this study it is recommended that there should be an increased retention of smaller-sized standing deadwood during harvesting.

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APPENDICES

APPENDIX I

Species abundance per stand origin type

Managed		Natural	
Species	Number of Individuals	Species	Number of Individuals
NAWA	114	WTSP	140
WTSP	102	RPVI	135
RPVI	93	OVEN	125
OVEN	86	NAWA	122
MAWA	73	SWTH	99
HETH	65	HETH	70
SWTH	63	GCKI	66
GCKI	51	MAWA	62
YBFL	47	LEFL	61
YRWA	45	VEER	60
VEER	36	CSWA	54
CSWA	34	RBNU	49
LEFL	32	MOWA	47
MOWA	31	BLBW	42
ALFL	30	YBFL	38
DEJU	25	CAWA	33
RCKI	24	WIWR	29
RBNU	24	YRWA	28
BLJA	21	RCKI	26
BBCU	21	AMRO	25
CONI	19	BLJA	25
WIWR	18	BRCR	24
AMRO	18	NOPA	24
PIWO	16	BCCH	23
BCCH	15	CONI	22
CAJA	14	BBCU	21
BLBW	14	BHVI	19
CEDW	13	PIWO	19
BRCR	13	BAWW	17
BHVI	12	TEWA	17
BBWA	12	DEJU	16
OSFL	11	ALFL	13
BOCH	11	CMWA	12
AMRE	10	EAWP	12
RUGR	9	RUGR	12
PUFI	9	BTBW	10
LISP	9	RBGR	10
CMWA	9	NOFL	9
BAWW	9	PUFI	9

WWCR	8	YBSA	9
PAWA	8	AMRE	8
YBSA	7	CEDW	8
TEWA	7	REVI	8
NOFL	7	CAJA	7
NOPA	6	OSFL	7
CAWA	6	BTNW	6
RBGR	5	DOWO	6
BTNW	5	PISI	6
REVI	4	BADO	4
EAWP	4	BBWA	4
CHSP	4	HAWO	4
BTBW	4	WWCR	4
PISI	3	BBWO	3
PHVI	3	NOWA	3
YEWA	2	PHVI	3
NOWA	2	YEWA	3
HAWO	2	AMGO	2
AMWO	2	CHSP	2
YBCU	1	LISP	2
WBNU	1	PAWA	2
SPGR	1	SPGR	2
SCTA	1	AMWO	1
KILL	1	BOCH	1
INBU	1	BWHA	1
EAKI	1	INBU	1
BWHA	1	WIWA	1
BBWO	1		
AMGO	1		

APPENDIX II

Four-letter species codes

Four-letter Species Code	Common Name	Scientific Name
ALFL	Alder flycatcher	<i>Empidonax alnorum</i>
AMGO	American goldfinch	<i>Carduelis tristis</i>
AMRE	American redstart	<i>Setophaga ruticilla</i>
AMRO	American robin	<i>Turdus migratorius</i>
AMWO	American woodcock	<i>Scolopax minor</i>
BADO	Barred owl	<i>Strix varia</i>
BAWW	Black-and-white warbler	<i>Mniotilta varia</i>
BBCU	Black-billed cuckoo	<i>Coccyzus erythrophthalmus</i>
BBWA	Bay-breasted warbler	<i>Setophaga castanea</i>
BBWO	Black-backed woodpecker	<i>Picoides arcticus</i>
BCCH	Black-capped chickadee	<i>Poecile atricapillus</i>
BHVI	Blue-headed vireo	<i>Vireo solitarius</i>
BLBW	Blackburnian warbler	<i>Setophaga fusca</i>
BLJA	Blue jay	<i>Cyanocitta cristata</i>
BOCH	Boreal chickadee	<i>Poecile hudsonicus</i>
BRCR	Brown creeper	<i>Certhia americana</i>
BTBW	Black-throated blue warbler	<i>Setophaga caerulescens</i>
BTNW	Black -throated green warbler	<i>Setophaga virens</i>
BWHA	Broad-winged hawk	<i>Buteo platypterus</i>
CAJA	Canada jay	<i>Perisoreus canadensis</i>
CAWA	Canada warbler	<i>Cardellina canadensis</i>
CEDW	Cedar waxwing	<i>Bombycilla cedrorum</i>
CHSP	Chipping sparrow	<i>Spizella passerina</i>
CMWA	Cape May warbler	<i>Setophaga tigrina</i>
CONI	Common nighthawk	<i>Chordeiles minor</i>
CSWA	Chestnut-sided warbler	<i>Setophaga pensylvanica</i>
DEJU	Dark-eyed junco	<i>Junco hyemalis</i>
DOWO	Downy woodpecker	<i>Dryobates pubescens</i>
EAKI	Eastern kingbird	<i>Tyrannus tyrannus</i>
EAWP	Eastern wood-pewee	<i>Contopus virens</i>
GCKI	Golden-crowned kinglet	<i>Regulus satrapa</i>
HAWO	Hairy woodpecker	<i>Dryobates villosus</i>
HETH	Hermit thrush	<i>Catharus guttatus</i>
INBU	Indigo bunting	<i>Passerina cyanea</i>
KILL	Killdeer	<i>Charadrius vociferus</i>
LEFL	Least flycatcher	<i>Empidonax minimus</i>
LISP	Lincoln's sparrow	<i>Melospiza lincolni</i>

MAWA	Magnolia warbler	<i>Setophaga magnolia</i>
MOWA	Mourning warbler	<i>Geothlypis philadelphia</i>
NAWA	Nashville warbler	<i>Leiothlypis ruficapilla</i>
NOFL	Northern flicker	<i>Colaptes auratus</i>
NOPA	Northern parula	<i>Setophaga americana</i>
NOWA	Northern waterthrush	<i>Parkesia noveboracensis</i>
OSFL	Olive-sided flycatcher	<i>Contopus cooperi</i>
OVEN	Ovenbird	<i>Seiurus aurocapilla</i>
PAWA	Palm warbler	<i>Setophaga palmarum</i>
PHVI	Philidelphia vireo	<i>Vireo philadelphicus</i>
PISI	Pine siskin	<i>Spinus pinus</i>
PIWO	Pileated woodpecker	<i>Dryocopus pileatus</i>
PUFI	Purple finch	<i>Haemorhus purpureus</i>
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
RBNU	Red-breasted nuthatch	<i>Sitta canadensis</i>
RCKI	Ruby-crowned kinglet	<i>Corthylio calendula</i>
REVI	Red-eyed vireo	<i>Vireo olivaceus</i>
RPVI	Red-eyed/Philadelphia vireo	<i>V. olivaceus/V. philadelphicus</i>
RUGR	Ruffed grouse	<i>Bonasa umbellus</i>
SCTA	Scarlet tanager	<i>Piranga olivacea</i>
SPGR	Spruce grouse	<i>Canachites canadensis</i>
SWTH	Swainson's thrush	<i>Catharus ustulatus</i>
TEWA	Tennessee warbler	<i>Leiothlypis peregrina</i>
VEER	Veery	<i>Catharus fuscescens</i>
WBNU	White-breasted nuthatch	<i>Sitta carolinensis</i>
WIWA	Wilson's warbler	<i>Cardellina pusilla</i>
WIWR	Winter wren	<i>Troglodytes hiemalis</i>
WTSP	White-throated sparrow	<i>Zonotrichia albicollis</i>
WWCR	White-winged crossbill	<i>Loxia leucoptera</i>
YBCU	Yellow-billed cuckoo	<i>Coccyzus americanus</i>
YBFL	Yellow-bellied flycatcher	<i>Empidonax flaviventris</i>
YBSA	Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>
YEWA	Yellow warbler	<i>Setophaga petechia</i>
YRWA	Yellow-rumped warbler	<i>Setophaga coronata</i>

APPENDIX III

Managed Summary

Plot Name	Sp Comp1	Sp Comp2	Age Class	Richness	Abundance
177001	Pj97 Pt2 Bw1	Pj pure	21-40	11	14
177002	Pt76 Bf14 Bw8 Sw2	Hwd pure	41-60	6	10
177003	Sb91 Bf5 Pt2 Bw1 Sw1	Sbup	61-80	20	21
177005	Sb93 Bw5 Sw2	Sbup	11-20	13	17
177008	Sb50 Bf26 Pt14 Pj9	Sbup	41-60	17	23
177011	Pj90 Sb10	Pj pure	11-20	22	33
177017		Pj pure	21-40	20	31
177021	Sw41 Bf26 Pj18 Bw13 Sb2	ConMx	41-60	12	14
177023	Pj100	Pj pure	11-20	18	23
177029	Pj54 Bf24 Bw16 Pt4 Sb3	ConMx	41-60	12	15
177030	Sb67 Bf19 Bw10 Pt3 Sw1	Sbup	21-40	13	20
177034	Sb80 Bf12 Bw6 Pt2	Sbup	21-40	19	24
177035	Sb52 Bw27 Bf10 Sw10	Sbup	61-80	16	18
177037	Pj70 Sb18 Pt10 Bf2	Pj pure	41-60	11	17
177042	Sb86 Bw11 Bf4	Sbup	11-20	13	23
177046	Bw30 Pj26 Pt24 Sb10 Sw5 Bf4	HwdMx	81-100	12	18
177052	Sb54 Pj27 La15 Pt4	ConMx	41-60	10	14
177053	Pt76 Bw16 Pb8	Hwd pure	61-80	9	14
177080	Pj58 Pt23 Sw19	ConMx	41-60	14	18
177083	Sb69 Bf17 Pt10 Bw4	Sbup	21-40	17	26
177097	Pj79 Sb21	Pj pure	41-60	10	13
177106	Pj58 Sb35 Pt8	ConMx	21-40	9	13
177108	Bf100	Sbup	21-40	21	31
177109	Bw100	Hwd pure	0-10	26	35
177111	Bw59 Pt21 Pj20	HwdMx	21-40	21	32
177112	Bf69 Sb29 Pj2	Sbup	21-40	9	13
177114	Pj92 Sb8	Pj pure	11-20	18	26
177123	Pt79 Bf11 Sw6 Sb5	Hwd pure	81-100	19	25
177124	Pt60 Bw21 Bf18 Sw1	HwdMx	61-80	15	20
177125	Pj94 Sb6	Pj pure	11-20	23	32
177126	Pt83 Bf9 Sb5 Bw3	Hwd pure	61-80	20	25
177129	Pj90 Sb8 Pt1	Pj pure	41-60	19	22
177131	Pj47 Bf39 Sb7 Mr6	ConMx	41-60	15	19
177138	Pj61 Sb34 Bf2 Bw2 Sw1	ConMx	61-80	21	26
177140	Bf50 Sb27 Bw15 Pj4 Pt3 Sw1	Sbup	21-40	14	18
177146	Sb47 Bf32 Pj20 Sw1	Sbup	21-40	15	20
177148	Pt78 Bw10 Mr8 Bf3 Am2	Hwd pure	41-60	10	14
177150	Pj89 Sb10 Bw1	Pj pure	41-60	16	19
177151	Pj72 Pt22 Bf5	Pj pure	41-60	17	23
177154	Sb49 Pt26 Bw14 Bf7 Sw3	ConMx	21-40	9	11
177155	Pt83 Sb9 Pj6 Bw2	Hwd pure	41-60	14	19

177156	Pt85 Bf8 Bw7	Hwd pure	41-60	13	18
177159	Pj99 Pt1	Pj pure	21-40	17	20
177160	Pj96 Sb3 Bf1	Pj pure	21-40	13	17
177161	Pj100	Pj pure	21-40	16	22
177162	Pt53 Sb16 Bw11 Pj11 Bf10	HwdMx	81-100	18	22
177163	Pt34 Pj31 Bf13 Sb12 Sw5 Bw4 Mr1	ConMx	61-80	13	18
177165	Pj97 Pt2 Sb1	Pj pure	21-40	13	16
177173	Pj69 Sb31	Pj pure	11-20	20	28
177175	Pj46 Sw42 Sb11 Bw1	ConMx	21-40	12	15
177177	Pt86 Bf14	Hwd pure	61-80	18	23
177182	Pj69 Pt17 Sb13 Bf1	ConMx	41-60	9	10
177188	Sb84 Bf16	Sbup	21-40	19	26
177189	Pt84 Bf7 Sb4 Bw3 Sw2	Hwd pure	61-80	20	22
177198		HwdMx	0-10	22	28
177199	Pt61 Bw39	HwdMx	61-80	14	17
177201	Pj100	Pj pure	21-40	11	13
177202	Pj99 Bf1	Pj pure	21-40	16	22
177203	Pj100	Pj pure	21-40	14	18
177206	Pt58 Pj34 Bw6 Sw1	HwdMx	41-60	14	16
177212	Pj100	Pj pure	11-20	14	21
177218	Sw93 Sb5 Pj3	Sbup	21-40	16	21
177219	Sw58 Pt38 Pj3	ConMx	41-60	11	15
177229	Bw51 Bf27 Sb22	HwdMx	0-10	21	27
177232	Sb49 Pt29 Bf16 Bw5 Sw1	ConMx	21-40	12	15
177233	Sw68 Bf32	Sbup	21-40	9	13
177234	Pj58 Sb30 Bf13	Pj pure	11-20	20	25

APPENDIX IV

Natural Summary

Plot Name	Sp Comp1	Sp Comp2	Age Class	Richness	Abundance
177004	Pt64 Sb20 Pj12 Bw4	HwdMx	61-80	15	20
177006	Pj70 Bf16 Sb14 Bw1	Pj pure	81-100	16	21
177007		Sbup	0-10	15	21
177009		Sbup	41-60	16	23
177013	Pt100	Hwd pure	81-100	18	24
177014	Pt49 Pj36 Sw10 Bw4 Mt2	HwdMx	61-80	18	21
177015	Bw74 Pj23 Sb2	Hwd pure	101+	16	18
177016	Pj44 Bw28 Pt26 Sb2	HwdMx	41-60	16	21
177018	Sb61 Pj37 Bf2	Sbup	61-80	15	21
177020	Bw79 Sw14 Bf7	Hwd pure	41-60	9	12
177022	Sw68 Bw32 Bf1	ConMx	81-100	15	20
177025	Pj63 Sb36 Pt1	ConMx	41-60	11	17
177026	Pj55 Bf32 Pt10 Sb1 Sw1 Bw1	ConMx	41-60	11	14
177027	Sb65 Bf19 Pt8 Bw8	Sbup	61-80	15	20
177031	Pt33 Sb30 Bf19 Pj15 Bw4	ConMx	21-40	12	17
177032	Sb52 La46 Bw1	Sbup	81-100	16	22
177038	Sb76 Pj12 Pt7 Bw4 Bf1	Sbup	41-60	18	24
177040	Pt52 Bw22 Pj21 Sb4 Sw1	HwdMx	61-80	17	24
177041	Pj100	Pj pure	41-60	13	17
177047	Pj98 Sb2	Pj pure	21-40	15	20
177049	Sb97 Bw3	Sbup	11-20	29	37
177050	Pj100	Pj pure	41-60	12	16
177058	Pt56 Sw44	HwdMx	81-100	17	23
177059	Pt100	Hwd pure	21-40	10	15
177061	Pt74 Bw22 Bf4	Hwd pure	41-60	7	12
177066	Pt79 Cp11 Bw9	Hwd pure	81-100	18	20
177073	Pt92 Bw4 Bf3	Hwd pure	81-100	10	15
177074	Bf66 Bw30 Sw3 Mt1	ConMx	61-80	16	21
177079	Pt100	Hwd pure	41-60	12	16
177081	Bw49 Pt41 Bf10	HwdMx	41-60	13	17
177085	Pj77 Sb13 Pt6 Sw3	Pj pure	81-100	13	17
177086	Pj71 Sb24 Bw5	Pj pure	101+	19	27
177087	Pt87 Sw7 Bw4 Sb2	Hwd pure	81-100	16	20
177088	Pt56 Pw40 Bf4	HwdMx	81-100	15	21
177091	Bf35 Mr31 Bw17 Cw10 Pt7 Mt1	HwdMx	61-80	14	17
177092	Bf49 Cw42 Bw9	Sbup	21-40	17	21
177095	La47 Pt45 Bf4 Sb4	ConMx	61-80	5	8
177096	Bw44 Pj25 Sb19 Bf7 Pt5	ConMx	81-100	23	27
177100	Pt47 Bw38 Sw6 Bf5 Sb3	HwdMx	61-80	17	22
177102	Sb83 Pt11 Pj7	Sbup	81-100	21	27
177107	Sb29 Bw24 Bf23 Pj14 Sw10	ConMx	81-100	16	24
177110	Pt73 Bf24 Bw3	Hwd pure	101+	19	23
177113	Bw76 Bf12 Pt12	Hwd pure	61-80	15	19
177116	Pj100	Pj pure	21-40	7	7
177119	Pt91 Bw5 Bf3 Sw1	Hwd pure	61-80	13	18
177121	Pt90 Mr7 Bw2 Sb1	Hwd pure	101+	14	19
177122	Pt81 Bf14 Sw5	Hwd pure	61-80	17	24
177127	Pj86 Bw8 Bf5	Pj pure	11-20	23	31

177128	Pt43 Bw35 Bf12 Sb8 Sw2	HwdMx	41-60	12	17
177130	Bf72 Mr16 Bw6 Sw6	Sbup	21-40	17	22
177132	Bw56 Pt17 Mr14 Bf10 Cp1 Sw1 Sb1	HwdMx	21-40	7	14
177133	Pj57 Pt19 Sb11 Bf7 Sw4 Bw2	ConMx	61-80	17	23
177134	Pj75 Sb14 Bf6 Pt3 Bw2	Pj pure	41-60	14	18
177135	Sb68 Bf18 Bw13 Mr1	Sbup	81-100	17	26
177137	Sb51 Pj31 Pt11 Bw5 Bf3	ConMx	61-80	8	11
177139	Pt59 Bf18 Sb12 Bw7 Mr3 Sw1	HwdMx	41-60	19	24
177143	Sb43 Pj34 Bw12 Bf6 Pt5	ConMx	41-60	15	18
177144	Pt94 Bw6	Hwd pure	41-60	13	19
177152	Bf52 Bw28 Pt15 Sw5	ConMx	101+	13	20
177153	Sb64 Bf28 Mr8	Sbup	101+	21	21
177158	Pt40 Bf37 Bw18 Sw3 Sb2	HwdMx	61-80	14	16
177168	Sb41 Pj28 Sw15 Pt9 Bw6	ConMx	41-60	18	26
177171	Pj36 Sb34 Bw24 Pt6	ConMx	21-40	14	17
177172	Pj84 Sb12 Sw2 Bf1	Pj pure	81-100	13	17
177174	Pj72 Pt16 Bw11 Sb1	Pj pure	81-100	16	21
177181	Pj66 Sb24 Bw8 Bf1	ConMx	81-100	12	20
177183	Pt100	Hwd pure	41-60	7	10
177186	Pt100	Hwd pure	21-40	9	13
177187	Pt61 Sw34 Bf4	HwdMx	61-80	12	14
177190	Pt95 Bw2 Bf2	Hwd pure	61-80	14	17
177192	Pj97 Bw2	Pj pure	101+	16	24
177193	Pj61 Sb39	Pj pure	101+	15	19
177194	Pj50 Bw27 Pt11 Sb11 Bf1	ConMx	81-100	20	23
177195	Sb84 Bw11 Pt5	Sbup	21-40	15	21
177197	Pj53 Pt38 Bw8 Pw1	ConMx	21-40	10	14
177205	Pj34 Sb33 Bw18 Pt8 Bf5 Mr1	ConMx	41-60	25	31
177207	Pt100	Hwd pure	41-60	15	19
177209	Pt92 Bf7 Sb1	Hwd pure	41-60	15	17
177210	Pj78 Pt17 Sb4 Bf2	Pj pure	41-60	8	11
177211	Sb78 Bw11 Bf8 Pt3	Sbup	41-60	19	24
177213	Pt61 Bw14 Sb9 Pj9 Bf7	HwdMx	61-80	13	17
177222	Pj97 Sb2 Bf1	Pj pure	41-60	10	15
177223	Pt72 Bw14 Bf9 Sb3 Sw2	Hwd pure	61-80	14	16
177231	Bw49 Pt28 Bf9 Mr7 Pw6 Sw1	HwdMx	61-80	15	18
177235	Pt77 Bf11 Bw10 Pj1 Sb1	Hwd pure	41-60	10	13
177236	Sb46 Bf32 Bw22	Sbup	61-80	18	22
177237	Bf64 Bw20 Sb13 Sw4	Sbup	61-80	13	16
177238	Pj87 Bw7 Sb4 Bf2	Pj pure	81-100	17	20
177239	Bw66 Pt33 Sb1	HwdMx	61-80	11	16
177240	Bw67 Pt32 Mr2	HwdMx	61-80	8	12

APPENDIX V

R codes

Richness

```

> ConMx_sprich <- ConMx %>%
group_by(PlotName, Origin, Age_Class3) %>%
summarize(distinct_species = n_distinct(Species))

> ConMx_meansdn <- ConMx_sprich %>%
group_by(Origin, Age_Class3) %>%
summarize(mean = mean(distinct_species), sd = sd(distinct_species), samp = n(), se =
sd / sqrt(samp))

> ggplot(ConMx_sprich, aes(x = Age_Class3, y = distinct_species, fill =Origin))+
geom_boxplot() +
geom_point(position = position_jitterdodge(), alpha=0.3) +
scale_x_discrete(limits = c("0-10", "11-20", "21-40", "41-60", "61-80", "81-100", "101+"))
+ scale_y_continuous(limits = c(0,40))

```

Abundance

```

> Sbup_abundance <- Sbup %>%
group_by(PlotName, Origin, Age_Class3, Species) %>%
summarize(abundance = max(SpeciesIndividualNumber))

> Sbup_abundance1 <- Sbup_abundance %>%
group_by(PlotName, Origin, Age_Class3) %>%
summarize(abundance1 = sum(abundance))

> ggplot(Sbup_abundance1, aes(x = Age_Class3, y = abundance1, fill = Origin)) +
geom_boxplot() +
geom_point(position = position_jitterdodge(), alpha=0.3) +
scale_x_discrete(limits = c("0-10", "11-20", "21-40", "41-60", "61-80", "81-100", "101+"))
+
scale_y_continuous(limits = c(0,40))

```

Shannon's Diversity Index

```

> Sbup_shannons <- Sbup_abundance %>%
group_by(PlotName, Origin, Age_Class3) %>%
summarize(N = sum(abundance), shannon.di = diversity(abundance, index =
"shannon", MARGIN = 2))

```

```
> ggplot(Sbup_shannons, aes(x = Age_Class3, y = shannon.di, fill = Origin)) +  
  geom_boxplot() +  
  geom_point(position = position_jitterdodge(), alpha=0.3) +  
  scale_x_discrete(limits = c("0-10", "11-20", "21-40", "41-60", "61-80", "81-100", "101+"))  
  +  
  scale_y_continuous(limits = c(0,4))
```