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RETENTION OF CANOPY TREES AS BIOLOGICAL LEGACIES FOR
BALANCING WOODY BIOMASS PRODUCTION AND BIODIVERSITY IN
MANAGED ASPEN FORESTS OF THE GREAT LAKES REGION

By

Amber M. Roth

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

(Forest Science)

MICHIGAN TECHNOLOGICAL UNIVERSITY

2012

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This dissertation, "Retention of Canopy Trees as Biological Legacies for Balancing Woody Biomass Production and Biodiversity in Managed Aspen Forests of the Great Lakes Region," is hereby approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in FOREST SCIENCE.

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ABSTRACT

Green-tree retention under the conceptual framework of ecological forestry has the potential to provide both biomass feedstock for industry and maintain quality wildlife habitat. I examined the effects of retained canopy trees as biological legacies (“legacy trees”) in aspen (*Populus* spp.) forests on above-ground live woody biomass, understory plant floristic quality, and bird diversity. Additionally, I evaluated habitat quality for a high conservation priority species, the Golden-winged Warbler (*Vermivora chrysoptera*). I selected 27 aspen-dominated forest stands in northern Wisconsin with nine stands in each of three legacy tree retention treatments (conifer retention, hardwood retention, and clearcuts or no retention) across a chronosequence (4-36 years post-harvest).

Conifer retention stands had greater legacy tree and all tree species biomass but lower regenerating tree biomass than clearcuts. Coniferous but not hardwood legacy trees appeared to suppress regenerating tree biomass. I evaluated the floristic quality of the understory plant assemblage by estimating the mean coefficient of conservatism (C). Mean C was lower in young stands than in middle-age or old stands; there was a marginally significant ($p=0.058$) interaction effect between legacy tree retention treatment and stand age. Late-seral plant species were positively associated with stand age and legacy tree diameter or age revealing an important relationship between legacy tree retention and stand development.

Bird species richness was greatest in stands with hardwood retention particularly early in stand development. Six conservation priority bird species were indicators of legacy tree retention or clearcuts. Retention of legacy trees in aspen stands provided higher quality nest habitat for the Golden-winged Warbler than clearcuts based on high pairing success and nesting activity.

Retention of hardwoods, particularly northern red oak (*Quercus rubra*), yielded the most consistent positive effects in this study with the highest bird species richness and the highest quality habitat for the Golden-winged Warbler. This treatment maintained stand biomass comparable to clearcuts and did not suppress regenerating tree biomass. In conclusion, legacy tree retention can enhance even-aged management techniques to produce a win-win scenario for the conservation of declining bird species and late-seral

understory plants and for production of woody biomass feedstock from naturally regenerating aspen forests.

CHAPTER 1. Introduction

Research Overview

Growth in foreign and domestic demand for fossil fuels and recent high fuel prices have brought increased attention to alternative sources of fuel such as plant-based ethanol and renewable biomass feedstocks. Ligno-cellulosic biomass from aspen (*Populus* spp.) presents an opportunity for producing an economically viable crop with high net energy yield while simultaneously supporting diverse plant and wildlife communities. The management of aspen forests for such purposes, however, will require an evaluation of trade-offs between tree productivity for biomass and retention of habitat for associated biodiversity. This study assessed trade-offs between aspen forest biomass production and wildlife (specifically bird assemblages) habitat as influenced by legacy tree retention, also called green-tree retention.

Biological legacies created by natural disturbances fill important ecological roles. Their retention in silvicultural prescriptions can create forest stand structure that emulates natural disturbances (Seymour et al. 2002, Lindenmeyer et al. 2006, Manning et al. 2006). Legacy trees, remnant live overstory trees not removed during the last harvest rotation, are increasingly being retained in even-aged management prescriptions to more closely mimic the structure of naturally disturbed sites and to improve wildlife habitat diversity, to improve aesthetics, and to reduce soil erosion (Kohm and Franklin 1997, Wisconsin Department of Natural Resources 2006). Clearcuts, or single-cohort stands, resemble infrequent catastrophic natural disturbance events where no canopy trees remain (Seymour et al. 2002). Aspen stands with legacy tree retention, or two-cohort stands, most closely resemble the structure of relatively more common intermediate-severity disturbance events where individual and patches of residual trees survive (Seymour et al. 2002). The impact of legacy tree retention requires evaluation to determine if wildlife species benefit as intended, to estimate changes to woody biomass, and to understand the impacts on carbon storage in these forests.

I will evaluate bird diversity, understory plant floristic quality, and woody plant productivity in 27 aspen forest stands in northern Wisconsin managed with one of three

silvicultural treatments (no legacy tree retention or clearcut, hardwood legacy tree retention, and conifer legacy tree retention) and across a chronosequence (4-36 years post-harvest). My goal is to understand how legacy tree retention in aspen forest stands affect relationships between stand-level tree productivity, understory plant floristic quality, and bird diversity and productivity for species of conservation concern (Figure 1.1).

Aspen forests provide an ideal study system that traditionally is harvested as a clearcut or coppice with the expectation that a near monotypic even-aged stand of young aspen will regenerate. Legacy tree retention, or green-tree retention, provides an alternative approach with the potential for being a win-win scenario that meets both biomass feedstock demand and bird conservation objectives. We hypothesized that legacy tree retention would not reduce stand productivity relative to a monotypic clearcut with no retention but that bird diversity and understory plant floristic quality would increase due to habitat for both early-seral associated species and some mature or late-seral forest associates.

I selected birds as a focal taxon in this study because early seral forest bird populations are declining in the Great Lakes Region and across eastern North America (Askins 1993, Hunter et al. 2001, Rich et al. 2005). The loss of early seral forest habitat due to maturation is frequently cited as a likely contributor to these declines (Litvaitis 1993, Trani et al. 2001). Aspen stands during the first ten years post-harvest are frequently utilized by shrubland bird species. Shrubland birds of eastern North America as a group have exhibited long-term population declines throughout their breeding range (Askins 1993).

In Chapter 2, my objective is to understand how legacy tree retention in aspen-dominated forest stands affects stand-level tree productivity and bird assemblage diversity, composition, and relative abundance. Optimizing biomass production potentially presents a trade-off in terms of reduced habitat quality for some bird species.

Repeated harvest of secondary forests has resulted in decreasing understory plant diversity in northern forests in the Great Lakes region (Rooney et al. 2004). In Chapter 3,

I evaluate the potential for legacy trees to reduce the negative impact of intensive forest harvesting, such as clearcutting, on disturbance-sensitive or late-seral understory plant species. Additionally, I hypothesized that legacy trees would produce a life-boating effect for some late-seral understory plant species and speed recovery of these species following harvest.

The Golden-winged Warbler (*Vermivora chrysoptera*) is a high conservation concern species that breeds in high densities in young aspen stands (Roth and Lutz 2004). The Golden-winged Warbler Working Group (GWWG) has identified the need to evaluate management practices that may generate quality breeding habitat as its top research priority (Buehler et al. 2007). In addition, the GWWG Breeding Grounds Management Committee listed developing timber harvest prescriptions that promote high-quality breeding habitat as its second highest priority. In Chapter 4, I identify the characteristics of aspen stands that produce high quality habitat for this species and that can be incorporated into commercial timber prescriptions.

The Golden-winged Warbler has often been identified as a forest edge associate (e.g. Confer et al. 2011). The design of this study provides a unique opportunity to better understand how this species reacts to edges of recently harvested aspen forest stands. In Chapter 5, I examine the difference in spatial orientation of male territories and female nest site selection which may suggest harvested stand edge preference or avoidance behavior. I hypothesize that the presence of at least intermediate densities of legacy trees would reduce the birds' use of these edges created by nearby mature forest.

Outcomes of this investigation include management recommendations to: 1) optimize both tree productivity for biomass feedstock production and biological diversity in aspen stands and 2) provide high quality habitat for bird species of conservation concern that depend on young forest habitat.

Animal Handling

Some of the research presented herein required the safe capture and handling of wild birds. My animal-handling procedures were authorized by Michigan Technological

University's Institutional Animal Care and Use Committee (IACUC Protocol no. L0111 and L0200). To our knowledge, no birds died as a result of this research.

Dissertation Format

The chapters of this dissertation are formatted for publication in different ecological journals. For this reason, I have written the text in first-person plural given that multiple people contributed to the research and would be recognized as co-authors. Also the writing style and scope are geared for different journal audiences depending on the chapter.

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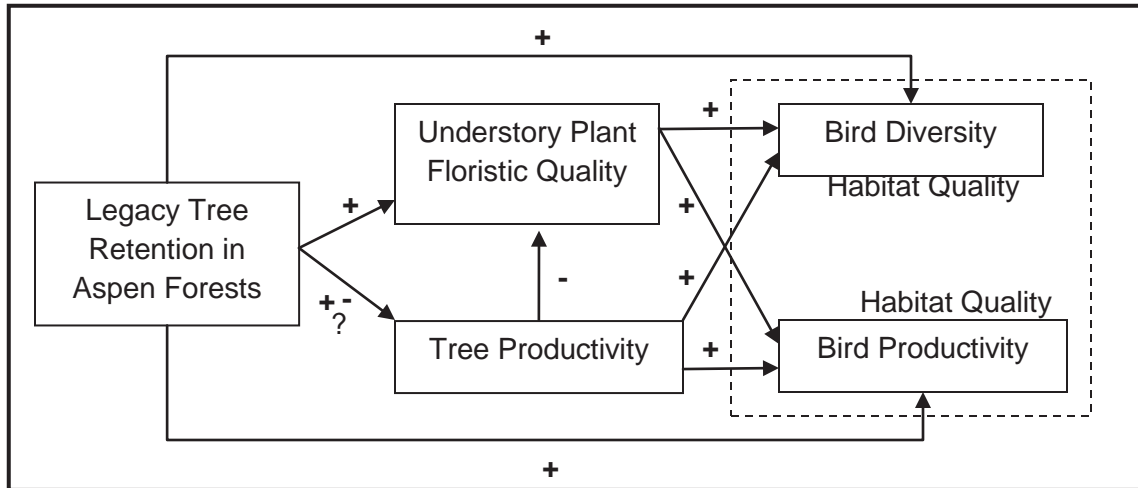


Figure 1.1. Predicted relationships between ecological components in aspen forest stands with legacy tree retention.

Chapter 2. Legacy Tree Retention Provides Win-Win Scenario for Increasing Bird Species Richness and Stand Productivity in Aspen Forests

Abstract

With increasing interest in using forests as a source for bioenergy feedstock, aspen (*Populus* spp.) forests may play an important role in meeting this new demand. To balance forest biomass harvesting with the habitat requirements of wildlife species, green-tree retention under the conceptual framework of ecological forestry provides potential for meeting both needs. We examined the effects of retained trees as biological legacies (“legacy trees”) on above-ground live woody biomass and bird assemblage species richness, diversity, abundance, and composition in 27 aspen-dominated forest stands in northern Wisconsin. We selected nine stands in each of two legacy tree retention treatments (conifer retention and hardwood retention) and clearcuts (no retention) across a chronosequence (4-36 years post-harvest). Hardwood retention stands and clearcuts had similar above-ground live woody biomass for regenerating trees, legacy trees, and all trees combined with minimal suppression of regenerating trees. Conifer retention stands had greater legacy tree and all tree biomass but lower regenerating tree biomass than clearcuts. Coniferous but not hardwood legacy trees appeared to suppress regenerating tree biomass. Bird species richness was greatest in the hardwood retention treatment particularly early in stand development likely reflecting the important compositional and structural role of the large-diameter northern red oak (*Quercus rubra*) trees in this system. Six conservation priority bird species (Black-throated Green Warbler, *Setophaga virens*; Brown Thrasher, *Toxostoma rufum*; Common Yellowthroat, *Geothlypis trichas*; Golden-winged Warbler, *Vermivora chrysoptera*; Mourning Warbler, *Geothlypis philadelphia*; White-throated Sparrow, *Zonotrichia albicollis*) were indicators of legacy tree retention or clearcuts with at least one species in each treatment suggesting that a mixture of these management strategies across the landscape may be necessary to aid declining species collectively. Legacy tree retention increased bird species richness with benefits to a group of conservation priority species, increased aspen forest biomass until 30 years post-harvest, and potentially maintained greater carbon stocks in young stands which could dampen carbon ecosystem fluxes

related to harvesting. This resulted in a win-win scenario for bird conservation and industries seeking woody feedstock from naturally regenerating forests.

Introduction

As fossil fuel prices increase, energy and fuel producers increasingly seek domestically produced sustainable fuel alternatives and are exploring use of a variety of feedstocks for the emerging bioenergy industry (Kszos et al. 2000, Dale et al. 2010). Aspen (*Populus* spp.) forests have the potential to play a major role (Johansson 2002, Richardson et al. 2002), given their cosmopolitan distribution in the northern hemisphere. Quaking aspen (*Populus tremuloides*) is the most widely distributed tree species in North America (Perala 1990), and the closely related European aspen (*Populus tremula*) has a similar broad temperate distribution across Eurasia (Worrell 1993).

Traditionally, aspen forests were clearcut with the tops and branches (i.e., residues or “slash”) left on site to decompose and provide nutrients to the naturally regenerating stand (Adams and Boyle 1981, Belleau et al. 2005). Bioenergy production is capable of using any plant material including these previously unused harvest residues as feedstock such that whole-tree harvest removal potentially provide increased economic returns relative to traditional cut-to-length operations (Adebayo et al. 2007, Becker et al. 2009). Additionally, short-rotation fast-growing woody crop plantations (e.g. hybrid poplar) can produce high volumes of feedstock on shorter timeframes than naturally regenerating aspen stands (Ruark et al. 2006). These new management practices come with potential costs in the form of reduced biodiversity, soil quality, and environmental quality leading to concerns about their large-scale implementation (Cook and Beyea 2000, Bockheim et al. 2005, Willyard and Tikalsky 2006, Firbank 2007, Flaspohler et al. 2009).

Ecological forestry promotes sustainable harvest of forests in such a way as to produce structural characteristics representative of naturally disturbed stands (Kohm and Franklin 1997). It provides a conceptual framework for creating management prescriptions that balance economic needs with maintenance of ecological integrity in managed forests

(Kohm and Franklin 1997, Janowiak and Webster 2010). Ecological forestry principles and practices thus provide the opportunity for evaluating tradeoffs in aspen forest management. For example, green-tree retention has been promoted to protect disturbance-sensitive and late seral species and to increase structural diversity resulting in habitat for a more diverse bird assemblage when compared to traditional clearcutting (Hansen et al. 1995a, Rodewald and Yahner 2000, Rosenvold and Lohmus 2008, McDermott and Wood 2009). This silvicultural practice involves the retention of large-canopy trees during a harvest such that they become biological legacies of the previous stand. These legacy trees thus have the potential for diversifying structural habitat for wildlife and providing a viable economic source of bioenergy biomass feedstock.

Our objective was to evaluate tree productivity and wildlife response to two prescriptions for legacy tree retention (conifer retention and hardwood retention) relative to traditional clearcuts in aspen forests. Retained large-canopy legacy trees cast shade on woody regeneration and potentially reduce the amount of above-ground live woody biomass available for harvest (Huffman et al. 1999, Edgar and Burk 2001). We measured both the contribution of legacy trees to the total stand biomass and their impact on biomass of the regenerating woody vegetation. We predicted that legacy trees will increase total stand biomass relative to clearcuts throughout the chronosequences if regenerating trees are not suppressed.

To evaluate wildlife response to these three prescriptions, we selected birds as our indicator group because they respond quickly to management and they include a large number of species with likely varying responses to management characteristics (Hansen et al. 1995b, Hutto 1998, Rodewald and Yahner 2000). For example, we predict that species associated with mature forests might be most abundant in stands with retention as opposed to species that prefer fully open canopy conditions that would be expected to be most abundant in young clearcuts. Thus there is the potential to identify groups of species that are indicators of the three harvest prescriptions. We expect species richness and diversity to be highest in young stands with legacy tree retention as these should attract species associated with both early and mature stages of stand development.

Hutto (1998) proposed the need for understanding which bird species occur in different land cover types particularly those resulting from specific land use and management practices. Through this understanding, we can identify bird species that can be indicators of a variety of forest types and characteristics resulting from specific management practices and not necessarily indicators of other species being present or abundant, a procedure which has been criticized (e.g. Niemi et al. 1997). Hutto (1998) suggested that surveying a broad list of landbirds would be preferred over a few high-profile species. He identified the following reasons why landbirds are a good indicator group relative to other taxa or bird groups: 1) they are easily surveyed as a group, 2) have patterns of occurrence that are easily identified, and 3) will include a combination of species with positive and negative responses to specific management actions such that broad spatial scales must be considered for conservation of all species. Thus we propose to survey all landbird species but to identify those that are indicative of the three silvicultural prescriptions of interest in this study such that trade-offs can be evaluated.

Methods

Study Area

We designed this study to compare three chronosequences of aspen-dominated forest stands in each of the following legacy tree retention treatments: conifer legacy tree retention, hardwood legacy tree retention, and traditional clearcut (i.e., no legacy tree retention). In 2006 we selected 27 aspen forest stands with nine in each retention treatment in northern Wisconsin (45° 43'N, 89° 32'W) ranging in age from 3-35 years post-harvest (Figure 2.1). We chose sites with similar soil types, primarily dry-mesic soils comprised of sandy loam and loamy sand (Soil Survey Staff 2011) within the Northern Highland Pitted Outwash (Bailey's Subsection 212Jm) based on the Ecoregions of the United States (Bailey et al. 1994; Figure 2.1). For stands with a green-tree retention prescription, all trees were harvested except for those that were marked and all large-diameter pine (*Pinus* spp.) and northern red oak (*Quercus rubra*) trees. This resulted in even-aged regeneration of primarily aspen species with retained canopy trees of varying ages. For stands with a clearcut prescription, all trees were harvested though occasionally scattered trees were retained for unknown reasons.

Tree Surveys

We conducted tree surveys during one visit in either 2007 or 2008 at ten 0.1 ha circular plots per stand. We randomly selected plot locations using the Random Points tool in ArcGIS version 9.2 (ESRI 2007) with the requirement that plots were at least 25 m from the stand edge, logging roads, log landings, wetland inclusions, and each other.

For each overstory tree greater than 10 cm dbh within the survey plot we recorded dbh, species, whether it was alive or dead, and whether it was a legacy tree based on having dbh greater than the surrounding regenerating trees. To sample saplings (i.e., trees or shrubs that were >1.37 m tall and <10 cm dbh), we established a 0.01 ha subplot centered on the 0.1 ha plot center. We only measured live individuals and recorded dbh and species for each one. Basal diameter at a height of 15 cm was measured for three saplings per species per subplot. Woody vegetation less than 1.37 m tall was not measured because it contributes negligible biomass to the stand total. In northern Wisconsin, Crow (1978) estimated above ground biomass for shrubs as 1.9% of the total stand woody biomass with 60% of this represented by *Corylus cornuta*, thus total stand woody biomass was probably not reduced by not including short woody biomass (less than 1.37 m tall).

Stand Characteristics

Aspen stand boundaries were acquired from the appropriate agency for publicly owned stands and were delineated from 2005 digital orthophotos for privately owned stands. Aspen stand area (ha) was calculated in ArcMap version 10.0 (ESRI 2010).

We estimated stand age based on trees regenerating since the last harvest by collecting core and cookie (a 1-2 cm section of the tree trunk) samples from aspen trees in each tree survey plot. If the regenerating trees were generally smaller than 10 cm dbh, we selected three dominant or codominant aspen trees per species present in the 0.01 ha sapling plot and collected a cookie at a basal height of 15 cm. If the regenerating trees were generally larger than 10 cm dbh, we cored one dominant or codominant aspen tree per species per 0.1 ha plot. All legacy trees were cored. We collected two perpendicular cores at dbh and mounted them on boards. Tree age was determined based on examination of tree rings in the cookie and core samples (Speer 2010). We added one

year to the age for all cored trees because we assumed that the first year's growth was likely less than 1.37m high given the relatively poor soils present. This assumption produced a conservative estimate of tree age given that some trees, esp. suppressed conifers, potentially took more than one year to reach a height of 1.37m. We averaged aspen tree ages across each stand to estimate stand age. We combined legacy tree ages from across each stand to calculate mean legacy tree age.

To describe general stand structural characteristics, we measured three variables (canopy closure, foliage height richness, and visual obstruction) at two sample points at a distance of 10m to the southeast and northwest from the tree plot center point. Canopy closure (%) was estimated using a spherical densitometer. Foliage height richness was an index (range of 0-16) of the number of 1-m intervals touching foliage along a 15m tall extension pole. A 16th interval was included that represented foliage that would have contacted the pole if we were able to extend it to the canopy height. Visual obstruction (%) was a horizontal measurement of understory vegetation height-density using a 3m x 0.5m density board divided into 0.1m x 0.1m squares of alternating black and white squares (Noon 1981). The percentage of squares obscured by vegetation was averaged for readings from 10-m in the cardinal directions. Contrary to Noon (1981), the density board was positioned at the sample point while the observer moved to the cardinal directions. This modification was necessary given the difficulty and slowness of moving the density board through the dense shrub layer.

Bird Surveys

We established two 250-m length transects in each aspen stand and conducted surveys twice per breeding season during the period of 26 May to 2 July. Transects were randomly placed such that the end points were a minimum of 25 m from the stand or clearcut edge and had a minimum width of 150 m without overlapping the stand or clearcut edge. Transect survey distance was unlimited but with the requirement that all recorded individuals occurred within the stand or clearcut boundaries. To avoid counting migrants, the earliest survey date each year was determined based on the absence of migrants during practice surveys conducted until only resident species remained. Surveys began approximately 15 minutes before sunrise and were completed by 10:00

AM CDT. We conducted surveys only when winds were below 19 km/hr and when there was no precipitation or dense fog.

We conducted line transect surveys in 2007-2009 using a double-observer dependent approach adapted from a similar point count methodology (Nichols et al. 2000). This method required a two-person team with one person designated the “primary” observer and the other the “secondary” observer who remained within 3m of one another during the survey. The primary reported all observations to the secondary who followed behind the primary, recorded the data, and added observations missed by the primary. Two stands were surveyed each morning, and the observers switched roles at the second stand surveyed each morning. On the second round of survey visits each year, the observer roles were the opposite of the first survey visit such that each observer was primary once for every transect and stand surveyed each year. We tallied each bird species by transect and compared transect survey maps to remove suspected duplicate observations.

Data Analysis

Results reported in the text are mean \pm se where se is the standard error of the mean.

Stand Characteristics

Based on tree measurements, we calculated tree density and basal area (m²/ha) for overstory trees and legacy trees in the 0.1 ha plot and sapling density in the 0.01 ha plot. From this data we also calculated the proportion of overstory trees, legacy trees, and saplings that were hardwoods relative to conifers.

Stand age-classes were created to simplify data presentation and for some categorical analyses. Aspen stands were grouped into three age-classes (relatively young, middle-age, and old) based on their sequence in the chronology for each legacy tree treatment.

Whole-tree above-ground live biomass was estimated using published species-specific allometric equations developed for trees and shrubs located in the Great Lakes, eastern United States, and adjacent areas of Canada. We used biomass equations from Perala and Alban (1994) and Ter-Mikaelian and Korzukhin (1997) for overstory trees and from

Grigal and Ohmann (1977), Roussopoulos and Loomis (1979), Smith and Brand (1983), and Perala and Alban (1994) for saplings. For saplings lacking basal diameter measurements in our dataset, we estimated missing values based on a species specific regression of dbh and basal diameter from the measured individuals. When more than one regional biomass equation was available, we averaged biomass estimates from two independent equation sources. Woody biomass was summed by legacy trees, regenerating trees (i.e., tree and tall shrub growth since the last harvest), and all trees (i.e., the sum of legacy trees and regenerating trees).

Bird Relative Abundance

Bird names follow the convention of The American Ornithologists' Union (2011) and all scientific names appear in Table 2.1. We classified species as conservation priority if they were categorized as one or both of the following: 1) continental concern species, regional concern species, continental stewardship species, or regional stewardship species in Bird Conservation Region 12 (BCR 12: Boreal Hardwood Transition) by Partners in Flight (Panjabi et al. 2005), and 2) State Wildlife Action Plans' Species of Greatest Conservation Need in Michigan, Minnesota, or Wisconsin representing the US portion of BCR 12 (Eagle et al. 2005, Wisconsin Department of Natural Resources 2005, Minnesota Department of Natural Resources 2006).

Species relative abundance (individuals/transect) was not adjusted for detectability as this was not possible for many species with small sample sizes (Nichols et al. 2000). Given that only 8% of individuals were added by the secondary observer, abundance adjustments due to detectability would likely be minor. We used the combined observations of the two observers to calculate relative abundance for each transect. We added the transect relative abundance values from the two transects to calculate relative abundance for each species in each stand.

Though we know detectability for each species likely decreased with increasing distance from the transect (Buckland et al. 2001), we assumed the detection function was similar for each species across stands allowing a reliable comparison of relative abundance among treatments and across the chronosequences. Varying habitat characteristics among stands especially those associated with stand development would be the most

likely reason for detectability to not be constant and thus violate this assumption (Bibby and Buckland 1987). We tested this assumption by comparing three stand structural characteristics (canopy closure, visual obstruction, and foliage height richness) among legacy tree retention treatments and by age-classes as a two-way analysis of variance in SigmaStat version 3.5 (Systat 2006).

To display species relative abundance patterns among legacy tree retention treatments and across the stand age chronosequences, we stacked the total relative abundance of the ten most abundant species from all surveys. We used the maximum relative abundance for each species observed for each stand in each year and totaled these values across the three survey years (Venier and Pearce 2005).

Bird Richness and Diversity

We calculated species richness (S ; number of species observed), Shannon's Diversity Index (H' ; $H' = -\sum p_i \log p_i$ where p_i is importance probability of species i), Shannon's Evenness (E ; $E = H' / \ln(S)$), and Simpson's Diversity Index (D ; $D = 1 / \sum p_i^2$) using the Row and Column analysis tool in PC-ORD version 5.0 (McCune and Mefford 2002). We selected the maximum relative abundance among the two survey visits each year (Venier and Pearce 2005) and averaged the maximum abundance among the three survey years for the richness and diversity analyses. We compared these richness and diversity metrics among legacy tree retention treatments in Minitab 16 Statistical Software (2010; version 16.1.1) using the General Linear Model tool to conduct an analysis of covariance with stand age as the covariate. In this analysis, we used a log transformation of stand age to meet the assumptions of a linear model. For post-hoc tests, we used Tukey's method. We considered statistical tests significant at $\alpha = 0.05$ and marginally significant at $\alpha = 0.10$.

Bird Assemblage Composition

To evaluate differences in bird assemblage composition based on stand characteristics, we conducted a non-metric multidimensional scaling (NMS) ordination. We ran the ordination in autopilot mode set to slow and thorough and using the Sorenson (Bray-Curtis) distance measure in PC-ORD (McCune and Mefford 2002). We constructed joint plots using the stand and bird species ordination scores. Displayed species or stand

points are considered compositionally more similar the closer they are together. We correlated stand characteristics measured with the ordination axes to identify mechanisms for observed compositional patterns. We included variables with $r^2 \geq 0.2$ in the joint plots.

To identify bird species associated with specific combinations of age-class and legacy tree treatment, we conducted an indicator species analysis in PC-ORD. We did not use this analysis to imply that a single bird species was indicative of a suite of bird species (Niemi et al. 1997) but rather to identify species with a strong association with specific silvicultural prescriptions and stages of stand development (Dufrêne and Legendre 1997, Carignan and Villard 2002, Venier and Pearce 2005). We totaled maximum abundance estimates across the three survey years and only included species with at least 10 observations (Venier and Pearce 2005). This reduced the number of species to 45. Importance values were calculated for nine age-class and legacy tree treatment combinations and ranged from 0 to 100 with 100 being a perfect indicator. To determine the statistical significance of the maximum indicator value among groups for each species, we used a Monte Carlo test with 5000 iterations. We reported the species with p-values ≤ 0.05 .

Results

Stand Characteristics

Stand areas ranged from 13.6-58.3 ha (Table 2.2). Above-ground live woody biomass for legacy trees was significantly greater in conifer retention stands (36.6 ± 6.1 10,000 kg/ha) than in clearcuts (1.4 ± 0.5 10,000 kg/ha) and hardwood retention stands (14.5 ± 3.7 10,000 kg/ha; $F_{1,23}=17.69$, $p \leq 0.001$). Conversely, regenerating tree biomass was significantly lower for conifer retention stands (18.3 ± 4.5 10,000 kg/ha) relative to clearcuts (27.8 ± 8.1 10,000 kg/ha) but neither were different from hardwood retention stands (28.3 ± 8.2 10,000 kg/ha; $F_{1,23}=5.10$, $p=0.015$). Total tree biomass was significantly greater for conifer retention stands (54.9 ± 6.0 10,000 kg/ha) relative to clearcuts (29.2 ± 8.4 10,000 kg/ha) but neither were different from hardwood retention stands (42.8 ± 7.4 10,000 kg/ha; $F_{1,23}=8.82$, $p \leq 0.001$).

Legacy tree biomass was constant across the legacy tree retention chronosequences ($F_{1,23}=0.01$, $p=0.924$, adjusted $R^2=55.6$) and represented a large proportion of biomass relative to regenerating trees in aspen stands with retention particularly early in stand development (Table 2.3, Figure 2.2). By around 25-30 years post-harvest, the clearcuts accumulated about the same total all tree biomass as the stands with retention thus reducing the benefits of the legacy trees at that point (Figure 2.2).

Most legacy tree biomass was comprised of eastern white pine (*Pinus strobus*; 29%±7%), red pine (*Pinus resinosa*; 20%±6%), and northern red oak (37%±9%; Table 2.4). As expected, most of the regenerating tree biomass (75%±1%) was comprised of the two aspen species (Table 2.4).

Visual obstruction was higher in young (79%±3%) and middle-aged (86%±3%) stands than in old stands (67%±3%; $F_{2,18}=10.380$, $p=0.001$) but there was no legacy tree retention treatment effect ($p=0.638$) or interaction effect ($p=0.859$). Foliage height richness was lower in young stands (2.8±0.4) than in middle-age (5.3±0.4) or old stands (5.8±0.4; $F_{2,18}=15.981$, $p\leq 0.001$); there was a marginal legacy tree retention treatment effect ($p=0.081$) but no interaction effect with age-class ($p=0.390$). Canopy closure varied by stand age-class ($F_{2,18}=19.801$, $p\leq 0.001$), legacy tree retention treatment ($F_{2,18}=4.849$, $p=0.021$), and their interaction ($F_{2,18}=3.122$, $p=0.041$). Among young stands, clearcuts (47.0±5.7) had lower canopy closure than conifer retention stands (81.8±5.7). Among hardwood retention stands and clearcuts, young stands (62.8±5.7 and 47.0±5.7, respectively) had lower canopy closure than middle-age (91.2±5.7 and 79.5±5.7, respectively) and old stands (92.9±7.0 and 92.1±4.9, respectively). Canopy closure and foliage height richness were significantly correlated ($r_P=0.848$, $p\leq 0.001$). These structural characteristic differences among retention treatments and stand age-classes suggested that bird detectability was likely not constant among stands.

Bird Relative Abundance

Most bird observations were based on audio cues alone (84.3%) with the remaining sightings based on either visual observation alone (5.5%) or combined audio and visual observation (10.2%). We observed 7450 individual birds representing 71 species of which 28 species (39%) were identified as conservation priority (Table 2.1). In addition,

we observed one phenotypic hybrid, Brewster's Warbler (*Vermivora chrysoptera* x *V. cyanoptera*), that was excluded from our analyses. Also, we removed two suspected late migrants (one Black-throated Blue Warbler (*Setophaga caerulescens*) and one Wilson's Warbler (*Cardellina pusilla*) from the analyses.

The two most abundant species were Chestnut-sided Warbler (*Setophaga pensylvanica*; $n=585$; 11.7% of all species observations) and Ovenbird (*Seiurus aurocapilla*; $n=571$; 11.4% of all species observations) with the former declining in unadjusted relative abundance with increasing stand age nearly proportionately to the increase in unadjusted relative abundance of the Ovenbird with increasing stand age (Table 2.1, Figure 2.3).

Of the sixteen conservation priority species (Table 2.1) with at least 10 observations among the three survey years, American Woodcock (*Scolopax minor*) and Northern Flicker (*Colaptes auratus*) reached their highest unadjusted relative abundance in young conifer retention stands. Chestnut-sided Warbler, Eastern Towhee (*Pipilo erythrophthalmus*), Golden-winged Warbler (*Vermivora chrysoptera*), Mourning Warbler (*Geothlypis philadelphia*), and Yellow-bellied Sapsucker (*Sphyrapicus varius*) reached highest unadjusted relative abundance in young hardwood retention stands. Brown Thrasher (*Toxostoma rufum*), Common Yellowthroat (*Geothlypis trichas*), Nashville Warbler (*Oreothlypis ruficapilla*), Purple Finch (*Carpodacus purpureus*), and White-throated Sparrow (*Zonotrichia albicollis*) reached their highest unadjusted relative abundance in young clearcuts. Rose-breasted Grosbeak and Veery reached their highest relative abundance in middle-age hardwood retention stands. Ruffed Grouse reached its highest relative abundance in middle-age conifer retention stands, and Black-throated Green Warbler was most abundant in old conifer retention stands. Single-tree and small patch blowdown in two old stands (conifer retention stand at age 25 and clearcut at age 27) likely resulted in an increase in relative abundance of species, such as Chestnut-sided Warbler and White-throated Sparrow, typically associated with young stands (Figure 2.3).

Bird Richness and Diversity

Based on the analysis of covariance with stand age as the covariate, species richness was significantly greater in aspen stands with hardwood legacy tree retention than in clearcuts but stands with conifer legacy tree retention were not different from either treatment ($F_{2,23}=5.84$, $p=0.009$; Figure 2.4). For Shannon's Diversity Index, we observed a significant legacy tree retention treatment effect ($F_{2,23}=3.42$, $p=0.050$) but the post-hoc tests suggested no difference between treatments (Figure 2.4). Shannon's Evenness ($p=0.601$) and Simpson's Diversity Index ($p=0.390$) did not differ among treatments (Figure 2.4). Increasing α to 0.10 for the post-hoc tests resulted in marginally significant higher species richness and Shannon's Diversity Index for both legacy retention treatments relative to clearcuts.

Diversity of conservation priority species did not differ by legacy tree retention treatment ($p=0.570$ - 0.967). The four richness and diversity metrics for all species declined significantly with increasing log of stand age consistently among legacy tree retention treatments ($F_{1,23}=14.53$ - 69.85 , $p\leq 0.001$, adjusted $R^2=32.1$ - 73.3 ; Figure 2.4). Similarly, conservation priority species declined significantly with increasing log of stand age for all richness and diversity metrics ($F_{1,23}=31.2$ - 59.6 , $p\leq 0.001$, adjusted $R^2=52.2$ - 68.8) except for Shannon's evenness ($F_{1,23}=0.33$, $p=0.570$, adjusted $R^2=0.00$).

Bird Assemblage Composition

The NMS ordination resulted in a two-dimensional solution with a final stress of 16.13 and most of the variance (0.852) represented by Axis 2. Of the 16 stand characteristics (not including stand area) (Table 2.2), stand age, proportion of hardwoods in the overstory, and legacy tree dbh were significantly correlated with Axis 2 (Table 2.5). Young aspen stands were spatially grouped (as indicated by circles in Figure 2.5) by legacy tree retention treatment suggesting there were consistent differences in bird assemblages among treatments early in stand development. Middle-age and old stands were not consistently grouped suggesting that bird assemblages were less distinctive later in stand development (Figure 2.5).

We identified 13 bird species as indicators of stand age-class and legacy tree treatment of which six were conservation priority. Seven of the 13 species were associated with

hardwood legacy tree retention, one with conifer legacy tree retention, and five with clearcuts (Table 2.6). Eleven species including five of the six conservation priority species were indicators of young stands (Table 2.6). In the NMS ordination, the indicator species in young stands were spatially grouped by legacy tree retention treatment in accordance with the ordination position of the stands in these treatments (Figure 2.5).

Discussion

Stand Productivity in Relation to Legacy Tree Retention

Conifer and hardwood legacy trees represented a large proportion of the biomass in aspen stands with retention particularly early in stand development. The biomass benefits of the legacy trees became negated by around 30 years post-harvest when the clearcuts accumulated about the same biomass as the stands with retention. This convergence was due to regenerating tree biomass increasing but legacy tree biomass remaining constant across the legacy tree retention chronosequences. The constant legacy tree biomass with increasing stand development was likely due to highly variable initial retention basal area and biomass at the time of the last harvest. Though legacy trees likely increased in biomass since the last stand harvest, the space for time substitution was unable to reflect this.

Conifer but not hardwood legacy trees appeared to suppress aspen growth and biomass. Given that the three dominant legacy tree species (red pine, eastern white pine, and northern red oak) have similar light tolerance, we might not expect a heavier shading effect by the conifers (Baker 1949, Messier et al. 1998). However sunlight penetrates deeper into conifer canopies relative to broad-leaf canopies (Walker and Kenkel 2000), thus we might expect greater suppression of regenerating trees under broad-leaf legacy trees relative to conifer legacy trees. However, the more important difference between broad-leaf and coniferous legacy trees may relate to the spring leaf-off period for deciduous, broad-leaf trees.

The leaf-off period for deciduous, broad-leaf canopies such as that dominated by northern red oak (*Quercus rubra*) may provide an adequate early spring window of near full sun penetration when regenerating aspen may be highly productive (Prévost and

Pothier 2003). In comparison, evergreen coniferous canopies provide perpetual shade despite the greater solar penetration through the canopy that may not be sufficient for regenerating aspen that requires near full sun conditions. Additionally, the generally higher density of legacy trees and higher canopy closure in the stands with conifer retention may have contributed to the observed suppression of the regenerating trees. It was unclear if the aspen biomass in the stands with conifer retention would eventually “catch up” to the other two treatments. A longer chronosequence was needed in the conifer retention treatment to provide insight into the answer.

If the carbon stored in legacy trees was proportionate to their biomass, then legacy trees have great capacity to reduce the carbon flux relative to traditional clearcutting. Additionally forest stands comprised of conifers and diverse mixes of tree species can store more carbon than monotypic broad-leaved forests (Bravo et al. 2008). Similarly, Edgar and Burk (2001) identified their most productive aspen stands in Minnesota as vertically stratified aspen-balsam fir-paper birch mixtures. Bravo et al. (2008) suggested several reasons for the greater carbon storing capacity of mixed forests including differences in stem and crown configuration between species, differences in forest structure, and differences in root biomass. Without legacy trees, our stands would be dominated by aspen species with a diverse minority of other, primarily broad-leaved species. Conifer species can store a greater amount of carbon per unit biomass than broad-leaved trees (Bravo et al. 2008). Though pine species in our study suppressed the regenerating tree biomass, they potentially have greater carbon storage capacity than oaks. Thus retention of conifers might be encouraged if carbon storage is the primary management goal.

Bird Species and Assemblage Response to Legacy Tree Retention Treatments

The legacy trees likely increased the structural complexity in young forests by creating a two-aged, two-storied forest stand rather than an even-aged, one-story aspen clearcut. As the regenerating trees reached the height of the legacy trees, the stand became one-storied thus the structural effects of the legacy trees were likely reduced. Across the chronosequences bird species assemblage differences were noted due to legacy tree compositional differences, particularly the ratio of large diameter overstory hardwoods to conifers. Bird species richness was greatest in the hardwood retention treatment

particularly early in stand development likely reflecting the important compositional and structural role of the large-diameter oak trees in this system. Though bird species richness in stands with conifer retention did not statistically differ from the other two treatments, it does suggest that it produced an intermediate effect that included the attraction of certain species (e.g. Black-throated Green Warbler) that were rare or absent in other treatments, a biologically important result.

Other studies examining effects of green-tree retention on forest birds have generally found an increase in bird richness, diversity and density for many species as compared to clearcut stands (Merrill et al. 1998, Rodewald and Yahner 2000, Harrison and Kilgo 2004, McDermott and Wood 2009) though exceptions exist (Atwell et al. 2008). Not all bird species responded the same to these treatments but consistent patterns observed included a positive response by early successional species to young retention stands and a positive response by some mature forest associates though often with reduced densities relative to uncut forest (Rodewald and Yahner 2000, Harrison and Kilgo 2004, McDermott and Wood 2009). Our results are consistent with these studies.

In our study, differences in forest stand characteristics among stand age-classes and legacy tree retention treatments indicated that detectability of different bird species and individuals within species likely varied among our aspen stands. Foliage height richness was lower and visual obstruction was higher in young stands relative to old stands. The lower foliage height richness in young stands was likely a reflection of the short height of the regenerating trees and the rarity of encountering legacy trees with the extension pole. Canopy closure increased with increasing stand age and overall was the lowest in young clearcuts. Thus, the regenerating woody vegetation in young stands was dense, short, but with a relatively more open canopy. As the canopy closed with age, the understory became more open due to reduced light penetration.

This structural shift from a dense understory to a more open one likely reduced our ability to detect individuals and perhaps certain species with the greatest underestimation of relative abundance being in young stands (Bibby and Buckland 1987). By adjusting relative abundance values for detectability we would expect that the differences we observed between young and old stands would become more extreme

with the greatest change in clearcuts and the smallest change in the conifer retention stands due to the more closed canopy. Our unadjusted relative abundance data represent a conservative estimate of the differences between age-classes and legacy tree retention treatments and thus likely represented true differences.

Of the 28 conservation priority species that we observed, six were indicator species for combinations of stand age-classes and legacy tree retention treatments. Five of these indicator species (Brown Thrasher, Common Yellowthroat, Golden-winged Warbler, Mourning Warbler, and White-throated Sparrow) were associated with young aspen stands. An additional seven conservation priority species with at least ten observations in our study reached their highest abundance in young stands. The decreasing number of conservation priority species relative to stand development may be a reflection of the overall importance of young forest habitat for many declining bird species (Askins 1993, Hunter et al. 2001, Trani et al. 2001).

Brown-headed Cowbird (*Molothrus ater*) was an indicator of young hardwood retention stands though only seven of the 14 total individuals were observed in these stands among the three survey years. This low relative abundance suggests that nest parasitism rates were likely low which is consistent with other studies in extensive, relatively unfragmented forested landscapes (Robinson et al. 1995, Hanski et al. 1996, Chace et al. 2005).

Conifer retention stands had high legacy tree biomass but low regenerating tree biomass compared to clearcuts. Though bird species richness was not different relative to the other two treatments, some bird species (e.g. Black-throated Green Warbler, Pine Warbler (*Setophaga pinus*), and Yellow-rumped Warbler (*Setophaga coronata*)) reached their highest unadjusted relative abundance in this treatment and the bird assemblage composition differed particularly early in stand development. In our study, the absence or low density of pines in a stand meant the near absence of these bird species.

Coniferous forest associations of Black-throated Green Warblers vary considerably across their breeding range (Collins 1983, Morse and Poole 2005) such that some studies have found an association with pines in the western Great Lakes region (e.g.

Collins 1983) and others have not (e.g. Beals 1960). In our study, the Black-throated Green Warbler (*Setophaga virens*) was an indicator of old conifer retention stands which supported their association with conifers and middle-aged to mature forests including mixed deciduous-coniferous forests as observed by Morse and Poole (2005).

Conservation priority birds were neither associated entirely with one legacy tree retention treatment nor one stand age-class. This emphasizes the conclusions of others that forest managers need a landscape perspective to provide a diverse range of forest age-classes and forest types to accommodate the full suite of declining forest bird species (Back 1979, Hutto 1998, Janowiak and Webster 2010).

Conclusions

Hardwood retention stands and clearcuts had similar above-ground live woody biomass for regenerating trees, legacy trees, and all trees combined with minimal suppression of regenerating trees. Hardwood retention stands also had higher bird species richness than the other two retention treatments. Several high conservation priority species associated with hardwood retention will benefit including the Golden-winged Warbler (see Chapter 4), a species recently petitioned for protection under the Endangered Species Act (U.S. Fish and Wildlife Service 2011). The dominant legacy tree species in this treatment was the northern red oak, a mast producing species important to many wildlife species (Tubbs et al. 1987, Johnson 1994, McShea et al. 2007).

Legacy tree retention can increase bird species richness with benefits to a group of conservation priority species, increase aspen stand biomass until 30 years post-harvest, and maintain greater carbon stocks in young stands which could dampen carbon ecosystem fluxes related to harvesting. This results in a win-win scenario for bird conservation and industries seeking woody feedstock from naturally regenerating forests.

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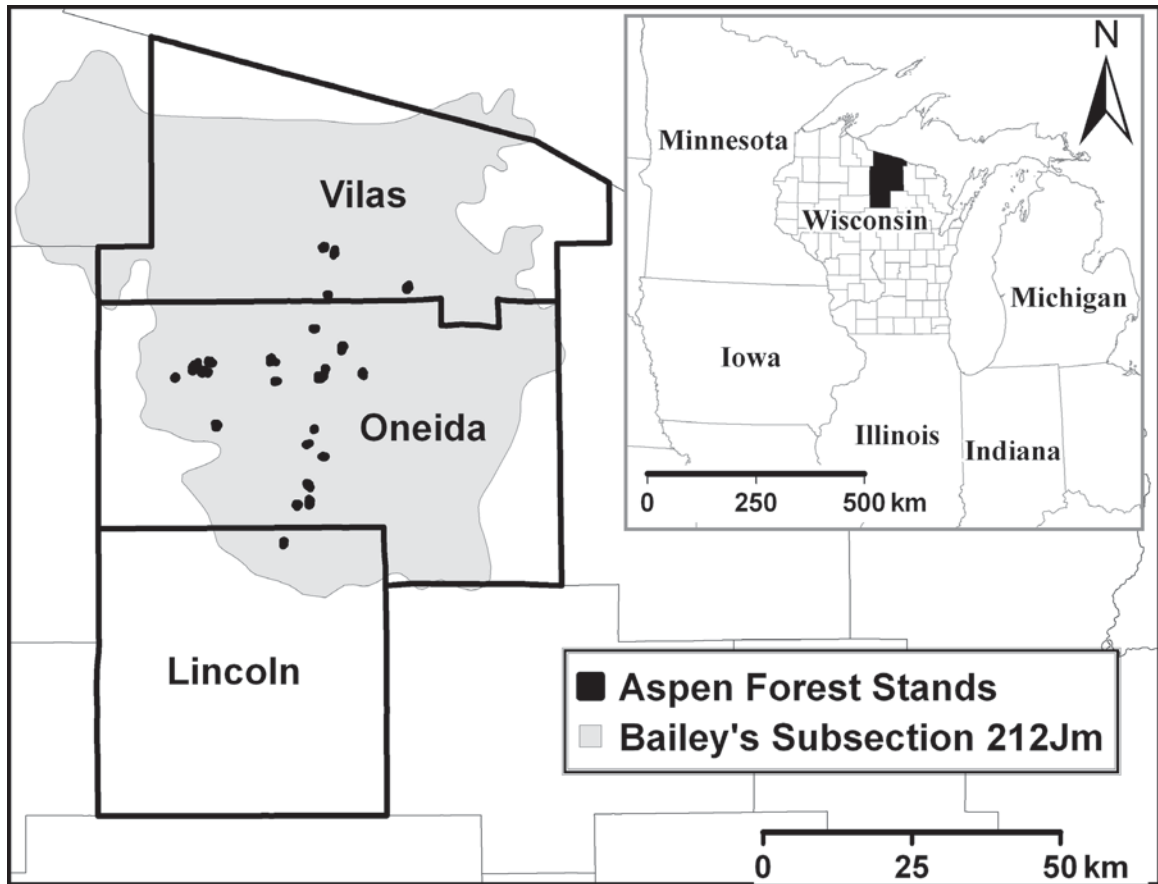


Figure 2.1. Twenty-seven aspen forest stands within the Northern Highland Pitted Outwash (Bailey's Subsection 212Jm). The three counties (Vilas, Oneida, and Lincoln) where these stands occur in northern Wisconsin are indicated in the inset map.

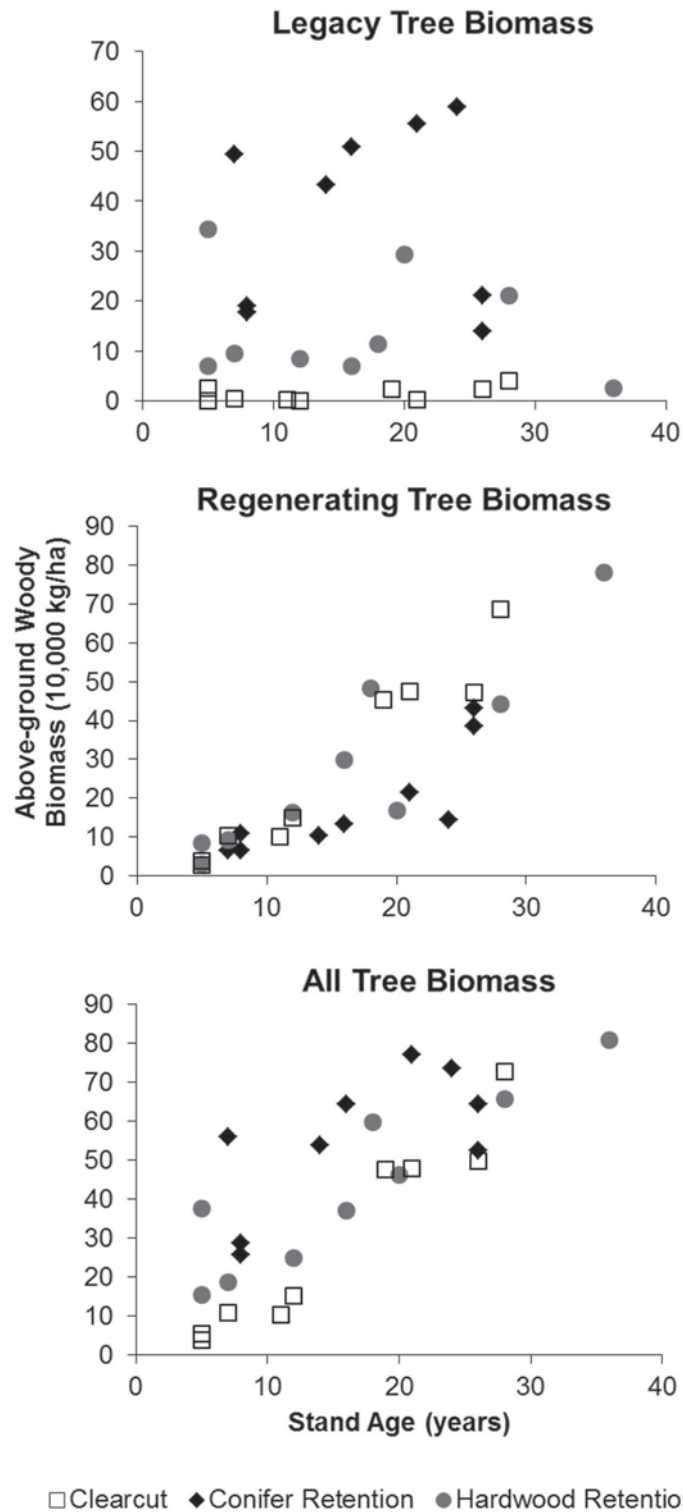


Figure 2.2. Above-ground live woody biomass for 27 aspen forest stands with estimates for legacy trees, regenerating trees (including tall shrubs), and their sum presented as all trees. Stands are identified by their legacy tree retention treatment (clearcut, conifer retention, and hardwood retention). Biomass was estimated based on regional allometric equations.

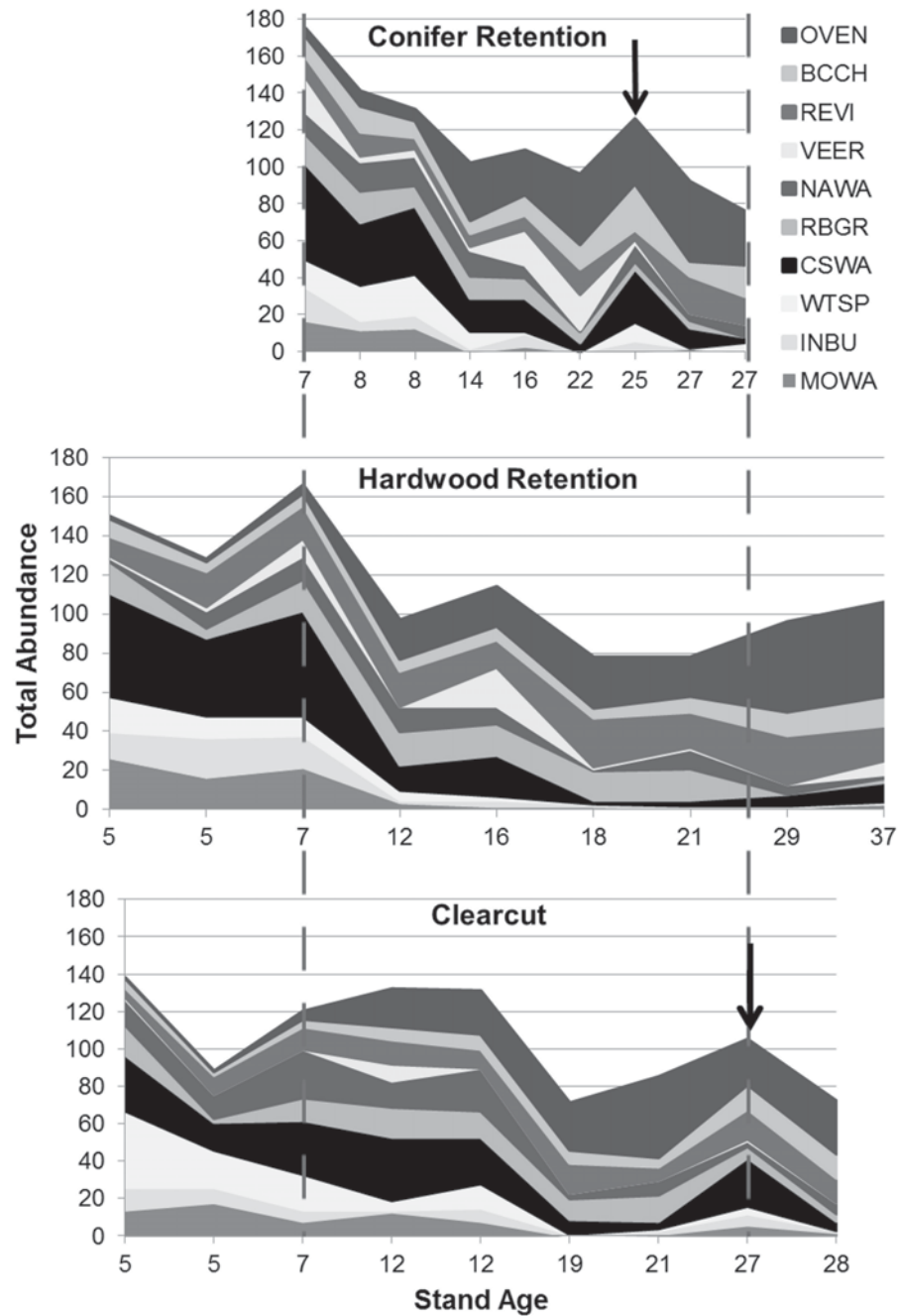


Figure 2.3. Total abundance of the ten most abundant bird species in 27 aspen forest stands in northern Wisconsin. For each stand, the total abundance for each species represents a three-year sum of the maximum relative abundance from each year and the stand age is the three-year mean. Vertical lines are guides for approximate alignment of the three legacy tree retention chronosequences. Arrows indicate stands with blowdown that created small-diameter canopy gaps. Bird species alpha codes are: OVEN=Ovenbird, BCCH=Black-capped Chickadee, REVI=Red-eyed Vireo, VEER=Veery, NAWA=Nashville Warbler, RBGR=Rose-breasted Grosbeak, CSWA=Chestnut-sided Warbler, WTSP=White-throated Sparrow, INBU=Indigo Bunting, and MOWA=Mourning Warbler.

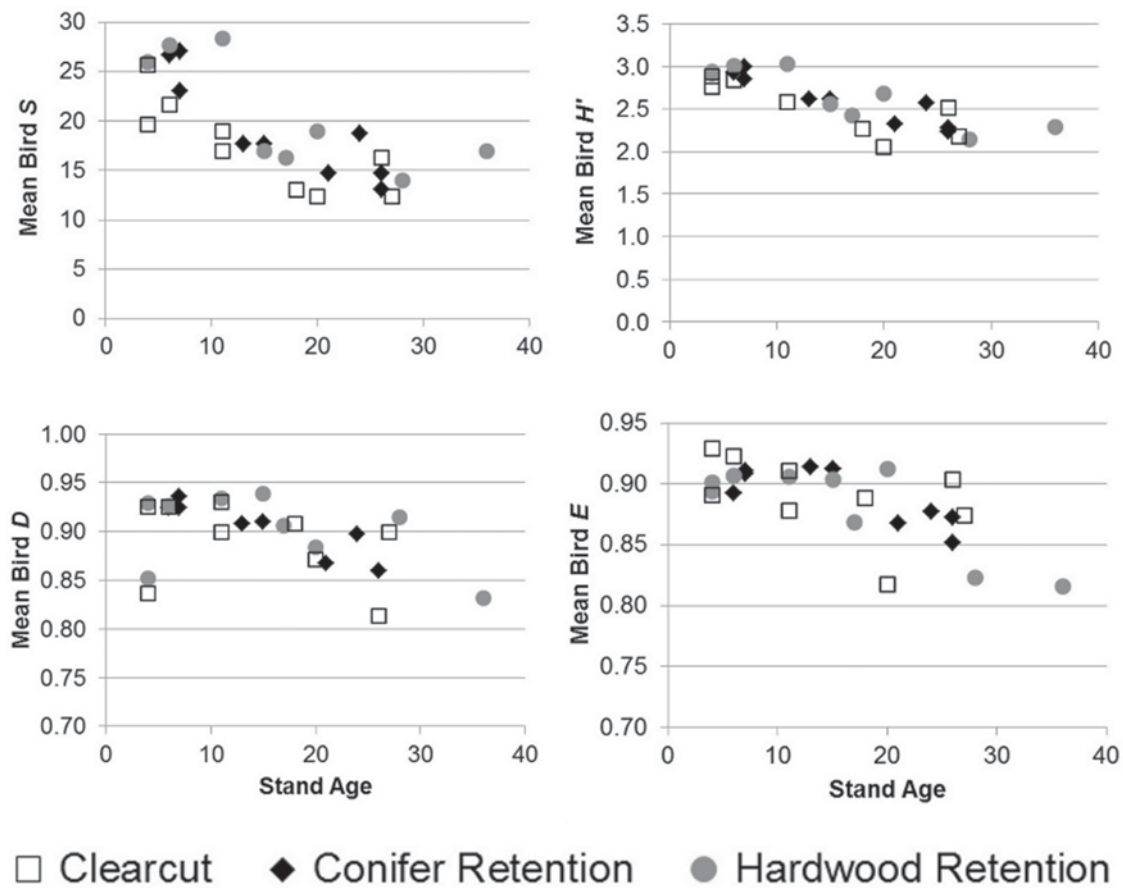


Figure 2.4. Mean bird species richness (S), Shannon's Diversity Index (H'), Shannon's Evenness (E), and Simpson's Diversity (D) trends relative to stand age and three legacy tree retention treatments (clearcut, conifer retention, and hardwood retention) in 27 aspen forest stands in northern Wisconsin. Bird data were collected along two 250m line transects in each stand surveyed twice annually during 26 May to 2 July. Plotted values represent a mean of the three survey years, 2007-2009.

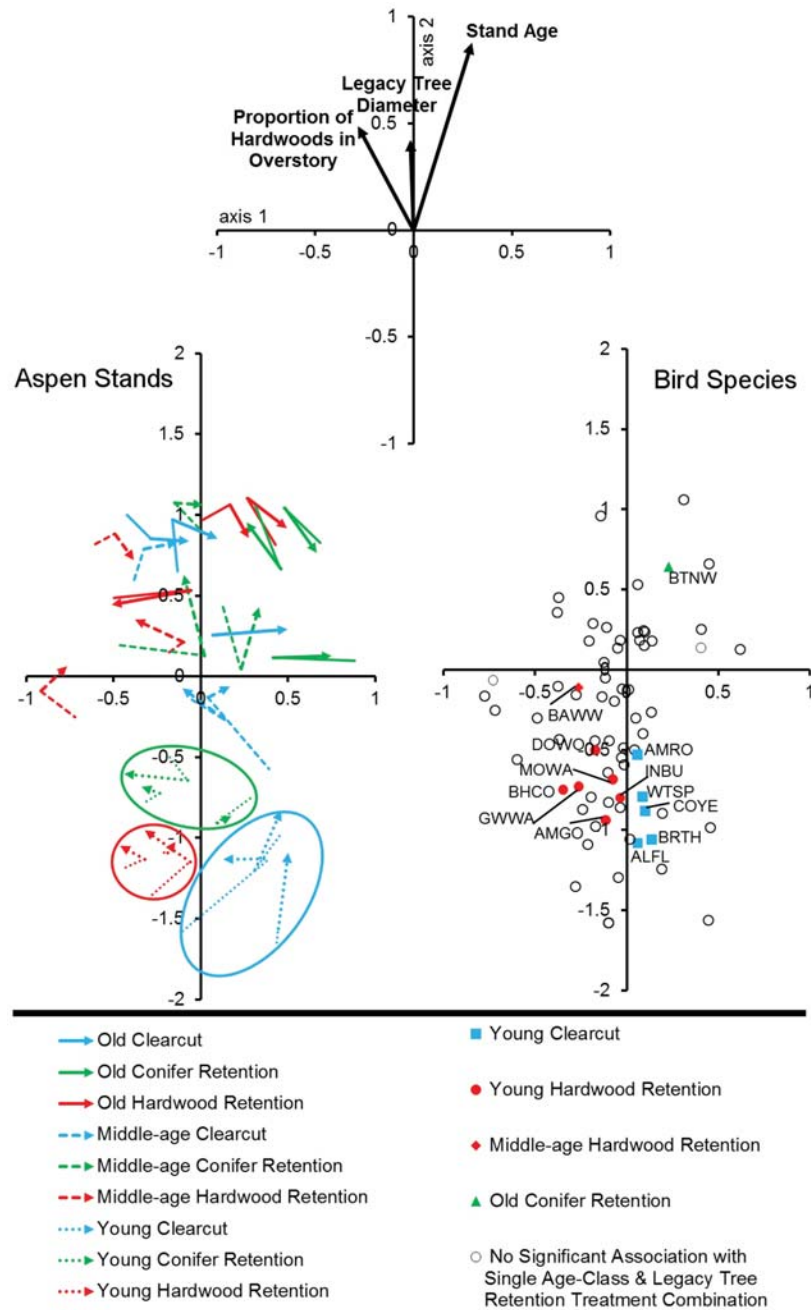


Figure 2.5. NMS ordination plots of 27 aspen forest stands and 71 bird species versus stand structural gradients. Stand variables are described in Table 2. Aspen stands are categorized based on their age-class (young, middle-age, and old) and legacy tree retention treatment (clearcut, conifer retention, and hardwood retention); the three surveys for each stand are connected with successional vectors. Young stands in each retention treatment are circled to indicate compositional similarity. Bird species identified as indicators of specific combinations of stand age-class and treatment are identified with alpha codes (ALFL=Alder Flycatcher, AMGO=American Goldfinch, AMRO=American Robin, BAWW=Black-and-white Warbler, BHCO=Brown-headed Cowbird, BRTH=Brown Thrasher, BTNW=Black-throated Green Warbler, COYE=Common Yellowthroat, DOWO=Downy Woodpecker, GWWA=Golden-winged Warbler, INBU=Indigo Bunting, MOWA=Mourning Warbler, and WTSP=White-throated Sparrow).

Table 2.1

Unadjusted mean relative abundance (individuals/500 m) of bird species on line transects for 27 aspen forest stands in northern Wisconsin, 2007-2009. Legacy tree retention treatments were clearcut ($n=9$), conifer retention (CR; $n=9$), and hardwood retention (HR; $n=9$). The highest value across age-classes and treatments is indicated in bold font for each species. Common names in bold font indicate conservation priority species.

Common Name	Scientific Name	Aspen Stand Age (years; in 2007) and Legacy Tree Retention Treatment					
		Young (4-7)		Middle-Age (11-21)		Old (20-36)	
		Clearcut	CR	HR	Clearcut	CR	HR
Alder Flycatcher	<i>Empidonax alnorum</i>	6.9	1.8	5.0	0.4	0.0	0.4
American Crow	<i>Corvus brachyrhynchos</i>	0.1	0.1	0.1	0.0	0.4	0.6
American Goldfinch	<i>Spinus tristis</i>	1.7	1.4	3.7	0.2	0.0	0.2
American Redstart	<i>Setophaga ruticilla</i>	0.0	1.0	1.6	0.2	0.2	0.3
American Robin	<i>Turdus migratorius</i>	4.0	1.6	1.8	1.3	0.3	1.0
American Woodcock	<i>Scolopax minor</i>	0.3	0.4	0.0	0.2	0.0	0.3
Baltimore Oriole	<i>Icterus galbula</i>	0.0	0.0	0.0	0.0	0.0	1.3
Belted Kingfisher	<i>Megasceryle alcyon</i>	0.0	0.0	0.1	0.0	0.0	0.0
Black-and-white Warbler	<i>Mniotilta varia</i>	0.2	1.2	0.9	0.4	0.3	1.8
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	0.2	0.0	0.1	0.1	0.0	0.3
Black-capped Chickadee	<i>Poecile atricapillus</i>	1.2	3.8	2.2	2.4	3.4	2.0
Black-throated Green Warbler	<i>Setophaga virens</i>	0.0	0.1	0.1	0.0	0.7	0.1
Blue Jay	<i>Cyanocitta cristata</i>	1.6	2.1	2.0	1.4	2.1	1.3
Blue-headed Vireo	<i>Vireo solitarius</i>	0.0	0.2	0.0	0.0	0.1	0.0
Brewster's Warbler	<i>Vermivora chrysoptera</i> x <i>V. cyanoptera</i>	0.0	0.0	0.1	0.0	0.0	0.0
Broad-winged Hawk	<i>Buteo platypterus</i>	0.0	0.0	0.0	0.0	0.1	0.0
Brown Creeper	<i>Certhia americana</i>	0.0	0.0	0.1	0.0	0.0	0.1
Brown Thrasher	<i>Toxostoma rufum</i>	1.7	0.8	1.1	0.2	0.0	0.1
Brown-headed Cowbird	<i>Molothrus ater</i>	0.2	0.1	0.8	0.0	0.0	0.3
Canada Warbler	<i>Cardellina canadensis</i>	0.0	0.0	0.0	0.0	0.4	0.3

Table 2.1, continued

Aspen Stand Age (years; in 2007) and Legacy Tree Retention Treatment										
Common Name	Scientific Name	Young (4-7)			Middle-Age (11-21)			Old (20-36)		
		Clearcut	CR	HR	Clearcut	CR	HR	Clearcut	CR	HR
Cedar Waxwing	<i>Bombycilla cedrorum</i>	1.6	1.2	2.3	0.0	1.4	1.2	0.3	0.2	0.7
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	8.2	13.7	16.3	7.4	4.6	4.0	3.9	4.8	2.1
Chipping Sparrow	<i>Spizella passerina</i>	0.1	0.1	0.1	0.1	0.0	0.1	0.0	0.2	0.0
Clay-colored Sparrow	<i>Spizella pallida</i>	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Common Raven	<i>Corvus corax</i>	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0
Common Yellowthroat	<i>Geothlypis trichas</i>	2.4	0.4	0.7	0.4	0.0	0.6	0.0	0.0	0.2
Dark-eyed Junco	<i>Junco hyemalis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Downy Woodpecker	<i>Picoides pubescens</i>	0.1	0.0	0.7	0.0	0.0	0.2	0.2	0.0	0.2
Eastern Bluebird	<i>Sialia sialis</i>	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Kingbird	<i>Tyrannus tyrannus</i>	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	3.1	3.0	3.6	1.7	0.1	0.8	0.0	0.1	0.0
Eastern Whip-poor-will	<i>Caprimulgus vociferus</i>	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Wood-pewee	<i>Contopus virens</i>	0.0	0.3	0.3	0.0	0.1	0.2	0.1	0.1	0.4
Golden-winged Warbler	<i>Vermivora chrysoptera</i>	0.4	2.9	4.0	0.1	0.0	1.3	0.1	0.1	0.1
Gray Catbird	<i>Dumetella carolinensis</i>	0.4	0.8	3.0	0.0	0.0	0.2	0.0	0.0	0.1
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0.0	0.2	0.1	0.0	0.1	0.1	0.0	0.1	0.2
Hairy Woodpecker	<i>Picoides villosus</i>	0.1	0.2	0.3	0.1	0.3	0.1	0.8	0.3	0.6
Hermit Thrush	<i>Catharus guttatus</i>	2.0	0.2	0.1	1.0	1.8	1.3	0.9	2.1	2.2
House Wren	<i>Troglodytes aedon</i>	2.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Indigo Bunting	<i>Passerina cyanea</i>	2.9	3.3	5.8	1.0	1.0	0.9	1.0	0.7	0.4
Least Flycatcher	<i>Empidonax minimus</i>	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.3
Lincoln's Sparrow	<i>Melospiza lincolni</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mourning Dove	<i>Zenaida macroura</i>	2.7	2.2	3.1	1.2	1.1	1.3	0.1	0.8	0.8
Mourning Warbler	<i>Geothlypis philadelphia</i>	4.4	4.7	7.0	2.3	0.3	0.6	1.0	0.2	0.3

Table 2.1, continued

Common Name		Aspen Stand Age (years; in 2007) and Legacy Tree Retention Treatment									
		Young (4-7)					Middle-Age (11-21)				
		Clearcut	CR	HR	Clearcut	CR	HR	Clearcut	CR	HR	CR
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	5.9	4.9	2.6	4.4	2.4	2.6	1.9	2.3	1.9	2.3
Northern Flicker	<i>Colaptes auratus</i>	1.4	1.7	1.1	0.8	0.2	0.3	0.2	0.3	0.4	0.4
Olive-sided Flycatcher	<i>Contopus cooperi</i>	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Osprey	<i>Pandion haliaetus</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ovenbird	<i>Seiurus aurocapilla</i>	0.4	2.0	0.7	7.6	10.3	7.3	10.6	11.9	12.7	11.9
Palm Warbler	<i>Setophaga palmarum</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pileated Woodpecker	<i>Dryocopus pileatus</i>	0.0	0.3	0.0	0.0	0.0	0.1	0.0	0.1	0.2	0.2
Pine Warbler	<i>Setophaga pinus</i>	0.0	1.8	0.4	0.0	2.3	0.0	0.1	2.6	0.7	0.7
Purple Finch	<i>Carpodacus purpureus</i>	0.7	0.3	0.3	0.2	0.1	0.1	0.0	0.0	0.2	0.2
Red-breasted Nuthatch	<i>Sitta canadensis</i>	0.3	1.2	0.6	0.0	0.9	0.1	0.3	0.9	0.3	0.3
Red-eyed Vireo	<i>Vireo olivaceus</i>	3.0	3.3	5.0	4.3	3.2	6.3	4.0	4.4	6.8	4.4
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.0	0.0	0.0
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	3.3	4.9	4.1	4.6	3.2	5.3	2.7	0.9	2.0	2.0
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	0.1	0.2	0.6	0.1	0.2	0.0	0.0	0.3	0.0	0.0
Ruffed Grouse	<i>Bonasa umbellus</i>	0.4	0.2	0.1	0.6	0.8	0.6	0.7	0.4	0.6	0.6
Scarlet Tanager	<i>Piranga olivacea</i>	0.1	0.3	0.6	0.4	1.0	1.3	0.9	0.6	0.8	0.8
Song Sparrow	<i>Melospiza melodia</i>	3.0	1.2	3.2	0.2	0.0	0.3	0.0	0.0	0.1	0.1
Swamp Sparrow	<i>Melospiza georgiana</i>	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Veery	<i>Catharus fuscescens</i>	0.3	5.6	2.1	3.3	5.1	6.4	4.6	0.4	2.6	2.6
White-breasted Nuthatch	<i>Catharus fuscescens</i>	0.1	0.4	0.7	0.0	1.2	0.1	0.1	0.2	0.4	0.4
White-throated Sparrow	<i>Zonotrichia albicollis</i>	8.9	6.2	4.3	2.0	1.1	0.8	0.6	1.7	0.1	0.1
Wilson's Snipe	<i>Gallinago delicata</i>	0.2	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Winter Wren	<i>Troglodytes hiemalis</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Wood Thrush	<i>Hylocichla mustelina</i>	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0

Table 2.1, continued

Common Name	Scientific Name	Aspen Stand Age (years; in 2007) and Legacy Tree Retention Treatment									
		Young (4-7)				Middle-Age (11-21)				Old (20-36)	
		Clearcut	CR	HR		Clearcut	CR	HR		Clearcut	CR
Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>	0.0	0.2	0.3		0.1	0.0	0.0		0.1	0.0
Yellow-rumped Warbler	<i>Setophaga coronata</i>	0.2	0.1	0.0		0.0	0.2	0.0		0.0	0.6
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0.0	0.0	0.1		0.0	0.0	0.0		0.0	0.1

Table 2.2

Mean±1 se stand characteristics for 27 aspen forest stands in northern Wisconsin, 2008-2009. Means were based on averaging ten plots per stand for nine stands in each legacy tree retention treatment.

Variable	<u>Clearcut (No Retention)</u>		<u>Conifer Retention</u>		<u>Hardwood Retention</u>	
	mean±se	range	mean±se	range	mean±se	range
Stand area (ha)	34.6±3.4	13.6-58.3	22.8±5.0	14.8-43.5	28.1±3.0	17.2-43.9
Stand age ^a (years)	14±3	4-27	16±3	6-26	16±4	4-36
Canopy closure (%)	75±7	33-96	87±3	72-95	81±6	47-98
Foliage height richness	4.2±0.7	1.8-7.4	5.3±0.5	3.6-6.8	4.5±0.6	2.1-6.5
Visual obstruction (%)	77±4	59-90	75±4	59-90	80±4	62-94
Legacy tree density (stems/ha)	5±1	0-14	91±15	29-166	33±5	14-59
Legacy tree basal area (m ² /ha)	0.3±0.1	0.0-0.8	7.9±1.2	3.3-11.4	2.3±0.5	0.4-4.3
Proportion of hardwood legacy trees	0.57±0.14	0-1.00	0.19±0.08	0-0.69	0.91±0.02	0.79-1.00
Legacy tree dbh ^b (cm)	25.5±2.0	15.3-31.5	32.4±3.1	22.0-51.1	27.3±1.5	20.5-31.7
Legacy tree age (years)	53±7	26-73	62±5	43-93	66±6	43-94
Overstory tree density (stems/ha)	325±124	0-964	242±63	89-617	164±59	14-531
Overstory tree basal area (m ² /ha)	4.0±1.8	0-14.6	10.1±1.1	4.4-13.3	5.6±1.9	1.1-17.4
Proportion of hardwoods in overstory	0.70±0.15	0.00-1.00	0.45±0.12	0.02-0.97	0.94±0.02	0.79-1.00
Overstory tree dbh ^c (cm)	17.1±2.2	11.8-31.5	23.1±1.9	14.5-31.8	20.8±2.4	12.8-31.7
Sapling density (stems/ha)	840±170	166-1641	597±121	138-1065	1005±172	360-1685
Proportion of hardwood saplings	0.99±0.00	0.97-1.00	0.97±0.02	0.79-1.00	0.99±0.00	0.98-1.00
Sapling dbh ^c (cm)	2.4±0.3	0.9-3.9	2.7±0.3	1.7-4.4	2.3±0.3	1.2-3.3

^aAge of regenerating aspen in 2007; age was determined by examining tree rings from samples of regenerating aspen.

^bDiameter at breast height.

Table 2.3

Mean±1 se aboveground live woody biomass (10,000 kg/ha) for all woody plants >1.37m tall in 27 aspen forest stands in 2007-2008, northern Wisconsin. Nine stands were in each legacy tree retention treatment and three stands were in each age-class (range of stand ages at time of survey are presented in parentheses) within treatment.

	Legacy Tree Retention Treatment								
	Clearcut			Conifer Retention			Hardwood Retention		
	Young (5-7 yrs) ^a	Middle-aged (12-18 yrs)	Old (20-36 yrs)	Young (7-8 yrs)	Middle-aged (14-21 yrs)	Old (24-26 yrs)	Young (5-7 yrs)	Middle-aged (11-19 yrs)	Old (21-28 yrs)
<u>Legacy Trees^b</u>									
Conifers	0.9±0.7	0.1±0.1	1.3±0.6	25.0±7.6	46.5±4.4	28.1±15.4	1.1±0.6	0.8±0.7	0.6±0.3
Hardwoods	0.1±0.1	0.8±0.8	1.0±0.5	3.6±2.8	3.4±2.4	3.2±2.5	15.8±9.1	8.9±1.9	17.1±7.6
All Species	1.0±0.8	0.9±0.7	2.3±1.1	28.6±10.3	49.9±3.6	31.3±14.0	16.9±8.7	9.0±1.3	17.7±7.9
<u>Regenerating Trees^c</u>									
Conifers	0.1±0.0	0.1±0.0	0.7±0.4	0.0±0.0	0.2±0.1	1.8±1.0	0.1±0.1	0.1±0.0	0.2±0.1
Hardwoods	5.5±2.4	23.4±11.0	53.7±6.8	8.0±1.5	14.9±3.3	30.2±8.4	6.8±2.0	31.5±9.2	46.2±17.9
All Species	5.6±2.4	23.4±11.0	54.4±7.1	8.0±1.5	15.0±3.3	32.0±8.9	6.9±1.9	31.5±9.3	46.4±17.8
<u>All Trees</u>									
Conifers	1.0±0.7	0.2±0.1	2.0±1.0	25.0±7.6	46.7±4.4	29.9±14.6	1.2±0.6	0.9±0.8	0.8±0.5
Hardwoods	5.7±2.3	24.1±11.8	54.7±7.3	11.6±2.6	18.2±3.2	33.4±10.6	22.6±7.2	39.7±10.4	63.3±10.5
All Species	6.6±2.2	24.3±11.7	56.7±8.0	36.6±9.6	65.0±6.7	63.3±6.1	23.8±6.9	40.2±10.2	64.1±10.0

^aStand age based on age of regenerating aspen as determined from tree cookies and cores from a sample of trees.

^bLegacy trees were retained during the last harvest and thus were representatives of a prior stand.

^cRegenerating trees (including tall shrubs) were established or sprouted since the last harvest.

Table 2.4

Legacy tree and regenerating tree (including tall shrubs) composition as a percent (mean \pm 1 se) of total above ground live woody biomass for 27 aspen forest stands in northern Wisconsin, 2007-2008.

Species	Regenerating Trees	Legacy Trees
<i>Populus</i> spp. ^a	75 \pm 1	5 \pm 3
<i>Acer rubrum</i>	8 \pm 2	6 \pm 4
<i>Quercus rubra</i>	5 \pm 1	37 \pm 9
<i>Betula papyrifera</i>	3 \pm 1	1 \pm 1
<i>Corylus</i> spp. ^b	3 \pm 1	na ^c
<i>Prunus serotina</i>	2 \pm 0	<1
<i>Abies balsamea</i>	1 \pm 0	1 \pm 11
<i>Pinus strobus</i>	1 \pm 0	29 \pm 7
<i>Pinus resinosa</i>	<1	20 \pm 6
Total	98	99

^aIncludes both *Populus tremuloides* and *Populus grandidentata*

^bIncludes both *Corylus cornuta* and *Corylus americana*

^cNot applicable

Table 2.5

Pearson correlations between non-metric multidimensional scaling ordination axes and stand variables for 27 aspen forest stands in northern Wisconsin, 2007-2009. The coefficient of determination is presented for each axis in parentheses.

Variable	Axis 1 (0.041)		Axis 2 (0.852)	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
Stand Age (years) ^a	0.298	0.089	0.878	0.771
Visual obstruction (%)	-0.367	0.135	-0.233	0.054
Legacy tree density (stems/ha) ^b	-0.055	0.033	0.008	0.000
Legacy tree diameter at breast height (cm) ^c	-0.016	0.000	0.424	0.180
Proportion of overstory trees that are hardwoods ^d	-0.282	0.079	0.488	0.239
Proportion of sapling trees that are hardwoods	-0.358	0.128	-0.201	0.040

^aCorrelated with canopy closure ($r=0.72$), foliage height diversity ($r=0.72$), overstory tree density ($r=0.86$), overstory tree basal area ($r=0.79$), overstory tree diameter ($r=-0.59$), sapling density ($r=-0.85$), sapling diameter at breast height ($r=0.64$)

^bCorrelated with legacy tree basal area ($r=0.85$)

^cCorrelated with legacy tree age ($r=0.69$)

^dCorrelated with proportion of legacy trees that are hardwoods ($r=0.80$)

Table 2.6

Indicator species analysis importance values (IV) by legacy tree treatment and stand age-class (years; in 2007) for 27 aspen forest stands with and without legacy tree retention, northern Wisconsin, 2007-2009. Only species with probability (p) values equal to or less than 0.050 are included. Species in each treatment-age group are sorted by highest indicator value. Species not in bold font had nearly equally high indicator values (within 75% of the maximum group indicator value) in one or more of the other groups, thus only species in bold font are good indicators for one treatment-age group. Species with asterisks are categorized as conservation priority. See Table 2.1 for species scientific names.

Species	Treatment & Age-class of Maximum IV	IV	p
Common Yellowthroat*	Clearcut–Young (4-7 yrs)	51.2	0.027
Alder Flycatcher	Clearcut–Young (4-7 yrs)	47.3	0.015
Brown Thrasher*	Clearcut–Young (4-7 yrs)	42.9	0.043
White-throated Sparrow*	Clearcut–Young (4-7 yrs)	34.6	0.018
American Robin	Clearcut–Young (4-7 yrs)	33.0	0.009
Brown-headed Cowbird	Hardwood Retention–Young (4-7 yrs)	50.0	0.028
American Goldfinch	Hardwood Retention–Young (4-7 yrs)	48.5	0.004
Downy Woodpecker	Hardwood Retention–Young (4-7 yrs)	46.2	0.049
Golden-winged Warbler*	Hardwood Retention–Young (4-7 yrs)	43.9	0.023
Indigo Bunting	Hardwood Retention–Young (4-7 yrs)	34.0	0.006
Mourning Warbler*	Hardwood Retention–Young (4-7 yrs)	33.5	0.007
Black-and-white Warbler	Hardwood Retention–Middle-age (11-21 yrs)	30.2	0.046
Black-throated Green Warbler*	Conifer Retention–Old (20-36 yrs)	56.5	0.027

CHAPTER 3. Canopy Trees as Biological Legacies Aid in Recovery of Late-seral Understory Plant Species in Managed Aspen Forests

Abstract

The decline of late-seral and disturbance-sensitive understory plants in managed forests has prompted the use of forestry practices such as retention of live, canopy trees (“legacy trees”) in commercial, even-aged forest management to protect native plant diversity. We compared aspen (*Populus* spp.) forests harvested with legacy tree retention to clearcuts across a chronosequence (8-40 years post-harvest) to determine if legacy trees increased understory plant diversity and floristic quality. We selected 27 aspen stands with nine in each of three harvest treatments: 1) no legacy tree retention or clearcut, 2) conifer legacy tree retention, and 3) hardwood legacy tree retention. Understory plant species richness, diversity, and evenness did not vary by harvest treatment or by stand age. Mean coefficient of conservatism (*C*) was lower in young stands than middle-age or old stands; there was a marginally significant ($p=0.058$) interaction effect between legacy tree retention treatment and stand age. Mean *C* was initially lower in stands with legacy tree retention than in clearcuts, but with stand development, mean *C* in stands with legacy tree retention exceeded that for clearcuts. Mean *C* for clearcuts remained relatively constant across the chronology suggesting that late-seral species were slow to germinate or invade. Late-seral plant species were positively associated with stand age and legacy tree diameter or age thus lending support for the importance of the relationship between legacy tree retention and stand development. Our data suggest that legacy tree retention may enhance traditional even-aged management techniques in aspen forest by conserving late-seral understory plants.

Introduction

Native understory plant diversity is declining in managed forests due to the decrease of habitat specialists and increase of habitat generalists resulting in increased compositional similarity (Rooney et al. 2004). This pattern highlights a general trend toward forest community homogenization that has prompted the need for forestry

practices that protect native plant diversity. Ecological forestry provides the framework around which silvicultural treatments may be crafted to provide elements in managed forests associated with natural disturbances (Kohm and Franklin 1997). The retention of biological legacies, pre-disturbance structures that persist post-disturbance, is a central concept in this framework (Franklin et al. 2007).

Aspen forests are important commercially across the northern hemisphere as feedstock for the paper and pulp industry and has attracted interest from the emerging bioenergy industry (Ragauskas et al. 2006). Aspen stands are regenerated with even-aged management techniques, generally a coppice or clearcut harvest (Perala 1977). Retention of live, canopy trees as biological legacies ("legacy trees") is recommended as an element of improving upon traditional even-aged forest management (Franklin et al. 2000, Franklin et al. 2007, Rosenveld and Lohmus 2008). As a practice this is referred to by a variety of names including legacy-tree retention, green-tree retention, variable retention, live-tree retention, partial harvest, even-aged management with reserves, or two-aged forest management.

Our objective was to assess changes in understory plant diversity, composition, and floristic quality in response to conifer and hardwood legacy tree retention relative to clearcuts in aspen forest stands across a chronosequence. Plant and forest ecologists have long explored the plant diversity and compositional effects of forest management but assessment of floristic quality in forests is relatively new (Francis et al. 2000, Spyreas and Matthews 2006, Wolff et al. 2008). Floristic Quality Assessment offers an assemblage-wide technique to determine if compositional changes tend toward historically undisturbed, intact forest (Swink and Wilhelm 1994). Though based on a subjective, qualitative species scoring method, this technique provides a quantitative tool to measure plant assemblage quality (Swink and Wilhelm 1994).

Bradbury (2004) offered three hypotheses to explain the influence of aggregated legacy tree retention on understory plant richness and diversity in boreal forests. These ideas could be adapted to predict effects of dispersed retention patterns and partially influenced our competing hypotheses in this study. First, based on successional niche theory and an understanding of resource characteristics, young stands with retention

represent an intermediate level of disturbance producing a high diversity of niches for a spectrum of early- to late-seral species resulting in the highest potential species richness and diversity earlier in stand development due to increases in both resource quantity and heterogeneity (Pacala and Reese 1998, Bartels and Chen 2010). The legacy tree retention effect will be greatest in young and middle-age stands but the effect will be reduced in old stands without retention and as aspen regeneration reaches the legacy tree canopy resulting in a reduction in niche diversity following canopy closure. Second, diversity may be lower in stands with retention given that conditions are suboptimal for both late-seral species and pioneering species and only benefitting species adapted to partial sun or shade conditions. Third, based on Hubell's Unified Neutral Theory that predicts no net gain in species richness or diversity through time though composition may change due to stochastic processes, we would predict no change in species diversity due to either stand development or legacy tree retention (Hubell 2001).

In regard to plant composition, we hypothesize that dispersed legacy trees will provide environmental conditions needed for persistence, invasion, and increased abundance of late-seral understory plant species earlier in stand development than would occur in the absence of legacy trees in aspen clearcuts. We predict that plant assemblage floristic quality and composition of young aspen stands with legacy trees will be similar to old aspen stands without legacy tree retention.

Past studies investigating ecological effects of legacy tree retention have focused primarily on the selection of specific tree species thus additional research was recommended to identify other important legacy tree characteristics such as age and size (Rosenveld and Lohmus 2008). By measuring a variety of legacy tree and retention characteristics including tree age and size, we can make recommendations to foresters for selection of legacy trees and to create stand characteristics for the protection of disturbance-sensitive plant species in commercially managed aspen forests.

Methods

Study area

In 2006, we selected 27 aspen-dominated forest stands in Oneida, Vilas, and Lincoln Counties, Wisconsin (45° 43'N, 89° 32'W) based on constructing a chronosequence of regenerating aspen stand developmental stages for nine stands in each of three legacy tree retention treatments: no legacy tree retention or clearcut, hardwood legacy tree retention, and conifer legacy tree retention (Figure 3.1). In this selection process, we minimized other stand differences such as soil type, landscape context, and management history. Climatically, this area averages 760-890 mm of annual precipitation and has an average annual temperature of 4-5°C with a 125-155 day freeze-free period (NRCS 2011).

All aspen stands were located within Subsection 212Jm (Northern Highland Pitted Outwash) of Province 212 (Laurentian Mixed Forest) based on the Ecoregions of the United States (Bailey et al. 1994; Figure 3.1). The study area fell within the boundaries of Major Land Resource Area 94D, Northern Highland Sandy Drift, in Soil Survey Region #10 (NRCS 2011). Based on mean percent of stand area, a majority of soils (~90%) were either sandy loam or loamy sand with the remaining ~10% being primarily sand (Soil Survey Staff 2011). Most soils were Entic or Alfic Haplorthods of the soil order Spodosols with the most common soil types being Padus-Pence Sandy Loam (21%), Keweenaw Sandy Loam-Vilas Loamy Sand Complex (17%), and Sayner Loamy Sand (15%; Soil Survey Staff 2011). These well- to excessively-drained soils were a product of glacial deposits in the form of outwash plains (Croswell, Rubicon, Vilas, Sayner, and Karlin series), loamy drift over sandy outwash (Pence and Padus series), and sediment or till on moraines and drumlins (Keweenaw series; NRCS 2011).

At the time of selection, aspen stand ages ranged from 3-35 years following the last clearcut harvest. Aspen stands in the region are typically harvested at around 45-60 years or as early as 35 years on poor quality soils and thus stands older than 40 years post-harvest were not included in the study (Perala 1977, WDNR 2011). We classified aspen stands into young, middle-age, or old age-classes based on order of stand ages within the chronosequence for each legacy tree retention treatment. Timber harvest

prescriptions called for removal of all aspen and tree species other than large-diameter (>12.7 cm diameter at breast height, dbh) oak (northern red oak, *Quercus rubra*) and pine (most often *Pinus strobus* and *Pinus resinosa*; C. Dalton pers. comm.). Retention pattern was not specified in the prescription, though most residual trees were generally dispersed, with several stands containing some residual tree aggregates that were a consequence of their spatial arrangement prior to harvest and not due to the prescription. Aspen stands were dominated by *Populus tremuloides* and *Populus grandidentata* and included other abundant regenerating species especially *Acer rubrum*, *Amelanchier* spp., *Prunus serotina*, *Quercus rubra*, and *Betula papyrifera*. The dominant tall shrubs (>1.37m) were *Corylus cornuta*, *Corylus americana*, and *Prunus virginiana*. Stand area ranged from 13.6 to 58.3 ha.

Field Methods

Ten 0.1-ha circular plots were randomly distributed within each stand without overlapping logging roads or other areas with ongoing vehicular disturbance. Random points were generated using the Generate Random Points tool using Hawth's Tools extension (Version 3.26; Beyer 2004) in ArcGis 9.2 (ESRI 2007). To minimize variability due to conditions other than legacy tree retention treatment and aspen stand characteristics, plots were placed at least 25m from: 1) the stand edge to minimize influence on understory vegetation by adjacent forest stands, 2) logging roads and log landings due to known differences in species diversity and composition compared to locations away from these areas (Wolf et al. 2008), and 3) one another to maintain independence. All herbaceous species and woody species less than 1m tall excluding tree seedlings were included in the understory plant survey. Surveys were conducted on one visit during 28 June - 20 September 2009 or 4-24 July 2010 during the part of the year when it was deemed possible to identify all understory species present.

Within each 0.1-ha circular plot, all herbaceous and target woody species were recorded as present. At 5m from plot center, a 1-m² subplot was placed at each heading of 30°, 150°, and 270° for a total of three subplots per plot. Within each subplot, the percent cover for each species present was estimated on a continuous scale from 1-100%; species with cover <1% were classified categorically as "trace".

For correlation with the ordination axes, we identified variables that reflected possible survey-related bias, environmental conditions, and stand characteristics which potentially affected understory plant assemblage composition and abundance. We selected one variable that represented potential bias in the data due to survey timing, the mean Julian date for the survey at each stand. We included one environmental variable, mean Palmer Drought Severity Index (PDSI), which is a good indicator of regional soil moisture conditions (Szép et al. 2005). We used this as indication of establishment conditions that may favor certain plant species over others. We averaged the PDSI for Wisconsin Climatic Division 2 (north-central Wisconsin) for the primary growing season months of May through Sept for the first two years following the most recent aspen harvest.

We selected three variables, canopy closure, foliage height richness, and visual obstruction, representing the structural characteristics of stand vegetation. These were measured at two subplots positioned at 10m from plot center to avoid trampling the understory plants measured in the subplots positioned at 5m from plot center within each 0.1ha circular plot. We measured canopy closure using a spherical densiometer. Foliage height richness was used as an index of vertical vegetation diversity using an extension pole marked with 1-m increments; vegetation contacting the pole was noted at each 1-m increment up to 15m and in an additional category combining all increments above 15m, the height of the pole. Visual obstruction was measured for shrub and understory vegetation height-density using a 3m x 0.5m density board divided into 0.1m x 0.1m squares of alternating black and white squares (Noon 1981). The percentage of squares obscured by vegetation was averaged for readings from 10-m in the cardinal directions. Contrary to Noon (1981), the density board was positioned at plot center while the observer moved to the cardinal directions. This modification was necessary given the difficulty and slowness of moving the density board through the dense shrub layer.

Within each 0.1ha circular plot, we recorded the following data for all overstory trees taller than 1.37m and greater than 10cm dbh: species, live vs. dead, dbh, and whether each was a biological legacy. A 0.01 ha circular plot was nested within the 0.1ha plot to measure sapling-sized woody vegetation, i.e., woody plants taller than 1.37m with a diameter at breast height less than 10cm. From these data, we calculated the following

variables for use in the ordination analysis: overstory tree density, overstory tree basal area, mean overstory tree dbh, proportion of hardwoods in the overstory, sapling density, legacy tree density, legacy tree basal area, mean legacy tree dbh, proportion of hardwood legacy trees, mean sapling dbh, and proportion of hardwood saplings.

To determine stand age, based on the regenerating aspen, and legacy tree age, we collected a sample of tree cores and cookies (a 1-2 section of tree trunk) at each stand. If aspen were generally larger than 10cm dbh in a stand, we removed two perpendicular cores per tree at a height of 1.37m for one co-dominant or dominant tree per aspen species present per plot. If aspen were generally smaller than 10cm dbh in a stand, we clipped three aspen saplings per species present in the 0.01ha sapling plot and collected a cookie at a basal height of 15cm for each tree clipped. Growth rings were counted for each tree core or cookie and then averaged across the stand to establish stand age since the last harvest. We cored all legacy trees present on each plot, counted the growth rings for each tree, and then averaged the ages to determine mean legacy tree age for each stand.

Plant Species Characteristics

For species included in the ordination, we classified each by forest seral association. We used geographically relevant field guides (e.g., Fassett 1997), web resources (e.g., USDA 2012), and scientific literature to appropriately classify each plant species. For some species, seral association was stated in this literature. For other species, seral association was determined based on light tolerance, plant community association, disturbance tolerance, forest stand age of maximum frequency and/or abundance, or a combination of these factors. Early-seral species were associated with full sun, open and disturbed plant communities, and/or declined in abundance with forest stand development. Late-seral species were associated with shade, mature forests, and/or increased in abundance with stand development. Mid-seral species were divided into early-mid seral or mid-late seral categories. Early-mid seral species were associated with full to partial sun and/or open to open woods vegetation communities. Mid-late seral species were associated with partial shade to full shade, woods, and/or a tendency to be found across a broad age range of closed canopy forest. Generalist species were associated with tolerance for a broad range of light conditions, both woods and open

vegetation communities, and/or similar frequency and abundance across all forest stand ages.

For each plant species present, we reported the coefficient of conservatism value from UWSP (2012). According to UWSP (2012), these values were developed based on survey results from 12 plant experts and finalized by a core group of six ecologists using the methods of Swink and Wilhelm (1994) and Wilhelm and Masters (1995). The coefficient of conservatism was used for floristic quality assessment of sites and has values on a scale from zero to ten that represents the probability that a species was found in a non-degraded natural community that represents a pre-European settlement condition. Invasive or weedy species with no likely association with an unaltered natural community were assigned a value of “0” and species that were certainly associated with undegraded natural communities were assigned a value of “10”. Non-native plant species introduced to Wisconsin were not given a value in the UWSP (2012) database, but we assigned these species a value of “0” to down-weight the means in our analyses (Spyreas et al. 2012).

Data Analysis

Species with less than 1% cover (“trace”) at the subplot level were assigned a value of 0.01% such that they could be included in analyses of cover as a continuous variable. All plant cover estimates were averaged by plot and then by stand. This “average-of-plots” method emphasizes frequently occurring species which may give a more realistic assessment of floristic quality by reducing the influence of rare or outlier species (Spyreas et al. 2012).

Understory Plant Diversity and Floristic Quality of Aspen Forest Stands

Understory plant species richness (S) was the total of all species (native and introduced) present at the plot scale. Shannon’s Diversity Index (H' ; where $H' = -\sum p_i \log p_i$ and p_i = the importance probability of species i), Shannon’s Evenness (E ; where $E = H' / \ln(S)$) and Simpson’s Diversity Index (D ; where $D = 1 / \sum p_i^2$) for understory plants were calculated for each aspen stand based on cover data collected at the subplot scale using the Row and Column Summary tool in PC-ORD Version 5 (McCune and Mefford 2002). To assess floristic quality of the aspen stands, we calculated the mean coefficient of conservatism

(C), also called the modified Floristic Quality Index (Rooney and Rogers 2002), and the Floristic Quality Index (FQI; Spyreas et al. 2012)). FQI was a product of mean C for a stand and the square root of the number of species observed or S (Spyreas et al. 2012). We conducted a two-way analysis of variance (ANOVA) using SigmaStat Version 3.5 (Systat 2006) to determine statistically significant differences in these diversity and floristic quality variables among three stand age-classes and the three legacy tree retention treatments. All variances for response variables were found to be normally distributed using the Kolmogorov-Smirnov test and were equal using Levene's Median test among groups; thus, no transformations were necessary.

Understory Plant Composition of Aspen Forest Stands

To evaluate understory plant compositional relationships with aspen stand and environmental characteristics, we used a non-metric multidimensional scaling (NMS) ordination using PC-ORD Version 5 (McCune and Mefford 2002). We ran the NMS procedure using the Sorensen distance measure in autopilot mode and the “slow and thorough” thoroughness setting. We selected the lowest dimensionality based on the best solution that notably improved the final stress. In other words, additional dimensions beyond the first were added only if they reduced the final stress by five or more. We generated joint plots for plant species and aspen stands using the two axes with the largest coefficients of determination. Displayed species or stand points are considered compositionally more similar the closer they are together. We reduced the set of 18 stand, environmental, and survey-related variables by examining Pearson correlations. Among the variables with correlations of 0.6 or more, we selected the variables that were likely representative of an underlying relationship. Based on the reduced set of eight variables, we selected those with $r^2 \geq 0.100$ for either of the two top ordination axes to construct a joint plot.

To identify plant species indicative of the three legacy tree retention treatments, we used an indicator species analysis in PC-ORD version 5.0 (McCune and Mefford 2002). We used the Monte Carlo Test set on the default of 1000 runs to identify species with a significant maximum importance value for a particular treatment relative to the importance value for randomized groups. The proportion (p) of randomized trials with an indicator value equal to or greater than the observed indicator value was deemed

significantly different at 0.050, though species with proportions between 0.050 and 0.100 were considered marginal indicators.

Results

Across aspen stands, we identified 195 understory plant species of which 170 were native and 25 (7 Graminoids and 18 forbs) were introduced to Wisconsin (Appendix A).

Understory Plant Diversity of Aspen Forest Stands

Understory plant richness, diversity, and evenness did not vary by stand age-class, legacy tree retention treatment, or their interaction (Table 3.1).

Floristic Quality of Aspen Forest Stands

The mean C was significantly lower for early-seral stands than for mid- and late-seral stands but did not vary for legacy tree retention treatments though there was a marginally significant interaction effect with stand age-class (Table 3.1). FQI did not vary by stand age-class, legacy tree retention treatment, or their interaction (Table 3.1). Plant species classified as mid-late seral, late-seral, and generalists had significantly higher mean C than early-seral species (Table 3.2).

Understory Plant Coverage and Compositional Patterns in Aspen Forest Stands

The coverage of some plant species had clear relationships with stand development (Table 3.3). In particular, we only observed *Comandra umbellata* ssp. *umbellata* and *Rubus flagellaris* in young clearcuts. *Oryzopsis asperifolia*, *Pedicularis canadensis*, *Pteridium aquilinum* var. *latiusculum* and *Vaccinium* spp., reached their highest coverage in young stands and declined with stand development. *Osmunda claytoniana* was the only species with observations restricted to middle-age stands. *Maianthemum racemosum* reached highest coverage in middle-age stands especially those with retained canopy trees. Species with coverage that increased with stand development included *Trientalis borealis* ssp. *borealis*, *Waldsteinia fragaroides* ssp. *fragaroides*, *Cornus canadensis*, and *Gaultheria procumbens*.

Retention of canopy trees affected plant species presence and coverage (Table 3.3). Several species (*Aralia nudicaulis*, *Eurybia macrophylla*, *Maianthemum canadense*, *Rubus allegheniensis*, *Uvularia sessilifolia*, *Waldsteinia fragaroides* ssp. *fragaroides*) reached higher coverage earlier in stand development in the presence of retained canopy trees (Table 3.3). We only observed *Clintonia borealis* in stands where canopy trees were retained (Table 3.3). Some species (e.g., *Rubus allegheniensis*) also dropped to relatively low coverage earlier in stand development in the presence of retained canopy trees (Table 3.3).

We summarized means, standard errors, and ranges by legacy tree retention treatment for all survey-related, environmental, and aspen stand variables used to correlate NMS ordination results (Table 3.4). Pearson correlations among these variables resulted in a reduced suite of variables used in the NMS ordination. Stand age was correlated with canopy closure ($r=0.72$), foliage height diversity ($r=0.72$), overstory tree dbh ($r=0.86$), overstory tree basal area ($r=0.79$), overstory tree diameter ($r=-0.59$), sapling density ($r=-0.85$), sapling dbh ($r=0.64$). Legacy tree density was correlated with legacy tree basal area ($r=0.85$). Legacy tree dbh was correlated with legacy tree age ($r=0.69$). The proportion of overstory hardwoods was correlated with the proportion of hardwood legacy trees ($r=0.80$).

The NMS ordination resulted in a three dimensional solution with a final stress of 9.234. Axis 3 of the ordination had the largest coefficient of determination (0.391) and was positively correlated with three aspen stand characteristics, stand age ($r=0.590$), proportion of hardwoods in the overstory ($r=0.472$), and legacy tree dbh ($r=0.387$) collectively representing 72.1% of the variation represented by this axis (Table 3.5). Axis 2 had the second largest coefficient of determination (0.321) and was positively correlated with the Palmer Drought Severity Index for the two years of stand establishment ($r=0.323$) and was negatively correlated with the proportion of overstory hardwoods ($r=-0.373$; Table 3.5). Axis 1 had the smallest coefficient of determination (0.182) and was poorly correlated with all survey-related, stand, and environmental variables ($r=-0.281-0.285$; Table 3.5).

Based on aspen stands with $r \geq 0.5$, younger stands (≤ 15 years post-harvest) were negatively associated and older stands (≥ 22 years post-harvest) were positively associated with axis 3 (Figure 3.2a, b). Middle-age and old stands with a hardwood overstory were positively associated with a hardwood overstory or a dry establishment period following harvest. In contrast, young stands and stands with a coniferous overstory were positively associated with a relatively high proportion of conifers in the overstory or had a moist establishment period following harvest (Figure 3.2a, b). Eleven stands (73% with legacy tree retention and 91% middle-age or old) were positively correlated and nine stands (44% with legacy tree retention and 78% young) were negatively correlated with legacy tree dbh (Figure 3.2a, b). The remaining seven stands had a weakly negative association ($r < 0.2$). The only positively correlated young stand, though a weak relationship, was in the conifer legacy tree retention treatment.

Early-seral and late-seral plant species generally had diametrically opposed associations with stand and environmental variables based on axes 2 and 3 of the NMS ordination (Figure 3.2a, c). Early-seral plant species were associated with aspen stands that were young, had a high proportion of conifer legacy trees or conifers in the overstory, had relatively small-diameter legacy canopy trees, and had relatively moist conditions at the time of establishment following harvest (Figure 3.2a,c). The ten late-seral plant species were associated with aspen stands that were old (9 spp.), had a high proportion of hardwoods or hardwood legacy trees in the overstory (7 spp.), had relatively large-diameter legacy canopy trees (10 spp.), and had relatively droughty conditions at the time of establishment following harvest (7 spp.; Figure 3.2a, c). *Streptopus lanceolatus* var. *longipes*, *Trientalis borealis* ssp. *borealis*, and *Aralia nudicaulis* were associated with moist establishment and/or relatively large conifer legacy trees. *Oxalis montana* was most strongly associated with a high proportion of hardwoods in the overstory or as legacy trees. *Dryopteris intermedia*, *Polygonatum pubescens*, *Brachyelytrum erectum*, and *Monotropa uniflora* were associated with overstory hardwoods and old stands. *Huperzia lucidula* and *Maianthemum racemosum* were most associated with old stands especially those with large legacy trees.

The indicator species analysis identified *Maianthemum canadense*, a mid- to late-seral species, as the only significant indicator of conifer legacy tree retention (Table 3.6)

though several other species were marginally significant (*Cornus canadensis*, *Eurybia macrophylla*, and *Lathyrus venosus*). Three species (*Hepatica nobilis* var. *obtus*, *Symphyotrichum ciliolatum*, *Vaccinium myrtilloides*) were significant indicators of aspen stands without legacy tree retention and five other species were marginally significant (Table 3.6). No species were indicative of hardwood legacy tree retention.

Discussion

Understory plant diversity in aspen stands

We found no relationship between plant diversity and either stand age or legacy tree retention treatment. The lack of a relationship may be affected by persistence of plant species following harvest and site conditions. Many forest plant species, regardless of forest type, persist following overstory removal with reduced abundance or density followed by eventual recovery to pre-harvest levels (Hughes and Fahey 1991, Crowell and Freedman 1994, Ruben et al. 1999, Sullivan et al. 2001, Aikens et al. 2007). Given that our youngest stands had at least six years of post-harvest recovery, early differences in diversity, if they existed, may have disappeared by the time of our surveys.

A review of studies that explored response of herbaceous plant species abundance and richness to dispersed and aggregated legacy tree retention produced inconsistent results (Rosenvold and Lohmus 2008). The reviewers attributed the variation in response to site specific characteristics such as forest type, percent canopy removal, soil characteristics, and number of pioneer species that invaded following harvest (MacDonald and Fenniak 2007, Rosenvold and Lohmus 2008). The latter two characteristics potentially contributed to the lack of relationship between plant diversity and retention treatments in our study.

In Michigan, understory plant diversity and composition in aspen clearcuts changed relative to mature forest on mesic sites but not on dry-mesic sites (Roberts and Gilliam 1995). Our results were consistent with this finding given that our aspen stands were dry-mesic with the oldest stands being younger than the mature forests in the Roberts and Gilliam (1995) study thus presenting even less of an age contrast across stands. We did not sample logging roads and log landings where many pioneering early-seral

species occur in greatest abundance such that this group may have increased diversity had these areas been included in our sampling design (Wolf et al. 2008). Also, differences in diversity related to varying retention in forest stands may be difficult to detect except at larger spatial scales (MacDonald and Fenniak 2007).

According to Hubell's (2001) Unified Neutral Theory model of zero-sum ecological drift, species richness and diversity within a community remain relatively constant though the membership by individual species and their abundance within a trophic level changes through time. Wiegmann and Waller (2006) found support for this model in shifting understory plant assemblage patterns of upland forests over a fifty-year period in northern Wisconsin. The lack of change in diversity metrics among legacy retention treatments and stand age in our study may be explained by this theory.

Effect of legacy tree retention on floristic quality and late-seral plant species

In terms of floristic quality of the plant communities, mean C but not FQI differed among stand age-classes and retention treatments. Mean C may be a better metric than FQI for assessing floristic quality given that our stand areas varied (Matthews et al. 2005), and this variable reduced the confounding influence of species richness (Rooney and Rogers 2002). The marginally significant interaction effect between stand age-class and legacy tree retention treatment suggested there was a weak treatment effect that was dependent upon the seral age-class of the aspen stand. Increasing the stand sample size may have produced a stronger treatment effect especially in the interaction. Nevertheless, this was consistent with our conclusion from the NMS ordination that stands with larger or older legacy trees had similar species composition as did the relatively old aspen stands in this study.

Overstory and legacy tree composition, particularly presence of conifers, influenced understory plant composition. Similarly, in Alberta, plant associations differed between forests managed with variable retention containing conifers and broadleaf forest (MacDonald and Fenniak 2007). Eight clearcut aspen stands in our study were divided into two groups with strong opposing associations to the proportion of hardwood in the overstory. Each group potentially reflected influence from the forest overstory composition prior to harvest with one group having a significant coniferous component

and the other not. MacDonald and Fenniak (2007) identified soil and forest structural characteristics pre- and post-harvest that differentiated plant communities in broadleaf forest from those in forests containing conifers.

PDSI at the time of stand establishment and the proportion of hardwoods in the overstory had opposite and potentially confounding influences on plant composition. Other studies have shown that drought conditions can decrease cover and alter dominance among understory plant species present in fields (Sandor et al. 2003), alter plant composition in secondary forests (Hutchinson et al. 1999, Yurkonis and Meiners 2006), and increase tree seedling mortality rates in savannas (Faber-Langendoen and Tester 1993). Thus it is likely that given the dry-mesic, well-drained soil conditions of our stands that drought conditions during early stages of plant invasion and recovery following harvest influenced plant composition. For early-seral species, relatively moist growing seasons potentially improved establishment conditions particularly in clearcuts and open areas of stands with legacy tree retention where soil temperatures and solar radiation exposure were relatively extreme (Childs and Flint 1987). Both PDSI during stand establishment and the proportion of conifers in the overstory may positively relate to moist environmental conditions favoring establishment of certain species. Beatty (1984) found that eastern hemlocks (*Tsuga canadensis*) in eastern deciduous forests influenced composition of understory plants due to higher soil moisture content and other soil characteristics near individual hemlock trees. Conifers in our study may have similarly influenced soil moisture and thus plant composition; however we did not measure microclimate characteristics associated with individual legacy trees.

We observed higher mean *C* in aspen stands where the plant assemblage composition included more mid-late to late-seral plant species that generally were scored with higher coefficients of conservatism than early-seral species. The weak interaction effect between stand age and retention treatment likely indicated the importance of legacy trees in middle-age to old aspen stands for retention or invasion of late-seral species. Wiegmann and Waller (2006) identified 21 understory plant species that were declining in frequency across northern Wisconsin forests over a 50-year period. We observed that five (*Aralia nudicaulis*, *Clintonia borealis*, *Eurybia macrophylla*, *Uvularia sessilifolia*, and *Waldsteinia fragaroides* ssp. *fragaroides*) of these species responded positively to

legacy tree retention and two (*Cornus canadensis* and *Eurybia macrophylla*) were indicators of stands with conifer retention. Two species (*Huperzia lucidula* and *Orthilia secunda*) were rare in our study and only associated with stands with legacy tree retention.

The response of late-seral plant species to legacy tree retention has been inconsistent across other studies. For example, in Douglas fir (*Pseudotsuga menziesii*) stands in the Pacific Northwest, frequency and cover of late-seral plants increased due to retention (North et al. 1996) in contrast to a lack of response by late-seral species to green-tree retention in boreal forests of Fennoscandia (Vanha-Majamaa and Jalonen 2001). The key reason cited for lack of late-seral species response to retention in the latter study included the need for a greater level of retention (>50 trees/ha). In support of this idea, early-seral plants were indicators of 25% canopy retention in boreal forest and late-seral plants were indicative of forests with 75% canopy retention or uncut control forests in Alberta (MacDonald and Fenniak 2007). Our results suggested that legacy tree size and age may be more important than retained tree density or basal area which may partially explain the inconsistent results elsewhere.

We identified two possible mechanisms explaining the greater importance of legacy tree size or age than legacy tree density or basal area. First, large legacy trees may have a greater life-boating effect than small legacy trees by better protecting understory plants from impact from the harvest machinery. Second, large legacy trees may have a greater influence on microclimate conditions than smaller legacy trees such that late-seral understory plant species either invade or establish earlier post-harvest or recover in abundance faster due to more favorable environmental conditions. If late-seral plants became established from the seed bank rather than by surviving harvest or by invasion, then we might expect the pattern of mean *C* that we observed with stand development. There would be three conditions needed for this pattern to develop for late-seral plant species: 1) parental plants (visible above-ground structures) disappeared following harvest, 2) seed remained viable in the soil for at least six years (the youngest stand age at the time of surveys), and 3) seed germination was delayed because microclimate conditions were initially unsuitable following harvest but became suitable later in stand development. Given the increased shading by the retained legacy trees, the resultant

microclimate conditions may become suitable for germination of seed for late-seral species earlier in stand development than in clearcuts with full sun exposure.

If any of these three conditions were not met, then late-seral plants would need to invade following harvest. We would then expect that mean *C* would be higher in the stands with legacy tree retention than in clearcuts among young stands. Instead, mean *C* was initially lower in stands with legacy tree retention than in clearcuts, but over time mean *C* in stands with legacy tree retention exceeded that for clearcuts. Mean *C* for clearcuts remained relatively constant across the chronology suggesting that late-seral species were slow to recover or invade. These trends support the second proposed mechanism that the legacy trees eventually allowed for earlier invasion or recovery of late-seral species. Additionally, this may explain rejection of our hypothesis that young stands with legacy tree retention had similar floristic quality as old clearcuts. Though legacy tree retention increased floristic quality in aspen stands, its role was most prevalent later in stand development when floristic quality in stands with retention surpassed that in the clearcuts among the older stands in our study.

Conclusions

Legacy tree retention was an improvement over traditional clearcutting in aspen forest by conserving late-seral understory plants. Given that the legacy tree retention pattern in our stands was more dispersed than aggregated, it is possible that retention of legacy trees in aggregates or patches may have produced a life-boating effect allowing for greater retention and faster recovery of late-seral species (Aubry et al. 2009). Future research should explore the potential for aggregated patterns of retention in aspen forests to have even greater benefits for late-seral understory plants.

Retention of non-aspen species requires consideration for their potentially impact on aspen regeneration. Retaining too much canopy cover can result in reduced aspen regeneration (Perala 1977), though some reduction in initial sucker density due to partial shading from retained legacy trees may increase early growth of the suckers (Stone et al. 2001). Given that the size or age of the retained trees were more important than retained tree density or basal area, foresters can create retention prescriptions that

benefit late-seral understory plant species without compromising aspen regeneration. Our results indicate that increasing the retention density of young or small legacy trees in a prescription likely would not compensate for large, old legacy trees. However, foresters can initially retain relatively small canopy trees and continue to retain them in future harvests to eventually attain the benefits of large legacy trees.

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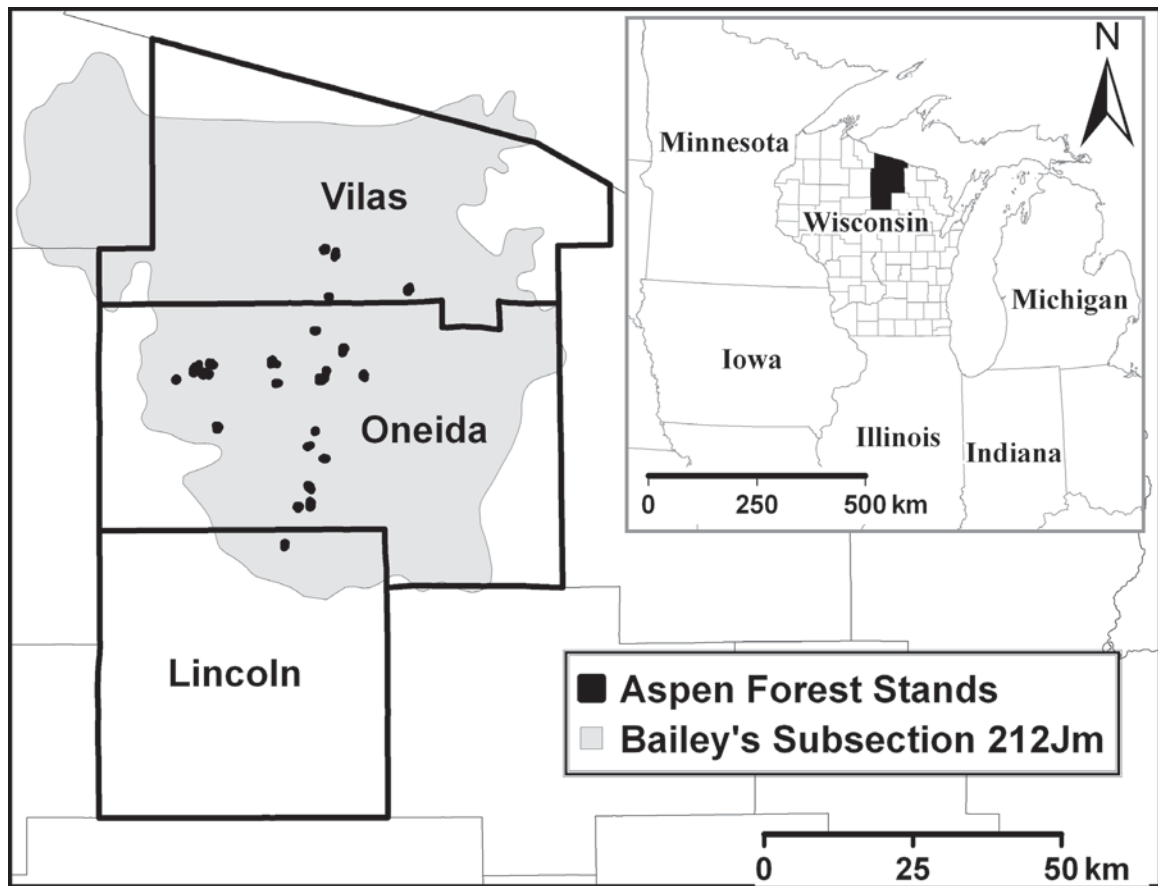


Figure 3.1. Study area depicting 27 aspen forest stands within the Northern Highland Pitted Outwash (Bailey's Subsection 212Jm) and in a three-county area of northern Wisconsin. The inset identifies the location of these three counties (Vilas, Oneida, and Lincoln) within Wisconsin and the Midwestern United States.

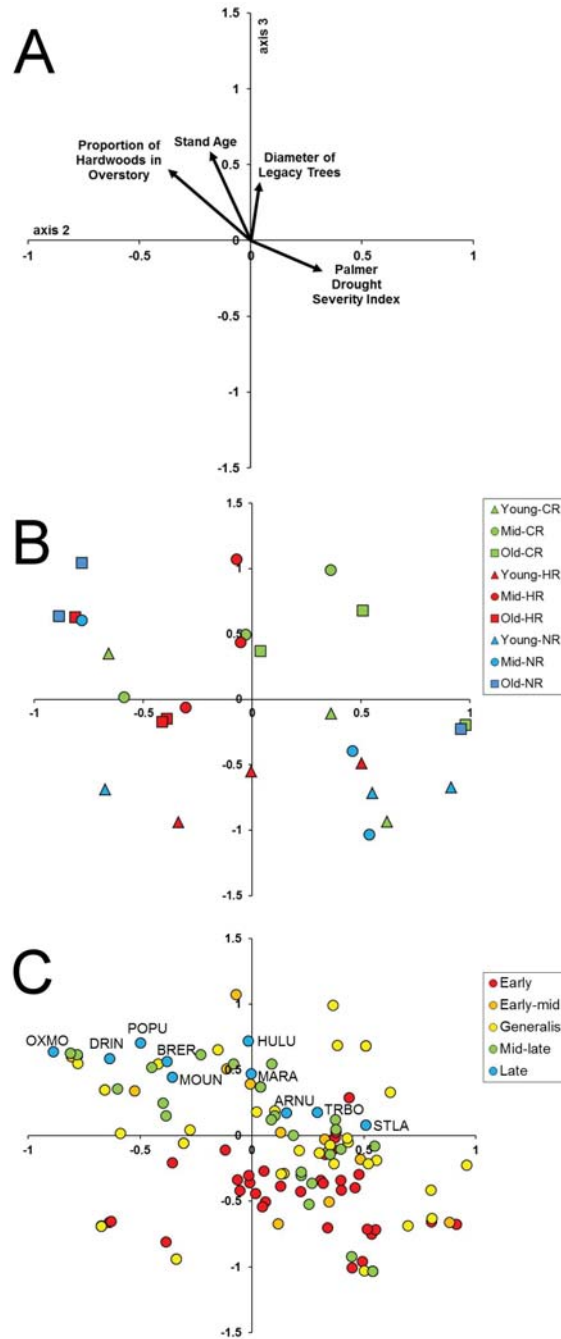


Figure 3.2. NMS ordination plots of 27 aspen forest stands (B) and 130 understory plant species (C) versus environmental and stand structural gradients (A). All plant species present within subplots for which cover was estimated were included in the ordination. Environmental and stand structural variables are described in Table 3.4. Aspen stands are categorized based on their age-class (young, mid, and old) and legacy tree retention treatment (CR=conifer legacy tree retention, HR=hardwood legacy tree retention, NR=no legacy tree retention or clearcut). Plant species are categorized based on their predetermined seral association. Late-seral species are identified with alpha codes (ARNU=*Aralia nudicaulis* L., BRER=*Brachyelytrum erectum*, DRIN=*Dryopteris intermedia*, HULU=*Huperzia lucidula*, MARA=*Maianthemum racemosum*, MOUN=*Monotropa uniflora*, OXMO=*Oxalis montana*, POPU=*Polygonatum pubescens*, STLA=*Streptopus lanceolatus* var. *longipes*, TRBO=*Trientalis borealis* subsp. *borealis*).

Table 3.1

Mean±1 se understory plant species diversity and floristic quality for 27 aspen forest stands in northern Wisconsin, 2008-2009. Diversity measures included species richness (S), Shannon's Diversity Index (H'), Simpson's Diversity Index (D), and Shannon's evenness (E). Measures of floristic quality included mean coefficient of conservatism (C) and floristic quality index (FQI).

Treatment	Measures of Diversity			Measures of Floristic Quality		
	S ^a	H ^b	E ^b	D ^b	mean C ^a	FQI ^a
<u>Young stands (6-9 years post-harvest)</u>						
Clearcut	57.0±9.3	1.77±0.36	0.49±0.11	0.67±0.10	4.62±0.07	34.64±2.93
Conifer retention	62.0±6.8	1.79±0.33	0.51±0.08	0.71±0.10	4.30±0.23	33.63±1.08
Hardwood retention	67.3±8.4	1.64±0.08	0.48±0.01	0.70±0.02	4.11±0.11	33.46±1.11
<u>Middle-age stands (13-23 years post-harvest)</u>						
Clearcut	59.7±5.4	1.68±0.25	0.44±0.07	0.66±0.07	4.54±0.23	35.14±3.20
Conifer retention	44.3±4.3	2.07±0.12	0.60±0.03	0.80±0.03	5.07±0.20	33.79±2.95
Hardwood retention	67.7±8.7	2.13±0.10	0.58±0.02	0.82±0.01	4.55±0.01	37.26±2.30
<u>Old stands (22-39 years post-harvest)</u>						
Clearcut	51.7±4.4	2.23±0.03	0.63±0.01	0.79±0.01	4.65±0.07	33.37±1.52
Conifer retention	55.0±6.2	2.06±0.12	0.57±0.04	0.78±0.03	4.73±0.14	34.86±1.76
Hardwood retention	51.0±1.5	1.94±0.22	0.55±0.07	0.69±0.08	4.79±0.13	34.20±2.03
<u>Two-way Analysis of Variance Results</u>						
Stand age-class	F _{2,18} = 1.60 p = 0.230	F _{2,18} = 2.05 p = 0.157	F _{2,18} = 1.77 p = 0.199	F _{2,18} = 1.10 p = 0.354	F _{2,18} = 6.33 p = 0.008 ^c	F _{2,18} = 0.41 p = 0.670
Legacy tree retention treatment	F _{2,18} = 1.26 p = 0.309	F _{2,18} = 0.13 p = 0.883	F _{2,18} = 0.34 p = 0.718	F _{2,18} = 0.55 p = 0.586	F _{2,18} = 1.58 p = 0.233	F _{2,18} = 0.13 p = 0.879
Stand age-class x legacy tree retention treatment	F _{4,18} = 1.38 p = 0.281	F _{4,18} = 0.95 p = 0.457	F _{4,18} = 1.17 p = 0.359	F _{4,18} = 1.07 p = 0.399	F _{4,18} = 2.79 p = 0.058	F _{4,18} = 0.37 p = 0.829

^aBased on 195 plant species present on study plots.

^bBased on 130 plant species with cover estimates from subplots.

^cPost-hoc multiple comparisons: Young stands (mean±se; 4.34±0.11) had a significantly lower mean coefficient of conservatism than the middle-age stands (4.72±0.12) and old stands (4.72±0.06).

Table 3.2

Mean \pm 1 se understory plant species coefficient of conservatism (C) by forest seral association classification for aspen forest stands in northern Wisconsin, 2008-2009.

Seral Association ^a	<i>n</i>	<i>C</i>
Early	48	2.73 \pm 0.36 A ^b
Early-mid	15	4.93 \pm 0.43 AB
General	31	5.29 \pm 0.36 B
Mid-late	26	6.12 \pm 0.24 B
Late	10	6.50 \pm 0.31 B

^aDetermined for each species using field guides, web resources, and/or scientific literature.

^b $H_4=44.023$, $p\leq 0.001$ for Kruskal-Wallis One Way Analysis of Variance on Ranks; multiple comparisons were conducted using Dunn's Method and seral groups that were significantly different from one another are indicated by different letters.

Table 3.3

Understory plant seral associations and mean±se cover (%) in 27 aspen forest stands in northern Wisconsin, 2008-2009. Species were included if present with a minimum mean cover of 1% at one or more stands. Stands were classified as young (6-9 years post-harvest), middle-age (13-23 years post-harvest), and old (22-39 years post-harvest) seral age-classes and by legacy tree retention treatments: no retention or clearcut (NR), conifer retention (CR), and hardwood retention (HR). Scientific names, common names, and authority followed the convention of the USDA (2012) and subspecies and variety names were identified in UWSP (2012). All species are native to Wisconsin.

Scientific Name and Authority	Seral Association ^a	Young			Middle-age			Old		
		NR (n=3)	CR (n=3)	HR (n=3)	NR (n=3)	CR (n=3)	HR (n=3)	NR (n=3)	CR (n=3)	HR (n=3)
Ferns										
<i>Athyrium filix-femina</i> (L.) Roth	mid-late	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.6±0.6	0.5±0.5
ssp. <i>angustum</i> (Willd.) R.T. Clausen										
<i>Osmunda claytoniana</i> L.	general	0.0±0.0	0.0±0.0	0.0±0.0	0.7±0.7	0.3±0.3	0.3±0.3	0.0±0.0	0.0±0.0	0.0±0.0
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>latiusculum</i> (Desv.) Underw. ex A.Heller	early	30.2±7.7	23.8±9.3	21.9±5.1	25.9±12.4	8.1±2.9	9.7±2.8	16.1±11.8	17.2±7.9	11.2±2.0
Forbs										
<i>Apocynum androsaemifolium</i> L.	early-mid	0.0±0.0	0.5±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	0.1±0.1	0.0±0.0
<i>Aralia nudicaulis</i> L.	late	0.1±0.1	1.4±1.2	0.8±0.1	0.2±0.1	1.3±0.4	1.2±0.2	1.5±0.6	1.2±0.2	0.2±0.1
<i>Clintonia borealis</i> (Aiton) Raf.	mid-late	0.0±0.0	0.2±0.2	0.1±0.1	0.0±0.0	0.1±0.1	0.5±0.4	0.0±0.0	0.3±0.3	0.1±0.0
<i>Comandra umbellata</i> ssp. <i>umbellata</i> (L.) Nutt.	early	0.6±0.6	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.3±0.3	0.0±0.0
<i>Doellingeria umbellata</i> (Mill.) Nees	early	0.5±0.5	0.1±0.1	0.3±0.2	0.0±0.0	0.0±0.0	0.2±0.1	0.2±0.1	0.0±0.0	0.3±0.3
<i>Eurybia macrophylla</i> (L.) Cass.	general	6.6±3.2	9.2±5.6	8.9±2.5	4.2±2.1	6.9±4.0	4.9±0.6	6.6±6.4	14.8±4.6	0.7±0.2
<i>Maianthemum canadense</i> Desf.	mid-late	0.3±0.3	2.1±1.6	0.6±0.3	0.2±0.1	2.0±0.7	0.9±0.6	1.3±0.9	4.4±3.7	0.5±0.1
<i>Maianthemum racemosum</i> (L.) Link	late	0.0±0.0	0.1±0.1	0.3±0.0	0.3±0.2	0.5±0.4	0.5±0.3	0.1±0.1	0.1±0.1	0.1±0.1
<i>Pedicularis canadensis</i> L.	mid-late	0.8±0.8	0.0±0.0	0.1±0.1	0.0±0.0	0.2±0.2	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0
<i>Thalictrum dioicum</i> L.	mid-late	0.0±0.0	0.1±0.1	0.1±0.1	0.0±0.0	0.3±0.2	0.2±0.2	0.2±0.2	0.0±0.0	1.0±1.0

Table 3.3, continued

Scientific Name and Authority	Seral Association ^a	Young			Middle-age			Old		
		NR (n=3)	CR (n=3)	HR (n=3)	NR (n=3)	CR (n=3)	HR (n=3)	NR (n=3)	CR (n=3)	HR (n=3)
<i>Trientalis borealis</i> ssp. <i>borealis</i> Raf.	late	0.1±0.1	0.6±0.3	0.0±0.0	0.2±0.2	1.0±0.6	0.4±0.1	2.1±1.4	1.8±0.9	0.6±0.2
<i>Uvularia sessilifolia</i> L.	general	0.2±0.2	0.8±0.7	0.5±0.2	0.2±0.1	0.8±0.4	0.4±0.3	1.0±1.0	1.2±0.7	0.2±0.1
<i>Waldsteinia fragarioides</i> ssp. <i>fragarioides</i> (Michx.) Tratt.	general	2.8±1.5	9.2±4.7	2.0±0.8	5.6±3.1	6.9±0.5	7.0±2.2	7.3±3.0	10.4±6.3	2.4±1.4
<u>Graminoids</u>										
<i>Carex pensylvanica</i> Lam.	general	1.0±0.8	0.8±0.5	0.5±0.2	0.1±0.1	0.5±0.1	1.2±1.0	1.1±0.3	0.2±0.1	0.4±0.4
<i>Oryzopsis asperifolia</i> Michx.	early-mid	2.7±0.9	1.9±0.6	1.4±0.6	2.2±1.0	1.5±0.9	0.6±0.2	1.3±0.3	2.2±1.6	0.5±0.2
<u>Shrubs and Subshrubs^b</u>										
<i>Comptonia peregrina</i> (L.) J.M. Coult.	early-mid	0.3±0.3	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
<i>Cornus canadensis</i> L.	general	0.2±0.2	0.4±0.1	0.0±0.0	0.1±0.1	0.4±0.3	0.2±0.2	0.9±0.9	1.3±1.1	0.1±0.1
<i>Diervilla lonicera</i> Mill.	early-mid	0.0±0.0	0.5±0.5	0.0±0.0	0.1±0.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
<i>Gaultheria procumbens</i> L.	general	0.2±0.2	0.0±0.0	0.2±0.1	0.0±0.0	0.3±0.3	0.0±0.0	0.7±0.4	0.8±0.7	0.4±0.3
<i>Rubus allegheniensis</i> Porter	early	1.6±0.9	8.1±2.8	16.4±6.8	7.5±3.0	1.0±0.6	2.8±2.6	0.8±0.7	0.6±0.2	1.3±0.8
<i>Rubus flagellaris</i> Willd.	general	1.1±1.1	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0
<i>Rubus idaeus</i> L. ssp. <i>strigosus</i> (Michx.) Focke	early	0.1±0.1	0.8±0.6	0.1±0.1	0.2±0.2	0.0±0.0	0.5±0.2	1.4±1.2	1.3±0.9	0.1±0.1
<i>Rubus pubescens</i> Raf.	general	0.4±0.4	0.3±0.2	0.2±0.2	0.2±0.1	0.0±0.0	0.3±0.3	1.2±0.9	0.4±0.3	0.2±0.1
<i>Vaccinium angustifolium</i> Aiton	early	3.6±3.2	0.1±0.1	0.6±0.6	0.1±0.0	0.3±0.1	0.1±0.0	1.3±1.0	1.5±1.4	0.4±0.2
<i>Vaccinium myrtilloides</i> Michx.	early	2.3±1.3	0.1±0.1	0.2±0.0	0.8±0.4	0.5±0.3	0.1±0.1	0.5±0.4	0.8±0.7	0.8±0.4

^aDetermined from field guides, web resources, and/or scientific literature.^bWoody non-tree species less than 1-m tall.

Table 3.4

Mean survey-related, environmental, and stand variables for 27 aspen forest stands in northern Wisconsin, 2008-2009. Means were based on averaging 10 plots per stand for nine stands per legacy tree retention treatment.

Variable	<u>Clearcut</u>		<u>Conifer Retention</u>		<u>Hardwood Retention</u>	
	mean±1 se	range	mean±1 se	range	mean±1 se	range
<u>Survey-related Variable</u>						
Julian date of survey	225±11	179-263	217±7	186-249	228±6	205-256
<u>Environmental Variable</u>						
Palmer Drought Severity Index ^a	-0.31±0.50	-3.62-1.39	0.69±0.30	-0.91-1.83	0.22±0.38	-1.30-1.83
<u>Stand Variables</u>						
Stand area (ha)	34.6±3.4	13.6-58.3	22.8±5.0	14.8-43.5	28.1±3.0	17.2-43.9
Stand age ^b (years)	16±3	6-29	18±3	8-29	18±4	6-39
Canopy closure (%)	75±7	33-96	87±3	72-95	81±6	47-98
Foliage height richness	4.2±0.7	1.8-7.4	5.3±0.5	3.6-6.8	4.5±0.6	2.1-6.5
Visual obstruction (%)	77±4	59-90	75±4	59-90	80±4	62-94
Legacy tree density (stems/ha)	5±1	0-14	91±15	29-166	33±5	14-59
Legacy tree basal area (m ² /ha)	0.3±0.1	0.0-0.8	7.9±1.2	3.3-11.4	2.3±0.5	0.4-4.3
Proportion of hardwood legacy trees	0.57±0.14	0-1.00	0.19±0.08	0-0.69	0.91±0.02	0.79-1.00
Legacy tree dbh ^c (cm)	25.5±2.0	15.3-31.5	32.4±3.1	22.0-51.1	27.3±1.5	20.5-31.7
Legacy tree age (years)	52±7	25-72	61±5	42-92	65±6	42-93
Overstory tree density (stems/ha)	325±124	0-964	242±63	89-617	164±59	14-531
Overstory tree basal area (m ² /ha)	4.0±1.8	0-14.6	10.1±1.1	4.4-13.3	5.6±1.9	1.1-17.4
Proportion of hardwoods in overstory	0.70±0.15	0.00-1.00	0.45±0.12	0.02-0.97	0.94±0.02	0.79-1.00
Overstory tree dbh ^c (cm)	17.1±2.2	11.8-31.5	23.1±1.9	14.5-31.8	20.8±2.4	12.8-31.7
Sapling density (stems/ha)	840±170	166-1641	597±121	138-1065	1005±172	360-1685
Proportion of hardwood saplings	0.99±0.00	0.97-1.00	0.97±0.02	0.79-1.00	0.99±0.00	0.98-1.00
Sapling dbh ^c (cm)	2.4±0.3	0.9-3.9	2.7±0.3	1.7-4.4	2.3±0.3	1.2-3.3

^aIndex based on mean values for May to September for the two years following the last aspen harvest.

^bAge of regenerating aspen at time of plant survey; age was determined by examining regenerating aspen tree rings.

^cDiameter at breast height.

Table 3.5

Pearson correlations between non-metric multidimensional scaling ordination axes and environmental, survey-related, and stand variables for aspen forests in northern Wisconsin, 2008-2009. The coefficient of determination is presented for each axis in parentheses.

Variable	Axis 1 (0.182)		Axis 2 (0.321)		Axis 3 (0.391)	
	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
Stand Age (years) ^a	-0.178	0.032	-0.183	0.033	0.590	0.348
Julian date of survey	-0.226	0.051	0.126	0.016	-0.296	0.087
Palmer Drought Severity Index during two years of post-harvest establishment	-0.281	0.079	0.323	0.104	-0.205	0.042
Visual obstruction (%)	0.228	0.052	0.112	0.013	-0.016	0.000
Legacy tree density (stems/ha) ^b	0.036	0.001	-0.060	0.004	0.075	0.006
Legacy tree diameter at breast height (cm) ^c	0.227	0.051	0.040	0.002	0.387	0.150
Proportion of overstory trees that are hardwoods ^d	0.012	0.000	-0.373	0.139	0.472	0.223
Proportion of sapling trees that are hardwoods	0.285	0.081	-0.078	0.006	-0.052	0.003

^aCorrelated with canopy closure ($r=0.72$), foliage height diversity ($r=0.72$), overstory tree density ($r=0.86$), overstory tree basal area ($r=0.79$), overstory tree diameter ($r=-0.59$), sapling density ($r=-0.85$), sapling diameter at breast height ($r=0.64$).

^bCorrelated with legacy tree basal area ($r=0.85$).

^cCorrelated with legacy tree age ($r=0.69$).

^dCorrelated with proportion of legacy trees that are hardwoods ($r=0.80$).

Table 3.6

Understory plant species that were indicators of legacy tree retention treatments based on indicator species analysis for 27 aspen forest stands in northern Wisconsin, 2008-2009. Only species with p -values ≤ 0.100 were included. Asterisks indicate species that were introduced to Wisconsin.

Species	Legacy Tree Retention Group Indicator Value	Randomized Group Indicator Value Mean	Randomized Group Indicator Value Standard Deviation	p
<u>Indicators of aspen clearcuts</u>				
<i>Danthonia spicata</i>	52.8	36.8	10.79	0.090
<i>Hepatica nobilis</i> var. <i>obtusata</i>	41.9	21.3	8.96	0.028
<i>Hieracium aurantiacum</i> *	48.5	34.9	8.88	0.080
<i>Lycopodium clavatum</i>	45.4	25.9	10.11	0.061
<i>Oryzopsis pungens</i>	36.3	22.5	9.75	0.100
<i>Symphotrichum ciliolatum</i>	55.7	40.6	7.15	0.035
<i>Vaccinium myrtilloides</i>	59.4	43.5	8.50	0.048
<u>Indicators of aspen stands with conifer legacy tree retention</u>				
<i>Cornus canadensis</i>	58.2	40.2	10.80	0.072
<i>Eurybia macrophylla</i>	49.6	42.6	5.12	0.096
<i>Lathyrus venosus</i>	37.9	21.0	9.48	0.086
<i>Maianthemum canadense</i>	68.6	52.6	7.75	0.027

CHAPTER 4. Legacy Trees in Aspen Clearcuts Improve Nest Habitat Quality for Golden-Winged Warblers

Abstract

Residual canopy trees as biological legacies in harvested aspen stands may mimic characteristics of naturally disturbed forests. We investigated the effects of legacy tree retention in young aspen (*Populus* spp.) forest stands on the quality of nest habitat for the Golden-winged Warbler (*Vermivora chrysoptera*), a species of conservation concern that is dependent upon recently disturbed forest and shrub habitats. Habitat quality was assessed by evaluating male density, male pairing success, percent of successful nests, daily nest survival, and productivity in young aspen stands (4-7 years post-harvest) with retained conifer legacy trees ($n=3$), retained hardwood legacy trees ($n=3$), and without legacy trees or clearcuts ($n=3$). Male pairing success was higher in stands with legacy trees (~75%) than in clearcuts (10%). In similarly aged regenerating aspen forests, only one nest was found in clearcuts. The percent of successful nests, daily nest survival rate, and productivity did not vary between stands with conifer legacy trees and stands with hardwood legacy trees. Retention of legacy trees in young aspen stands provided higher quality nest habitat than clearcuts based on high pairing success resulting in high nesting activity. Male density was an excellent indicator of pairing success (pseudo $R^2=0.976$). For nest habitat to be occupied by a cluster of nesting pairs, land managers must consider the roles of both habitat characteristics and conspecific attraction. Aspen stands harvested for nest habitat should support at least four territorial males at a minimum density of 0.2 males/ha for a breeding cluster to have approximately 75% of males successfully paired. High male densities (>0.2 males/ha) were achieved by retaining at least 13 legacy trees/ha with at least nine as hardwood species and hardwoods with a mean diameter at breast height ≥ 16 cm.

Introduction

One of the tenets of ecological forestry is the use of natural disturbance-based management strategies that promote ecological resilience (Drever et al. 2006, North and Keeton 2008). Biological legacies, such as scattered live trees, in post-disturbance

environments fill important ecological roles, and their retention may allow silvicultural treatments to more closely emulate natural disturbances (Seymour et al. 2002, Lindenmeyer et al. 2006, Manning et al. 2006). Legacy canopy trees as individuals or patches in managed aspen (*Populus* spp.) forests are known to increase bird diversity (Merrill et al. 1998) and benefit certain bird habitat-guilds or individual species in other forest communities (Hansen et al. 1995a, Schiek and Hobson 2001, Tittler et al. 2001, Lefort and Grove 2009). The impact of legacy canopy trees on bird habitat quality using demographic or physiological variables has been investigated using proxies for quality such as nest success (Titler and Hannon 2000, Duguay et al. 2001, Stuart-Smith and Hayes 2003) and body condition in the post-breeding season (McDermott and Wood 2010). Such demographic traits are generally accepted as better indicators of habitat quality than abundance or density estimates alone (Van Horne 1983). Most previous research has found that nest predation across the bird community was not higher in stands harvested with retention relative to unharvested stands and did not vary with the density of retained trees (Titler and Hannon 2000, Duguay et al. 2001, Stuart-Smith and Hayes 2003). Only Duguay et al. (2001) reported species-specific nest success for five passerine species with higher predation rates in harvested stands with retained trees versus unharvested stands for one species, Acadian Flycatcher (*Empidonax vireescens*).

We investigated the impact of legacy canopy tree retention, also called green-tree retention, in young aspen stands on a high conservation priority migratory songbird, the Golden-winged Warbler (*Vermivora chrysoptera*), during the breeding season. This species is dependent on disturbance events in forest ecosystems to create appropriate breeding habitat; the species' recent declines have been blamed in part on the maturation of forests in eastern North America (Confer et al. 2011). The Golden-winged Warbler, like other shrubland-dependent species, likely evolved to utilize forest openings regenerating with shrubs and young trees created by natural disturbances such as wind, fire, and beaver activity in forested landscapes (Hunter et al. 2001, Lorimer 2001). These openings likely contained both live and dead legacy canopy trees in varying densities with scattered individuals and patches depending on the intensity of the disturbance (Foster and Boose 1992, Frelich 2002; Figure 4.1a). Retention of legacy canopy trees in harvested even-aged forest stands, i.e., green-tree retention, has been proposed as a

silvicultural practice that mimics this natural disturbance pattern (Seymour et al. 2002, Lindenmeyer et al. 2006; Figure 4.1b).

An estimated 76% of the global population of Golden-winged Warblers breeds in the Boreal-Hardwood Transition Bird Conservation Region (Blancher et al. 2007). Thus, management practices that create high quality breeding habitat in this region are critical to the species' future. Regenerating aspen forests supported the highest relative abundance of Golden-winged Warblers among several habitat types occupied by Golden-winged Warblers in northern Wisconsin (Martin et al. 2007). Among regenerating aspen stands, Golden-winged Warbler abundance or density was quite variable suggesting that not all stands are equally attractive and that stand characteristics may explain differences in use and quality (Roth and Lutz 2004, Martin et al. 2007). Our objectives were to: 1) evaluate effects of legacy tree retention and legacy tree type on nest habitat quality for Golden-winged Warblers in young aspen stands using a combination of density, pairing success, nest survival, and productivity 2) determine if male density reflects habitat quality based on demographic indicators, and 3) recommend aspen forest silvicultural guidelines for foresters and land managers interested in providing high quality nest habitat for Golden-winged Warblers.

Methods

Study Area

We selected nine young aspen-dominated forest stands in Oneida and Vilas Counties, Wisconsin (45° 43'N, 89° 32'W) in an area defined by glacial moraines and outwash plains (Figure 4.2). Soils were characterized as sand, sandy loams, or loamy sands and ranged from moderately well drained to excessively drained (Soil Survey Staff 2010). Three stands were selected for each of three treatments: 1) aspen stands with no legacy tree retention or clearcut, 2) aspen stands with conifer retention, and 3) aspen stands with hardwood retention. Stands ranging from 17-44 ha in area and were commercially harvested using green-tree retention guidelines between 1997 and 2002 thus the regenerating aspen was 4-7 years-old (mean \pm se; 5 \pm 0) at the start of the study in 2007. Timber harvest prescriptions called for removal of all aspen and most tree species except those that were marked and all large diameter pine (*Pinus* spp.) and oak

(*Quercus* spp.; C. Dalton pers. comm.). Aspen stands were dominated by *Populus tremuloides* and *Populus grandidentata* and included other abundant regenerating species especially *Acer rubrum*, *Amelanchier* spp., *Prunus serotina*, *Quercus rubra*, and *Betula papyrifera*. The dominant shrubs were *Rubus* spp. and *Corylus* spp. All sites were selected without prior knowledge of Golden-winged Warbler occupancy.

Field Methods

Golden-winged Warbler territory and nest surveys were conducted 10 May-2 July 2007, 19 May-21 July 2008, 19 May-15 July 2009, and 16 May-3 July 2010. We captured and banded 88% of territorial adult male and 9% of adult female Golden-winged Warblers among all sites. Adults were targeted for capture using mistnets with tape playback (Kubel and Yahner 2007) and then given a unique color band combination including a silver U.S. Fish & Wildlife Service band for individual identification. In subsequent years, resighted birds were used to calculate annual return rates.

To determine territorial male densities in nest habitat, we mapped locations for all territorial males using a modification of the protocol of Robbins (1970). Surveys for the same individual or stand were conducted at least three days apart. When possible, we used teams of two observers with one observer recording locations on a map and marking song perches while the second observer tracked the bird. Because of the dense vegetation, it was difficult to continually track a bird and thus considerable time was spent checking bands to make sure the same individual was resighted before resuming the survey. An identifiably unique individual was tracked until the observer(s) completed a full circuit of the bird's territory such that the bird primarily began using marked perch trees. Unbanded males prior to capture were identifiable by unique song characteristics, favorite song perches, discrimination from banded neighboring males, or other characteristic behaviors. We did not survey males into the fledgling period. All perches were flagged and coordinates were collected later with a handheld Trimble XM Geographic Positioning System. From these locations, we used minimum convex polygons to delineate territorial boundaries. Not all males were intensively mapped with each stand visit but at a minimum, the presence-absence of each male was noted within previously known territorial boundaries. Territorial male densities were calculated based

on the number of territories for males observed on at least eight visits per harvested stand area.

Pairing success was defined as a territorial adult male observed interacting with an adult female (e.g. copulation or a male following a female) on two or more occasions though every attempt was made to document male visitation to a nest or fledglings (Askins et al. 2007). Contrary to Askins et al. (2007), we deemed one observation of a female with a male as inadequate due to occasional “prospecting” behavior by females especially early in the breeding season or following nest failures. Pairing success was generally determined incidentally to nest searching which was conducted in every territory and represented dozens of person hours of observation per territory often with multiple observers present. Territorial males without females were visited on most site visits throughout the nesting season until nesting activity was largely completed for most other pairs, and thus we had high confidence that these males did not acquire social mates. However, in stands with high male densities, we were conservative in our assignment of pairing success because we could not always differentiate unbanded females especially near territorial boundaries and other complicating issues such as females leaving their territory for extra-pair copulations (EPCs) and when females switched social mates or territories following nest failure. Extra-pair copulations are common in other Golden-winged Warbler populations (up to 55% of nests) so males without social mates may have sired offspring (Vallender et al. 2007). We did not determine paternity for nestlings so we could only define pairing success based on behavioral observations.

Nests were located by searching the entire stand for females exhibiting nesting behavior, adults feeding nestlings, and good potential nest sites within male territories. After egg laying was completed, nests were monitored every three days or sooner if the predicted fledging date fell before the next routine visit. Fledging was considered successful based on observation of fledglings, banded adults carrying food, or substantial fecal material on the rim of the nest or on nearby perches.

To determine legacy tree basal area and density at the stand scale, we randomly established ten 1000-m² circular plots separated by at least 30 m in each stand. These plots were visited 19 May-14 August 2008. We defined legacy trees as trees that were

retained during the most recent harvest rotation and were identified as live trees with diameter at breast height (DBH) at least 5 cm greater than the DBH of surrounding regenerating aspen trees and that were at least 1m taller than surrounding regenerating aspen trees in order to be used as a song perch. For each tree with DBH>10 cm, we recorded species, DBH, and whether it was alive or dead. To estimate regenerating tree stem density, a 100-m² nested plot was centered at the same point as the 1000-m² plot. All tree saplings ≥ 1.37 m tall and with DBH <10 cm were counted. Density estimates were calculated and averaged across each stand.

Data Analysis

Aspen Clearcut Characteristics

Comparisons of legacy tree characteristics and regenerating aspen stem densities among legacy tree retention treatments were conducted using One Way Analysis of Variance (ANOVA) using SigmaStat version 3.5 (Systat 2006). We used the Holm-Sidak test for multiple comparisons between treatments because it is more powerful than other tests such as Tukey and Bonferroni (Systat 2006). A simple linear regression was performed in SigmaStat to relate legacy tree density to legacy tree basal area. Both variables were log transformed to meet normality and equal variance assumptions for the residual errors.

Golden-winged Warbler Demographic Characteristics and Legacy Tree Retention Effects

Differences in territorial male numbers and densities between legacy tree retention treatments and years were determined using Two Way ANOVA for normally distributed datasets using SigmaStat (Systat 2006). Both of these dependent variables were transformed using square root transformation and the Holm-Sidak test was used for post-hoc comparisons. The Holm-Sidak test was used because it is a more conservative approach than other tests such as the Student-Newman-Keuls test (Systat 2006). The difference in male pairing success among legacy tree retention treatments was evaluated using a Chi-square test. The nest success (i.e. percent of successful nests) difference among legacy tree retention treatments by year and pooled across years was

evaluated using Fisher's Exact Test due to at least one cell in the contingency table having an expected value less than five.

To determine if daily nest survival rate (DSR) varied by year and legacy tree retention treatment, we used Program MARK version 5.1 (White and Burnham 1999). We compared six *a priori* models to evaluate whether daily nest survival varied by: 1) year, 2) site, 3) legacy tree retention treatment, 4) year and legacy tree retention treatment, and 5) year and site as compared to 6) an intercept only model. All models were constructed using constant survival through the nesting season. Independent variables were coded as dummy variables. We used MARK to apply an information theoretic approach to evaluate the models using Akaike Information Criterion for small sample sizes (AICc). Models with an AICc difference of two or less of the best model were considered equivalent models (Anderson 2008). Models with AICc differences between four and seven of the best model were given considerably less support for inference of results (Burnham and Anderson 2002). Model deviance was calculated in MARK.

Productivity was calculated as the number of fledglings per nesting territory based on procedures in Kubel and Yahner (2008). A nesting territory was defined as a territory for which we found at least one active nest during the course of a nesting season; we never found more than one successful nest per territory. In SigmaStat (Systat 2006), the difference in productivity between legacy tree retention treatments was determined using Kruskal-Wallis Analysis of Variance on Ranks due to a non-normal distribution, and the Tukey test was used for the post-hoc comparisons.

Male Density as an Indicator of Habitat Quality

To evaluate whether territorial male density was a good measure of habitat quality in aspen forest stands, we correlated territorial male Golden-winged Warbler density to pairing success among stands. We explored a variety of regression functions to fit this data by year and by the mean across years in SigmaPlot 9.0 (Systat 2004). For the yearly datasets, an exponential transformation of pairing success and a square root transformation of male density was required to meet normality and equal variance assumptions for the regression errors. A three-parameter sigmoid function consistently provided the best fit of the data among datasets and was used in a nonlinear regression

procedure (NLMIXED) in SAS. We used a Newton-Raphson fitting algorithm which is a derivative dependent method as recommended by SAS (Schabenberger 2011). Parameter start values were based on the fitted line parameters produced by SigmaPlot. Individual males were treated as a random effect. Pseudo- R^2 values were calculated with the following formula recommended by Schabenberger (2011): $\text{pseudo-}R^2 = 1 - \frac{\text{Sum of Squares(Residual)}}{\text{Sum of Squares(Total}_{\text{Uncorrected}})}$.

To identify the minimum number of territorial males per stand needed to produce the highest relative pairing success, we fitted a nonparametric general additive model using the GAM procedure in SAS to produce a smooth relationship that is the best fit of the data. We selected the generalized cross validation function (GCV) to optimizing the amount of smoothing from the data (Craven and Wahba 1979).

Male Density and Aspen Clearcut Characteristics

We selected variables *a priori* that might influence Golden-winged Warbler use or densities based on past studies. Stand age (i.e., regenerating aspen age) was selected as a proxy for successional stage given that peak Golden-winged Warbler use is thought to occur between 2 years and 10 years post-clearcutting in aspen forests (Roth and Lutz 2004, Martin et al. 2007). Regenerating aspen stem density has been found to be among the most important variables differentiating aspen stand use and preference among different early successional community types in Wisconsin (Roth and Lutz 2004, Martin et al. 2007).

Given our prediction that the presence of legacy trees will increase Golden-winged Warbler densities, we included variables that would describe stand-scale legacy tree characteristics such as mean basal area of legacy trees by group (hardwood species, coniferous species, and all species) and mean stem density of legacy trees by the same groups.

The Golden-winged Warbler feeds by gleaning or probing for insects amongst foliage and spends a majority of its time foraging in the upper quarter of tree and shrub canopies in breeding habitat (Ficken and Ficken 1968). The Golden-winged Warbler's propensity to probe particularly by inserting its bill into curled leaves, leaf clusters, buds,

and flowers suggests that hardwood species may offer greater foraging opportunities than conifers (Ficken and Ficken 1968). In general, Airola and Barrett (1985) found that migrant species were more likely to forage in deciduous trees compared to coniferous trees in mixed-conifer forests. Thus the proportion of hardwood to conifer legacy trees might be important in evaluating habitat quality and thus male density.

We selected tree size based on mean DBH as a variable given males frequent use of tall, canopy trees for song perches and foraging (Ficken and Ficken 1968, Rossell 2001). Bent (1963) noted that the species' preferred food is Lepidopteron larvae obtained from large trees. Moth larvae from Family Tortricidae (commonly referred to as leaf-roller caterpillars) are favored (Bent 1963, Will 1986) and for which the most commonly used host plants are cotyledons, though the three most common legacy tree species in the current study are each known host plants for 18-21 *Tortricid* species (Brown et al. 2008). Will (1986) noted that these larvae were most frequently extracted from aspen, hawthorn (*Crataegus* spp.), maple (*Acer* spp.), and alder (*Alnus* spp.) which are all broad-leaved, deciduous species. These studies did not indicate presence of conifers so it is unclear if broad-leaved, deciduous trees are the preferred foraging substrate when conifers are present as an alternate choice.

We used Pearson correlation to reduce the set of variables where correlation coefficients ≥ 0.60 were considered significant. The final set of variables included year, stand age, and mean values of regenerating aspen density, legacy tree stem density, conifer legacy tree size, hardwood legacy tree size, and proportion of hardwood to conifer legacy tree stem density. Nine models were developed to explain differences in male density across the aspen stands based on our literature review.

Male density may not be independent between years given that nearly half of all males returned to the same stand from one year to the next. To account for this, year was treated as a random effect in our linear mixed effect models. Non-linear mixed effects candidate models were evaluated using program R (version 2.9.1; The R Foundation for Statistical Computing) and package nlme. For model-selection we used AIC_c and package AICcmodavg to rank the candidate models. We fitted the models using the maximum likelihood procedure to generate the AIC_c rankings. We refitted the models

using the restricted maximum likelihood procedure to estimate parameter values. For nested models considered competitive based on the differences in AIC_c , final parameter values and confidence intervals were estimated using the model averaging procedure in package *AICcmodavg* which was based on the recommendations of Burnham and Anderson (2002).

To determine the minimum values or thresholds for legacy tree characteristics needed to achieve high male densities, we explored the correlation of each independent variable to mean male density in SigmaPlot. A three parameter sigmoidal function consistently provided the best fit of the data among datasets and was used in a nonlinear regression procedure (NLIN) in SAS. Parameter start values were based on the fitted line parameters produced by SigmaPlot. Individual males were treated as a random effect. Pseudo- R^2 values were calculated as described above.

Results

Aspen Stand Characteristics

In the conifer legacy tree retention treatment, the legacy trees were primarily *Pinus strobes* (55%), *Pinus resinosa* (23%), *Quercus rubra* (13%), and *Abies balsamea* (5%). In the hardwood legacy tree retention treatment, the legacy trees were primarily *Quercus rubra* (93%), *Pinus resinosa* (3%), and *Pinus strobes* (2%). In clearcuts, though legacy trees were rare as expected, they were *Quercus rubra* (31%), *Pinus resinosa* (23%), and *Abies balsamea* (23%).

Legacy tree density was significantly higher in stands with conifer retention, lowest in clearcuts, and intermediate in stands with hardwood retention (Table 4.1). Not surprisingly, conifer legacy tree density and basal area were highest in stands with conifer retention (Table 4.1). Legacy tree density and basal area were highly correlated (Adj. $R^2=0.916$, $F=88.291$, $P\leq 0.001$) based on the following relationship: $\log(\text{density})=1.420+(0.571*\log(\text{basal area}))$. Legacy tree size (mean DBH) and regenerating aspen stem density did not vary by legacy tree retention treatment (Table 4.1). Most (97%) aspen saplings were $\leq 5.0\text{cm}$ DBH.

Golden-winged Warbler Demographic Characteristics and Legacy Tree Retention Effects

We mapped territories for 36 males in 2007, 32 males in 2008, 31 males in 2009, and 32 males in 2010. Male return rates were 44% in 2008, 51% in 2009, and 51% in 2010; no females were resighted though only four were banded in 2007-09. No territorial Blue-winged Warblers (*Vermivora cyanoptera*) were observed. We observed one territorial phenotypic hybrid, a Brewster's Warbler (*V. chrysoptera* x *V. cyanoptera*), in 2007 that returned in 2008 to defend the same territory; we did not include this individual in any analyses.

Among the four survey years, there were more territorial males and a higher density of territorial males in stands with conifer or hardwood retention than in clearcuts (Table 4.2). The number of territorial males was not affected by the survey year ($F_{3,24}=0.107$, $p=0.955$) or an interaction effect between year and treatment ($F_{6,24}=0.534$, $p=0.777$). Similarly, male density neither varied by year ($F_{3,24}=0.032$, $p=0.992$) nor by interaction between year and treatment ($F_{6,24}=0.345$, $p=0.906$). However, given the rate of return for males between years, there was potentially some lack of independence. Despite this, we feel that the clear difference in male density between stands with legacy trees versus clearcuts was biologically significant.

Male pairing success across years was much higher in the conifer and hardwood retention treatments with conservative estimates of 68% and 71% respectively (Table 4.2). Pairing success was low for males in the clearcuts with only one male of eight individuals with 10 opportunities (10%) successfully acquiring a mate across four years. This particular male acquired a female during his third breeding season defending the same territory (i.e., one male with three opportunities for acquiring a mate).

We found 50 Golden-winged Warbler nests over four years (Table 4.2). Only one nest was found in clearcuts despite considerable time spent searching for both females and nests. Nests were located by behavioral cues usually by observing females (65%), searching likely nest sites (20%), and by luck (15%). Of the 25 nests that failed, 56% were depredated and 44% were abandoned. No double-brooding was observed. The

percentage of successful nests was similar between stands with hardwood legacy trees and stands with conifer legacy trees (Table 4.2).

Nest DSR was 0.975 ± 0.015 in 2007, 0.977 ± 0.013 in 2008, 0.971 ± 0.014 in 2009, and 0.960 ± 0.012 in 2010. DSR was similar between the conifer (0.968 ± 0.010) and hardwood retention (0.967 ± 0.010) treatments. The DSR for the one nest among clearcuts was 1.000 ± 0.000 . Based on a 24-day nest cycle, nest success was estimated at 0.46 for the conifer retention, 0.45 for the hardwood retention, and 1.00 for the no retention legacy tree treatments.

Of the models assessed to explore the effects of year, site, and legacy tree treatment on DSR, site was an improvement over the null (intercept only) model though both the intercept only model and legacy tree treatment model were competitive (Table 4.3). This suggests that nest survival did not vary by year but that site and legacy tree retention treatment explained some of the variation in DSR. Though DSR appeared to be lowest in 2010, this was not significant despite a 42% reduction in the percent of successful nests in 2010 (33%) compared to 2007-2009 (mean of 57%). Removal of the one nest in a clearcut still produced a competitive model ($\Delta AIC_c = 2.01$) suggesting that the slight difference in DSR (0.001) between stands with conifer retention and stands with hardwood retention may be important though it seems doubtful that this would produce significant differences in nest productivity. In fact, productivity did not vary by legacy tree retention treatment and was consistently 2.2 fledglings/nesting territory between the two treatments with legacy tree retention when four nests abandoned due to research-related causes were removed (Table 4.2).

Male Density as an Indicator of Habitat Quality

Pairing success related significantly to male density in all years (pseudo $R^2 = 0.885$ - 0.994 , $P < 0.001$) and for mean values among years (pseudo $R^2 = 0.976$, $P < 0.001$) (Table 4.4, Figure 4.3). The probability of a male successfully finding a mate was >40% when four or more territorial males were present at a male density above 0.1 individuals/ha, the inflection point in the sigmoid curve (Figures 4.3 and 4.4). Pairing success was consistently high (~75% on average) across years when male density was ≥ 0.2 individuals/ha, the asymptote of the curve (Figure 4.3).

Male Density and Aspen Clearcut Characteristics

The most parsimonious model explaining male densities in aspen forest stands included legacy tree density and hardwood legacy tree size (Table 4.5). The second best model was considered competitive and included the same two variables with the addition of the proportion of hardwood and conifer legacy trees (Table 4.5). Male densities increased with increasing legacy tree density, hardwood legacy tree size, and the proportion of legacy trees comprised of hardwood species (Table 4.6). Mean male density reached an asymptote when hardwood legacy tree size was 16 cm DBH (Table 4.7). Mean male densities increased notably above a legacy tree density threshold at 13 stems/ha (Figure 4.5), the point where the relationship first reached an asymptote (Table 4.7). Similarly, the asymptote for the relationship between male density and hardwood legacy tree density was first reached at around nine stems/ha for hardwood legacy tree density (Table 4.7). There was a marginally significant relationship between male density and conifer legacy tree density with an asymptote at three stems/ha suggesting that Golden-winged Warblers were tolerant of conifer presence as long as a minimum density of hardwood legacy trees was retained (Table 4.7). At relatively low legacy tree densities, a high proportion (>80%) of relatively large (≥ 16 cm DBH) hardwood trees attracted high male densities (Figure 4.5). If stands have a high proportion of conifer legacy trees (>70%), retaining a minimum of nine hardwood trees/ha was necessary to attract high male densities (Figure 4.5).

Discussion

Male Density Indicates Habitat Quality

Because we expected that male density alone would be an inadequate indicator of habitat quality, we also examined male pairing success, nest survival, and nest productivity as part of our evaluation. Pairing success in our study was comparable to the 42-80% rate reported for a Golden-winged Warbler population in central Michigan (Will 1986). For the closely related Blue-winged Warbler in a study in Connecticut (Askins et al. 2007), pairing success (54%) and nesting activity were higher in small habitat patches (supporting 1-2 territories) relative to large habitat patches (potentially supporting 2+ territories). However, their study sites were separated by as little as 10m

of forest, suggesting that sites or potential habitat may not be independent from a social contact perspective and thus conspecific attraction could be occurring among sites.

Contrary to our expectations, male density appeared to be an excellent indicator of pairing success. Similarly, Perot and Villard (2009) found that Ovenbird (*Seiurus aurocapilla*) territory density was a good indicator of productivity. In our study, only one male in four years acquired a mate and then successfully nested in a clearcut. Thus low male numbers and densities were indicative of low pairing success and low nesting probability. Male densities above 0.2 males/ha appear to indicate consistently high pairing success and nesting activity. Male densities indicate habitat quality but defining optimal habitat quality for Golden-winged Warbler likely requires an understanding of a combination of habitat characteristics and social behavior as suggested for other species (Ahlering and Faaborg 2006).

Legacy Tree Retention Improves Habitat Quality

DSR did not vary by year despite a 42% drop in the percentage of successful nests in 2010 compared to 2007-2009. A larger annual sample size may have produced a significant year effect. According to the multimodel inference results, legacy tree retention treatment contributed to explaining DSR despite the small difference between the two treatments with legacy trees. This somewhat puzzling result was possibly due to the difference in how the data were analyzed and presented. DSRs were presented as pooled estimates among stands in each legacy treatment whereas the nest survival analysis in MARK used individual nests to model the effect of legacy tree treatment. DSR may vary by an interaction of site and legacy tree treatment that was not modeled in this analysis and that was not apparent in how we presented the DSR results. In addition, given that only three sites comprise each legacy tree treatment, it is possible that one or two sites could be driving the legacy treatment result and thus might explain why the site model was ranked as the best. A detailed DSR analysis of all site specific characteristics including stand geometry, legacy tree characteristics, and habitat structure were beyond the scope of this study but would likely produce results that would better explain DSR variation. Based on the pooled results among sites in a legacy tree treatment, the small differences between the number of successful nests, DSR, and

productivity suggests that legacy trees (particularly the difference between hardwoods vs. conifers) have little impact on nesting success.

The most striking result of the demographic characteristics was the overall poor quality of clearcuts based on low male densities and low pairing success resulting in little nesting activity. Retention of legacy trees in aspen stands provided higher quality nest habitat based on relatively high pairing success (70%) and nearly identical DSR and productivity for Golden-winged Warbler nests as was found in aspen clearcuts in Pennsylvania (Kubel and Yahner 2008).

We have demonstrated the importance of legacy trees for improving habitat quality from the perspective of territorial male densities and pairing success. Other studies have documented the importance of scattered mature trees for Golden-winged Warbler occupation (Huffman 1997, Cumming 1998) and others have suggested that increasing scattered mature trees across large patches of open habitat potentially could improve occupancy especially away from transitional edges between open and mature forest habitat (Patton et al. 2010).

Golden-winged Warblers preferred residual canopy trees (> 6m tall) over shrub-sapling layer song perches (< 6m tall) in Minnesota aspen forests (Back 1982). This preference for large canopy trees as song perches was also documented for this species in mountain wetlands in North Carolina (Rossell 2001). A majority of song perches (78%) were in the upper 25% of the tree crown; and this positioning was thought to optimize vocal display and attraction of a mate, an idea supported by acoustic research (Henwood and Fabrick 1979, Mathevon and Aubin 1997).

We speculate that retaining legacy trees in aspen stands mimics the appearance of forests disturbed by wind and other weather events that provided suitable nest habitat for Golden-winged Warblers. Moderately severe natural disturbances often did not fell all canopy trees in the disturbed area and left behind a combination of injured and healthy trees (Figure 4.1). The canopy was opened up enough to allow dense shrub development and the patchiness characteristic of Golden-winged Warbler territories. Clearcuts where no legacy trees were retained likely resemble rare, severe natural

disturbances where no trees are left standing and appear to be less attractive to Golden-winged Warblers.

Conspecific Attraction Effects Habitat Occupancy

The inability of males to attract female mates at low densities and the corresponding rare instances of nesting suggest that there was also a social, conspecific attraction component to habitat occupancy. We documented that low densities of territorial males or the presence of only one or two territorial males at a site were not indicative of breeding activity or viable breeding habitat given the low likelihood of attracting a female social mate. Other studies have suggested that the Golden-winged Warbler appears to occur as loose aggregations or clusters (Confer and Knapp 1981, Klaus and Buehler 2001, Bulluck and Harding 2010). Confer (1992) reported that these clusters often include 2-6 or more pairs and that 10-15 ha of suitable habitat would be necessary to support six pairs. Across the four years of this study, the five sites that consistently had both males with pairing success above 50% and consistent annual nesting activity had at least four territorial males present each year. Thus, in addition to density, a minimum number of territories (0.1 territories/ha) may also be important for stability of breeding clusters. This suggests that either females are selective of locations with some minimal male density threshold or, due to lack of success in retaining females at a site, prospecting males are quickly rejecting territories and searching for sites more attractive to females. This pattern is indicative of a couple hypotheses that may explain the association of pairing success with territorial densities or clustering behavior.

The first hypothesis, posed by Brown et al. (1995) was based on evidence that most species are not evenly distributed across a landscape but instead form many “cool spots” where a species occurs in low abundance and a few “hot spots” where the species exists in high abundance. Further, they found that populations persisted long beyond the typical lifespan or generation time of the species owing to some unidentified ecological processes. Muller et al. (1997) proposed an alternate hypothesis where conspecific attraction may account for the persistence of hot spots. They proposed that females may be more attracted to habitat with high densities of males rather than low densities and thus settlement patterns may be based on a combination of habitat and conspecific characteristics. Further, they found that older more experienced males may

be more attractive to females than isolated naïve males. A dispersing or second year male with no breeding experience may be greatly influenced by conspecifics as an indicator of habitat quality. Older males can use their knowledge from previous nesting attempts and territories to select quality habitat. This may involve returning to a territory they defended in previous breeding seasons or selecting a neighboring territory deemed to be higher quality. Thus older males are less influenced by conspecifics than are young males. Our result of individual male pairing success as a function of the number of males present offers possible support for this hypothesis. As the number of males present exceeded five, an individual male's pairing success declined. This was potentially due to there being more young inexperienced males in larger populations that were unable to attract social mates.

The social mate attraction hypothesis suggests that sexual selection favors male aggregation and thus the clustering behavior of males will be more attractive to females. Clusters may be characterized by older males in better physical condition and thus may be more attractive to females. This would suggest that females prefer clusters of males rather than solitary males due to increased opportunity for EPCs particularly with high quality males. With the advent of genetic fingerprinting, many monogamous bird species were more promiscuous than previously thought such that females may be selecting clusters of males where they have multiple opportunities for EPCs (Wagner 1993, Tarof and Ratcliffe 2004). The hidden lek hypothesis adds that females seek matings from central or "hot shot" males and that the EPCs benefit the female in some way such as genetically.

The evolution of hidden leks includes several potential models, one of which is a female selection model which seems most consistent with our observations (Fletcher and Miller 2006). This model predicts that females prefer clusters of males and avoid solitary males. Reasons for this behavior include the opportunity to appraise relative male quality among a group and the likelihood that average male quality will increase with increasing aggregation size. This model also predicts that larger aggregations provide increased opportunity for EPCs which is a common practice in Golden-winged Warblers (Vallender et al. 2007). Our results best fit the female selection model though this should be examined more closely.

To understand the persistence of breeding clusters between years, we must also consider site fidelity and annual adult survival rates. Murray and Gill (1976) reported a conservative return rate of 60% for Golden-winged Warblers in Michigan as compared to a mean return rate of 49% in our study. In other regions of the breeding range, male return rates were higher with 75% in Ontario and 85% in Tennessee (Bulluck 2007). From a meta-analysis of site fidelity for shrubland birds of eastern North America, Schlossberg (2009) estimated a mean site fidelity rate of 38% for shrubland birds in general and 40% for Golden-winged Warblers specifically. Thus Golden-winged Warblers in our study have relatively average site fidelity compared to other species but lower site fidelity than Golden-winged Warbler populations in other parts of the breeding range. This could be an indication of lower quality breeding habitat or alternatively it could suggest a difference in habitat availability. In areas of the breeding range where there is little nest habitat in the landscape and where new nest habitat is generated infrequently, site fidelity and occupancy persistence may be higher and for longer duration than in regions where new nest habitat is more ubiquitous and consistently generated in the landscape (i.e. disturbance is common and more predictable; Donner et al. 2010). The relatively low site fidelity rate in our population may suggest that the likelihood of breeding cluster persistence was lower in our study area than elsewhere in the breeding range. This may be due to relative higher abundance of nest habitat and its frequent generation in the landscape. Additionally, other factors such as nest success from the previous year and habitat succession into an undesirable condition may also account for differences in site fidelity or occupancy rates (Haas 1998, Amarasekare and Possingham 2001).

Annual adult survival rates have been estimated in Tennessee (see Bulluck 2007) and could play an important role in breeding cluster persistence especially for sites where the number of pairs in a cluster was near the low critical threshold. For example, one site in our study had a cluster of breeding pairs for the first two years but did not in the last two years though floating males were observed. In the first year, there were two after-second-year males and two after-hatch-year males. In the second year, two of the banded males returned plus the addition of an unbanded second-year male. In the third and fourth years, no banded birds returned and only a floater was observed. If the two

after-second-year males from the second year died the following non-breeding season, then there may have been no veteran males to recreate the cluster in the third year thus leading to the collapse of that breeding cluster. This suggests that small clusters of Golden-winged Warblers were potentially less stable or indicative of habitat quality decline and thus less persistent than larger population clusters, though this idea should be tested with greater replication.

Studies of other warbler species have found that pairing success increased as habitat patch area increased (Burke 1998, Butcher 2011). We did not find that nest habitat area restricted pairing success given that much of the clearcut areas were unoccupied where there were low male densities. Regardless of the mechanism, when low densities (<0.2 males/ha) and small populations (three or fewer territorial males) are present additional evidence of pairing and reproductive success should be documented when evaluating habitat quality.

Recommendations for Managing High Quality Habitat

Habitat management at a site should be conducted with a specific Golden-winged Warbler population goal in mind, specifically attracting a breeding cluster comprised of at least four territorial males at a minimum density of 0.2 males/ha. Stands that support one or two territorial males will not likely result in nesting activity. Though stand area was not an important variable in predicting male density, nest habitat should be extensive enough to attain the population goal. The smallest area of nest habitat required per territorial male among stands with at least four males was 2.2 ha/male suggesting that at least 9 ha of nest habitat was required to support a population cluster. Confer and Knapp (1981) found that most Golden-winged Warbler territories were located in 10-50 ha habitat patches. Confer (1992) suggested that 10-15 ha might be close to the optimal patch size in old field habitats. Thus a minimum of 9-10 hectares of nest habitat seemed to be preferred by Golden-winged Warblers among these studies. However, at moderately low densities like our recommended minimum male density of 0.2 males/ha, at least 20 ha of suitable habitat may be necessary to support a breeding cluster. Thus land managers could assess male densities at other similarly managed sites in the area to determine the likely male density range that they can expect.

Kubel (2005) found that a minimum area of 1.0 ha was sufficient to attract breeding pairs though clearcuts were only 100m apart such that males were likely able to detect one another between clearcuts (Kubel and Yahner 2007). Similarly Roth and Lutz (2004) found that habitat area distributed as one large clearcut or two to three smaller clearcuts in close proximity attracted high densities of territorial males. Thus managers have some flexibility in how they configure nest habitat patches.

The support we found for a social mate attraction hypothesis (specifically a female selection model) as driven by habitat characteristics suggests focusing creation of new nest habitat near areas where clusters of breeding pairs currently exist. Bulluck and Harding (2010) found that the probability of Golden-winged Warblers occupying a nest habitat patch was higher when other occupied patches were in close proximity. This suggests that a strategy where land managers either expand the area of existing nest habitat or create new nest habitat in close proximity to existing populations is likely to be occupied. Creating nest habitat where there are no or few breeding pairs in proximity may have low probability of occupancy and pairing success would likely be low if only one or two territorial males arrive. More research especially with experimental manipulation is needed to better understand the spatial and temporal interplay of habitat vegetation characteristics and conspecific attraction in defining optimal habitat quality and also should include an examination of the roles of site fidelity and annual adult survival for persistence of optimal breeding habitat for this high conservation priority species.

Land managers, especially foresters, have a great opportunity for creating high quality Golden-winged Warbler nest habitat in aspen forests within the species' breeding range. For the Golden-winged Warbler, not all aspen clearcuts are created equal. When quantifying habitat for this species, it is important to also consider quality of habitat, in this case, the quality of the aspen forest. Retaining canopy trees can increase habitat quality in an even-aged harvest in aspen forest.

Based on the range of legacy tree densities observed for the aspen clearcuts in this study, we did not find an upper density limit where Golden-winged Warbler densities declined. However, there was a lower limit around 13 trees/ha (or 0.9 m²/ha) where there

was a notable increase in male density and also male pairing success. Huffman (1997) recommended a residual basal area of 4.6 m²/ha or approximately 20% residual canopy cover in aspen forests in Minnesota. They also observed that Golden-winged Warbler numbers declined and the composition of the bird community shifted at around 9.2 m²/ha or approximately 40% residual canopy cover. This suggests that optimal residual basal area and density for Golden-winged Warbler is likely higher than our minimum 0.9 m²/ha and 13 trees/ha minimum threshold.

The high proportion of hardwood to coniferous legacy trees was likely only important where legacy tree density was low thus stands with a high proportion of conifer legacy trees was acceptable if the minimum of 12 hardwood legacy trees/ha was retained. Retained trees should have an average DBH \geq 17cm. The dominant hardwood legacy tree was northern red oak (93%) and it is unclear what role this species, as compared to other hardwood species, has in attracting Golden-winged Warblers to a site.

Anecdotally, males spent much time singing and foraging in the canopies of large oak trees (personal observation). On sites where retention of oak is not an option, retention of other hardwood species may be adequate but we have no data on the relative attractiveness of oak to other species. In reclaimed mine habitat in Kentucky, black locust (*Robinia pseudoacacia*) was an important forage tree and planting new trees was recommended to improve habitat quality (Patton et al. 2010). In New York, Ficken and Ficken (1968) identified apple (*Pyrus malus*), black cherry (*Prunus serotina*), and hawthorn as the principal species utilized for foraging. Thus it is likely that there are a variety of hardwood species that could be retained or planted in open, shrub habitats that Golden-winged Warblers would find attractive and retention options will depend on which species are locally available, abundant, and tolerant of removal of the surrounding canopy.

For our study, the dominant legacy trees were northern red oak, eastern white pine, and red pine. Care should be taken when selecting trees for retention as some species will not tolerate the post-harvest exposure and will die or fall within the first few years after clearcutting. In our study, paper birch was occasionally retained but rarely survived the first years of post-harvest exposure (Roth, personal observation). Ideal legacy tree

species such as pines are deep rooted, and healthy dominant individuals will be more likely to withstand windthrow (Franklin et al. 1997). Based on research in British Columbia, managers were encouraged to select trees with low height-diameter ratios and deep, sparse crowns (Scott and Mitchell 2005).

Habitat management should be evaluated to determine if Golden-winged Warblers are responding as expected to specific prescriptions. From our results, we found that male density based on a minimum of number of territorial males was a good indicator of habitat quality when minimum thresholds were well understood. Given that nest searching or even establishing pairing success requires considerable time, personnel, and financial resources, we find it fortunate that male density has the potential to be a reliable metric of habitat quality for this species in young aspen stands and possibly in other vegetation communities occupied by Golden-winged Warblers.

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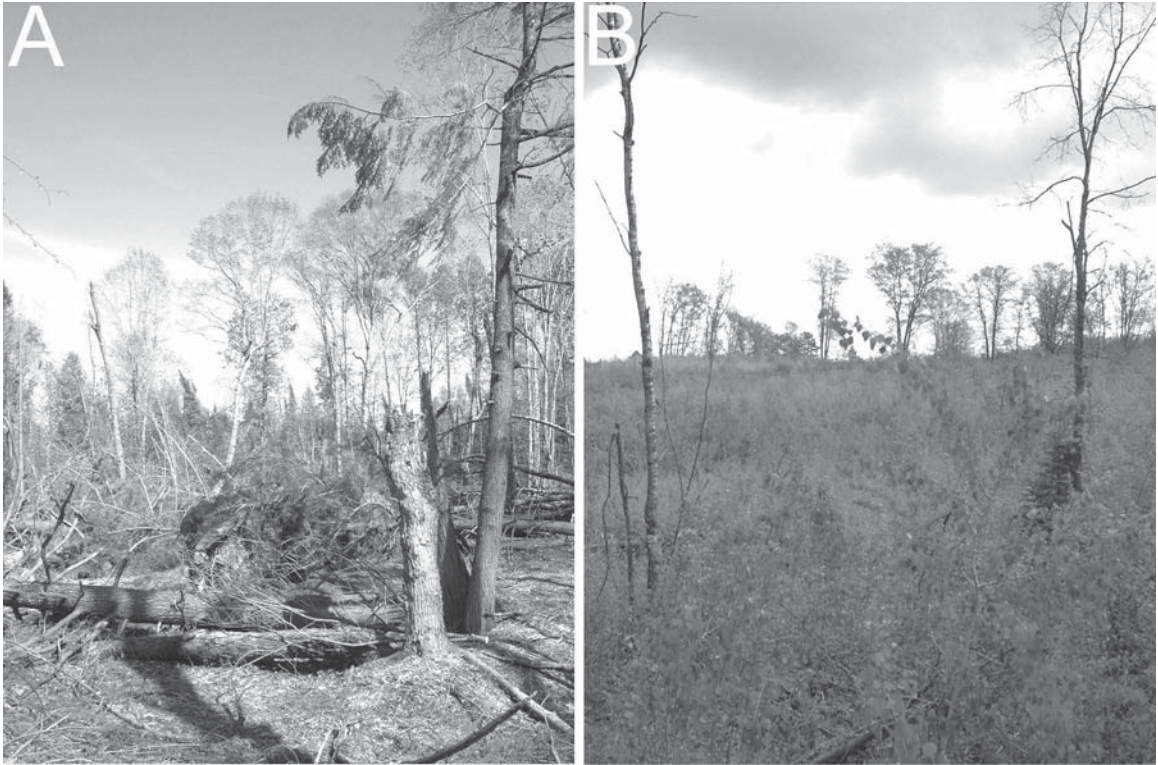


Figure 4.1. (A) Blowdown caused by a thunderstorm down burst in a northern hardwood-hemlock (*Tsuga canadensis*) stand in northern Wisconsin. (B) Commercially-managed aspen stand with retention of hardwood legacy trees, primarily northern red oaks, in northern Wisconsin. Photos courtesy of Christopher Webster.

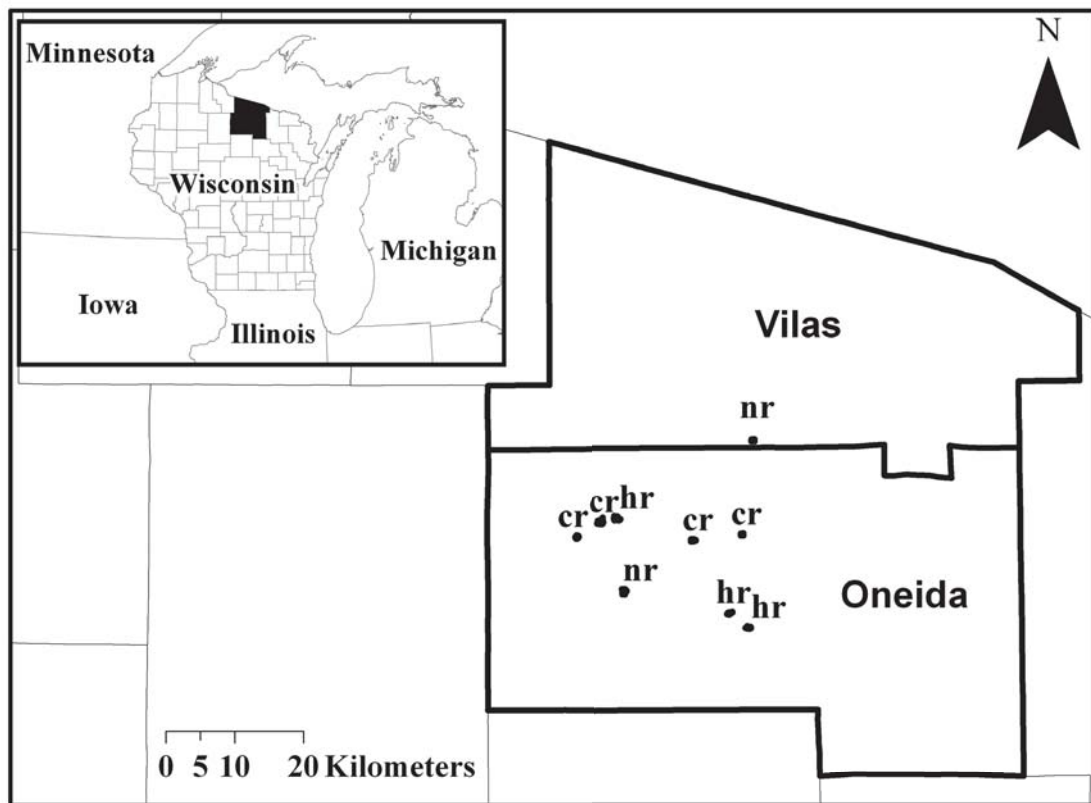


Figure 4.2. Nine aspen forest stands in Oneida and Vilas Counties, Wisconsin. Each stand is labeled by treatment: nr=no legacy tree retention or clearcut, cr=conifer legacy tree retention, and hr=hardwood legacy tree retention.

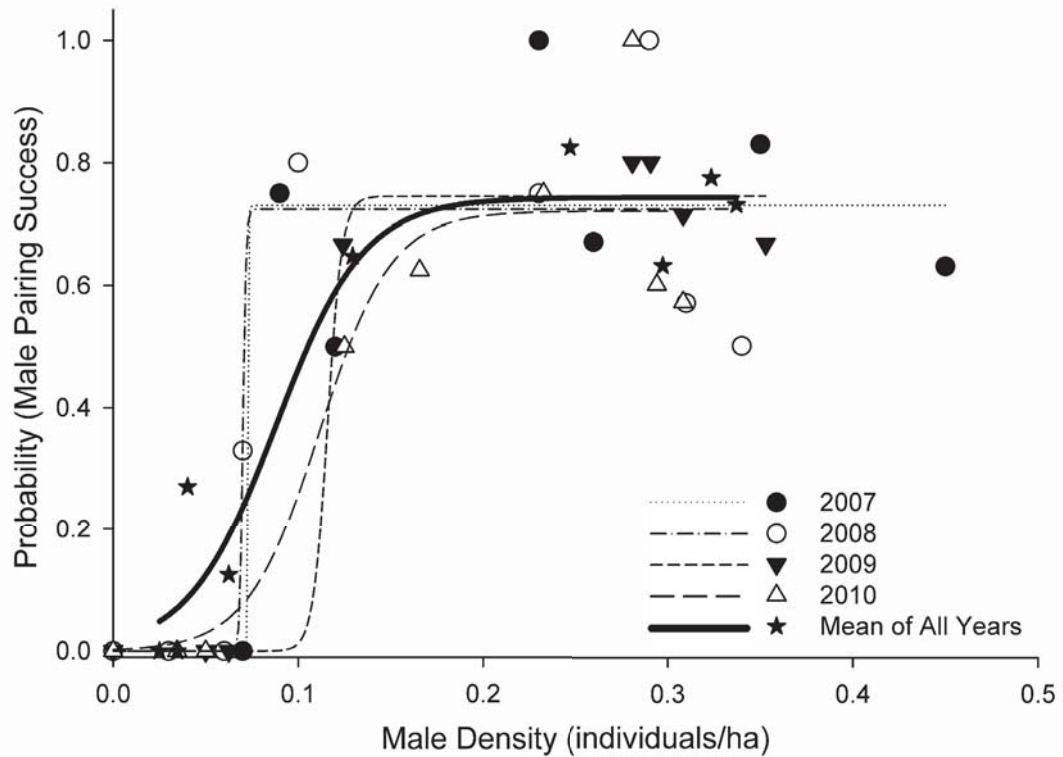


Figure 4.3. Golden-winged Warbler male pairing success was a three-parameter sigmoid function of male density (See Table 4.4 for equations). Data was not transformed for easier interpretation and followed a similar pattern among years. A minimum threshold of 0.1 males/ha appeared to be necessary for pairing success to be greater than 40% (the inflection point of the curve representing the mean male density across years) and a minimum of 0.2 males/ha consistently supported pairing success around 75% (the density where the asymptote of the curve representing the mean male density across years was reached).

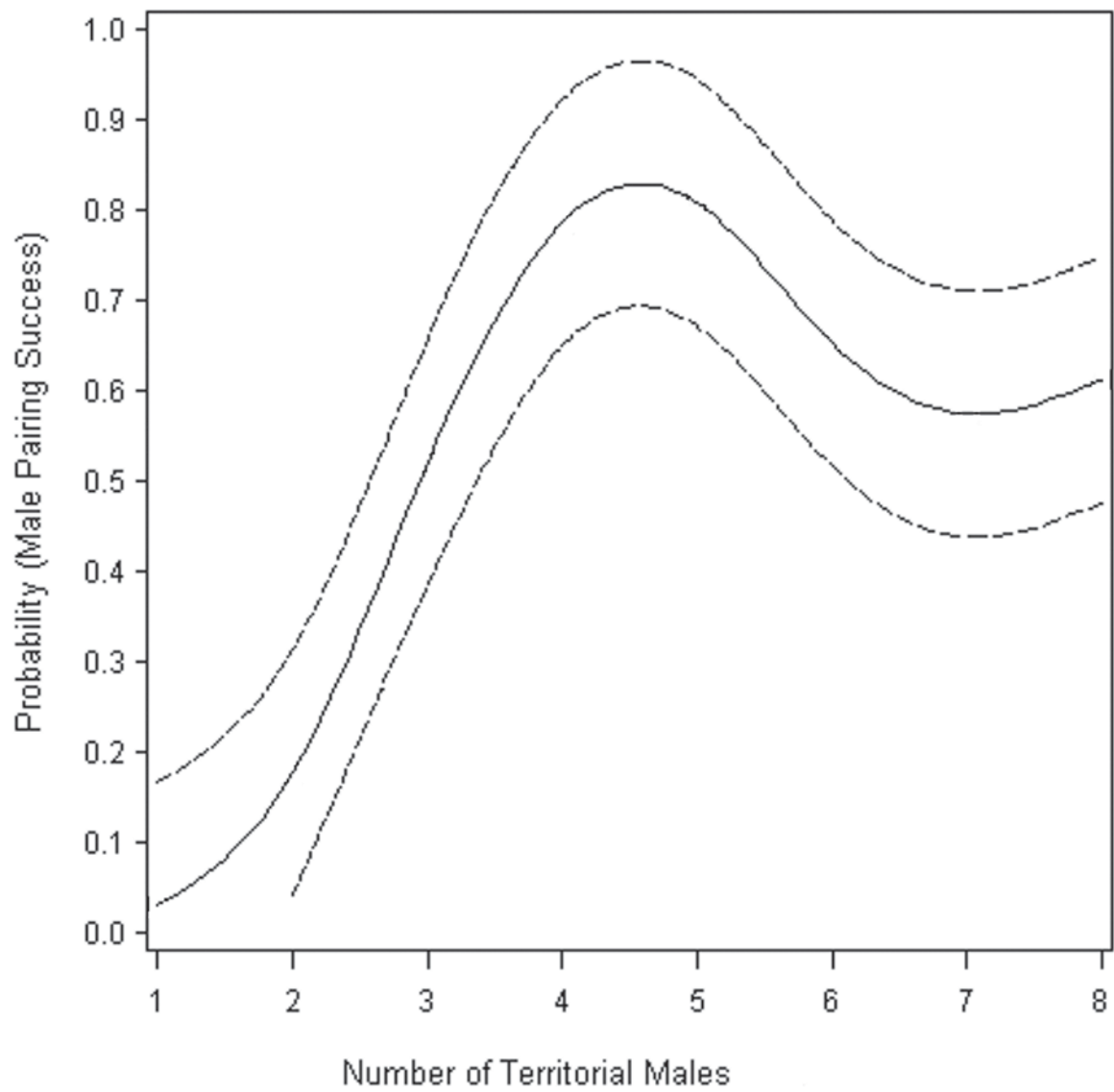


Figure 4.4. Probability of an individual male Golden-winged Warbler's pairing success as a function of the number of territorial males in an aspen forest stand based on the spline from a general additive model. Dashed lines indicate the standard error (0.135) of the spline. A minimum threshold of four males appeared to be necessary to support relatively high pairing success (>60% probability).

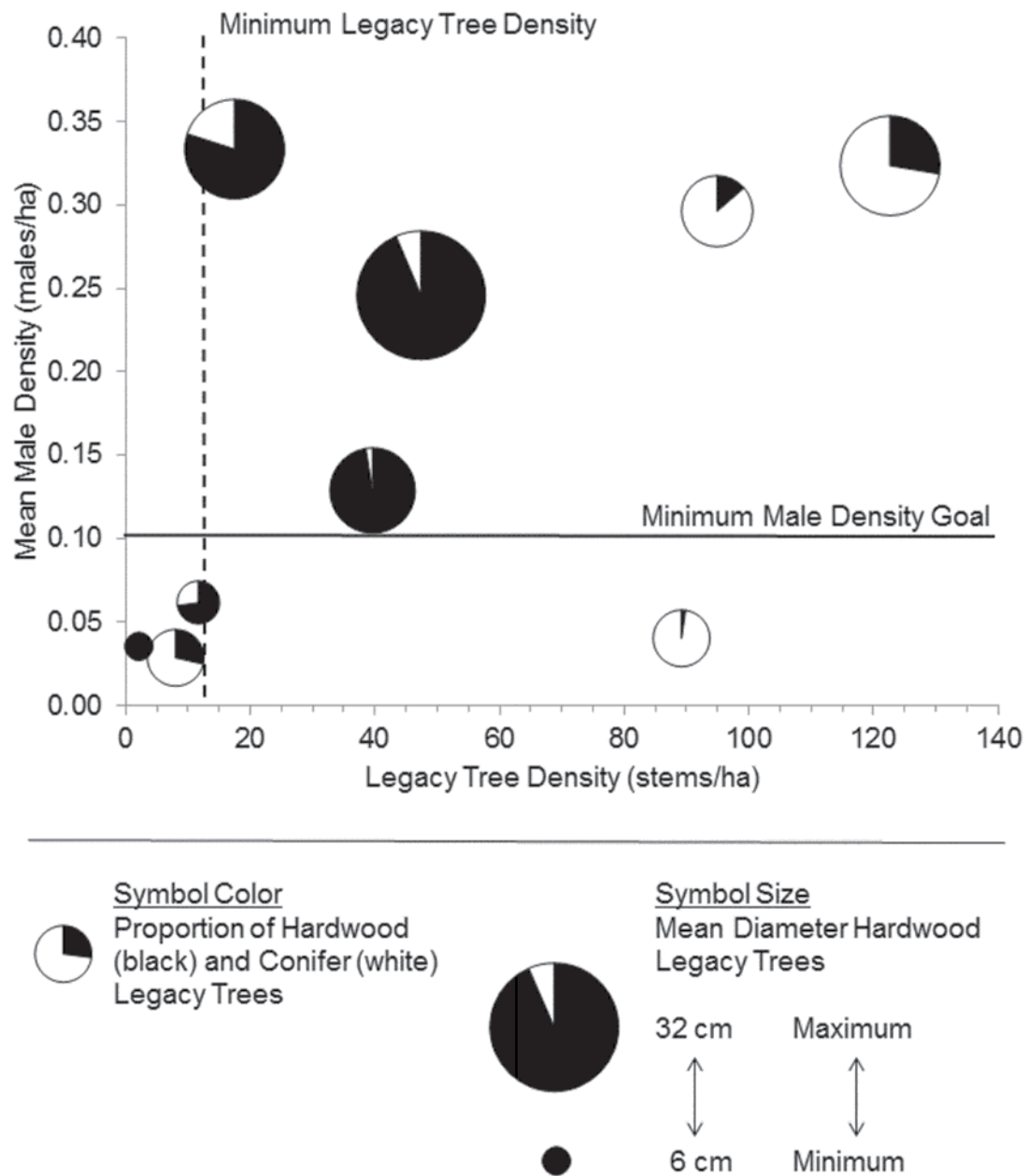


Figure 4.5. Golden-winged Warbler territorial male densities in nine aspen forest stands were related to three legacy tree characteristics: legacy tree density, proportion of hardwood and conifer legacy trees, and size of hardwood legacy trees. Based on Figure 4.3, a minimum density of 0.10 males/ha was needed to obtain >40% pairing success. Large, hardwood legacy trees were an important characteristic of aspen forest stands above the minimum male density goal, particularly at low legacy tree densities.

Table 4.1

Legacy tree characteristics and regenerating aspen stem density (mean \pm 1 se) in young aspen forest stands in three legacy tree retention treatments in Oneida and Vilas Counties, Wisconsin, 2008. Significant differences based on $\alpha=0.05$ between treatments in the post-hoc test comparisons are indicated by different letters.

	Legacy Tree Treatment			$F_{2,6}$	p
	No Retention or Clearcut ($n=3$)	Conifer Retention ($n=3$)	Hardwood Retention ($n=3$)		
<u>Legacy Tree Density (stems/ha)</u>					
Conifers	2.67±1.45 A	86.00±2.08 B	2.33±0.67 A	1012.113	<0.001
Hardwoods	4.00±2.00	16.33±9.39	31.33±9.82	2.981	0.126
All Species	6.67±2.60 A	102.33±10.48 B	33.67±9.62 C	34.919	<0.001
<u>Legacy Tree Basal Area (m²/ha)</u>					
Conifers	0.18±0.13 A	6.10±1.65 B	0.23±0.10 A	28.292 ^a	<0.001
Hardwoods	0.03±0.02	0.57±0.42	2.08±1.08	2.506	0.162
All Species	0.21±0.15 A	6.67±2.06 B	2.31±1.02 AB	6.077	0.035
<u>Legacy Tree Size (dbh, cm)</u>					
Conifers	26.72±6.57	27.83±3.82	34.31±5.65	0.562	0.597
Hardwoods	9.80±2.18 A	16.71±2.76 AB	25.18±3.60 B	7.027	0.027
All Species	12.17±3.46 A	26.15±2.89 B	26.34±3.03 AB	6.712	0.029
<u>Mean Regenerating Aspen Density (stems/ha)</u>					
All Species	1280±184	769±112	1005±320	1.322	0.335

^aBased on a square root transformation of conifer basal area.

Table 4.2

Demographic characteristics for Golden-winged Warblers (*Vermivora chrysoptera*) in young aspen forest stands without legacy tree retention or clearcuts, with conifer legacy tree retention, and with hardwood legacy tree retention in northern Wisconsin. Significant differences based on $\alpha=0.05$ between treatments in the post-hoc test comparisons are indicated by different letters.

	Legacy Tree Retention Treatment					
	No Retention (n=3)	Conifer Retention (n=3)	Hardwood Retention (n=3)	Test Statistic _{df}		p
<u>Mean Number of Territorial Males, mean±se</u>						
2007	0.7±0.7 A	5.3±0.7 B	6.0±1.2 B			
2008	0.7±0.3	5.0±1.2	5.0±0.6			
2009	0.7±0.3	4.3±2.2	5.3±0.3			
2010	1.3±0.3	4.0±2.1	5.7±1.2			
All Years ^a	0.8±0.2 A	4.7±0.7 B	5.5±0.4 B	F _{2,24}	15.915	≤0.001
<u>Mean Territorial Male Density, individuals/ha; mean±se</u>						
2007	0.02±0.02	0.24±0.08	0.27±0.10			
2008	0.03±0.02	0.22±0.08	0.22±0.07			
2009	0.04±0.02	0.22±0.11	0.23±0.05			
2010	0.07±0.03	0.20±0.10	0.23±0.03			
All Years ^a	0.04±0.01 A	0.22±0.04 B	0.24±0.03 B	F _{2,24}	10.569	≤0.001
<u>Male Pairing Success Rate (total territorial males)</u>						
2007	0% (2)	81% (16)	67% (18)			
2008	0% (2)	67% (15)	67% (15)			
2009	0% (2)	62% (13)	75% (16)			
2010	25% (4)	58% (12)	76% (17)			
All Years	10% (10)	68% (56)	71% (66)	χ ² , df=2	14.65	0.001
<u>Number of Nests (% successful^b)</u>						
2007	0 (0%)	7 (71%)	3 (67%)	Fisher's		1.000
2008	0 (0%)	6 (60%)	3 (67%)	Fisher's		1.000
2009	0 (0%)	6 (75%)	7 (57%)	Fisher's		1.000
2010	1 (100%)	6 (17%)	11 (40%)	Fisher's		0.273
All Years	1 (100%)	25 (55%)	24 (52%)	Fisher's		0.671
<u>Productivity, number of fledglings/nesting territory^b</u>						
All Years ^c	5.0±0.0	2.2±0.5	2.2±0.5	H ₂	1.67	0.434

^aANOVA test statistics based on a square root transformation of the dependent variable.

^bCalculation does not include four nests removed due to research-related abandonment.

^cKruskal-Wallis ANOVA on Ranks performed and Tukey Test used for post-hoc pairwise multiple comparisons. Due to small sample sizes of successful nests by legacy tree treatment, data were pooled across years.

Table 4.3

Model-selection results for models of nest survival (S) for Golden-winged warbler daily nest survival rates in aspen forest stands without legacy tree retention or clearcuts ($n=3$), with conifer legacy tree retention ($n=3$), and with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. Four nests that were abandoned due to research-related causes were removed from this analysis.

Model	K^a	AIC_c	ΔAIC_c	w_i	Deviance
$S_{(site)}$	6	149.59	0.00	0.36	137.46
$S_{(intercept\ only)}$	1	149.94	0.35	0.31	147.93
$S_{(legacy\ tree\ treatment)}$	2	150.50	0.91	0.23	146.49
$S_{(site + year)}$	8	153.53	3.93	0.05	137.30
$S_{(year)}$	4	154.90	5.31	0.03	146.84
$S_{(legacy\ tree\ treatment + year)}$	5	154.97	5.38	0.02	144.88

^aNumber of model parameters.

Table 4.4

Nonlinear models relating Golden-winged Warbler (*Vermivora chrysoptera*) territorial male pairing success to male density in aspen clearcuts without legacy tree retention ($n=3$), with conifer legacy tree retention ($n=3$), and with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin. Both dependent and independent variables were transformed in the four yearly models to meet assumptions of normality and equal variances of the errors.

Year	Model	<i>F</i>	<i>p</i>	Pseudo- <i>R</i> ²
2007	$\exp(\text{Male Pairing Success}_{2007}) = 2.390 / (1 + \exp(-(\sqrt{\text{Male Density}_{2007}} - 0.097) / 0.215))$	47.64	<0.001	0.960
2008	$\exp(\text{Male Pairing Success}_{2008}) = 2.351 / (1 + \exp(-(\sqrt{\text{Male Density}_{2008}} - 0.151) / 0.197))$	36.14	<0.001	0.948
2009	$\exp(\text{Male Pairing Success}_{2009}) = 5.273 / (1 + \exp(-(\sqrt{\text{Male Density}_{2009}} - 0.748) / 0.466))$	99.53	<0.001	0.980
2010	$\exp(\text{Male Pairing Success}_{2010}) = 3.742 / (1 + \exp(-(\sqrt{\text{Male Density}_{2010}} - 0.449) / 0.333))$	64.72	<0.001	0.970
Mean of All Years	$\text{Male Pairing Success}_{\text{Mean}} = 0.743 / (1 + \exp(-(\text{Male Density}_{\text{Mean}} - 0.088) / 0.024))$	80.63	<0.001	0.976

Table 4.5

Selection results for linear mixed effects models of Golden-winged Warbler (*Vermivora chrysoptera*) territorial male density in aspen stands without legacy tree retention or clearcuts ($n=3$), with conifer legacy tree retention ($n=3$), and with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. Year was treated as a random effect in each model.

Model	K^a	AIC _c	Δ AIC _c	w_i	Deviance
Density _{(Legacy Tree Stem Density + log(Hardwood Legacy Tree Size))}	5	-59.259	0.000	0.566	35.629
Density _{(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees + log(Hardwood Legacy Tree Size))}	6	-58.703	0.556	0.429	36.800
Density _(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees)	5	-48.438	10.821	0.003	30.219
Density _(Legacy Tree Stem Density + Proportion of Hardwood & Conifer Legacy Trees+ Conifer Legacy Tree Size)	6	-46.983	12.276	0.001	30.940
Density _(Legacy Tree Stem Density + Conifer Legacy Tree Size)	5	-46.880	12.379	0.001	29.440
Density _(Legacy Tree Stem Density)	4	-44.122	15.136	0.000	26.706
Density _(Regenerating Aspen Density)	4	-39.515	19.744	0.000	24.402
Density _(.)	3	-38.068	21.190	0.000	22.409
Density _(Stand Age)	4	-35.586	23.672	0.000	22.438

^aNumber of model parameters.

Table 4.6

Average beta estimates and 95% confidence intervals for parameters based on the top models in Table 5 receiving AIC_c weights for Golden-winged Warbler densities in aspen forest stands with and without legacy tree retention ($n=9$) in Oneida and Vilas Counties, Wisconsin, 2007-2010.

Parameter	β	95% Confidence Interval	
		Lower	Upper
Intercept	-0.172	-0.628	0.283
log (Hardwood Tree Size)	0.160	0.090	0.231
Legacy Tree Stem Density	0.001	0.000	0.002
Proportion of Hardwood & Conifer Legacy Trees	0.097	-0.033	0.226

Table 4.7

Nonlinear models relating Golden-winged Warbler (*Vermivora chrysoptera*) mean territorial male density to three legacy tree density characteristics in aspen stands without legacy tree retention or clearcuts ($n=3$), with conifer legacy tree retention ($n=3$), and with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin.

Independent Variable	Model	<i>F</i>	<i>p</i>	<i>Pseudo-R</i> ²
Legacy Tree Density (LTD)	Mean Male Density = $0.205/(1+\exp(-(LTD-11.164)/0.168))$	14.39	0.001	0.753
Hardwood Legacy Tree Density (HLTD)	Mean Male Density = $0.229/(1+\exp(-(HLTD-8.6941)/0.725))$	17.09	0.002	0.832
Conifer Legacy Tree Density (CLTD)	Mean Male Density = $0.190/(1+\exp(-(CLTD-0.661)/0.406))$	4.52	0.056	0.693
Hardwood Legacy Tree Size (DBH)	Mean Male Density = $0.0.267/(1+\exp(-(DBH-13.977)/0.278))$	20.39	0.002	0.911

CHAPTER 5. Behavioral and Demographic Measures of Edge Effect Reveal Contradictory Patterns for a Migratory Shrubland Songbird

Abstract

The Golden-winged Warbler (*Vermivora chrysoptera*) has frequently been referred to as a shrubland-forest edge associate. Clearcutting aspen (*Populus* spp.) forest creates a distinct shrub habitat edge, often defined by older adjacent forest. We examined the influence of scattered legacy canopy trees in aspen forests managed with green-tree retention on habitat spatial use by male and female Golden-winged Warblers during the breeding seasons of 2007-2010. In northern Wisconsin, we selected nine young aspen stands with three in each of the following legacy canopy tree retention treatments: no legacy tree retention or clearcut, conifer legacy tree retention, and hardwood legacy tree retention. We mapped male territories to examine two response variables, the percentage of male locations in the young aspen stands vs. adjacent habitat and whether male territories overlap the stand edge. Both response variables indicated higher male use of the harvested stand interior vs. the stand edge. Male behavioral patterns suggested that edges were used less or were avoided as the percent of interior harvested stand area increased and as the density of residual canopy trees increased within the harvested stand. Females choose nest sites, so we used nest site selection as an indicator of female avoidance or attraction to harvested stand edges. Median nest distance (67m; $n=50$) into the harvested stand from the edge was greater than the expected median distance compared to a random point distribution (51m). Nest predation did not explain female preference for nesting toward the harvested stand interior and was higher toward the interior of stands with hardwood legacy tree retention but unrelated to edge distance in stands with conifer legacy tree retention. A combined approach of using behavioral and demographic metrics for evaluating edge effects produced contradictory conclusions about edge avoidance or association for this species due to site context. The role of scattered trees, e.g. legacy trees in young aspen stands, to optimize usage of large patches of nesting habitat should be an important consideration for Golden-winged Warbler habitat management and conservation planning.

Introduction

The Golden-winged Warbler (*Vermivora chrysoptera*) is a high conservation priority migratory songbird for which information is needed to describe quality breeding habitat and to create habitat management recommendations for land managers (Buehler et al. 2007). The Golden-winged Warbler nests in young forests and shrublands in forested landscapes of the eastern United States and Canada and has been historically associated with forest edge habitat (Confer et al. 2011). Over eighty years ago, H.O. Green provided a historical account of Golden-winged Warbler nesting habitat in eastern Massachusetts: “For their summer home these birds prefer the border of deciduous woods, where tall trees give plenty of shade, to an adjacent clearing with a growth of briars, bushes and grass, and the nest is usually placed just outside the line of the forest proper, but within the shade of the trees (p. 209; Forbush 1929).” Collins et al. (1982) reported that the Golden-winged Warbler was associated with deciduous edge vegetation though no specific edge metrics were included in their habitat measurements so the edge association seems speculative. DeGraaf et al. (1991) listed the special habitat requirements of Golden-winged Warbler as brushy edge habitats or openings.

Descriptions of Golden-winged Warbler territories also frequently mention a forest edge or border (Ficken and Ficken 1968, Gill and Murray 1972, Confer et al. 2011). Studies specifically investigating territorial characteristics also identify forest edge as a key component (Rossell et al. 2003, Confer et al. 2003). Rossell (2001) found that Golden-winged Warblers preferred tall trees near forest edges (0.6m from edge) compared to randomly selected tall trees (2.3m from edge). Though this was a statistically significant difference, it seems that the habitat studied generally did not have many trees greater than 3m from the forest edge, given that the mean distance for random trees was 2.3 ± 0.6 m. Frech and Confer (1987) mentioned that territories may extend up to 20m into adjacent forest.

Golden-winged Warbler nesting habitat is generally characterized by the following components: 1) dense herbaceous cover, 2) patches of shrubs, and 3) tall trees often at the territory border (Confer et al. 2011). Nests are located on the ground and frequently at or near the edge between the relatively recently disturbed open-habitat and mature

forest (Ficken and Ficken 1968, Will 1986, Demmons 2000, Kubel 2005, Patton et al. 2010).

Based on this evidence, it is not surprising that the Golden-winged Warbler has received the label as a forest edge associate (e.g. Hanowski et al. 2006, Bowen et al. 2007, Patton *et. al.* 2010) though this label has been found unwarranted in many other shrub-scrub bird species (Schlossberg and King 2008). We suggest that the Golden-winged Warbler's association with forest edges is not a universal characteristic of habitat selection in this species and is partly an artifact of two ways that past study areas were chosen. First, some studies were conducted in patches of habitat too small to allow territories to occur away from edges. For example, Kubel (2005) studied aspen clearcuts in Pennsylvania that were cut as 1-ha blocks with little or no "interior" habitat. Roth and Lutz (2004) observed that 10% of Golden-winged Warbler territories within aspen clearcuts did not include the clearcut edge and speculated that this was due to continuous shrub cover across the clearcuts along with the fact that some clearcuts were large enough (>55 ha) for territories to be located away from edges. They speculated that if patches of continuous habitat were large enough, Golden-winged Warblers would not be restricted to the edges.

A second pattern of past studies was that they were located in the eastern USA and Canada where the focus has been on abandoned farmland (or, similarly, reclaimed minelands in the Appalachians) surrounded by forest or on wetland-forest ecotones. Roth and Lutz (2004) suggested that these past studies have focused on habitats where the pattern of woody succession and encroachment would result in rings of habitat around the field periphery where woody vegetation encroaches from the forest boundary. Confer (1992) suggested that the middle of large fields may not provide the forest edge usually part of territories thus implying that trees are generally absent in the field interior. Similarly, in wetland-forest ecotones, trees and shrubs are sometimes more prevalent at the wetland edge adjacent to forest and decrease in cover as the site grades toward wetter soil and eventually into deeper water where herbaceous vegetation becomes dominant and trees are absent. Based on these successional patterns, Golden-winged Warbler territories would be expected to occur in the forest-shrub

ecotone particularly in the absence of tall canopy trees and shrubs in the field or wetland interior.

Here, our objective was to evaluate Golden-winged Warbler spatial use of breeding habitat when breeding pairs are presented with large, continuous patches such that adequate area is available for birds to choose territories near or far from the edge of recently harvested aspen stands. Commercially managed aspen (*Populus* spp.) stands provide an ideal system to investigate breeding territory selection because the size of the habitat patch and the retention pattern of tall trees can be controlled. Golden-winged Warblers are known to be present in high densities in young aspen clearcuts in northern Wisconsin (Roth and Lutz 2004, Martin et al. 2007). Typical timber harvest prescriptions, such as clearcutting, for aspen forest usually creates a distinct edge between the regenerating aspen and surrounding forest that is usually older and thus contains tall trees. Newly harvested aspen stands provide all of the critical nesting habitat components including dense herbaceous cover and patches of shrubs and regenerating aspen trees continuously throughout the clearcut area (Roth and Lutz 2004).

One potential difference between silvicultural prescriptions for aspen forest is whether or not tall canopy trees are retained during the timber harvest, also called green-tree retention. We hypothesized that when tall trees are found throughout a large timber harvest, Golden-winged Warbler territories and nests will be found throughout the stand. In contrast, when the only tall trees are found in an adjacent forest stand, i.e., at the harvest area edge, we expected to find territories restricted to the harvested stand edges. Similarly, Patton et al. (2010) suggested that the lack of residual mature trees in a reclaimed mine area may restrict Golden-winged Warbler use to the edges adjacent to mature forest and proposed a similar hypothesis as ours. They suggested that by increasing the number of scattered mature trees across mine lands away from the mature forest edge could increase use of mine lands in places where Golden-winged Warblers are currently absent. Specifically, we evaluated the effects of legacy tree retention on spatial use by both male and female Golden-winged Warblers in young aspen stands and identify the mechanisms for observed spatial patterns. We also hypothesized that nest success is unrelated to nest distance to the stand edge based on a similar study system in Minnesota (Hanski *et al.* 1996).

Methods

Study area

We selected nine young aspen-dominated forest stands in Oneida and Vilas Counties, Wisconsin (45° 43'N, 89° 32'W; Figure 5.1) in an area defined by glacial moraines and outwash plains. We selected stands with similar soil types, tree composition, structural characteristics, and management history. Soils were characterized as sand, sandy loams, or loamy sands and ranged from moderately well drained to excessively drained (Soil Survey Staff 2010). Three aspen stands were selected for each of three legacy tree retention prescriptions: 1) no legacy tree retention or clearcut, 2) conifer legacy tree retention, and 3) hardwood legacy tree retention. Aspen stands were dominated by *Populus tremuloides* and *Populus grandidentata* and included other abundant regenerating species especially *Acer rubrum*, *Amelanchier* spp., *Prunus serotina*, *Quercus rubra*, and *Betula papyrifera*. The dominant shrubs were *Rubus* spp. and *Corylus* spp. Legacy trees were primarily *Pinus strobus*, *Pinus resinosa*, and *Quercus rubra*. Stands ranging from 17-48 ha were commercially harvested between 1996 and 2001 thus the regenerating aspen was 4-7 years-old at the start of the study in 2007. Timber harvest prescriptions called for removal of all aspen and most other tree species with retention of large diameter pine and oak species. Clearcuts contained a small number of scattered legacy trees that were retained for unknown reasons. All sites were selected without prior knowledge of Golden-winged Warbler occupancy.

Field Methods

Golden-winged Warbler territory and nest surveys were conducted 10 May-2 July 2007, 19 May-21 July 2008, 19 May-15 July 2009, and 16 May-3 July 2010. We captured unbanded territorial adult male Golden-winged Warblers and a few adult females across all sites. Males were targeted for capture using mistnets with tape playback (Kubel and Yahner 2007) and then given a unique color band combination including a silver U.S. Fish & Wildlife Service band for individual identification.

Other studies have used male territory placement to evaluate spatial relationships of forest passerines relative to forest edges (Kroodsma 1984, King et al. 1997). We mapped locations for all territorial males using a modification of the protocol by Robbins

(1970). Surveys for the same individual or stand were conducted at least three days apart. When possible, we used teams of two observers with one observer recording locations on a map and marking perches while the second observer tracked the bird. Because of dense vegetation, it was difficult to continually track a bird and thus considerable time was spent checking bands to make sure the same individual was resighted before resuming the survey. Unique individuals were tracked until the observer(s) completed a full circuit of the bird's territory such that the bird primarily began using marked perch trees. Mapping continued on subsequent visits until the male was primarily using marked perch trees. Unbanded males prior to capture were identifiable by unique song characteristics, favorite song perches, discrimination from banded neighboring males, and/or other characteristic behaviors. We did not survey males into the fledgling period. All perches were flagged and coordinates were collected later with a handheld Trimble XM Geographic Positioning System (GPS). Only males present on a minimum of eight site visits spanning a minimum of 22 days were included in analyses. Based on the GPS locations, we used the Hawth's Tools Extension in ArcMap (ESRI 2010) to generate minimum convex polygons to delineate territorial boundaries. Male locations were identified as at or beyond the harvested stand edge if a point was within a 5m buffer of the stand edge or outside of the stand boundary. The 5m buffer was chosen given that a Trimble XM GPS has an accuracy of 1-3m thus this would capture any positioning errors (see www.Trimble.com for equipment specifications).

Nests were located by searching the entire stand for females exhibiting nesting behavior, adults feeding nestlings, and good potential nest sites within male territories. Nests found during nest building were not revisited until it was likely that the nest had a complete clutch of eggs to avoid abandonment by the female (Confer et al. 2011). Only nests with at least one egg were included in analysis; nests abandoned prior to egg laying were omitted. After nests were no longer in use, we used the GPS to collect the nest site coordinates.

To determine legacy tree density in young aspen stands, we randomly established ten 1000-m² circular plots in each stand separated by at least 30 m. We defined legacy trees as trees that were retained during the most recent harvest rotation and were identified as

live trees with diameter at breast height (DBH) at least 5 cm greater than the DBH of surrounding regenerating aspen trees. All of these trees were ≥ 10 cm DBH and classified as emergent. These plots were visited 19 May-14 August 2008. For each tree with DBH ≥ 10 cm, we recorded species, DBH, and whether it was alive or dead. Dead trees were not included in the analyses.

Harvested stand boundaries were acquired through one of three methods. Wisconsin Department of Natural Resources provided shapefiles of stand boundaries for state-owned lands. For sites with no electronic data, we delineated the boundary from a digital orthoquad photo for stands with clear boundaries; and for stands where boundaries could not be delineated with this method, we used the GPS to map the boundary in the field.

Data Analysis

Means and standard errors of the mean are reported as mean \pm 1 se.

Territorial Male Spatial Behavior

To determine if the percentage of male locations at or beyond the harvested stand edge and territories overlapping the edge varied by legacy tree retention treatment, we conducted a one-way analysis of variance (ANOVA) in SAS version 9.2 (SAS Institute Inc. 2008). Year effects were evaluated using ANOVA for male locations and chi square for territory placement. To assess the mechanisms for the observed spatial differences in male spatial use, we treated each male's observations independently as a random effect due to the potential lack of independence between observations for the same male in different years. The percent of territorial male locations at or beyond the harvested stand edge is a continuous variable and thus we used a general linear mixed effects modeling procedure (GLIMMIX) with individually identified males (i.e., color-banded) as the random effect in SAS version 9.2 (SAS Institute Inc. 2008). Across the four years, there were 132 territory records for 91 distinct males. Of these, 12 territories included the harvested stand edge adjacent to another aspen forest of similar enough age and structure to be deemed indiscernible by the birds and thus were not indicated as overlapping an edge in the analyses.

Male territory placement relative to the stand edge was a binary variable (0=no overlap with edge or “interior”, 1=overlap with edge) so we used a nonlinear mixed effects modeling procedure (NLMIXED) with individual males as the random effect in SAS. Sample sizes were the same as for the GLIMMIX procedure. Initial parameter values were derived from output of the GLIMMIX procedure, though a grid was used for the random effects variance. Differences in parameters between territories at the stand edge versus the stand interior were performed using a Mann-Whitney Rank Sum test given that the variables were not normally distributed.

We used a multimodel inference approach to evaluate the suite of nine *a priori* models for each male dataset (Burnham and Anderson 2002). The best model for each dataset was identified based on the smallest Akaike Information Criterion score adjusted for small sample sizes (AIC_c) though models with an AIC_c value within 2.0 were considered competitive. AIC_c values and their associated log-likelihood scores were generated by the NLMIXED and GLIMMIX procedures in SAS. The parameter statistics for the best models were generated by these same procedures.

The nine *a priori* models were based on a literature review and our hypothesized role of legacy trees as an important habitat component. Model variables included stand interior area (Batary and Baldi 2004), percent interior area (i.e., stand interior area/stand area*100; Batary and Baldi 2004), edge density (i.e., harvested stand perimeter-to-area ratio; Spanhove et al. 2009a), legacy tree density (stems/ha), size of legacy trees (i.e., mean DBH), and year. Legacy tree size was only used in models that also included legacy tree density because legacy trees must be present in order for their size to be a factor. Legacy tree basal area was highly correlated with legacy tree stem density (Adj. $R^2=0.916$, $F=88.291$, $P\leq 0.001$) based on a log transformation of both variables and was not included as a separate model.

Geometric values for stand interior area, percent interior area, and edge density were calculated in ArcMap. Interior area was defined as being 50m from the harvested stand edge based on this generally being the distance that explains edge-related nest predation impacts (Batary and Baldi 2004). All territories and male locations regardless of position within a stand were attributed the variable values of that stand.

Nest Placement and Predation Rates

To determine if female Golden-winged Warblers avoided nesting near edges, we compared nest distances to random distances from the harvested stand edge. We used the Create Random Point tool within ArcMap to generate the random points with the same number of random points as there were nests for each aspen stand. We used ModelBuilder to generate 30 and 50 iterations of random point sets. Thus the total number of random points in a set was equal to the total number of nests found across all four years of the study. We used the Near tool in ArcMap to measure the distance between nests or random points and the nearest stand edge. There was no difference in the number of random points in five distance categories between 30 and 50 iterations so the means were considered converged. The range of distances for each category was determined based on equal division of random points into five categories. Given that the random point data was not normally distributed, differences in median distances to edge for nests and random points were compared using a nonparametric Mann-Whitney Rank Sum Test. To determine whether nest sites were concentrated at varying distance, we used a chi square analysis to compare observed nest distances to expected random point distances in the five discrete distance categories.

Nest predation is one mechanism that may influence whether birds choose to nest near or far from clearcut edges (Lahti 2001). Nest predation rates were based on Mayfield (1961), and exposure days were calculated based on the first date of eggs or nestlings observed in the nest until nest failure or fledging of nestlings. The nest period was 24 days based on 4 days for egg laying, 11 days for incubation, and 9 days for the nestling period (Bulluck and Buehler 2008). Based on nests with known hatch and fledge dates ($n=5$), our nestling period was 9 days rather than 10 days as in Bulluck and Buehler (2008). Mean clutch size was 4.6 ± 0.1 (median=5) and incubation was assumed to begin on the day that the last egg was laid. To test the hypothesis that nest failure due to predation of eggs or nestlings is related to distance from the harvested stand edge, we fitted a simple logistic regression to the data with nest success (0) or failure due to predation (1) as the dependent variable and distance to stand edge as the independent variable using SigmaStat 3.5 (Systat 2006). Nests that were abandoned or had unknown outcomes were omitted from this analysis. The simple logistic regression model used was:

$$\text{Predicted logit of (NEST_FATE)} = \beta_0 + \beta_1 (\text{EDGE_DISTANCE})$$

where β_0 is the Y-intercept and β_1 is the regression coefficient. The likelihood ratio test was used to evaluate the overall model. The Hosmer-Lemeshow test was used to evaluate goodness-of-fit.

Results

We marked 462 territorial male locations in 2007, 311 locations in 2008, 304 locations in 2009, and 332 locations in 2010. Only 11% of these locations were at the edge of the harvested stands or in adjacent mature forest. There was no year effect for the percentage of territorial male locations at or beyond the harvested stand edge ($F_{3,128}=1.29$, $p=0.28$) and male locations related significantly to legacy tree retention treatments ($F_{2,129}=5.17$, $p=0.007$; Table 5.1). Edge density was the most parsimonious model explaining the variation in male locations though the percent of interior stand area was also considered a competitive model (Table 5.2). These variables were highly correlated (Pearson $r=-0.91$) and likely reflect similar information about harvested stand geometry. The percentage of male locations at the edge increased as edge density increased and as interior stand area became smaller (Table 5.3, Figure 5.2). Harvested stands with edge density >125 had large standard errors; the two with the longest error bars had small sample sizes for number of territories ($n=2$ and 4).

We mapped territories for 36 males in 2007, 32 males in 2008, 31 males in 2009, and 33 males in 2010. Thirty-two (24%) of these territories included the harvested stand edge based on at least one male location at or beyond the stand edge. There was no year effect for the percentage of territories that included the stand edge ($\chi^2=0.592$, $df=3$, $p=0.90$) and these differed by legacy tree retention treatment ($F_{2,27}=4.519$, $p=0.02$; Table 5.1). Examples of minimum convex polygons for two aspen forest stands, one is a clearcut (Figure 5.3a, b) and the other a stand with conifer legacy tree retention (Figure 5.3c, d), show the typical spatial relationship of territories to harvested stand edge. Territories overlapping the stand edge had significantly higher edge density and legacy tree size than territories in the stand interior (Table 5.4). Interior territories were

associated with significantly higher stand interior area and higher legacy tree density than edge territories (Table 5.4). Of these, the combination of legacy tree density and legacy tree size best explained the difference in likelihood of a territory being at the edge or toward the interior of the harvested stand (Table 5.2).

We found and monitored 50 Golden-winged Warbler nests across four years, 2007-2010 (Table 5.5). Median nest distance from stand edge (67m) was significantly greater than for random points (51m; $U=52350.0$, $p=0.049$). There were fewer nests than expected within 39.8m of the stand edge and more nests than expected at 63.2-233.6m from the stand edge ($\chi^2=12.08$, $df=4$, $p=0.017$; Figure 5.4).

Successful nests were closer to the stand edge than depredated nests ($p=0.002$, $n=41$; Table 5.6). Successful nests averaged 51 ± 7 m from the edge compared to depredated nests that averaged 91 ± 10 m. When the nests were analyzed by legacy tree treatment (omitting clearcuts as there was only one nest), the observed relationship was similar between nests in stands with hardwood legacy tree retention ($p=0.016$, $n=20$; Table 5.6) and nests in stands with conifer legacy tree retention ($p=0.040$, $n=20$; Table 5.6).

Discussion

Spatial Use by Territorial Males

Male spatial behavior provided evidence for stand edge avoidance. Males were found less frequently at the edges when there was a large enough interior in the harvested area, with relatively low edge density, for them to defend a territory away from edges. This supports the hypothesis of Roth and Lutz (2004) that given a large enough patch of continuous habitat, Golden-winged Warblers distributed their territories throughout the site including the harvested stand interior and without concentration at the edges. However, our study had a much higher ratio of males with interior territories (63-76%) compared to the 10% reported in Roth and Lutz (2004). This suggests that a large interior area for territories to be positioned away from the clearcut edge is inadequate alone but that other clearcut characteristics contribute to explaining the spatial patterns observed.

Whether a territory overlapped the harvested stand edge or not was best explained by the stem density and size of legacy trees. Though the size of legacy trees was statistically different between territories at the edge versus the interior, the 1 cm difference in mean diameter was not likely meaningful from the birds' perspective. Thus legacy tree density was more likely to be driving the relationship. Legacy tree densities in stands with legacy tree retention supported a majority of territories in the interior as compared to clearcuts where most males had territories at the edge. The conifer retention treatment had the highest stem density and, as expected, the clearcut treatment had the lowest stem density; stem density in the hardwood retention treatment was intermediate. This is consistent with observed differences in spatial territory patterns observed between legacy tree retention treatments.

The combination of large interior area with low edge density and scattered canopy trees (e.g. stands with legacy tree retention) was necessary for territories to occur throughout a large site. Our results also suggest that creation of breeding habitat with high edge density is not necessary if legacy trees are retained throughout the stand during aspen cutting which is an important consideration for other forest birds that may be edge sensitive. Our data suggest that large patches of breeding habitat can be created as long as legacy trees are retained throughout the site. Though the behavioral evidence suggests that harvested stands with interior area > 2 ha (i.e. >1 ha of suitable nest habitat more than 50m from harvested stand edges) and retention of legacy trees may be preferred, an understanding of demographic characteristics such as nest success or fledgling survival is necessary to evaluate the overall quality of habitat.

Spatial Use by Nesting Females

Our nest site selection data suggested that Golden-winged Warblers either preferred to nest away from harvested stand edges or that the spatial arrangement of suitable nest sites varied between sites. Nest sites were frequently located near logging roads and may contribute to the observed patterns (Figure 5.5). Anecdotally, logging road location may account for the location of the seven nests within 10m of the harvested stand edge. Six of these were from the same site where the main logging road delineates the southern edge of the harvest area (Figure 5.5b) and provides many of the best nesting sites at the road margins. The rest of this stand either contained dense aspen with low

herbaceous cover or extensive herbaceous cover lacking shrubs in large oak openings. The other stands in the study appeared to provide suitable nest sites at both the harvested stand edge and throughout the rest of the harvest interior area providing birds with a greater selection of nest sites at varying distances.

Our results differ from other nesting studies for this species where nests were generally located at or near the edge between the open, shrubby habitat and adjacent mature forest (Ficken and Ficken 1968, Will 1986, Demmons 2000, Kubel 2005, Patton et al. 2010). Kubel (2005) is the only other Golden-winged Warbler nest study in aspen clearcuts where nesting distance to forest edge (mean of 9.9m) was measured; clearcut area was 1.0 ha so nest placement would necessarily be within 50m of the edge. Rodewald and Vitz (2005) found that seven of eight shrubland birds, including the closely related Blue-winged Warbler (*Vermivora cyanoptera*), tended to avoid clearcut edges bordered by mature forests based on mist net capture locations. They rejected spatial variation in food resources and habitat characteristics as explanations for the observed edge avoidance and proposed nest predation as a possible mechanism.

Nest predation in our study was higher toward the interior of aspen stands with hardwood legacy tree retention. However, this result is based on a small number of nests ($n=11$) across three distance categories spanning nearly 200m so results should be interpreted cautiously. Nevertheless, other bird studies found a similar pattern of lower nest predation near clearcut-mature forest edges (Storch 1990), in forest fragments bounded by terrestrial habitat (Small and Hunter 1988), and in forest-farmland edges with the use of artificial nests (Santos and Telleria 1992, Spanhove et al. 2009b). Also, our results were consistent with known patterns of edge effects on avian nest success due to two key characteristics of our study identified as important by Batary and Baldi (2004): 1) use of natural, ground nests and 2) the hardwood legacy tree retention treatment being applied to harvest deciduous forest. Woodward et al. (2001) investigated the relationship between natural nest placement and nest predation rates at varying distances to edge in shrublands adjacent to forest and found either no relationship between the two metrics with distance to edge (three species) or that preferred nest placement distances were correlated with low predation rates (two species) suggesting that some species may select nest sites based on accurate

knowledge of nest predation risk. Our results from the aspen stands with hardwood retention suggest that Golden-winged Warblers may not be selecting nest sites based on nest predation risk or that this risk is spatially and/or temporally inconsistent.

If nest predation is indeed higher toward the interior of harvested stands with hardwood legacy tree retention, additional study is needed to understand the mechanism for this pattern. Based on six other ground nesting songbirds at the same sites, no relationship was found between nest predation rate and distance to harvested stand edge for all species combined ($p=0.721$) or for individual species ($p=0.16-0.78$; Roth unpublished data) which is consistent with other studies in similar study systems using natural nests (Yahner and Wright 1985, Yahner 1991) and artificial nests (Ratti and Reese 1988, Rudnicki and Hunter 1993, Hanski et al. 1996). We hypothesize that the observed nest predation pattern was a result of Golden-winged Warblers selecting nest sites with characteristics that were different from other species and this put them at higher risk of nest predation by a specific predator or predator guild (i.e., avian versus mammalian). Perhaps nest sites with relatively high herbaceous vegetation and low shrub cover resulted in higher predation rates (Chasko and Gates 1982) and attracted a specific nest predator species that is associated with the same microhabitat preferences and with higher abundance in the harvested stand interior.

Hansson (1994) found that there is a difference between the vertebrate community in large clearcuts versus adjacent mature forest with at least one small mammal (*Microtis agrestis*) being more abundant in clearcut interiors than at the edges. He hypothesized that low nest predation rates near clearcut edges may be a result of high rates of predation by owls on small mammals. The relative role of specific mammalian nest predators is context dependent and varies by availability and abundance of alternate prey species (Angelstam et al. 1984), relative influence of direct (predation) and indirect (competition with other predators) pathways (Schmidt et al. 2001), patch size (Arango-Velez and Kattan 1997), forest stand age (King et al. 1998), and composition and relative abundance of species within the predator community (Nour et al. 1993). Also, pulses in mast production for oaks (Schmidt 2003, Schmidt and Ostfeldt 2008) and pines (Huhta et al. 1996, King et al. 1998) are known to influence nest success and predator population dynamics, and the asynchronous mast pulses of oaks and pines may factor

into the observed treatment difference though it is not likely the sole predictor of nest predation given that other ground nesting songbirds did not show the same inverse relationship with edge distance. Identification of the primary predators for Golden-winged Warbler nests and information about their spatial, temporal, and interspecific interactions are critical to understanding the species-specific patterns of nest predation observed in this study and may be a better approach to understanding nest predation dynamics (Lahti 2001).

We found no relationship between nest predation and distance to edge in harvested aspen stands with conifer legacy tree retention and yet we did find such a relationship among stands with hardwood legacy tree retention. This suggests that in otherwise similar habitat types, the type of legacy tree may influence patterns of nest predation. As others have concluded, site context is critical to understanding predation rate patterns (Lahti 2001, Chalfoun et al. 2002).

We hypothesized that the lower use of edges and the higher than expected nest placement away from edges was due to higher nest predation rates near the harvested stand edges. We reject this given that there was no relation to edge distance in one legacy tree treatment and an inverse relationship between nest predation and proximity to edge in the other. The latter case suggests that the harvested aspen edge may provide higher quality habitat in hardwood legacy tree retention sites and contradicts the male behavioral metric results indicating that territorial males have a spatial preference for the interior of harvested stands. The quality of edge habitat appears to be context dependent even for sites such as ours that were selected for similar structural characteristics, landscape context, and management history. A notable difference between stands was the composition of the legacy trees, with the conifer legacy tree retention sites dominated by pines and the hardwood legacy tree retention sites dominated by oaks. Another difference between clearcuts was legacy tree density which may affect microhabitat conditions for nest predators. These two variables should be considered in future research and their effects on nest predation and nest predator dynamics.

Conclusions

Our findings suggest that labeling the Golden-winged Warbler as an edge associate is overly simplistic given that this species' relationship with habitat edges varies with site characteristics. Labeling any species as edge-associated should be done cautiously and only with an understanding of both behavioral and demographic characteristics. The implications are that apparent edge avoidance or association by shrub-scrub bird species depends on habitat context and can be inconsistent among different demographic metrics. It is critical to understand this for the Golden-winged Warbler given its high conservation status and the need to understand conditions for providing optimal breeding habitat quality. Conservation planning for this species should consider the role of legacy tree retention and nesting habitat geometry in forest management recommendations. Contrary to some past guidance (Confer 1992), creating habitat with a distinct forest-shrub edge or a high density of mature forest edge is not necessary to provide nesting habitat for this species.

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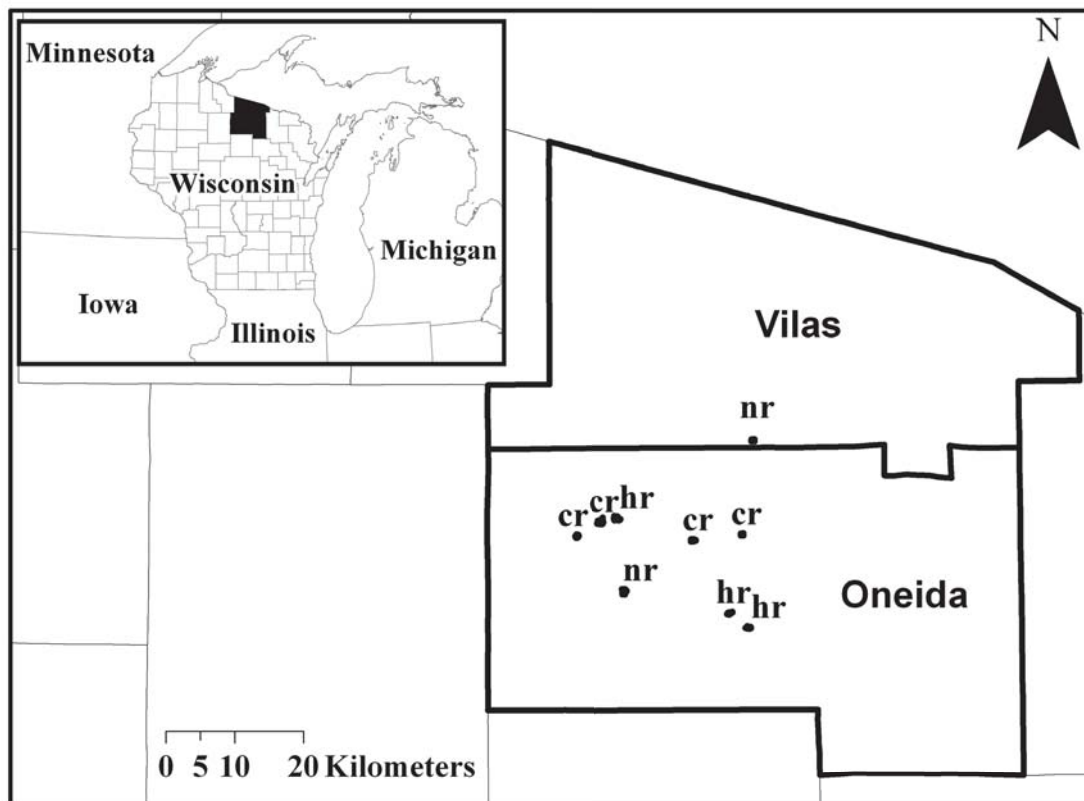


Figure 5.1. Nine aspen forest stands in Oneida and Vilas Counties, Wisconsin. Each stand is labeled with treatment: nr=no legacy tree retention or clearcut, cr=conifer legacy tree retention, and hr=hardwood legacy tree retention.

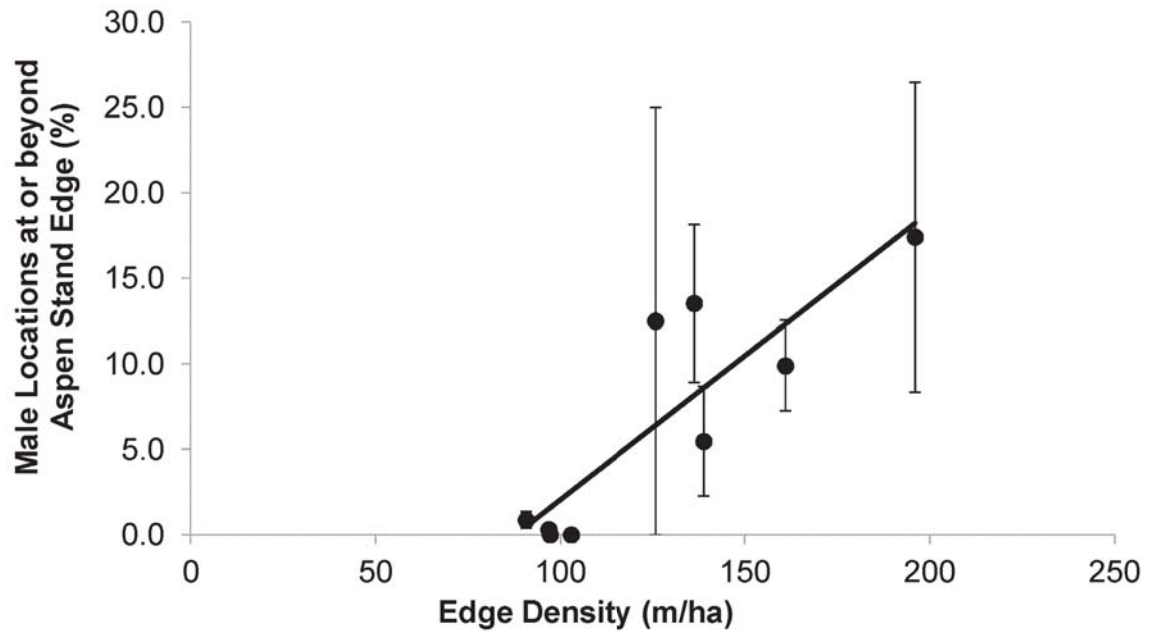


Figure 5.2. Percentage of Golden-winged Warbler male territory locations on or beyond the aspen forest stand edge as relates to edge density. Standard errors bars reflect low sample sizes for the number of territories in two stands with the longest error bars or the greater variability in male locations due to higher edge density in the case of the other three stands.

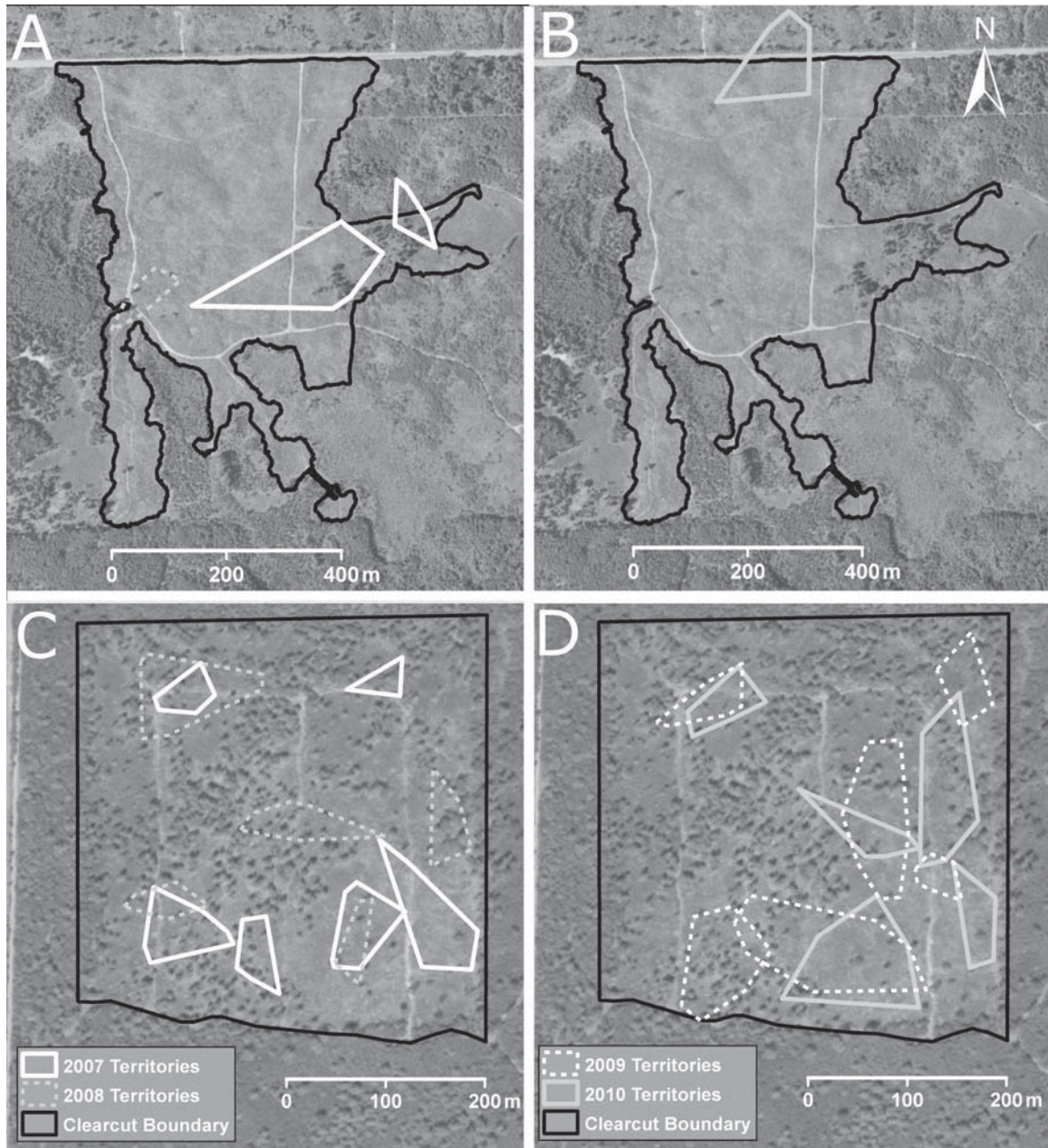


Figure 5.3. Golden-winged Warbler territories mapped in 2007-2010 in an aspen clearcut (Photos A and B) and in an aspen stand with conifer legacy tree retention (Photos C and D). Territories are projected on a digital orthoquad air photo from 2005 for clearer harvest boundaries and easier identification of legacy trees. Note that the clearcut does contain a cluster of legacy trees on the east side and a few scattered trees elsewhere that appear to attract territorial males to these areas in addition to using the clearcut's edge. The territories in the stand with conifer legacy trees do not include the edge of the harvested area. For this site, the southernmost point of the 2009 territory in the southwest corner is actually 10m north of the harvest boundary and does not overlap it as it appears on the map.

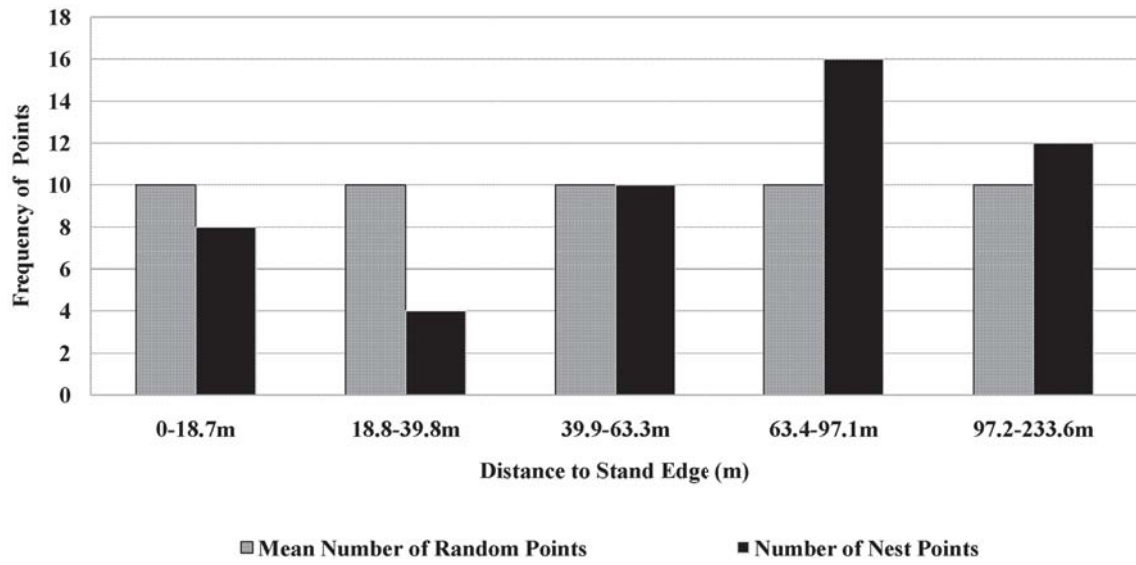


Figure 5.4. Golden-winged Warbler nest locations were farther from the harvested stand edge than we expected based on random points ($\chi^2=12.08$, $df=4$, $p=0.017$).

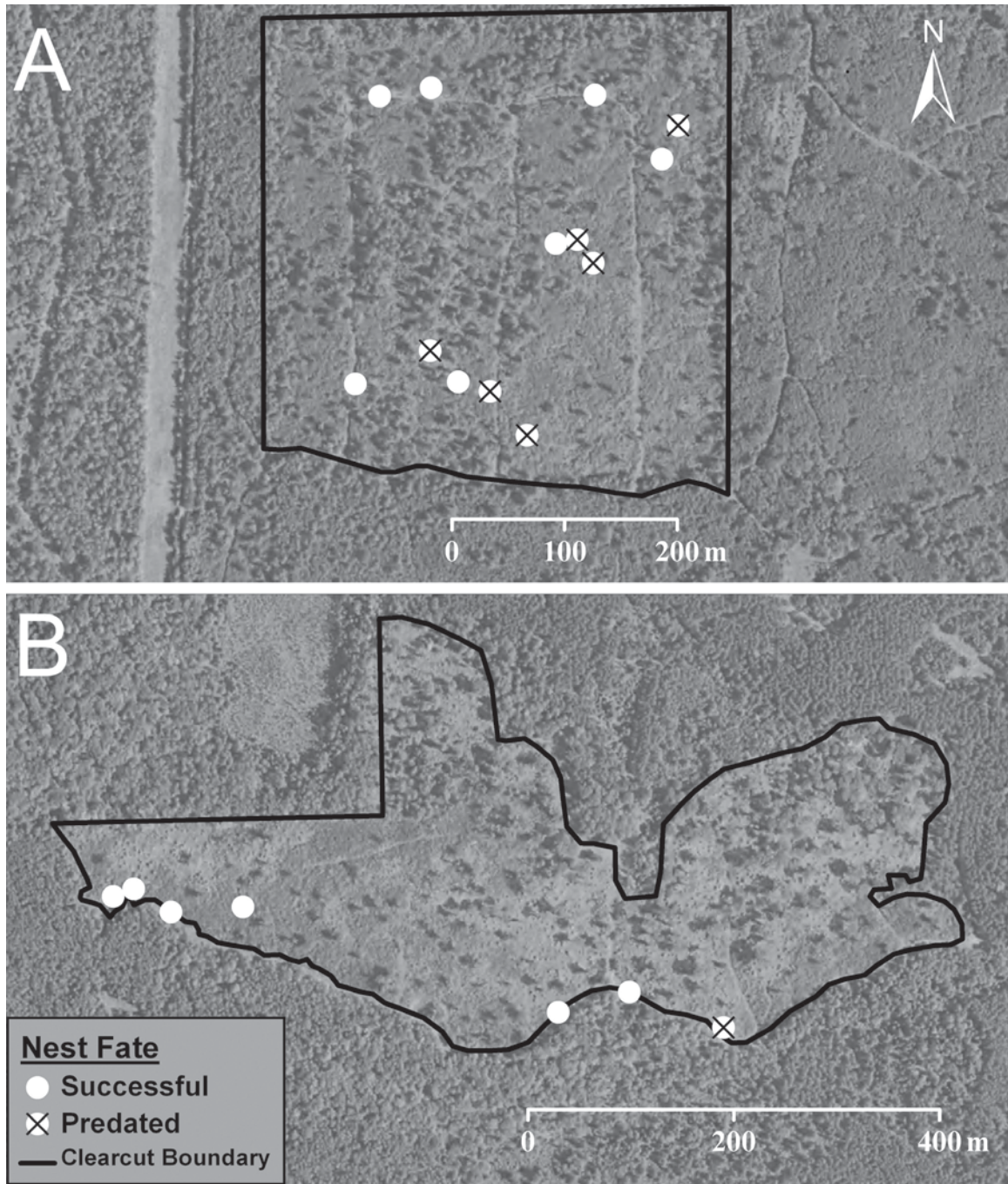


Figure 5.5. Golden-winged Warbler nest site locations relative to harvested aspen forest boundaries are depicted in the above maps. Aspen stands and nests are projected on a digital orthoquad air photo from 2008. Map A is a typical stand with conifer legacy tree retention where all nests were located away from the edge though several were near logging roads. Map B is a stand with hardwood legacy retention where nests were located primarily near the stand edge along the main logging road marking the southern harvest boundary.

Table 5.1

Mean \pm 1 se percent of Golden-winged Warbler (*Vermivora chrysoptera*) male locations at or beyond the harvested stand edge and territories that overlap the stand edge for aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$), and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin. There was no year effect for the percentage of territories that included the harvested stand edge ($\chi^2=0.592$, $df=3$, $p=0.90$) and for the percentage of territorial male locations at or beyond the harvested stand edge ($F_{3,128}=1.29$, $p=0.28$).

Legacy Tree Retention Treatment	2007	2008	2009	2010	All Years
<u>Male Locations at or beyond Harvested Stand Edge^a</u>					
Conifer Retention	3 \pm 2	0 \pm 0	0 \pm 0	1 \pm 1	1 \pm 1 A ^b
Hardwood Retention	5 \pm 1	14 \pm 7	5 \pm 2	7 \pm 3	8 \pm 2 B
Clearcut or No Retention	28 \pm 15	7 \pm 7	0 \pm 0	6 \pm 6	8 \pm 4 AB
					$F_{2,129}=5.17$, $p=0.007$
<u>Territories that Overlap the Harvested Stand Edge^c</u>					
Conifer Retention	33 \pm 21	25 \pm 21	7 \pm 26	25 \pm 26	24 \pm 7 A
Hardwood Retention	33 \pm 21	39 \pm 21	39 \pm 21	38 \pm 21	37 \pm 8 AB
Clearcut or No Retention	100 \pm 36	50 \pm 26	50 \pm 26	83 \pm 21	69 \pm 16 B
					$F_{2,27}=4.519$, $p=0.02$

^aExperimental units are the individual males.

^bMultiple comparisons using Holm-Sidak are indicated by letters; treatments with the same letter are not different from one another.

^cExperimental units are the harvested stands.

Table 5.2

Nine *a priori* models explaining variation in territorial Golden-winged Warbler (*Vermivora chrysoptera*) male locations and territory placement in aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$) and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. Models are listed from best to worst with the top two models for each dependent variable considered competitive as most parsimonious based on the smallest AIC_c value. Model statistics were generated using the GLIMMIX procedure for territorial male locations and the NLMIXED procedure for territory placement using SAS; individual males were the random effect in both procedures. The NLMIXED models used a binary dependent variable, territory placement, with territories either overlapping the harvested stand edge (1) or not overlapping the harvested stand edge (0).

Model	K^a	AIC _c	ΔAIC_c	Akaike Weight	-2 Log Likelihood
<u>Dependent Variable: Percent Male Locations at or beyond Harvested Stand Edge</u>					
Edge Density	3	-182.49	0.00	0.610	-186.6
Percent Interior Area	3	-181.11	1.38	0.306	-185.2
Legacy Tree Density + Legacy Tree Size	4	-177.41	5.08	0.048	-181.5
Intercept	2	-176.13	6.36	0.025	-180.2
Legacy Tree Density	3	-172.69	9.80	0.005	-176.8
Interior Stand Area	3	-172.02	10.47	0.003	-176.1
Edge Density+Legacy Tree Density +Legacy Tree Size	5	-170.39	12.10	0.001	-174.5
Legacy Tree Density + Edge Density	4	-169.53	12.96	0.001	-173.6
Year	3	-162.57	19.92	0.000	-166.7
<u>Dependent Variable: Territory Placement overlaps Harvested Stand Edge</u>					
Legacy Tree Density + Legacy Tree Size	4	104.8	0.0	0.559	96.5
Percent Interior Area	3	105.3	0.5	0.436	99.1
Edge Density	3	115.3	10.5	0.003	109.1
Legacy Tree Density + Edge Density	4	116.7	11.9	0.001	108.4
Edge Density+Legacy Tree Density +Legacy Tree Size	5	118.7	13.9	0.001	108.2
Interior Stand Area	3	137.2	32.4	0.000	131.0
Legacy Tree Density	3	137.7	32.9	0.000	131.5
Intercept	2	154.6	49.8	0.000	146.3
Year	3	152.4	47.6	0.000	146.2

^aNumber of model parameters.

Table 5.3

Statistical model parameter estimates for the most parsimonious models explaining variation in territorial Golden-winged Warbler (*Vermivora chrysoptera*) male locations and territory placement in aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$) and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. The top two models for territorial male locations and territory placement are included and are based on the smallest AIC_c values for competing models. Coefficient statistics were generated using the GLIMMIX procedure for territorial male locations and the NLMIXED procedure for territory placement using SAS.

	Coefficient	se	<i>t</i>	<i>P</i>
Percent Territorial Male Locations~ $\beta_0+\beta_1$ (Edge Density)				
β_0	-0.1499	0.0427	-3.51	0.0007
β_1	0.0017	0.0004	4.78	<0.0001
Percent Territorial Male Locations~ $\beta_0+\beta_1$ (Percent Interior Area)				
β_0	0.1553	0.0251	6.19	<0.0001
β_1	-0.0024	0.0005	-4.67	<0.0001
Territory Placement~ $\beta_0+\beta_1$ (Legacy Tree Density)+ β_2 (Legacy Tree Size)+random effect(MaleID)				
β_0	-11.7912	3.9820	-2.96	0.0036
β_1	-0.0255	0.0285	-0.89	0.3740
β_2	32.9956	51.2745	0.64	0.5210
random effect variance	1576.89	0563.42	1.01	0.3150
Territory Placement~ $\beta_0+\beta_1$ (Percent Interior Area)+random effect(MaleID)				
β_0	24.9440	6.4178	3.89	0.0002
β_1	-0.5975	0.1428	-4.18	<0.0001
random effect variance	199.88	174.12	1.15	0.2531

Table 5.4

Mean \pm 1 se aspen forest stand parameters for Golden-winged Warbler (*Vermivora chrysoptera*) territories that included the harvested stand edge and those that were interior from the edge for aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$), and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. A Mann-Whitney Rank Sum test was performed for each variable due failure to meet the assumption of a normal distribution.

Stand Parameter	Edge Territories	Interior Territories	<i>U</i>	<i>P</i>
Edge Density (m/ha) ^a	144.0 \pm 4.8	108.3 \pm 2.4	633.5	<0.001
Stand Interior Area (ha) ^b	9.8 \pm 1.0	15.7 \pm 0.9	2377.5	<0.001
Stand Interior Area (%) ^c	41.4 \pm 1.6	54.0 \pm 0.9	2380.5	<0.001
Legacy Tree Density (stems/ha)	37.7 \pm 5.5	67.7 \pm 4.1	2209.5	0.001
Legacy Tree Size (DBH; cm)	15.0 \pm 3.5	14.0 \pm 2.6	1165.5	0.019

^a=harvested stand perimeter length/harvested stand area.

^bBased on a 50-m interior buffer of the harvested stand edge.

^c=harvest stand interior area/harvest stand area x100.

Table 5.5

Daily nest predation rates for 41 of 50 active Golden-winged Warbler (*Vermivora chrysoptera*) nests divided into five distance to harvested stand edge intervals in aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$) and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. Eight nests were abandoned and one had unknown outcome, and thus they were not included in Probability of Daily Nest Predation calculations.

Stand Edge Distance (m)	No. of Active Nests ^a	No. Successful Nests	No. Predated Nests	Probability of Nest Predation ^b			
				HR	CR	NR	All Sites
0.0-18.7	8	6	1	0.208 ($n=7$)	NA ($n=0$)	NA ($n=0$)	0.208 ($n=7$)
18.8-39.8	4	3	0	0.000 ($n=2$)	0.000 ($n=1$)	0.000 ($n=1$)	0.000 ($n=4$)
39.9-63.3	10	4	4	0.585 ($n=4$)	0.563 ($n=4$)	NA ($n=0$)	0.688 ($n=8$)
63.4-97.1	16	8	5	0.837 ($n=4$)	0.279 ($n=9$)	NA ($n=0$)	0.451 ($n=13$)
97.2-233.6	12	2	7	0.761 ($n=3$)	0.933 ($n=6$)	NA ($n=0$)	0.884 ($n=9$)

^aA nest became active upon laying of the first egg.

^bBased on Mayfield (1961); nest period was 24 days.

Table 5.6

Logistic regression model coefficients and test statistics relating Golden-winged Warbler (*Vermivora chrysoptera*) nests that failed due to nest predation (0=successful, 1=predated) to distance to harvested stand edge in aspen forest clearcuts ($n=3$), stands with conifer legacy tree retention ($n=3$) and stands with hardwood legacy tree retention ($n=3$) in Oneida and Vilas Counties, Wisconsin, 2007-2010. There was only one nest in the clearcut treatment so a separate analysis using logistic regression was not possible.

							Likelihood Ratio Test	Hosmer & Lemeshow Test		
Predictor	β	SE	Wald's χ^2	df	P	e^{β} (odds ratio)	χ^2	P	χ^2	P
<u>All Nests (n=41)</u>							9.519	0.002	5.202	0.736
Constant (β_0)	-2.252	0.818	7.578	1	0.006	0.105				
Edge distance (β_1)	0.027	0.010	6.968	1	0.008	1.028				
<u>Nests in Conifer Retention Sites (n=20)</u>							4.208	0.040	11.805	0.160
Constant (β_0)	-2.778	1.503	3.415	1	0.065	0.062				
Edge distance (β_1)	0.030	0.017	3.187	1	0.074	1.030				
<u>Nests in Hardwood Retention Sites (n=20)</u>							5.828	0.016	6.809	0.557
Constant (β_0)	-2.092	1.003	4.352	1	0.037	0.123				
Edge distance (β_1)	0.032	0.016	4.176	1	0.041	1.033				

CHAPTER 6: Conclusion

Summary of Research Conclusions

Green-tree retention under the conceptual framework of ecological forestry can provide for both biomass feedstock for industry and quality wildlife habitat. I examined the influence of retained canopy trees as biological legacies (“legacy trees”) in aspen (*Populus* spp.) forests on above-ground live woody biomass, understory plant floristic quality, and species richness of bird assemblages. Additionally, I evaluated habitat quality for a high conservation priority species, Golden-winged Warbler (*Vermivora chrysoptera*). I selected 27 aspen-dominated forest stands in northern Wisconsin with nine stands in each of two legacy tree retention treatments (conifer retention and hardwood retention) and clearcuts (no retention) across a chronosequence (4-36 years post-harvest).

Conifer retention stands had greater legacy tree and total overstory tree biomass but lower biomass of regenerating aspen than clearcuts. Though conifer canopies allow greater solar penetration (Walker and Kenkel 2000), they also produced perpetual year-round shade as compared to stands with hardwood retention dominated by a deciduous broad-leaf species. Stands with oak legacy trees have an early spring leaf-off period when regenerating aspen can be productive. Additionally, stands with conifer retention had higher retained legacy tree densities on average than in stands with hardwood retention. Thus stands with high densities of conifer legacy trees may cast a greater area of shade than stands with relatively lower densities of oak legacy trees. The relative influences of legacy tree density and composition on regenerating aspen can be assessed in future analyses.

I evaluated the floristic quality of the understory plant assemblage by estimating the mean coefficient of conservatism (*C*), an index of how closely the assemblage resembled an undisturbed native community. Mean *C* was lower in young stands (6-9 years post-harvest) than middle-age (13-23 years post-harvest) or old (22-39 years post-harvest) stands; there was a marginally significant ($p=0.058$) interaction effect between legacy tree retention treatment and stand age. Late-seral plant species were positively

associated with stand age and legacy tree diameter or age thus suggesting that large-diameter legacy trees can produce suitable understory conditions for these species that are typically associated with later stages of stand development. Mean *C* in young stands was highest in aspen clearcuts and was driven largely by shade intolerant species with above average *C* values. Mean *C* remained constant with stand development in clearcuts but increased with stand development in stands with legacy tree retention. This pattern may be due to late-seral species with above average *C* values dispersing from adjacent unharvested older forests. Alternatively, the pattern may be due to delayed regeneration from the seed bank following the demise of parental individuals immediately during and after harvest. Such species would need to have viable seeds in the soil at least 6-years-old post-harvest, the beginning of plant surveys for the youngest stands in this study. The retention of large, canopy trees could provide hospitable germination conditions (i.e. shade and a cooler, moister microclimate) earlier in stand development than in clearcuts.

Early in aspen stand development, bird species richness was greatest in stands with hardwood retention, lowest in clearcuts, and intermediate in stands with conifer retention. Six conservation priority birds were indicators of legacy tree retention or clearcuts with at least one species in each treatment. Retention of legacy trees in aspen stands provided higher quality nest habitat for Golden-winged Warbler than clearcuts based on high pairing success resulting in high nesting activity.

Retention of hardwoods, particularly northern red oak, yielded the most consistent positive effects over traditionally clearcutting with no retention as indicated by: 1) higher bird species richness, 2) higher quality habitat for Golden-winged Warbler, and 3) comparable stand biomass compared to clearcuts without suppressing regenerating tree biomass. Though composition of legacy trees was generally more important than their density, though there is a point where density can reduce aspen growth (Perala 1977), the size of legacy trees was important in influencing both bird and understory plant assemblage composition in addition to Golden-winged Warbler use. Large legacy trees in young aspen stands produced compositionally similar results as relatively old stands. These large diameter trees resulted in greater bird species richness by providing habitat that attracted some mature forest species to young aspen stands that would not

ordinarily be present in young, traditional aspen clearcuts comprised entirely of small-diameter trees. Specifically, the presence of large diameter hardwoods (≥ 16 cm diameter at breast height) was an important characteristic of high quality habitat for Golden-winged Warblers.

Legacy tree retention can enhance even-aged management techniques and produce a win-win scenario for the conservation of declining bird species and late-seral understory plants and for production of woody biomass feedstock from naturally regenerating aspen forests. This should not imply that green-tree retention should replace traditional clearcutting. The latter potentially produces higher quality habitat for some bird species than green-tree retention. Green-tree retention should be considered in stands where aspen is mixed with other tree species that are resistant to windthrow and thus appropriate as legacy trees. Non-aspen trees cannot be retained where they do not exist and in these cases, traditional clearcutting is likely a more practical option.

At the landscape-scale, forests should be managed using a variety of silvicultural practices, including green-tree retention, to diversify forest structure, forest types and ages, and tree composition. This should be implemented in a strategic pattern across the landscape to create long-term balance to maintain habitat for a broad suite of forest wildlife species, to provide a sustainable harvest of timber and feedstock for the forest products and bioenergy industries, and to maintain forest health.

Future Research and Publication Considerations

In this study, there were three common species of legacy trees retained in aspen forests: white pine (*Pinus strobus*), red pine (*Pinus resinosa*), and northern red oak. What is the future of these legacy tree species in aspen forests? Given that deer browse can be high in some forests, regeneration of some tree species may be in doubt (Horsley et al. 2003, Randall and Walters 2011). Additionally, climate change is predicted to influence habitat suitability for many tree species resulting in loss of some species from their current range (Iverson et al. 2008). Thus, foresters may not have the same tree species to retain in future timber harvest rotations once the existing legacy trees die or are harvested. I

did not present the age structure of the common legacy tree species though this is a subject I could address in future publications.

In terms of forest stand biomass, I focused on live above-ground woody biomass. I did not estimate below-ground woody biomass which may differ between legacy tree retention treatments and vary with stand development. This is potentially important from the perspective of below-ground carbon storage and sequestration, an important component to understanding how forests factor into global carbon and climate models (Gough et al. 2008).

I compared deciduous legacy trees to coniferous legacy trees but was unable to compare the importance of different species of legacy trees within these two groups in terms of their potentially differing effects on bird assemblages, Golden-winged Warbler use, etc. Retention of spruce (*Picea* spp.) and fir (*Abies* spp.) on sites with moister, richer soils may attract a different suite of bird species than retention of pine on drier, poorer soils (Beals 1960). In the case of Golden-winged Warbler management, the emerging body of research investigating habitat quality suggests that deciduous trees are critically important (Roth et al. 2012); however it is unclear how important different deciduous tree species are relative to each other in this context. If land managers have a choice, are certain tree species more important for retention in forests or planting in reclamation/restoration projects? Perhaps species composition is not as important as structure. Providing scattered large deciduous trees in a landscape with a high proportion of deciduous, broad-leaf forest may be adequate for creating high quality Golden-winged Warbler habitat.

When measuring habitat for birds, demographic characteristics tend to best reflect habitat quality. Though Golden-winged Warbler pairing success, nest success and productivity were used to evaluate habitat quality for this species, similar information for the other bird species observed in this study would provide a better picture of how the bird assemblage is responding as a whole. Though I collected this information, I was unable to present it here but hope to do so in future publications.

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Appendix A

Table A.1

Understory plants present in 27 aspen forest stands in northern Wisconsin, 2008-2009.
Asterisks indicate species that are introduced to Wisconsin.

Scientific Name ^a	Common Name ^a	C ^b
<u>Ferns</u>		
<i>Adiantum pedatum</i> L.	northern maidenhair	7
<i>Athyrium filix-femina</i> (L.) Roth ssp. <i>angustum</i> (Willd.) R.T. Clausen	common ladyfern	5
<i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	spinulose woodfern	7
<i>Dryopteris cristata</i> (L.) A. Gray	crested woodfern	7
<i>Dryopteris intermedia</i> (Muhl. ex Willd.) A. Gray	intermediate woodfern	7
<i>Gymnocarpium dryopteris</i> (L.) Newman	western oakfern	7
<i>Onoclea sensibilis</i> L.	sensitive fern	5
<i>Osmunda cinnamomea</i> L.	cinnamon fern	7
<i>Osmunda claytoniana</i> L.	interrupted fern	6
<i>Pteridium aquilinum</i> (L.) Kuhn var. <i>latiusculum</i> (Desv.) Underw. ex A.Heller	western brackenfern	2
<u>Fern Allies</u>		
<i>Huperzia lucidula</i> (Michx.) Trevis.	shining clubmoss	7
<i>Lycopodium annotinum</i> L.	stiff clubmoss	7
<i>Lycopodium clavatum</i> L.	running clubmoss	6
<i>Lycopodium dendroideum</i> Michx.	tree groundpine	7
<i>Lycopodium hickeyi</i> W.H. Wagner, Beitel & Moran	Pennsylvania clubmoss	7
<i>Lycopodium lagopus</i> (Laest. ex Hartm.) Zinserl. ex Kuzen	one-cone clubmoss	8
<i>Lycopodium obscurum</i> L.	rare clubmoss	7
<i>Lycopodium tristachyum</i> Pursh	deeproot clubmoss	7
<u>Forbs</u>		
<i>Achillea millefolium</i> L.	common yarrow	1
<i>Actaea pachypoda</i> Elliott	white baneberry	6
<i>Actaea rubra</i> (Aiton) Willd.	red baneberry	7
<i>Agrimonia gryposepala</i> Wallr.	tall hairy agrimony	2
<i>Anaphalis margaritacea</i> (L.) Benth.	western pearly everlasting	3
<i>Anemone cylindrica</i> A. Gray	candle anemone	6
<i>Anemone quinquefolia</i> L. var. <i>quinquefolia</i>	wood anemone	6
<i>Antennaria neglecta</i> Greene	field pussytoes	3
<i>Apocynum androsaemifolium</i> L.	spreading dogbane	2
<i>Aquilegia canadensis</i> L.	red columbine	5
<i>Arabis drummondii</i> A. Gray	Drummond's rockcress	6
<i>Arabis glabra</i> (L.) Bernh.	tower rockcress	5
<i>Aralia nudicaulis</i> L.	wild sarsaparilla	6
<i>Asclepias exaltata</i> L.	poke milkweed	7
<i>Calystegia spithamea</i> (L.) Pursh	low false bindweed	4
<i>Campanula rotundifolia</i> L.	bluebell bellflower	5

Table A.1, continued

Scientific Name ^a	Common Name ^a	C ^b
<i>Cerastium arvense</i> L.	field chickweed	4
<i>Cerastium fontanum</i> Baumg. emend Jalas ssp. <i>vulgare</i> (Hartm.) Greuter & Burdet*	big chickweed	0
<i>Cerastium nutans</i> Raf.	nodding chickweed	0
<i>Cirsium vulgare</i> (Savi) Ten.*	bull thistle	0
<i>Clinopodium vulgare</i> L.	wild basil	3
<i>Clintonia borealis</i> (Aiton) Raf.	bluebead	7
<i>Comandra umbellata</i> (L.) Nutt. ssp. <i>umbellata</i>	bastard toadflax	6
<i>Comarum palustre</i> L.	purple marshlocks	8
<i>Conyza canadensis</i> (L.) Cronquist var. <i>canadensis</i>	Canadian horseweed	0
<i>Corallorhiza maculate</i> (Raf.) Raf.	summer coralroot	7
<i>Corallorhiza trifida</i> Chatelain	yellow coralroot	7
<i>Cynoglossum virginianum</i> L. var. <i>boreale</i> (Fernald) Cooperr.	wild comfrey	8
<i>Doellingeria umbellata</i> (Mill.) Nees	parasol whitetop	6
<i>Epilobium ciliatum</i> Raf.	fringed willowherb	3
<i>Erigeron annuus</i> (L.) Pers.	eastern daisy fleabane	0
<i>Erigeron philadelphicus</i> L.	Philadelphia fleabane	2
<i>Eurybia macrophylla</i> (L.) Cass.	bigleaf aster	4
<i>Euthamia graminifolia</i> (L.) Nutt. var. <i>graminifolia</i>	flat-top goldentop	4
<i>Fragaria vesca</i> L. ssp. <i>americana</i> (Porter) Staudt	woodland strawberry	3
<i>Fragaria virginiana</i> Duchesne	Virginia strawberry	1
<i>Galeopsis tetrahit</i> L.*	brittlestem hempnettle	0
<i>Galium boreale</i> L.	northern bedstraw	5
<i>Galium triflorum</i> Michx.	fragrant bedstraw	5
<i>Helenium flexuosum</i> Raf.*	purplehead	0
<i>Helianthus hirsutus</i> Raf.	sneezeweed	5
<i>Helianthus strumosus</i> L.	hairy sunflower	5
<i>Hepatica nobilis</i> (Pursh) Steyerl. var. <i>obtusata</i>	paleleaf woodland sunflower	4
<i>Hieracium aurantiacum</i> L.*	roundlobe hepatica	3
<i>Hieracium piloselloides</i> Vill.*	orange hawkweed	0
<i>Hieracium scabrum</i> Michx.	tall hawkweed	0
<i>Hieracium umbellatum</i> L.	rough hawkweed	6
<i>Hypericum perforatum</i> L.*	narrowleaf hawkweed	6
<i>Iris versicolor</i> L.	common St. Johnswort	0
<i>Lactuca biennis</i> (Moench) Fernald	harlequin blueflag	5
<i>Lathyrus venosus</i> Muhl. ex Willd.	tall blue lettuce	3
<i>Leucanthemum vulgare</i> Lam.*	veiny pea	6
<i>Linnaea borealis</i> (Forbes) Hultén ssp. <i>americana</i> ex R.T. Clausen	oxeye daisy	0
<i>Lobelia inflata</i> L.	twinflower	9
<i>Lycopus americanus</i> Muhl. ex W. Bartram	indian-tobacco	2
<i>Lysimachia ciliata</i> L.	american water horehound	4
	fringed loosestrife	5

Table A.1, continued

Scientific Name ^a	Common Name ^a	C ^b
<i>Lysimachia quadrifolia</i> L.	whorled yellow loosestrife	6
<i>Maianthemum canadense</i> Desf.	Canada mayflower	5
<i>Maianthemum racemosum</i> (L.) Link	feathery false lily of the valley	5
<i>Melampyrum lineare</i> Desr.	narrowleaf cowwheat	7
<i>Mitchella repens</i> L.	partridgeberry	6
<i>Monarda fistulosa</i> L. ssp. <i>fistulosa</i>	wild bergamot	3
<i>Monotropa hypopithys</i> L.	pinemap	7
<i>Monotropa uniflora</i> L.	indianpipe	5
<i>Orthilia secunda</i> (L.) House	sidebells wintergreen	7
<i>Osmorhiza claytonia</i> (Michx.) C.B. Clarke	Clayton's sweetroot	5
<i>Oxalis montana</i> Raf.	mountain woodsorrel	8
<i>Oxalis stricta</i> L.	common yellow oxalis	0
<i>Pedicularis canadensis</i> L.	Canadian lousewort	8
<i>Plantago major</i> L.*	common plantain	0
<i>Polygala paucifolia</i> Willd.	gaywings	7
<i>Polygonatum biflorum</i> (Walter) Elliott	smooth soloman's seal	4
<i>Polygonatum pubescens</i> (Willd.) Pursh	hairy soloman's seal	6
<i>Potentilla norvegica</i> L.	Norwegian cinquefoil	0
<i>Potentilla recta</i> L.*	sulphur cinquefoil	0
<i>Potentilla simplex</i> Michx.	common cinquefoil	2
<i>Prenanthes alba</i> L.	white rattlesnakeroot	5
<i>Prunella vulgaris</i> L.	common selfheal	1
<i>Pseudognaphalium macounii</i> (Greene) Kartesz	Macoun's cudweed	2
<i>Pseudognaphalium obtusifolium</i> (L.) Hilliard & B.L. Burt ssp. <i>obtusifolium</i>	rabbit-tobacco	3
<i>Pyrola chlorantha</i> Sw.	greenflowered wintergreen	7
<i>Pyrola elliptica</i> Nutt.	waxflower shinleaf	6
<i>Ranunculus hispidus</i> Michx.	bristly buttercup	6
<i>Rumex acetosella</i> L.*	common sheep sorrel	0
<i>Sanicula marilandica</i> L.	Maryland sanicle	5
<i>Silene vulgaris</i> (Moench) Garcke*	maidenstears	0
<i>Smilax ecirrhata</i> (Engelm. ex Kunth) S. Watson	upright carrionflower	5
<i>Solidago canadensis</i> L.	Canada goldenrod	1
<i>Solidago gigantea</i> Aiton	giant goldenrod	3
<i>Solidago hispida</i> Muhl. ex Willd. var. <i>hispida</i>	hairy goldenrod	6
<i>Stachys palustris</i> L.	marsh hedgenettle	5
<i>Streptopus lanceolatus</i> (Aiton) Reveal var. <i>longipes</i> (Fernald) Reveal	twistedstalk	7
<i>Symphyotrichum ciliolatum</i> (Lindl.) A. Löve & D. Löve	Lindley's aster	4
<i>Symphyotrichum cordifolium</i> (L.) G.L. Nesom	common blue wood aster	6
<i>Symphyotrichum laeve</i> (L.) Á. Löve & D. Löve var. <i>laeve</i>	smooth blue aster	6
<i>Symphyotrichum lanceolatum</i> (Willd.) G.L. Nesom	white panicle aster	4
<i>Taraxacum officinale</i> F.H. Wigg.*	common dandelion	0
<i>Thalictrum dioicum</i> L.	early meadow-rue	7

Table A.1, continued

Scientific Name ^a	Common Name ^a	C ^b
<i>Trientalis borealis</i> subsp. <i>borealis</i> Raf.	starflower	7
<i>Trifolium aureum</i> Pollich*	golden clover	0
<i>Trifolium pretense</i> L.*	red clover	0
<i>Trifolium repens</i> L.*	white clover	0
<i>Trillium grandiflorum</i> (Michx.) Salisb.	white trillium	6
<i>Uvularia sessilifolia</i> L.	sessileleaf bellwort	6
<i>Verbascum thapsus</i> L.*	common mullein	0
<i>Veronica officinalis</i> L.*	common gypsyweed	0
<i>Veronica serpyllifolia</i> L.	thymeleaf speedwell	0
<i>Vicia americana</i> Muhl. ex Willd. ssp. <i>americana</i>	American vetch	4
<i>Viola adunca</i> Sm.	hookedspur violet	6
<i>Viola canadensis</i> L.	Canadian white violet	7
<i>Viola labradorica</i> Schrank	alpine violet	4
<i>Viola pubescens</i> Aiton	downy yellow violet	5
<i>Viola renifolia</i> A. Gray	white violet	7
<i>Viola sororia</i> Willd.	common blue violet	3
<i>Waldsteinia fragarioides</i> (Michx.) Tratt. ssp. <i>fragarioides</i>	Appalachian barren strawberry	6
<u>Graminoids</u>		
<i>Agropyron repens</i> (L.) Gould*	quackgrass	0
<i>Agrostis gigantea</i> Roth*	redtop	0
<i>Agrostis hyemalis</i> (Walter) Britton, Sterns & Poggenb.	winter bentgrass	4
<i>Brachyelytrum erectum</i> (Schreb. ex Spreng.) P. Beauv.	bearded shorthusk	7
<i>Bromus ciliatus</i> L.	fringed brome	7
<i>Calamagrostis canadensis</i> (Michx.) P. Beauv.	bluejoint	5
<i>Carex arctata</i> Boott ex Hook.	drooping woodland sedge	5
<i>Carex brunnescens</i> (Pers.) Poir. ssp. <i>sphaerostachya</i> (Tuck.) Kalela	brownish sedge	7
<i>Carex communis</i> L.H. Bailey var. <i>communis</i>	fibrousroot sedge	6
<i>Carex deweyana</i> Schwein. var. <i>deweyana</i>	Dewey sedge	7
<i>Carex intumescens</i> Rudge	greater bladder sedge	5
<i>Carex leptoneura</i> (Fernald) Fernald	nerveless woodland sedge	6
<i>Carex pedunculata</i> Muhl. ex Willd.	longstalk sedge	7
<i>Carex pensylvanica</i> Lam.	Pennsylvania sedge	3
<i>Carex projecta</i> Mack.	necklace sedge	4
<i>Carex scoparia</i> Schkuhr ex Willd. var. <i>scoparia</i>	broom sedge	4
<i>Carex tosa</i> (Fernald) E.P. Bicknell	shaved sedge	4
<i>Carex tuckermanii</i> Dewey	Tuckerman's sedge	8
<i>Cinna latifolia</i> (Trevis. ex Goepp.) Griseb.	drooping woodreed	7
<i>Danthonia spicata</i> (L.) P. Beauv. ex Roem. & Schult.	poverty oatgrass	4
<i>Dichanthelium clandestinum</i> (L.) Gould*	deertongue	0
<i>Dichanthelium depauperatum</i> (Muhl.) Gould	starved panicgrass	4
<i>Dichanthelium latifolium</i> (L.) Gould & C.A. Clark	broadleaf rosette grass	7
<i>Elymus repens</i> (L.) Gould*	quackgrass	0
<i>Festuca subverticillata</i> (Pers.) Alexeev	nodding fescue	4
<i>Juncus bufonius</i> L.	toad rush	3

Table A.1, continued

Scientific Name ^a	Common Name ^a	C ^b
<i>Juncus bufonius</i> L.	toad rush	3
<i>Juncus greenei</i> Oakes & Tuck.	Greene's rush	7
<i>Luzula acuminata</i> Raf. var. <i>acuminata</i>	hairy woodrush	6
<i>Muhlenbergia frondosa</i> (Poir.) Fernald	wirestem muhly	3
<i>Oryzopsis asperifolia</i> Michx.	roughleaf ricegrass	6
<i>Oryzopsis pungens</i> (Torr. ex Spreng.) Dorn	mountain ricegrass	8
<i>Panicum capillare</i> L.	witchgrass	1
<i>Phleum pratense</i> L.*	timothy	0
<i>Poa alsodes</i> A. Gray	grove bluegrass	5
<i>Poa compressa</i> L.*	Canada bluegrass	0
<i>Poa pratensis</i> L.*	Kentucky bluegrass	0
<i>Schizachne purpurascens</i> (Torr.) Swallen	false melic	7
<i>Scirpus cyperinus</i> (L.) Kunth	woolgrass	4
<u>Shrubs and Subshrubs</u>		
<i>Alnus viridis</i> (Chaix) DC. ssp. <i>crispa</i> (Aiton) Turrill	mountain alder	8
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	kinnikinnick	7
<i>Chimaphila umbellata</i> (L.) W. Bartram ssp. <i>cisatlantica</i> (S.F. Blake) Hultén	pipsissewa	8
<i>Comptonia peregrina</i> (L.) J.M. Coult.	sweetfern	4
<i>Cornus canadensis</i> L.	bunchberry dogwood	7
<i>Diervilla lonicera</i> Mill.	northern bush honeysuckle	6
<i>Epigaea repens</i> L.	trailing arbutus	7
<i>Gaultheria procumbens</i> L.	eastern teaberry	6
<i>Ilex verticillata</i> A. Gray	common winterberry	7
<i>Rosa acicularis</i> Lindl. ssp. <i>sayi</i> (Schwein.) W.H. Lewis	prickly rose	6
<i>Rosa carolina</i> L.	Carolina rose	4
<i>Rubus allegheniensis</i> Porter	Allegheny blackberry	2
<i>Rubus flagellaris</i> Willd.	northern dewberry	3
<i>Rubus hispidus</i> L.	bristly dewberry	4
<i>Rubus idaeus</i> L. ssp. <i>strigosus</i> (Michx.) Focke	grayleaf red raspberry	3
<i>Rubus pubescens</i> Raf.	dwarf red blackberry	7
<i>Spiraea alba</i> Du Roi var. <i>alba</i>	white meadowsweet	4
<i>Toxicodendron rydbergii</i> (Small ex Rydb.) Greene	western poison ivy	2
<i>Vaccinium angustifolium</i> Aiton	lowbush blueberry	4
<i>Vaccinium myrtilloides</i> Michx.	velvetleaf huckleberry	6
<u>Vines</u>		
<i>Amphicarpaea bracteata</i> (L.) Fernald	American hogpeanut	5
<i>Clematis occidentalis</i> (Hornem.) DC. var. <i>occidentalis</i>	western blue virginsbower	8
<i>Polygonum cilinode</i> Michx.	fringed black bindweed	1
<i>Smilax tamnoides</i> L.	bristly greenbrier	5

^aScientific names, common names, and authority followed the convention of USDA (2012) and subspecies and variety names were identified in UWSP (2012).

^bCoefficient of Conservatism; C values were obtained from UWSP (2012). Introduced species did not have a C value but were given a value of zero for our analyses.