Effectiveness of riparian buffers. Breeding bird response to riparian buffer width: 10 years post-harvest.

By:
Scott F. Pearson, Jack Giovanini, Jay E. Jones and Andrew J. Kroll

WASHINGTON STATE DEPARTMENT OF
Natural Resources
PETER GOLDMARK - Commissioner of Public Lands

August 2014

CMER #12-1204

Washington State Forest Practices Adaptive Management Program

The Washington State Forest Practices Board (FPB) has established an Adaptive Management Program (AMP) by rule in accordance with the Forests & Fish Report (FFR) and subsequent legislation. The purpose of this program is to:

> *Provide science-based recommendations and technical information to assist the FPB in determining if and when it is necessary or advisable to adjust rules and guidance for aquatic resources to achieve resource goals and objectives. The board may also use this program to adjust other rules and guidance.* (Forest Practices Rules, WAC 222-12-045(1)).

To provide the science needed to support adaptive management, the FPB established the Cooperative Monitoring, Evaluation and Research (CMER) committee as a participant in the program. The FPB empowered CMER to conduct research, effectiveness monitoring, and validation monitoring in accordance with WAC 222-12-045 and Board Manual Section 22.

Report Type and Disclaimer

This technical report contains scientific information from research or monitoring studies that are designed to evaluate the effectiveness of the forest practices rules in achieving one or more of the Forest and Fish performance goals, resource objectives, and/or performance targets. The document was prepared for the Cooperative Monitoring, Evaluation and Research Committee (CMER) and was intended to inform and support the Forest Practices Adaptive Management program. The project is part of the Eastside Type F Riparian Effectiveness Program, and was conducted under the oversight of the Riparian Scientific Advisory Group (RSAG).

This document was reviewed by CMER and was assessed through the Adaptive Management Program’s independent scientific peer review process. CMER has approved this document for distribution as an official CMER document. As a CMER document, CMER is in consensus on the scientific merit of the document. However, any conclusions, interpretations, or recommendations contained within this document are those of the authors and may not reflect the views of all CMER members.

The Forest Practices Board, CMER, and all the participants in the Forest Practices Adaptive Management Program hereby expressly disclaim all warranties of accuracy or fitness for any use of this report other than for the Adaptive Management Program. Reliance on the contents of this report by any persons or entities outside of the Adaptive Management Program established by WAC 222-12-045 is solely at the risk of the user.

Proprietary Statement

This work was developed with public funding, as such it is within the public use domain. However, the concept of this work originated with the Washington State Forest Practices Adaptive Management Program and the authors. As a public resource document, this work should be given proper attribution and be properly cited.

Full Reference

Pearson, Scott F., Giovanini, Jack, Jones, Jay E., Kroll, Andrew J. 2014. Effectiveness of riparian buffers. Breeding bird response to riparian buffer width: 10 years post-harvest. Cooperative Monitoring Evaluation and Research Report CMER 12-1204. Washington State Forest Practices Adaptive Management Program. Washington Department of Natural Resources, Olympia, WA.

Author Contact Information

Scott F. Pearson
Wildlife Research Division
Washington Department of Fish and Wildlife
1111 Washington St. SE
Olympia, Washington, USA

Jack Giovanini
Statistics, Mathematics, and Operations Research
Weyerhaeuser NR
Federal Way, Washington, USA

Jay E. Jones
Statistics, Mathematics, and Operations Research
Weyerhaeuser NR
Federal Way, Washington, USA

Andrew J. Kroll
Timberlands Technology
Weyerhaeuser NR
Federal Way, Washington, USA

Effectiveness of riparian buffers.
Breeding bird response to riparian buffer width: 10 years post-harvest.

August 2014

Prepared for:

The State of Washington
Forest Practices
Adaptive Management Program
Department of Natural Resources
Personal Service Contract #11-350

Prepared by:

Scott F. Pearson
Wildlife Research Division
Washington Department of Fish and Wildlife
1111 Washington St. SE
Olympia, Washington, USA

Jack Giovanini
Statistics, Mathematics, and Operations Research
Weyerhaeuser NR
Federal Way, Washington, USA

Jay E. Jones
Statistics, Mathematics, and Operations Research
Weyerhaeuser NR
Federal Way, Washington, USA

Andrew J. Kroll
Timberlands Technology
Weyerhaeuser NR
Federal Way, Washington, USA

Effectiveness of riparian buffers

Breeding bird response to riparian buffer width: 10 years post-harvest

Scott F. Pearson[1], Jack Giovanini[2], Jay E. Jones[2] and Andrew J. Kroll[3]

[1]Wildlife Research Division, Washington Department of Fish and Wildlife, 1111 Washington St. SE, Olympia, Washington, USA
[2]Statistics, Mathematics, and Operations Research, Weyerhaeuser NR, Federal Way, Washington, USA
[3]Timberlands Technology, Weyerhaeuser NR, Federal Way, Washington, US

ABSTRACT

Buffer strips of intact native vegetation are often left between harvested forest cutblocks or between agricultural fields and aquatic habitats in order to reduce potentially negative effects of tree harvest and agriculture activities on aquatic systems. Previously, we described the 1-2 year post-harvest bird community responses to two riparian buffer treatments: 1) a relatively uniform width forested riparian buffer (~13m) and, 2) a wider and more variable width buffer (~30m) (unharvested reserves), both created after clearcut harvest of the uplands adjacent to small streams in western Washington, USA. In this study, we revisited study sites (10 years post-harvest) to examine longer-term bird community effects. Using the same Before-After-Control-Impact (BACI) experimental approach and temporally replicated point counts, we estimated population- and community-level avian responses while incorporating variation in the detection process across treatments and years, an aspect not previously included.

Post-harvest, average riparian buffer width was 13 (±2.0 SE) and 29 m (±2.2 SE) on the Narrow and Wide treatments respectively. Across all years [1993 (pre-treatment year), 1995-1996 (immediate post-harvest sample), and 2003-2004 (10 year post-harvest sample)] and treatments (Control, Wide and Narrow buffer), 28 species were detected at least 10 times for a total of 2,064 detections. We did not find a treatment effect on total bird abundance. Buffer treatments exhibited a 31-44% increase in mean species richness in the post-harvest years, relative to their respective pre-harvest year, a pattern most evident 10 years post-harvest. In contrast, we found a 13-18% increase in species richness post-harvest on controls. When comparing probability of species turnover between the pre-harvest year and either the two immediate post-harvest years or the two~10 year post-harvest years, turnover was much higher on both treatments (63-74%) relative to the controls (29%). Post-harvest, we found strong evidence (no overlap in 95% credible intervals) for an increase in site occupancy on treatments relative to the controls for approximately 29% and 100% of the species in the immediate post-harvest and the ~10 year post-harvest sample respectively. Occupancy increased for more species on the wider buffer treatment, but we found no clear evidence for a species-level decrease in occupancy on either treatment after harvest. Taking advantage of the existing variation in vegetation characteristics and buffer width among harvested sites and ignoring site treatment assignments (Wide vs. Narrow), our model predicted an increase in total bird abundance with increasing buffer width but the evidence was weak (a 16% probability of no/negative change). Some of the narrowest buffered sites had lower bird abundance and species richness than the controls. When assessing the relationship between buffer width and site level abundance of the four species associated with riparian habitats, Pacific-slope flycatcher (*Empidonax difficilis*), Pacific wren (*Troglodytes troglodytes*), American robin (*Turdus migratorius*), and black-throated gray warbler (*Dendroica nigrescens*), we found weak evidence that Pacific wren abundance was reduced on some of the very narrow buffered sites. Our results suggest that local extinction does not occur even on the very narrow buffers that we examined, that buffer treatments increased species richness regardless of their width, and that birds continued to colonize riparian buffers for up to 10 years post-harvest.

Key words: Riparian buffers, riparian zones, riparian birds, species turnover, site-level extinction, forest practices. Key phrases: Effects of riparian buffer width; bird species richness vs. riparian buffer width, local bird species extinction vs. riparian buffer width, breeding bird abundance vs. riparian buffer width, riparian associates in riparian zones; breeding birds in riparian zones

INTRODUCTION

Riparian areas associated with rivers and streams are dynamic portions of the landscape because they integrate aquatic and terrestrial communities (Pollock et al. 1998, Swanson et al. 1988, Naiman et al. 2005). They are dynamic because of seasonal and episodic changes in hydrology that influence soil erosion and deposition and ultimately plant and animal composition and structure. As a consequence, riparian areas are typically more structurally diverse (Bull 1978, Planty-Tabacchi et al. 1996, Pollock et al. 1998) and more productive (Pollock et al. 1998) than adjacent uplands. In some cases, riparian zones support a greater number of plant and vertebrate species (Thomas et al. 1979, Oakley et al. 1985, Gregory et al. 1991, NRC 2002) but in others, they support different but not necessarily more species (Sabo et al. 2005). Many of these riparian-associated species are uniquely adapted to exploit the temporally and spatially variable nature of river systems (Naiman and Bilby 1998).

Buffer strips of standing trees or intact native vegetation are often left between harvested stands or agricultural fields and aquatic environments because of the ecological importance of riparian areas and to reduce the negative effects of harvest on terrestrial, riparian and aquatic systems, (Stauffer and Best 1980, Knopf et al. 1988, Keller et al. 1993, Peak and Thompson 2006). Buffer strips are left to: (1) maintain natural processes and functions of the aquatic system (e.g., shading, sedimentation interception, inputs of large wood and leaf litter, etc.)(Chamberlin et al. 1991), (2) maintain aquatic species and communities (Osmundson et al. 2002, Kiffney et al. 2003), and (3) protect riparian vegetation and animals (Naiman et al. 2000, 2005, Richardson et al. 2005). Buffer strips may also serve as dispersal corridors or as important connections between fragmented forest patches, and consequently, may counteract some of the problems associated with landscape fragmentation [(Wilcox and Murphy 1985, Saunders et al. 1991) but see Hannon and Schmiegelow (2002) and Schmiegelow and Monkkonen (2002)]. When conserving riparian systems in forest landscapes, riparian buffer width is the primary variable influenced by state and provincial guidelines in the United States and Canada (Blinn and Kilgore 2001, Lee et al. 2004). Despite their apparent importance and substantial research devoted to their effectiveness in conserving species and ecological process, considerable variation in buffer width guidelines exists among jurisdictions (Blinn and Kilgore 2001, Lee et al. 2004). From an ecological perspective, the discrepancy is understandable given the variation in how biotic and abiotic factors respond to riparian buffers. For example, in a meta-analysis using data from 397 comparisons of species abundance in riparian buffers and unharvested riparian sites, responses of terrestrial species were not consistent between taxonomic groups (Marczak et al. 2010). In general, bird and arthropod abundances increased in buffers relative to unharvested areas, whereas amphibian abundance decreased (Marczak et al. 2010).

To examine effectiveness of riparian buffer width on avian community abundance and richness in forested landscapes, investigators have used a variety of approaches. Some have looked at changes in species richness with distance from the stream in unharvested forests (e.g. Spackman and Hughes 1995). Others have correlated buffer width with species abundance and richness after timber harvest (Kinley and Newhouse 1997, Hagar 1999, Whitaker and Montevecchi 1999). A few studies have used an experimental approach to examine the effect of buffer width on species and communities (e.g., Darveau et al. 1995, Pearson and Manuwal 2001) and others have experimentally examined the effects of tree harvest within riparian habitats (Hanowski et al. 2003). To date, few studies focused on species responses to buffer width have: (1) documented the long-term effectiveness of the buffer in maintaining the presence or abundance of riparian associated species; (2) quantitatively identified riparian associates and consequently the effectiveness of the buffer in maintaining those species; and (3) addressed issues of detectability that may have been confounded with treatment (Gimenez et al. 2008, Perry et al. 2011, Jones et al. 2011, Archaux et al. 2012) and consequently resulted in apparent effects (Perry et al. 2011). Estimated effects of forested buffers on riparian fauna that have been calculated from short-term data (≤ 5 years post-harvest) should be "viewed with caution" (Marczak et al. 2010, page 132) because both short- and long-term effects may be associated with harvesting forests adjacent to buffers. Interior forest species that exhibit some degree of philopatry may "pack" into the adjacent forested buffer resulting in a higher density than expected in the years immediately following harvest (Hagan et al. 1996). Over the longer-term, regeneration of trees and shrubs in the adjacent harvest area may "soften" the contrast between the harvested upland and unharvested riparian buffer resulting in an increased use by species sensitive to "hard" or high contrast edges (Fletcher and Koford 2003, Ries et al. 2004). The animal species composition and structure within the buffer is also likely to change over time. Changes in temperature and light and wind speeds can penetrate as much as 40 m into buffers, which results in changes in the structure and composition of the shrub and canopy layers and potentially increases in downed wood resulting from blow down (Brosofske et al. 1997, Harper and Macdonald 2001, Hannon et al. 2002, Kiffney et al. 2003). Although, longer-term changes in buffer structure and composition post-harvest are likely to influence abundance and composition of the animals that reside in the buffer, these long-term effects are unexamined to date (Marczak et al. 2010).

For many studies, it is difficult to evaluate the effect of buffer width on species that are highly dependent upon riparian zones because we do not know which species are in fact highly dependent upon riparian environments (but see Whitaker and Montevecchi 1999 and Pearson and Manuwal 2001). As a consequence, species that decline or disappear in riparian buffers may not be species dependent upon riparian zones for reproduction or survival but are simply responding to the loss of forest.

When considering issues of detectability, we know that patch occupancy is not generally detected with certainty (MacKenzie et al. 2002). It therefore follows that a researcher's ability to assess patterns in species richness or abundance in riparian buffers before and after harvest in forested landscapes could be influenced by changes in species detectability post-harvest. This potential change in detectability can occur for a variety of reasons including: 1) real changes in species abundance that influences their detectability (e.g., in the case of birds, singing frequency which is related to density); 2) changes in the structure and composition of the riparian buffer or the adjacent cutblock (see below), such as vegetation density that influences an observer's ability to detect the individual or species; or 3) changes between sampling periods, such as in environmental conditions (weather, stream noise) or observers that differ in their ability to detect the species. In our review of the riparian buffer literature, we found only one study (Perry et al. 2011) that explicitly accounted for changes or differences in detectability when examining the effectiveness of riparian buffers.

In the precursor to our study, Pearson and Manuwal (2001) described the immediate post-harvest (1-2 year post-harvest) responses to two buffer treatments: 1) a relatively uniform width riparian buffer and, 2) wider and more variable width buffers created after clearcut logging the uplands adjacent to small streams in western Washington, USA (Figure 1). For this current study, we revisited our study sites (~10 years post-harvest) and used the same Before-After-Control-Impact (BACI) experimental approach to examine longer-term effects on the avian community. Specifically, we looked at buffer treatment effects on species abundance and richness, local extinction (site-level species loss) and turnover, and similarity in community composition between treatments and controls. At the species level, we examine treatment effects on occupancy and abundance. In a second analysis that was not conducted with the short-term data, we took advantage of the variability in buffer width both within and among treatments to examine the relative influence of riparian buffer width and vegetation (trees and shrubs) on species occupancy and abundance. This new analysis allows us to identify thresholds in the effects of buffer width on species associated with riparian habitats. Unlike our previous study and most riparian studies to date, we incorporate contemporary statistical methods to account for potential influence of detectability on apparent treatment effects (e.g., Dorazio and Royle 2005, Zipkin et al. 2009, Russell et al. 2009, Archaux et al. 2012, Giovanini et al. 2013).

METHODS

Study area and experimental design

The experiment was conducted on the west side of the southern Cascade Mountains and the coast range of Washington, USA. All sites were located in the Western Hemlock forest zone (Franklin and Dyrness 1973; Figure 1). Forests in this zone are dominated by conifers including Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*). Deciduous tree species are not common in this zone except in recently disturbed sites, talus slopes, and riparian habitats. Riparian habitats are often dominated by red alder (*Alnus rubra*) and big-leaf maple (*Acer macrophyllum*) in early seral stages and by western hemlock and red cedar in later stages. The region is characterized by ridges and steep valleys and the climate consists of warm dry summers and cool wet winters. Lands used in this research were owned by the State of Washington, the City of Seattle, and private timber companies (see Acknowledgments). The primary management objective on these lands is the production of even-aged conifer stands dominated by Douglas-fir and much of the landscape has been harvested once or twice previously.

We used a Before-After-Control-Impact experimental design (McDonald et al. 2000) to examine bird response to narrow and wider, forested riparian buffers left along streams after clearcut harvest of the uplands. In 1991 and 1992, 18 sites were selected along small streams between the Cedar River watershed (east of Seattle) to the north and the Columbia River to the south. Sites were randomly assigned to treatments (Figure 1). Site selection was based on the following criteria: 1) low elevation (< 620 m); 2) second growth forest (45 - 65 yrs old); 3) dominated by Douglas-fir and western hemlock in the uplands; 4) second and third order streams (Strahler 1957); 5) predominantly coniferous riparian canopy with deciduous tree component; 5) at least 500 m in stream length and 300 m wide (150 m wide on each side of the stream) to accommodate point counts (see Bird Sampling below); and 6) experienced a common management history (e.g., harvested and thinned at the same time in the past) and were likely to be harvested as a single unit in the future. Sites size ranged from~33 to 50 ha, and each site was located along a different stream. The experimental design consisted of three treatments each with six replicates. The treatments were: 1) forested control sites with no harvest; 2) sites harvested according to 1992 Washington State Forest Practices regulations that consisted of clearcut uplands on each side of the stream with narrow unharvest forest reservers or buffers (~ 13m) along each side of the stream (Narrow treatment); and 3) sites harvested with a variable width unharvested buffer reserve that was wider and more variable than the Narrow treatment (~ 30 m; Wide treatment). Wide buffered sites were modified to accommodate local features such as seeps and structural components such as snags and down wood. Sites were harvested in 1994. We collected pre-harvest data in the spring of 1993 from all 18 sites; immediate post-harvest data in the spring of 1995 and 1996 (n = 6 Control, 6 Narrow buffer, and 6 Wide buffer); and long-term data approximately 10 years after harvest in 2003 and 2004 (n = 5 Control, 5 Narrow buffer, and 5 Wide buffer). Three sites in each treatment category were lost to harvest or not available for sampling in the second post-harvest period, resulting in a reduction in sample size between sampling periods from 18 to 15 sites.

Bird Sampling

We surveyed the avian community using 15-m fixed radius point counts (Verner 1985). In each site, we established 10 riparian point count stations along the edge of the stream with five stations spaced evenly on each side of the stream. The center of each riparian station was located 15 m (perpendicular distance) from the usual high water line, 100 m from other stations and at least 50 m from the edge of the study site. Ten additional point count stations were located parallel and 100 m upslope from the riparian stations in the adjacent uplands. Data from the upland stations were only used in the pre-harvest year to identify birds that were more abundant in the riparian habitat (Pearson and Manuwal 2001). Reference flags were placed 15 m to each side of each station. Small radius point counts allowed us to examine differences in bird abundance along narrow strips of potential habitat post-harvest and also to reduce detection issues associated with adjacent stream noise. Point counts rather than strip transects were used because it would have been difficult to both walk and observe birds in the dense vegetation and rugged terrain. However, we note that point count stations in the Narrow treatment will sample small areas outside of the riparian buffer after harvest. As a result, all inference about bird community responses to buffer treatments is made with reference to distance from the stream channel. Censuses usually started within 30 minutes of dawn and were completed within 5 hours. Upon arriving at a survey point, observers remained stationary and quiet for a minimum of 1 minute to allow birds to settle and then recorded all birds heard or seen during a 6-minute period. To avoid biases among observers, observers were rotated among the 18 study sites. To avoid biases associated with visiting riparian or upland sites first, we alternated travel routes. Each site was visited 6 times between mid-April and late-June. The surveys were evenly spaced throughout the breeding season to account for differences in breeding phenology among species. We did not conduct surveys during heavy precipitation or high winds. Every attempt was made to avoid counting individual birds more than once.

Habitat before and after harvest

We measured habitat variables in 15-m^2 square plots at each bird point count station (n = 10 per site) and the variables included in this study were: 1) counts of Douglas-fir, western hemlock/red cedar, and deciduous tree stems > 10 cm at 1.5 m above the ground (hereafter referred to as DBH or Diameter at Breast Height), and 2) visually estimated percent cover of shrubs (> 1m tall). At each point count station, we also measured the distance between the mean high water mark and the outer edge of the standing trees on all treatment sites. Upland habitats on both buffer treatments were clearcut leaving approximately two standing trees per acre as required by State law. In most cases, these standing trees were incorporated into the riparian buffer.

Data analyses

For all analyses, detections of Hermit (*Setophaga occidentalis*) and Townsend's (*Setophaga townsendi*) warblers were grouped as one species (hereafter hermit/Townsend's warbler) because these species hybridize extensively in this region (Rohwer and Wood 1998) and cannot be distinguished by song in regions of hybridization (Pearson and Rohwer 1998). In addition, we excluded from all analyses individuals that flew over the site, migrants that did not breed in the area [e.g., Ruby-crowned Kinglet (*Regulus calendula*) and Golden-crowned Sparrow (*Zonotrichia leucophrys*)], and all species not adequately sampled by point counts (grouse, raptors, and waterfowl). In addition, we excluded all species that were not detected on at least ten total occasions from all analyses; these species tended to be those for which we had no evidence of breeding on the experimental units, which generally do not breed in western hemlock forests, or have very large territories that are not adequately sampled using small radius point counts (e.g., pileated woodpecker *Dryocpus pileatus*).

For all analyses we aggregated over all point count stations within a site to obtain one response per site. This was done to avoid spatial autocorrelation of point count stations within sites, to help with model convergence by reducing the number of species that are not observed at the analysis level, and because the experimental unit was the site. All sites had the same 10 station × 15 meters radius sampling area. However given that the buffer widths varied between treatments, the samples represent bird populations within 30 meters of the stream edge, not bird within the riparian buffer.

We used multispecies site occupancy and abundance models (Dorazio and Royle 2005, Zipkin et al. 2009, Yamaura et al. 2012) to estimate species level covariate effects as well as population level summaries of occupancy and abundance, such as species richness, species similarity, and total abundance. We estimated occupancy dynamics, including species turnover and extinction (Russell et al. 2009, Giovanini et al. 2013). For both occupancy and abundance, we constructed three models. First, we fit the design-based model, in which treatment is modeled as a categorical covariate. Second, we fit a model in which buffer-width and vegetation effects are modeled as continuous covariates (we expect the treatments to modify buffer width as well as vegetation composition and structure). Finally, in order to understand how species richness and total abundance varied solely as a function of buffer width, we fit a model with a random effect for site but without treatment or covariate effects for either occupancy or abundance. We plotted these estimates against buffer width to determine if any thresholds existed in the association. We fit the third model to avoid forcing a linear relationship of buffer width. Following Russell et al. (2009), we do not account for the contribution of unobserved species in our population estimates, instead conditioning on the set of observed breeding species in our study.

Occupancy models--We let $z_{i,j,k}$ denote true the occupancy status, in which $z_{i,j,k} = 1$ if species i in year j occupies site k or $z_{i,j,k} = 0$ otherwise. The occupancy state is taken to be a Bernoulli random variable, $z_{i,j,k} \sim Bern(\psi_{i,j,k})$, where $\psi_{i,j,k}$ is the probability that species i in year j occupies site k. We take species detection, also, to follow a Bernoulli distribution, $y_{i,j,k,l} \sim Bern(p_{i,j,k,l} \cdot z_{i,j,k})$, where $y_{i,j,k,l}$ is 1 if the species i in year j is detected at site k during visit l, or 0 otherwise and where $p_{i,j,k,l}$ is the detection probability. Note that under this parameterization, the probability of detecting species i during year j at site k during will be zero if it does not occupy site k, since $z_{i,j,k} = 0$.

The first model that we considered was the model based on the experimental design, in which detection probability varied by treatment type (Control, Narrow, and Wide treatments) and year. For the detection model, the treatment status effect is the treatment at time of measurement. Therefore, in 1993, all sites had control for the detection model. In addition, we included linear and quadratic terms for Julian date (January 1 = 1, December 31=365) because avian detection rates are known to vary seasonally (Kéry et al. 2005). We centered and scaled the date covariate. The species-specific detection probability mean model is:

$$logit\left(p_{i,k,j,l}\right) = \beta_{oi} + \beta_{1i} \cdot Year.1995_j + \beta_{2i} \cdot Year.1996_j + \beta_{3i} \cdot Year.2003_j +$$
$$\beta_{4i} \cdot Year.2004_j + \beta_{5i} \cdot Trt.Narrow.det_{k,j} + \beta_{6i} \cdot Trt.Wide.det_{k,j} + \beta_{7i} \cdot Date_{j,k,l} +$$
$$\beta_{8i} \cdot Date^2_{j,k,l}$$

Occupancy was allowed to vary by species, site, year, treatment, and by an interaction of treatment type and year. The occupancy mean model is:

$$
\begin{aligned}
&logit\left(\psi_{i,j,k}\right) = \alpha_{0i} + \alpha_{0k} + \alpha_{1i} \cdot Year.1995_j + \alpha_{2i} \cdot Year.1996_j + \alpha_{3i} \cdot Year.2003_j + \\
&\alpha_{4i} \cdot Year.2004_j + \alpha_{5i} \cdot Narrow_k + \alpha_{6i} \cdot Wide_k + \alpha_{7i} \cdot Year.1995_j \cdot Narrow_k + \\
&\alpha_{8i} \cdot Year.1996_j \cdot Narrow_k + \alpha_{9i} \cdot Year.2003_j \cdot Narrow_k + \alpha_{10i} \cdot Year.2004_j \cdot Narrow_k + \\
&\alpha_{11i} \cdot Year.1995_j \cdot Wide_k + \alpha_{12i} \cdot Year.1996_j \cdot Wide_k + \\
&\alpha_{13i} \cdot Year.2003_j \cdot Wide_k + \alpha_{14i} \cdot Year.2004_j \cdot Wide_k
\end{aligned}
$$

The terms α_{0i} and α_{0k} are random effects for species and site, respectively. Even though there substantial variability of buffer widths within the Narrow and Wide buffer treatments (Table 2), this analysis allows us to examine how the buffer treatments would act within the context of operational variability of harvest prescriptions.

To examine how species occupancy differed among buffer prescriptions, we estimated treatment effect sizes (Christensen 1996, Kroll et al. 2012, Betts et al. 2013). In our parameterization, the year × Narrow and year × Wide coefficients compare occupancy of the respective treatments to the Control, and are estimates of the treatment effects on occupancy. After back transformation, these terms are interpreted as the multiplicative change in odds of occupancy. We estimated species richness (*s*), where *nspp* is the total number of species across all sites by year, for treatment and control plots separately as:

$$\hat{s}_{j,k} = \sum_{i=1}^{i=nspp} \sum_{k=1}^{k=sites} \hat{z}\left(i, j, k\right).$$

To examine the effect of buffer treatment on species richness, we estimated the mean species richness for the three treatment × five year combinations. In addition to estimated species richness, we estimated species similarity both between and among treatment and control sites (Dorazio and Royle 2005) by calculating the proportion of species that occupy both sites. Species similarity in year *j* for sites k_1 and k_2, is defined as:

$$S_{j,k_1,k_2} = \frac{2\sum_i \left(z_{i,j,k_1} \times z_{i,j,k_2}\right)}{\sum_i z_{i,j,k_1} + \sum_i z_{i,j,k_2}}.$$

Within each year, we estimated the similarity for all pairwise combinations of sites. This set of summary statistics allows us to determine the impact of buffer treatment on species similarity.

We estimated species turnover (τ), the probability that a species chosen at random from the community at time *j* is a species not present at time *j* – 1, and local-extinction rates (ε) as:

$$\tau\left(j\right)=\frac{\sum_{i=1}^{i=nspp}\sum_{k=1}^{k=sites}z\left(i,k,j\right)\times\left[1-z\left(i,k,j-1\right)\right]}{\sum_{i=1}^{i=nspp}\sum_{k=1}^{k=sites}z\left(i,k,j-1\right)}$$

$$\varepsilon\left(j\right)=\frac{\sum_{i=1}^{i=nspp}\sum_{k=1}^{k=sites}1-z\left(i,k,j\right)\times z\left(i,k,j-1\right)}{\sum_{i=1}^{i=nspp}\sum_{k=1}^{k=sites}z\left(i,k,j-1\right)}.$$

The second model that we used examined effects of buffer width (the treatment) and vegetation covariates on occupancy for sites that were harvested. Observations from the pre-treatment year and all control sites were not included in this analysis. The detection model included effects of year, average buffer width (based on 10 measurements) at each site (BufferWidth), percent shrub cover (Shrub), number of Douglas-fir stems > 10 cm DBH (DougFir), number of deciduous stems > 10 cm DBH (Decid), and number of western hemlock and western red cedar stems > 10 cm DBH (HemCedar). We included linear and quadratic terms for Julian date. We centered and scaled all continuous covariates. The species-specific detection probability mean model is:

$$logit\left(p_{i,k,j,l}\right)=\beta_{oi}+\beta_{1i}\cdot Year.1996_j+\beta_{2i}\cdot Year.2003_j+\beta_{3i}\cdot Year.2004_j+$$
$$\beta_{4i}\cdot BufferWidth_{k,j}+\beta_{5i}\cdot Shrub_{k,j}+\beta_{6i}\cdot DougFir_{k,j}+\beta_{7i}\cdot Decid_{k,j}+\beta_{8i}\cdot HemCedar_{k,j}+$$
$$\beta_{9i}\cdot Date_{j,k,l}+\beta_{10i}\cdot Date^2_{j,k,l}.$$

The occupancy model had the same terms as the detection model, except for the date covariates, and also included a site effect. The species-specific occupancy probability mean model is:

$$logit\left(\psi_{i,k,j}\right)=\alpha_{oi}+\alpha_{ok}+\alpha_{1i}\cdot Year.1996_j+\alpha_{2i}\cdot Year.2003_j+\alpha_{3i}\cdot Year.2004_j+$$
$$\alpha_{4i}\cdot BufferWidth_{k,j}+\alpha_{5i}\cdot Shrub_{k,j}+\alpha_{6i}\cdot DougFir_{k,j}+\alpha_{7i}\cdot Decid_{k,j}+\alpha_{8i}\cdot HemCedar_{k,j}.$$

We constructed a third model to provide site-specific estimates of species richness without any covariate effects except year. We used only the 2003 and 2004 data because we were interested in finding a buffer width that matched the control in the longer-term time frame. The detection model included effects of year, average buffer width (based on 10 measurements) at each site (BufferWidth), percent shrub cover (Shrub), number of Douglas-fir stems > 10 cm DBH (DougFir), number of deciduous stems > 10 cm DBH (Decid), and number of western hemlock and western red cedar stems > 10 cm DBH (HemCedar). We included linear and quadratic terms for Julian date. We centered and scaled all continuous covariates. The species-specific logistic detection probability model is:

$$logit\left(p_{l,k,j,i}\right) = \beta_{oi} + \beta_{1i} \cdot Year.2004_{j} +$$
$$\beta_{2i} \cdot BufferWidth_{k,j} + \beta_{3i} \cdot Shrub_{k,j} + \beta_{4i} \cdot DougFir_{k,j} + \beta_{5i} \cdot Decid_{k,j} + \beta_{6i} \cdot HemCedar_{k,j} +$$
$$\beta_{7i} \cdot Date_{j,k,l} + \beta_{8i} \cdot Date^{2}_{j,k,l}.$$

The occupancy model included site and year effects. We did not include either buffer width or vegetation effects because we did not want to 'force' a relationship between buffer width and occupancy. The species-specific logistic occupancy probability model is:

$$logit\left(\psi_{i,k,j}\right) = \alpha_{oi} + \alpha_{ok} + \alpha_{1i} \cdot Year.2004_{j}.$$

Abundance models-- For the abundance data, we fit a multispecies version of the N-mixture model (Yamaura et al. 2012, Chandler et al. 2013). This model is a natural extension of the single species N-mixture model (Royle 2004, Kéry 2008) and the multispecies occupancy model (Dorazio and Royle 2005). We let $n_{i,j,k,l}$ be the number of individuals of species *i* in year j that are detected at site *k* , and during visit *l*. We define $N_{i,j,k}$ as the unobserved site level abundance, assumed constant over visits. We then model the observed count, $n_{i,j,k,l}$ as a $\text{Binomial}\left(N_{i,j,k}, p_{i,j,k,l}\right)$ random variable. Following Royle (2004), we assume the site level abundance $N_{i,j,k}$ follows a $\text{Poisson}\left(\lambda_{i,j,k}\right)$ distribution. Abundance covariates are incorporated in the model by assuming that the log-transform of $\lambda_{i,j,k}$ is described by a linear function of the covariates. Detection probability is modeled similarly, where we assume that the logit transform of $p_{i,j,k,l}$ is a linear function of the covariates.

The first model that we constructed was based on the experimental design, in which detection probability varied by treatment type (Control, Narrow, and Wide buffers) and year. For the detection model, the treatment status effect is the treatment at time of measurement. Therefore in 1993, all sites had control for the detection model. Similar to the occupancy models, we included linear and quadratic effects of date. We centered and scaled the date covariate. The species-specific logistic detection probability model is:

$$logit\left(p_{i,k,j,l}\right) = \beta_{oi} + \beta_{1i} \cdot Year.1995_j + \beta_{2i} \cdot Year.1996_j + \beta_{3i} \cdot Year.2003_j + \beta_{4i} \cdot Year.2004_j + \beta_{5i} \cdot Trt.Narrow.det_{k,j} + \beta_{6i} \cdot Trt.Wide.det_{k,j} + \beta_{7i} \cdot Date_{j,k,l} + \beta_{8i} \cdot Date^2_{j,k,l}$$

Similar to occupancy, abundance was allowed to vary by site and by an interaction of treatment type and year. The log linear abundance model is:

$$log\left(\lambda_{i,j,k}\right) = \alpha_{0i} + \alpha_{0k} + \alpha_{1i} \cdot Year.1995_j + \alpha_{2i} \cdot Year.1996_j + \alpha_{3i} \cdot Year.2003_j + \alpha_{4i} \cdot Year.2004_j + \alpha_{5i} \cdot Narrow_k + \alpha_{6i} \cdot Wide_k + \alpha_{7i} \cdot Year.1995_j \cdot Narrow_k + \alpha_{8i} \cdot Year.1996_j \cdot Narrow_k + \alpha_{9i} \cdot Year.2003_j \cdot Narrow_k + \alpha_{10i} \cdot Year.2004_j \cdot Narrow_k + \alpha_{11i} \cdot Year.1995_j \cdot Wide_k + \alpha_{12i} \cdot Year.1996_j \cdot Wide_k + \alpha_{13i} \cdot Year.2003_j \cdot Wide_k + \alpha_{14i} \cdot Year.2004_j \cdot Wide_k.$$

As with the occupancy model, the year × Narrow and year × Wide coefficients compare abundance of the respective treatments to the Control, adjusting for differences due to year. After back transforming, a treatment contrast of 1 indicates that abundance is equal across treatments.

We estimated the total abundance of all individuals for all species that occupy a site for treatment and control plots separately as:

$$Total\ \hat{N}_{j,t} = \sum_{i=1}^{i=nspp} \sum_{k=1}^{k=sites} \hat{N}_{i,j,k},$$

where *nspp* is the total number of species across all sites and t is an indicator variable for treatment type. This estimate represents the total number of individuals across all species, where abundance for each species is adjusted by a species-specific detection probability.

The second model that we considered examined the effect of buffer width and vegetation covariates on abundance for sites that were harvested. Observations from the pre-treatment year and all control stands were not included in this analysis. The detection model included effects of year, site buffer width, percent shrub cover, number of Douglas-fir stems > 10 cm DBH, number of deciduous stems > 10 cm DBH, and number of western hemlock and western red cedar stems > 10 cm DBH. We centered and scaled all continuous covariates. The species-specific detection probability mean model is:

$$logit\left(p_{i,k,j,l}\right) = \beta_{oi} + \beta_{1i} \cdot Year.1996_j + \beta_{2i} \cdot Year.2003_j + \beta_{3i} \cdot Year.2004_j + \beta_{4i} \cdot Width_{k,j} + \beta_{5i} \cdot Shrub_{k,j} + \beta_{6i} \cdot DougFir_{k,j} + \beta_{7i} \cdot Decid_{k,j} + \beta_{8i} \cdot HemCedar_{k,j} + \beta_{9i} \cdot Date_{j,k,l} + \beta_{10i} \cdot Date^2_{j,k,l}.$$

The abundance model had the same terms as the detection model and also included a site effect. The species-specific abundance mean model is:

$$log\left(\lambda_{i,k,j}\right)=\alpha_{oi}+\alpha_{ok}+\alpha_{1i}\cdot Year.1996_{j}+\alpha_{2i}\cdot Year.2003_{j}+\alpha_{3i}\cdot Year.2004_{j}+$$
$$\alpha_{4i}\cdot Width_{k,j}+\alpha_{5i}\cdot Shrub_{k,j}+\alpha_{6i}\cdot DougFir_{k,j}+\alpha_{7i}\cdot Decid_{k,j}+\alpha_{8i}\cdot HemCedar_{k,j}.$$

We wanted to determine at what buffer width abundance of riparian-associated species and total avian abundance were similar to abundance in the Control sites. To estimate these quantities for each site, we averaged the posterior medians of total abundance and species richness over the years in the study. The resulting means were plotted vs. buffer width of the site.

The third model that we constructed examined the association between buffer width and total abundance for harvested sites as compared to control sites. We used only the 2003 and 2004 data because we wanted to identify a buffer width that matched the control in the longer-term time frame. The detection model included effects of year, average buffer width (based on 10 measurements) at each site (BufferWidth), percent shrub cover (Shrub), number of Douglas-fir stems > 10 cm DBH (DougFir), number of deciduous stems > 10 cm DBH (Decid), and number of western hemlock and western red cedar stems > 10 cm DBH (HemCedar). We included linear and quadratic terms for Julian date. We centered and scaled all continuous covariates. The species-specific detection probability mean model is:

$$logit\left(p_{l,k,j,i}\right)=\beta_{oi}+\beta_{1i}\cdot Year.2004_{j}+$$
$$\beta_{2i}\cdot BufferWidth_{k,j}+\beta_{3i}\cdot Shrub_{k,j}+\beta_{4i}\cdot DougFir_{k,j}+\beta_{5i}\cdot Decid_{k,j}+\beta_{6i}\cdot HemCedar_{k,j}+$$
$$\beta_{7i}\cdot Date_{j,k,l}+\beta_{8i}\cdot Date_{j,k,l}^{2}.$$

The abundance model included site and year effects. We did not include either buffer width or vegetation effects because we did not want to force a relationship between buffer width and abundance. The species-specific abundance probability mean model is:

$$log\left(\lambda_{i,k,j}\right)=\alpha_{oi}+\alpha_{ok}+\alpha_{1i}\cdot Year.2004_{j}.$$

To examine the association of buffer width and vegetation covariates with species richness and total abundance in the continuous covariate model (2nd model), we used average predictive comparisons (Gelman and Pardoe 2007, Jones et al. 2012,) to quantify directly associations (and uncertainty) between *predicted* species richness and *predicted* total abundance with each model covariate. Predictive comparisons evaluate the difference in expected response for a unit difference in an input covariate, using the fitted model, and averaging over the distribution of all other covariates. Following Jones et al. (2012), we extend this approach to species richness and total abundance by summing over the species-specific predictions to obtain averaged expected differences in species count. For dataset $(x, y)_j$, $j = 1, ..., n$, we denote our input of interest *u*, and all other inputs *v*, such that *x=(u,v)*, where n is the number of sites. We let $i = 1, ..., N$, be the index of species, where N is the total number of observed species. We estimated the average predictive comparison for species richness using the following equation:

$$\hat{\Delta}_u = \frac{\sum_{j=1}^{n}\sum_{k=1}^{n}\sum_{s=1}^{S} w_{jk}\sum_{i=1}^{N}\left(E(y\,|\,u_k, v_j, \theta^S) - E(y\,|\,u_j, v_j, \theta^S)\right) sign(u_k - u_j)}{\sum_{j=1}^{n}\sum_{k=1}^{n}\sum_{s=1}^{S} w_{jk}(u_k - u_j) sign(u_k - u_j)}$$

Let θ^s be a set of $s = 1, ..., S$ simulations were sampled from the posterior distribution. Let w_{jk} be a weight that reflects how likely a transition from u_j to u_k when $v=v_j$. We calculated predictive comparisons for all model inputs, treating each in turn as the input of interest. Standard errors for $\hat{\Delta}_u$ are estimated following Gelman and Pardoe (2007), and account for the uncertainty in model parameter estimates, while treating all covariates as fixed.

For all four of the hierarchical community models, we assume that the species-specific effects for a given parameter are drawn from a common normal distribution, e.g., that $\alpha_{1,i} \sim N\left(\mu_1, \sigma_1^2\right)$ for parameter α_1 of species *i*, where the mean and variance of $\alpha_{1,i}$ are population-level hyper-parameters. This population-level distribution provides a summary of community response, both in terms of the mean behavior as well as the variability in behavior. The extent to which information is shared across species depends on both the degree of uniformity across the population, as estimated by the population-level parameters, and the amount of information available for each species. For species with little information, those with low detection probabilities, estimates will tend to shrink toward the population mean value. To account for the fact that the same sites are sampled in multiple years, we included a site level random effect, $\alpha_{0k} \sim N\left(0, \sigma_k^2\right)$. This approach is analogous to a 'compound symmetric' correlation structure for years within a site (Littell et al. 2006).

We fit our model using JAGS (Plummer 2003) called from R version 2.15.2 (R Development Core Team 2010) using the 'jags' function in package R2jags version 0.03-08 (Su and Yajima 2012). For all models, we ran 3 Markov chains of length 400,000 with a burn-in period of 200,000 and 1/50 thinning. We provide all code for the models in the supplementary material. We assessed convergence using the Gelman-Rubin statistic (Gelman et al. 2004) and visual inspection of the chains, with both measures indicating a reasonable assumption of convergence. To assess consistency between our models and data, we used posterior predictive checks (Gelman and Hill 2007). We did not find any evidence of lack of fit in the models that we evaluated (Appendix 2). We provide details and an example for the posterior predictive checks in the supplementary material.

RESULTS

Experimental Approach

Overall.--Across all years (1993, 1995-1996, and 2003-2004) and treatments (Control, Wide and Narrow buffer), we had 28 species detected at least 10 times total for a total of 2064 detections (Table 1). A few species constituted the majority (60%) of the detections including the Pacific wren (*Troglodytes pacificus*), Pacific-slope flycatcher (*Empidonax difficilis*), chestnut-backed chickadee (*Poecile rufescens*), Wilson's warbler (*Cardellina pusilla*), Swainson's thrush (*Catharus ustulatus*), and American robin (*Turdus migratorius*). For reference, we provide the effect (95% credibility interval) of three riparian buffer treatments on detection and capture probabilities for all 28 species in Table S3 and S4.

The average riparian buffer was 13.1 (±9.1SD) and 29.9 m (±15.5SD) on the Narrow and Wide treatments, respectively, but we found considerable within-treatment variation (Table 2). In fact, the widest forested buffer on the Narrow treatment (25.5±12.1SD) overlaps with the narrowest buffer on the Wide treatment (21.7±5.1SD). In our "*covariate effects*" and "*buffer width thresholds*" analysis below, we took advantage of this variation in buffer width both within and among treatments to examine effect of buffer width on abundance and occupancy while ignoring treatment assignments (see the X axis in Figures 9 and 10 for the distribution of all site buffer widths). In general, the treatments resulted in greater shrub cover and number of deciduous and Douglas-fir trees in the riparian and fewer western hemlock and western red cedar trees 10 years post-harvest (Table 3) than the control.

Community responses.—We found broad overlap in the credible intervals associated with our estimates of total bird abundance for controls and treatments for the pre- and post-harvest time periods (Figure 2). Within sampling year, we found less variation in the mean point estimates of abundance among treatments relative to the uncertainty associated with those estimates (Figure 2). Note that the credible intervals are wide indicating uncertainty about parameter estimates and a lack of power to detect treatment effects. In general, avian abundance moved up and down between time periods similarly among all sites post-treatments (Figure 2). Across all years and treatments, mean estimates of species richness ranged from approximately 13-24 avian species with lower pre-harvest richness on all treatments. Estimates of post-harvest richness change little on Control sites relative to pre-harvest levels (Figure 3), while both treatments exhibit a similar 31-44% increase post-harvest (Figure 3). Richness estimates on both treatments continued to increase by about 1-2 species between the immediate post-harvest survey (slight credible interval overlap between treatments and controls) and the 10 year post-harvest survey (no credible interval overlap between treatments and control; Figure 3). Species similarity among treatments overlapped broadly before and after harvest (Figure 4). Site-level estimates of species local-extinction rates were almost identical between treatments and controls regardless of the time periods compared (Figure 5). Species turnover was also almost identical for the two buffer treatments and controls for all years compared except when comparing the pre-harvest sample to the 10 year post-harvest sample when there was little overlap in credible intervals between the Narrow treatment and the Control (Figure 5) and with much higher turnover on both treatments (63% and 74%) relative to the controls (29%).

Species responses. — Pre-harvest, species-level estimated probability of site occupancy was very similar for the control and each treatment (95% credible intervals for differences broadly overlap 0 for all species; Figure 6). Post-harvest, 7 and 21% of the species increased their probability of site occupancy (95% credible intervals associated with the probability of species occupancy did not overlap zero) in the short-term and 29 and 93% increased their probability of site occupancy in the long-term on the Narrow and Wide buffer treatment respectively (Figure 6). Probability of site occupancy did not decrease for any species (Figure 6). This increase in the probability of occupancy held for interior conifer forest species like the golden-crowned kinglet (*Regulus satrapa*) and for species associated with edge and more open habitats like the northern flicker (*Colaptes auratus*). We found no clear evidence for species-level differences (all credible intervals overlapped zero) in abundance between buffer treatments and the Control for either time period assessed (Figure 6).

Moving Beyond the Experiment

Covariate effects.--When taking advantage of the existing variation in vegetation characteristics and buffer width among harvested sites only (excluding controls) and ignoring site treatment assignments (Wide vs. Narrow), we found no effect of vegetation (deciduous trees, Douglas-fir trees, western hemlock/red cedar trees, and shrubs) or buffer width covariates on species richness or total avian abundance (Figure 7). For buffer width, we found little (16%) overlap between total avian abundance and zero, providing some evidence (84%) for a positive effect of buffer width on avian abundance.

Nearly all credible intervals broadly overlapped zero for the relationship between individual species abundance/occupany and either buffer width or the vegetation variables (Figure 8). The few relationships (8 out of 280) where credible intervals did not overlap zero were: 1) a positive effect of buffer width on chestnut-backed chickadee abundance, 2) negative effect of deciduous tree density on Pacific-slope flycatcher, chestnut-backed chickadee, golden-crowned kinglet, and dark-eyed junco abundance, 3) positive effect of Douglas-fir tree density on Steller’s jay abundance, 4) negative effect of western hemlock and western red cedar density on Wilson’s warbler abundance, and 5) a positive effect of shrub cover on warbling vireo occupancy (Figure 8).

Buffer width thresholds.--Again, taking advantage of the variability in average site buffer widths within and among treatments and ignoring treatment assignments, we compared species richness and total avian abundance across buffer widths (Figure 9). Averaged across all years post-treatment, richness was generally similar between various width buffers and Controls except for lower richness on a on a very narrow buffer and greater richness on a wider buffer (Figure 9). Abundance was less than controls on two relatively narrow buffers and greater than controls on one wider buffer (Figure 9). For all species associated with riparian habitats (Pacific-slope flycatcher, Pacific wren, black-throated gray warbler, and American robin; Figure 10), overlap occurred between the credible intervals between controls and all stands regardless of width. Although Pacific wren abundance point estimates for two relatively narrow treatments were below the credible intervals of the Controls, their credible intervals overlapped those for controls.

DISCUSSION

Long- and short-term effects of buffer width – the experimental approach

Using an experimental approach, we found no evidence for a long- or short-term change in estimated total avian abundance among riparian buffer treatments, regardless of the year compared. Similarly, we did not find any site-level loss of species (local-extinction) due to buffer treatments. Instead, turnover in the avian community on both the Narrow and Wide treatments resulted in the addition of species (43-47% increase; Figure 5). As a result of this increase in richness on the two buffer treatments, treatments were more similar to each other in species composition than either was to the control. The increase in richness on the two treatments was manifested by greater odds of site occupancy for a number of species on the treatments post-harvest (Figure 6). Many species had twice the odds of occupying treatment sites compared to the control. Interestingly, for most species, strong evidence for an increase in probability of occupancy on treatments relative to the controls did not become evident until~10 years post-harvest, suggesting that colonization was occurring over an extended period of time (compare the long- to short-term occupancy effects in Figure 6). The change in the avian community within the riparian buffers on the treatments post-harvest was driven by the colonization of early successional species such as spotted towhee (*Pipilo maculatus*) and song sparrow (*Melospiza melodia*) and edge species like the northern flicker and olive-sided flycatcher (*Contopus cooperi*) (Figure 6). The harvest resulted in more varied forest conditions relative to controls – the buffers contained forest, edge and early successional conditions - which, in turn, resulted in an increase in the detections of edge and open habitat species. The potential competitive interaction among the new species assemblages within riparian buffers remains unexplored.

All studies included in Marczak et al.’s (2011) meta-analysis were short-term (<5 years following forest harvest) and consequently, they recommend that the results be viewed with “caution”. This is the case because species may be lost or they may colonize riparian buffers with increasing time since buffer establishment, a pattern that may not be evident in short-term studies (Marczak et al. 2010). For example, philopatric and territorial forest-associated species returning to their previous years' territory may pack into the remaining habitat in the forested buffer resulting in an increase in abundance immediately post-harvest but with a gradual reduction in density as birds sort out territorial boundaries. We found no short-term increase in avian abundance following our treatments and therefore no support for the packing hypothesis. Alternatively, one might predict delayed colonization or extinction within a buffer as the result of gradual changes in the buffer plant community. For example, edge effects created by clearcutting the forest adjacent to riparian buffers can penetrate as much as 40 m into buffers (Brosofske et al. 1997), resulting in greater risk of blow-down, larger quantities of downed wood, and other structural and compositional forest changes (Harper and Macdonald 2001, Hannon et al. 2002). Edge effects can continue to influence forest structure and composition for upwards of 15 years post-harvest (Harper and Macdonald 2001). Interestingly, in our study, species richness and probability of individual species occupancy continued to increase between the immediate post-harvest surveys and the 10 year post-harvest surveys with no similar evidence for local species extinction over the same time period. In addition, this pattern appeared to be driven primarily by the treatments and not by other structure or compositional changes within the buffer. Because the increase in species richness on buffer treatments was gradual and may well continue beyond the time frame of this experiment, the effect of treatment (buffer width) on species turnover did not become pronounced until 10 years post-harvest lending support to being cautious in assuming that short-term results are necessarily reflective of the long-term.

Moving beyond the experiment – the influence of buffer width and vegetation

Relatively few studies differentiate the effect of buffer width from the effect of vegetation composition and structure on the breeding bird community. Although we had clear differences between treatments in buffer width (see averages in Table 2), we also had considerable variability in buffer width within and among our treatments (range = 6.7 - 40.7 m; Table 2). This variability allowed us to move beyond site (stand) treatment assignments and our experimental approach to an analysis where we could examine the influence of buffer width and tree and shrub characteristics on species abundance and occupancy (this analysis did not include controls). On the treated sites, we found weak evidence for a positive relationship between total avian abundance and buffer width was positive but weak (84% for a positive relationship; Figure 7). At the same time, we found almost no estimated effect of the other shrub and tree covariates on abundance suggesting that buffer width alone is responsible for nearly all of the positive patterns observed (Figure 7). Perry et al. (2011) examined both forest structure and buffer width on species occupancy in the southeastern U.S. and found that, for many species, both variables were important. However, they examined the structure of the surrounding forests (not that of the riparian buffer) on the avian community in the buffer. In our study, the forest adjacent to the riparian buffer was clearcut on all treatments and as a consequence, we examined forest composition/structure variables within the riparian buffer and not in the adjacent harvest unit. To understand how species richness and total abundance varied solely as a function of buffer width, we fit a model with a random effect for site but without treatment or covariate effects. We plotted these site estimates of buffer width and compared them to that of controls to determine if any thresholds existed in the association (Figures 9 and 10). These results suggest that there is no difference or greater species richness and abundance for forested buffers ≥ 21m when compared to controls and there is some evidence for reduced abundance and richness on a few sites with buffers ≤ 12m (Figure 9). Some sites with very narrow buffers (<12m) appear to have similar total avian abundance and richness to controls suggesting considerable variation in avian response even at the narrowest buffer widths. Because we were unable to identify other vegetation covariates that might provide insight into this variation in response, we recommend research focused on identifying those mechanisms responsible for variation in narrow buffer effectiveness. This information can direct site-specific prescriptions for maintaining avian abundance and richness when narrow buffers are desired.

Riparian associates

When establishing buffer guidelines, agencies rarely differentiate between supporting organisms at their original abundance and simply maintaining the presence of a species (Marczak et al. 2010, Richardson and Thompson 2009). In addition, few studies have identified which species are more abundant in riparian zones when compared to adjacent uplands. In our previous research (Pearson and Manuwal 2001), we identified “riparian associates” by comparing the relative abundance of all species in un-harvested riparian to upland habitats. This comparison identified four species that were more abundant in riparian habitats, the Pacific wren, Pacific-slope flycatcher, black-throated gray warbler and American robin (Pearson and Manuwal 2001). This result is supported, in part, by other studies (e.g., McGarigal and McComb 1992). The black-throated gray warbler, for example, forages and nests almost exclusively in deciduous trees or mixtures of deciduous and conifer trees (Morrison 1982, Guzy and Lowther 1997) which are most abundant in the riparian zone in this region (Swanson et al. 1982). Also, when compared to adjacent upslope conifer dominated habitats, Pacific-slope flycatchers in riparian habitats are more likely to attract mates, pair earlier, and have higher fecundity (Leu 2000). As a result, the riparian habitat is particularly important to these species. Despite the disproportionate use of riparian environments, we found no evidence that the Narrow or Wide buffer treatment reduced the abundance of these species relative to the controls (Figure 6). When attempting to identify buffer width thresholds for riparian associates, only the Pacific wren abundance demonstrated very weak evidence for reduced abundance on two of the Narrow sites (Figure 10). Our results suggests that the riparian buffer guidelines in the Pacific region are close to the minimum needed to maintain the abundance of riparian-associated birds but more than adequate to maintain the species on the landscape (especially when also considering the forested portions of the landscape).

Buffer guidelines

Are current riparian buffer guidelines adequate for maintaining riparian-associated species? In a quantitative review of riparian buffer width guidelines and regulations from Canada and the United States, average buffer width varied from 15.1 - 29.0 m (Lee et al. 2004). This variation was driven by the water body type (lake, stream, wetland, etc.) being buffered and its size and the average width varied geographically, with larger buffers in Canada and particularly narrow buffers in the Southeastern United States (Lee et al. 2004). In addition, buffer width guidelines are likely to vary depending on the biotic and abiotic focus of the guideline or political considerations. Although forested buffers can be established to maintain species associated with aquatic and riparian conditions (e.g.,Wesche et al. 1987), other factors such as minimizing sedimentation (Steedman and France 2000), moderating stream temperature and light penetration

(Johnson and Jones 2000), and maintaining riparian vegetation (Harper and MacDonald 2001) and input of large organic debris (Fetherston et al. 1995) may be dominant factors when establishing buffer width guidelines. In the Pacific region where our research was conducted, average buffer width on small and large permanent streams ranged from 22.7-24.3 m (Lee et al. 2004). These guidelines for this region are within the range of buffers included in our study. They are also within a range where we observed no evidence (>12 m) for avian species loss or for a decline in species abundance (including that of riparian associated species). Based on our results, buffers in this range are likely to maintain or increase avian species richness and abundance and not result in site-level species extinction.

In contrast to our results, several authors have suggested that buffers ≥ 100 m are needed to maintain the complete pre-harvest avian community (Tiquet et al. 1990, Hodges and Krementz 1996, Kilgo et al. 1998, Lambert and Hannon 2000, Shirley and Smith 2005, Perry et al. 2011) while others have suggested that buffers ≥ 60 m or even narrower are needed to maintain the pre-harvest avian community (Darveau et al. 1995, Hagar 1999). The relationship between buffer width and avian abundance or species composition appears to vary geographically, and it appears that wider buffers are needed in eastern deciduous forests than in the relatively wet coastal coniferous forests.

Landscape context and study limitations

Landscape context beyond the riparian buffer can also influence abundance of species within the buffer (Lambert and Hannon 2000, Hannon et al. 2002, Martin et al. 2006) and ultimately might influence buffer width guidelines. For example, characteristics of the landscape matrix, particularly amount of urban development surrounding a forest, can be better predictors of avian community composition than forest buffer width (Miller et al. 2003, Rodewald and Bakermans 2006). Our research was conducted in a landscape with little urban development. Our study sites were embedded in large contiguous blocks of commercial or state forest properties (primarily in blocks > 30,000 ha). These large blocks consist of a tapestry of stands differing in size and age but generally composed of stands where the dominant trees range from 0-60 years in age and nearly all stands on the landscape had been harvested 1-3 times previously. Adjacent to these very large blocks of commercial/state timberlands were rural/agricultural lands at lower elevations and hundreds of thousands of hectares of forested federal lands (National Forest and Parks) at upper elevations. Other studies have classified landscapes similar to ours as “wildlands” (Hepinstall et al. 2008) where the human footprint is relatively low (Leu et al. 2008). In this context, landscape structure (composition and configuration) typically explains a relatively small amount of the variation in avian species abundance and species’ abundances are generally greater in more heterogenous landscapes (McGarigal and McComb 1995). Although we do not evaluate the effect of landscape context on our observed treatment effects, it is important to consider that the landscape backdrop was relatively consistent among our study sites, that all sites had to meet specified criteria for inclusion, and that the assignment of treatments and controls was random. Finally, we included a random effect for “site” in our model that can incorporate hetereogeneity resulting from unmodeled landscape-scale variation. Even though we consider it unlikely that a landscape scale factor is influencing the observed results, it is important to consider the landscape context of this experiment when thinking about the application of our results to other areas. For example, riparian zones appear to be more influential in relatively arid environments. In arid regions of the western United States, riparian habitats make up less than 1% of the landscape, yet 82% of all avian species annually breeding in northern Colorado occur in riparian vegetation (Knopf 1985), and 51% of all avian species in southwestern states are completely dependent upon this habitat type (Johnson et al. 1977). In this context, we might expect very different influences of buffer width on species composition, abundance, and local extinction probabilities.

We did not evaluate the effects of riparian buffers on avian reproduction and survival and the potential exists that birds within narrow riparian buffers or forest fragments may not reproduce as successfully as those located in large blocks of intact forests (Robbinson et al. 1995, Vander Haegen and Degraaf 1996). This relationship between reduced fecundity and habitat fragmented may not hold in all western riparian forests (Tewksbury et al. 1998, Davidson and Knight 2001). Geographical differences may be associated with the occurrence of brown-headed cowbirds (*Molothrus ater*), a brood parasite that is common in eastern U.S. forests but rarely encountered in some western forests (Carey et al., 1991; Bryant et al., 1993; Schieck et al.,1995). In addition, abundance of nest predators such as crows (*Corvus* spp.) and jays (*Cyanositta*) are not related to patch size in the western United States (Lehmkuhl et al., 1991; Schieck et al., 1995; Tewksbury et al., 1998) although they do prefer fragmented habitats

(Marzluff et al., 2004) and respond favorably to human habitation (Marzluff and Netherlin 2006). The only corvid detected frequently enough to assess treatment effects in our study was the Steller's jay (*Cyanocitta stelleri*). Abundance of Steller’s jays on treatments did not differ from Controls although it was twice as likely to occupy the Wider buffer treatment compared to the Control, which could result in higher nest predation within wide buffers. Without data on nest success or other vital rates, we cannot evaluate the potential influence of this nest predator on fecundity.

Conclusion

We conducted a large-scale manipulation using a BACI experimental design where we accounted for time lag-effects and inherent variability among treatments through replication and by selecting sites from similar managed forest landscapes and by randomly assigning treatments and controls. Finally, we used recent statistical developments that allow us to address issues of detectability among treatments and years by using replicated counts within season. Depending on the landscape context, land owner, and individual forester, considerable variability in how the boundaries riparian buffers are designated on-the-ground is likely. This variation was apparent within and among our treatments. This variability provided an opportunity to examine the relative effect of buffer width as a quasi-continuous variable to identify potential thresholds on avian abundance and occupancy. Taken together, our results suggest that local site-level extinction does not occur regardless of the buffer width that we examined, that buffer treatments increased species richness regardless of their width and that birds continued to colonize riparian buffers for up to 11 years post-harvest. We found only weak evidence for a positive effect of buffer width on total avian abundance and some suggestion that some very narrow buffered sites have lower total avian abundance and richness than controls.

ACKNOWLEDGMENTS

We thank Virgil C. Hawkes for coordinating the 2003-2004 re-sample. We thank Marc Hayes with Washington Department of Fish and Wildlife, the Cooperative Management and Research Committee, the Landscape-Wildlife Advisory Group, and the Scientific Advisory Group for having the foresight to establish and continue this study. For contractual assistance and oversight, we thank the following agencies and land owners/managers for their help in providing research sites and facilitating this work: Champion Pacific Timberlands, City of Seattle, Hampton Tree Farms, Hancock Timber, International Paper, Olympic Resource Management, Plum Creek Timber, The Campbell Group, Washington Department of Natural Resources, Washington Department of Fish and Wildlife, and Weyerhaeuser. We thank the field assistants that made this work possible for both the original sample (see Pearson and Manuwal 2001) and the 10 year post-harvest sample (Hawkes 2007). We thank Dr. John Richardson and three anonymous reviewers from the scientific review committee under Cooperative Monitoring, Evaluation and Research Committee for very helpful comments on an early draft of this manuscript.

LITERATURE CITED

Archaux, F., P.-Y. Henry, and O. Gimenez. 2012. When can we ignore the problem of imperfect detection in comparative studies? Methods in Ecology and Evolution 3:188-194.

Betts, M.G., J. Verschuyl, J. Giovanini, T. Stokely, and A.J. Kroll. 2013. Initial experimental effects of intensive forest management on avian abundance. Forest Ecology and Management 310:1036-1044.

Blinn, C.R., and M.A. Kilgore. 2001. Riparian management practices: a summary of state guidelines. Journal of Forestry 99:11-17.

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Bryant, A.A., J.P. Savard, and R.T. McLaughlin. 1993. Avian communities in old-growth and managed forests of western Vancouver Island, British Columbia. Technical Report Series, Canadian Wildlife Service, Nanaimo, British Columbia. pp. 1–115.

Bull, E. L. 1978. Specialized habitat requirements of birds: snag management, old growth, and riparian habitat. Pages 74-82 *in* R. M. DeGraaf, technical coordinator. Proceedings of the workshop on nongame bird habitat management in the coniferous forests of the western United States. U. S. Forest Service General Technical Report, PNW-64.

Carey, A.B., M.M. Hardt, S.P. Horton, and B.L. Biswell. 1991. Spring bird communities in the Oregon Coast Range. Pages 123–144 *in* Wildlife and Vegetation of Unmanaged Douglas Fir Forests. Vol. PNW-GTR-285. United States Department of Agriculture Forest Service General Technical Report, Portland, Oregon.

Chamberlin, T.W., R.D. Harr, and F.H. Everest. 1991. Timber harvesting, silviculture, and watershed processes. American Fisheries Society Special Publication 19:181–206.

Chandler, R.B., D.I. King, R. Raudales, R. Trubey, C. Chandler, and V.J.A. Chávez. 2013. A small-scale land-sparing approach to conserving biological diversity in tropical agricultural landscapes. Conservation Biology 27: 785-795.

Christensen, R. 1996. Analysis of variance, design and regression. Boca Raton, Florida, USA: Chapman and Hall/CRC.

Darveau, M., P. Beauchesne, L. Bélandger, J. Huot, and P. Larue. 1995. Riparian forest strips as habitat for breeding birds in boreal forest. Journal of Wildlife Management 59:67-78.

Davidson, A.S., and R.L. Knight. 2001. Avian nest success and community composition in a western riparian forest. Journal of Wildlife Management 65: 334–344.

Dorazio, R. M. and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association 100:389-398.

Fetherston, K.L., R.J. Naiman, and R.E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology 13: 133–144.

Fletcher, R.J., and R.R. Koford. 2003. Spatial responses of bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. Auk 120:799–810.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis, 2nd edition. Chapman & Hall/CRC, Boca Raton, FL, USA.

Gelman, A. and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, England.

Gelman, A., and I. Pardoe. 2007. Average predictive comparisons for models with nonlinearity, interactions, and variance components. Sociological Methodology 37:23-51.

Gimenez, O., A. Viallefont, A. Charmantier, R. Pradel, E. Cam, C.R. Brown, M.D. Anderson, M.B. Brown, R. Covas, J.-M. Gaillard. 2008. The risk of flawed inference in evolutionary studies when the detectability is less than one. American Naturalist 172:441-448.

Giovanini, J., A. J. Kroll, J. Jones, B. Altman, and E. B. Arnett. 2013. Effects of management intervention on post-disturbance community composition: an experimental analysis using Bayesian hierarchical models. PLOS ONE 8:e59900.

Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41: 540-551.

Guzy, M.J., and P.E. Lowther. 1997. Black-throated gray warbler (*Dendroica nigrescens*). In A. Poole, and F. Gill, eds., The Birds of North America, No. 319. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, D.C.

Hagan, J. M., III, W. M. Vander Haegen, and P.S. McKinley. 1996. The early development of forest fragmentation effects on birds. Conservation Biology 10:188-202.

Hagar, J. C. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. Journal of Wildlife Management 63:484-496.

Hannon, S. J., C. A. Paszkowski, S. Boutin, J. DeGroot, S. E. MacDonald, M. Wheatley, and B. R. Eaton. 2002. Abundance and species composition of amphibians, small mammals, and songbirds in riparian forest buffer strips of varying widths in the boreal mixedwood of Alberta. Canadian Journal of Forest Research 32:1784–1800.

Hannon, S.J. and F.K.A. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. Ecological Applications 12: 1457-1468.

Hanowski, J., N. Danz, J. Lind, and G. Niemi. 2003. Breeding bird response to riparian forest harvest and harvest equipment. Forest Ecology and Management 174:315–328

Harper, K. A., and S. E. Macdonald. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. Ecology 82:649–659.

Hawkes, V.C. 2007. Effectiveness of riparian management zones in providing habitat for wildlife: Resampling at the 10-year post-treatment interval. LGL Limited, Environmental Research Associates, Sidney, BC, Canada V8T 3C3.

Hepinstall, J. A., M. Alberti, and J. M. Marzluff. 2008. Predicting land cover change and avian community responses in rapidly urbanizing environments. Landscape Ecology 23:1257-1276.

Hodges, M.F and D.G. Krementz. 1996. Neotropical migratory breeding bird communities in riparian forests of different widths along the Atlanta River, Georgia. Wilson Bulletin 108:496-506.

Johnson, R. R., L. T. Haight, and J. M. Simpson. 1977. Endangered species vs. endangered habitats: A concept. Pages 68-97 in R. R. Johnson and D. A. Jones, technical coordinators. Importance, preservation and management of riparian habitat: A symposium. U.S. Forest Service, General Technical Report, RM-166.

Johnson, S.L., and J.A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57:30-39.

Jones, J.E., A.J. Kroll, J. Giovanni, S.D. Duke, and M.G. Betts. 2011. Estimating thresholds in occupancy when species detection is imperfect. Ecology 92:2299-2309.

Jones, J.E., A.J. Kroll, J. Giovanini, S.D. Duke, T.M. Ellis, and M.G. Betts. 2012. Avian species richness in relation to intensive forest management practices in early seral tree plantations. PLOS ONE 7: e43290. doi:10.1371/journal.pone.0043290.

Keller, C.M.E., C.S. Robbins, and J.S. Hatfield. 1993. Avian communities in riparian forests of different widths in Maryland and Delaware. Wetlands 13:137-144.

Kéry, M. 2008. Estimating abundance from bird counts: binomial mixture models uncover complex covariate relationships. Auk 125: 336-345.

Kéry, M., J. A. Royle, and H. Schmid. 2005. Modeling avian abundance from replicated counts using binomial mixture models. Ecological Applications 15:1450-1461.

Kiffney, P.M., J.S. Richardson, and J.P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams Journal of Applied Ecology 40:1060–1076.

Kilgo, J. C., R. A. Sargent, B. R. Chapman, and K. V. Miller. 1998. Effect of stand width and adjacent habitat on breeding bird communities in bottomland hardwoods. Journal of Wildlife Management 62:72-83.

Kinley, T. and N. J. Newhouse. 1997. Relationship of riparian reserve zone width to bird density and diversity in southeastern British Columbia. Northwest Science 71:75-86.

Knopf, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105-111 in R. R. Johnson, C. D. Ziebell, D. R. Patten, P. F. Ffolliot, and R. H. Hamre, technical coordinators. Riparian ecosystems and their management: Reconciling conflicting uses. U.S. Forest Service General Technical Report, RM-120.

Knopf, F.L., R.R. Johnson, T. Rich, F.B. Samson, and R.C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100: 272-284.

Kroll, A.J., J. Giovanini, J. Jones, E.B. Arnett, and B. Altman. 2012. Effects of salvage logging of beetle-killed forests on avian species and foraging guild abundance. Journal of Wildlife Management 76: 1188-1196.

Lambert, J.D., and S. Hannon. 2000. Short-term effects of timber harvest on abundance, territory characteristics, and pairing success of ovenbirds in riparian buffer strips. Auk 117:687-698.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165-180.

Lehmkuhl, J.F., L.E. Ruggiero, and P.A. Hall. 1991. Landscape patterns of forest fragmentation and wildlife richness and abundance in the southern Washington Cascade Range. Pages 425–442 *in* Wildlife and Vegetation of Unmanaged Douglas Fir Forests. Vol. PNW-GTR-285. United States Department of Agriculture Forest Service General Technical Report, Portland, Oregon.

Leu, M. 2000. Breeding territory settlement patterns and mate choice in a monochromatic Tyrannid flycatcher. Ph.D. Dissertation, University of Washington, Seattle.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: A large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119-1139.

Littell, R.C., G.A. Milliken, W.W. Stroup, R.D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models, Second Edition. SAS Institute Inc., Cary, North Carolina, USA.

MacKenzie, D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A. and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Marczak, L.B., T. Sakamaki, S.L. Turvey, I. Deguise, S.L.R. Wood, and J.S. Richardson. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications 20:129-134.

Martin, T.G., S. McIntyre, C.P. Catterall, and J.P. Possingham. 2006. Is landscape context important for riparian conservation? Birds in grassy woodland. Biological Conservation 127:201-214.

Marzluff, J.M., J.J. Millspaugh, P. Hurvitz, and M.S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller’s Jays. Ecology 85: 1411–1427.

Marzluff, J.M., and E. Neatherlin. 2006. Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. Biological Conservation 130:301–314.

McDonald, T.L., W.P. Erickson, and L.L. McDonald. 2000. Analysis of count data from Before-after control-impact studies. Journal of Agricultural, Biological, and Environmental Statistics 5:262-279.

McGarigal, K., and W. C. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management 56:10-23.

McGarigal K., and W.C. McComb. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecological Monographs 65:235-260.

Miller, J.R., J.A. Wiens, N.T. Hobbs, and D.M. Theobold. 2003. Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecological Applications 3:1041-1059.

Morrison, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of the Black-throated Gray and Hermit Warblers. Auk 99:503-513.

Naiman, R.J. and R.J. Bilby. 1998. River ecology and management in the Pacific Coastal Ecoregion. Pages 1-10 in R.J. Naiman, and R.E. Bilby, Eds. River ecology and management: Lessons from the Pacific Coastal Ecoregion. Springer-Verlag: New York.

Naiman, R.J., R.E. Bilby, and P. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. BioScience 50:996–1011.

Naiman, R.J., H. De´camps, and M.E. McClain. 2005. Riparia: ecology, conservation, and management of streamside communities. Elsevier Academic Press, San Diego, California, USA.

NRC (National Research Council). 2002. Riparian areas: functions and strategies for management. National Academy Press, Washington, D.C., USA.

Oakley, A.L., J.A. Collins, L.B. Everson, D.A. Heller, J.C. Howerton and R.E. Vincent. 1985. Riparian zones and freshwater wetlands. Pp 57-80 *in* E.R. Brown (Tech. Editor). Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. U.S. Department of Agriculture, R6-F & WL-192-1985.

Osmundson, D.B., R.J. Ryel, V.L. Lamarra, and P. Pitlick. 2002. Flow-sediment-biota relations: implications for river regulation on native fish abundance. Ecological Applications 12:1719–1739.

Peak, R.G., and F.R. Thompson, III. 2006. Factors affecting avian species richness and density in riparian areas. Journal of Wildlife Management 70:173-179.

Pearson, S.F., and D.A. Manuwal. 2000. Influence of niche overlap and territoriality on hybridization between hermit warblers and Townsend’s warblers. Auk 117: 175-183.

Pearson, S.F., and D.A. Manuwal. 2001. Breeding bird response to riparian buffer width in managed Pacific Northwest Douglas-fir forests. Ecological Applications 11:840-853.

Pearson, S. F., and S. Rohwer. 1998. Influence of breeding phenology and clutch size on hybridization between Hermit and Townsend's Warblers. Auk 115:739-745.

Perry, R.W., T.B. Wigley, M.A. Melchoirs, R.E. Thill, P.A. Tappe, and D.A. Miller. 2011. Width of riparian buffer and structure of adjacent plantations influence occupancy of conservation priority birds. Biodiversity and Conservation 20:625-642.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). March, pp. 20–22.

Rodewald, A.D., and M.H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation. Biological Conservation 128:193-200.

Planty-Tabacchi, A.M., E. Tabacchi, R.J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology 10:598-607.

Pollock, M.M., R.J. Naiman, and T.A. Hanley. 1998. Plant species richness in riparian wetlands: a test of biodiverstity theory. Ecology 79:94-105.

R Development Core Team. 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Richardson, J.S., R.J. Naiman, F.J. Swanson, and D.E. Hibbs. 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. Journal of the American Water Resources Association 41:935–947.

Richardson, J.S., and R.M. Thompson. 2009. Setting conservation targets for freshwater ecosystems in forested catchments. Pages 244-263 *in* M.A. Villard and B.G. Jonsson, editors. Setting conservation targets for managed forest landscapes. Cambridge University Press, Cambridge, UK.

Ries, L., R.J. Fletcher Jr., J. Battin, and T.D. Sisk. 2004. The ecology of habitat edges: mechanisms, models and variability explained. Annual Review of Ecology, Evolution and Systematics 35: 491–522.

Robinson, S.K., F.R. Thompson III, T.M. Donovan, D.R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990.

Rohwer, S., and C. Wood. 1998. Three hybrid zones between Hermit and Townsend's Warblers in Washington and Oregon. Auk 115:284-310.

Royle, J.A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60: 108-115.

Russell, R.E., J.A. Royle, V.A. Saab, J.F. Lehmkuhl, W.M. Block, and J.R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. Ecological Applications 19:1253-1263.

Sabo, J.L., R.Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and J. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56-62.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32. Schieck, J., K. Lertzman, B. Nyberg, and R. Page. 1995. Effects of patch size on birds in old-growth montane forests. Conservation Biology 9: 1072–1084.

Schmiegelow, F.K.A. and M. M Monkkonen. 2002. Habitat loss and fragmentation in dynamic landscapes: avian perspectives from the boreal forest. Ecological Applications 12: 375-389.

Shirley, S.M., and J.N.M. Smith. 2005. Bird community structure across riparian buffer strips of varying width in a coastal temperate forest. Biological Conservation 125: 475–489.

Spackman, S. C., and J. W. Hughes. 1995. Assessment of minimum stream corridor with for biological conservation: Species richness and distribution along mid-order streams in Vermont, USA. Biological Conservation 71:325-332.

Stauffer, D.I. and L.B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44:1-15.

Steedman, R.J., and R.L. France. 2000. Origin and transport of Aeolian sediment from new clearcuts into boreal lakes, northwestern Ontario, Canada. Water, Air, and Soil Pollution 122:139-152.

Strahler, A.N. 1957. Quantitative analysis of watershed geomorphology. American Geophysics Union Transactions 38:913-920.

Su, Y.-S. & Yajima, M. (2012) R2jags: A Package for Running Jags from R. http://CRAN.R-project.org/package=R2jags.

Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee. 1988. Landform effects on ecosystem patterns and processes. BioScience 38:92-98.

Swanson, F.J., S.V. Gregory, J.R. Sedell, and A.G. Campbell. 1982. Land-water interactions: The riparian zone. In: Analysis of Coniferous Forest Ecosystems in the Western United States. US/IBP Synthesis Series 14 Stroudsburg, Pa. Hutchinson Ross Publishing Co.

Thomas, J.W., C. Maser, and J.E. Rodiek. 1979. Riparian zones. Pp. 40-47 *in* Wildlife habitats in managed forest -- the Blue Mountains of Oregon and Washington (J. W. Thomas, tech. ed.). U.S. Forest Service Handbook No. 553, Washington, D. C.

Tewksbury, J.J., S.J. Hejl, and T.E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.

Triquet, A.M. G.A. McPeek, and W.C. McComb. 1990. Songbird diversity in clearcuts with and without a riparian buffer strip. Journal of Soil Water Conservation 45:500-503.

Vander Haegen, W. M., and R. M. DeGraaf. 1996. Predation on artificial nests in forested riparian buffer strips. Journal of Wildlife Management 60:542–550.

Verner, J. 1985. Assessment of counting techniques. Current Ornithology 2:247-302.

Wesche, T.A., C.M. Goertler, and C.B. Frye. 1987. Contribution of riparian vegetation to trout cover in small streams. North American Journal of Fisheries Management 7:151-153.

Whitaker, D.M., and W.A. Montevecchi. 1999. Breeding bird assemblages inhabiting riparian buffer strips in Newfoundland, Canada. Journal of Wildlife Management 63:167-179.

Wilcox, B.A., and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879-887.

Yamaura, Y., Royle J.A., Shimada N., Asanuma S., Sato T., H. Taki, S. Makino. 2012. Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodiversity and Conservation 21: 1365-1380.

Zipkin, E.F., A. DeWan, and J.A. Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. Journal of Applied Ecology 46:815-822.

Table 1. Number of detections by species, year, and riparian buffer treatment, western Washington, USA, 1993, 1995-1996, and 2003-2004. C = Control, N = Narrow, and W = Wide prescriptions, respectively.

		1993			1995/1996			2003/2004			
Species	Code	C	N	W	C	N	W	C	N	W	TOTAL
Rufous hummingbird *Selasphorus rufus*	RUHU	1	1	3	5	10	12	5	24	18	79
Red-breasted sapsucker *Sphyrapicus ruber*	RBSA	0	0	1	0	3	6	0	13	16	39
Hairy woodpecker *Picoides villosus*	HAWO	0	2	1	13	15	8	6	11	8	64
Northern flicker *Colaptes auratus*	NOFL	0	0	0	0	1	0	0	6	6	13
Olive-sided flycatcher *Contopus cooperi*	OSFL	0	0	0	0	7	4	0	6	3	20
Hammond's flycatcher *Empidonax hammondii*	HAFL	0	1	1	3	5	7	2	0	1	20
Pacfic-slope flycatcher *Empidonax difficilis*	PSFL	21	21	11	44	50	34	49	33	32	295
Hutton's vireo *Vireo huttoni*	HUVI	0	0	0	2	4	1	1	3	0	11
Warbling vireo *Vireo gilvus*	WAVI	2	0	0	5	20	16	2	17	3	65
Steller's jay *Cyanocitta stelleri*	STJA	3	1	0	6	7	6	5	18	23	69
Chestnut-backed chickadee *Poecile rufescens*	CBCH	21	25	17	25	18	20	32	31	28	217
Brown creeper *Certhia americana*	BRCR	3	3	2	6	1	5	20	0	1	41
Winter wren *Troglodytes troglodytes*	WIWR	21	26	18	44	52	38	52	41	34	326
Golden-crowned kinglet *Regulus satrapa*	GCKI	9	11	7	15	2	2	29	4	8	87
Varied thrush *Ixoreus naevius*	VATH	0	2	0	3	0	1	11	0	2	19
Swainson's thrush *Catharus ustulatus*	SWTH	4	4	3	14	8	13	20	18	21	105
American robin *Turdus migratorius*	AMRO	7	0	1	12	22	13	11	16	14	96

Cedar waxwing	CEWA	0	0	0	0	7	4	1	17	6	35
Bombycilla cedrorum											
Hermit/Townsend's warbler	HETO	3	4	1	3	0	1	0	0	0	12
Dendroica occidentalis/townsendi											
Black-throated gray warbler	BTYW	3	2	1	4	0	0	2	4	1	17
Dendroica nigrescens											
Macgillivray's warbler	MGWA	0	0	0	0	0	0	1	11	4	16
Oporornis tolmei											
Wilson's warbler	WIWA	10	4	7	26	15	28	22	38	29	179
Wilsonia pusilla											
Western tanager	WETA	1	0	2	2	4	12	6	13	11	51
Piranga ludoviciana											
Spotted towhee	SPTO	0	0	0	0	0	0	0	15	3	18
Pipilo maculatus											
Song sparrow	SOSP	0	0	0	0	26	11	0	31	5	73
Melospiza melodia											
Dark-eyed junco	DEJU	0	0	0	5	27	11	0	1	1	45
Junco hyemalis											
Black-headed grosbeak	BHGR	0	0	0	3	9	2	2	12	11	39
Pheucticus melanocephalus											
Evening grosbeak	EVGR	1	1	0	0	1	4	3	2	1	13
Coccothraustes vespertinus											
TOTAL		110	108	76	240	314	259	282	385	290	2064

Table 2. Summary of post-treatment riparian buffer widths by treatment type (n=5 for each treatment type), western Washington, USA, 1993, 1996, and 2004.

Site Name	Treatment	Year	Average (m)	Standard deviation
Blue Tick	Wide	1996	32.0	13.9
Blue Tick	Wide	2003	36.1	22.1
Eleven 31	Wide	1996	21.9	10.8
Eleven 31	Wide	2003	21.9	10.4
Ms Black	Wide	1996	31.0	10.7
Ms Black	Wide	2003	28.1	9.3
Ryderwood 860	Wide	1996	21.7	5.1
Ryderwood 860	Wide	2003	21.7	5.1
Side Rod	Wide	1996	34.4	14.1
Side Rod	Wide	2003	40.7	24.9
	All wide buffers		29.9	15.5
Eleven 32	Narrow	1996	8.8	4.0
Eleven 32	Narrow	2003	6.7	5.2
Kapowsin	Narrow	1996	14.5	4.0
Kapowsin	Narrow	2003	6.7	4.7
Night Dancer	Narrow	1996	10.4	3.8
Night Dancer	Narrow	2003	9.3	5.4
Potpourri	Narrow	1996	25.5	12.1
Potpourri	Narrow	2003	21.3	6.7
Simmons Creek	Narrow	1996	15.6	8.8
Simmons Creek	Narrow	2003	8.7	5.4
	All narrow buffers		13.1	9.1

Table 3. Summaries (average and standard error) of four vegetation covariates, percent shrub cover and total number of stems >10 cm in diameter for all deciduous trees combined, Douglas-fir, and western hemlock and western red cedar combined, by treatment type (n=5 for each treatment type), western Washington, USA, 1993, 1996, and 2004.

Treatment and year	Shrub cover	SE	Deciduous	SE	Douglas-fir	SE	Western hemlock/ western red cedar	SE
Control 1993	15.7	2.8	97.8	25.8	13.8	1.0	57.6	22.7
Control 1996	19.8	3.9	74.4	23.1	17.4	3.3	80.8	23.2
Control 2004	4.3	1.9	61.2	36.0	26.4	5.2	121.4	16.1
Narrow 1993	14.0	2.9	78.4	10.6	22.4	6.6	79.8	22.8
Narrow 1996	18.0	4.1	99.6	14.3	31.4	16.9	73.4	18.9
Narrow 2004	6.5	2.0	89.4	15.3	44.8	13.0	85.4	22.6
Wide 1993	7.8	3.4	82.8	33.2	29.6	9.2	101.4	25.4
Wide 1996	6.8	3.3	68.8	31.1	11.8	1.9	97.8	18.3
Wide 2004	9.5	1.4	148.8	10.4	42.6	9.5	86.2	15.2

Figure 1. Distribution of study sites and treatments in western Washington, USA.

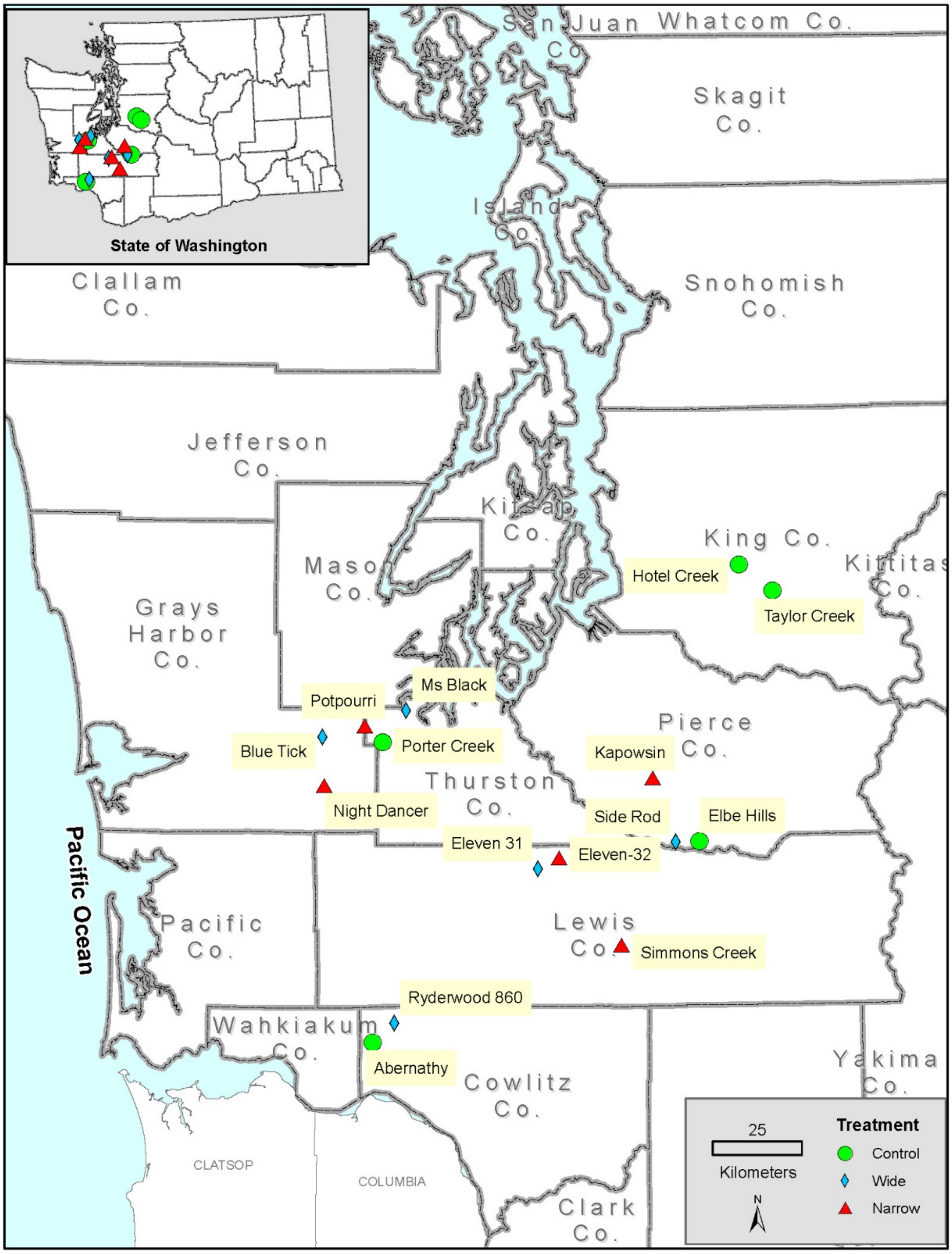


Figure 2. Estimated total number (95% credible interval) of birds of all species per point count station by treatment (C, Control; N, Narrow; and W, Wide) in western Washington, USA, 1993 (pre-harvest), 1995-1996, and 2003-2004. Each treatment had 5 experimental units (n=15). Estimates were corrected for species-specific detection. In some instances, 95% CRI extend beyond the range of the y-axis.

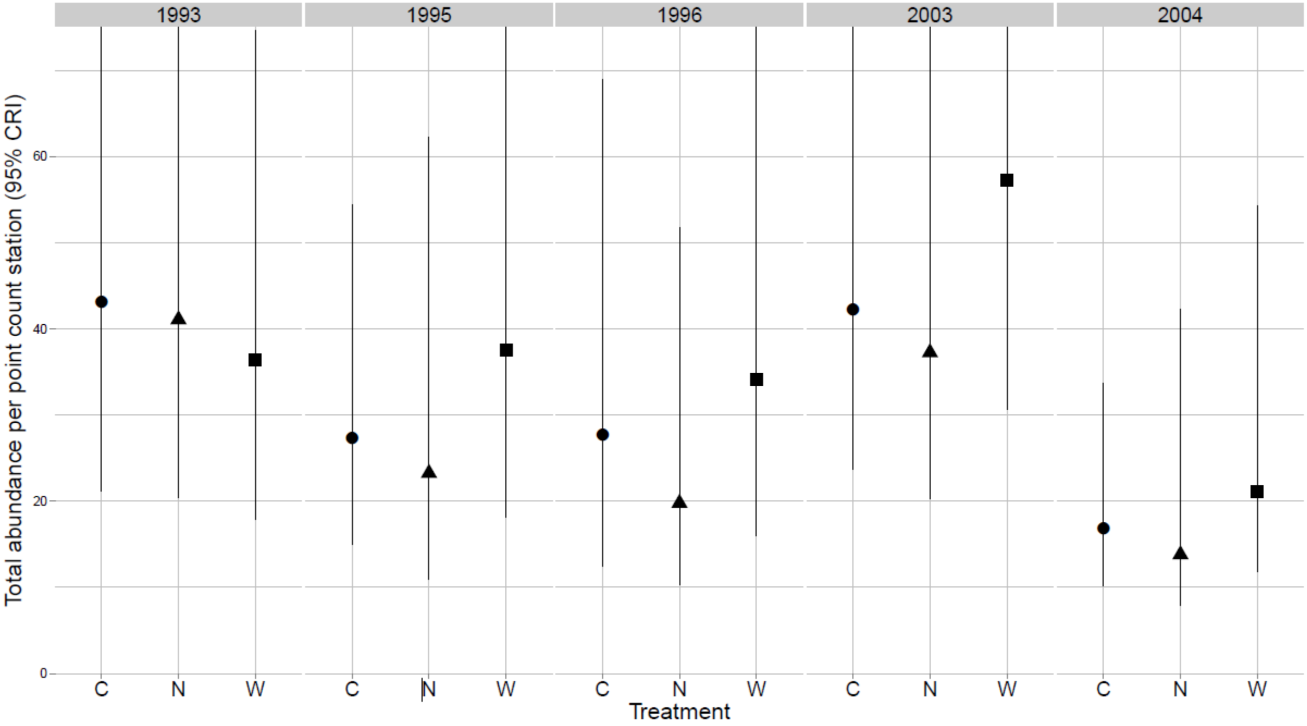


Figure 3. Estimated median number of species (95% credible interval) by year and treatment (C, Control; N, Narrow; and W, Wide) in western Washington, USA, 1993 (pre-harvest), 1995-1996, and 2003-2004. Each treatment had 5 experimental units (n=15).

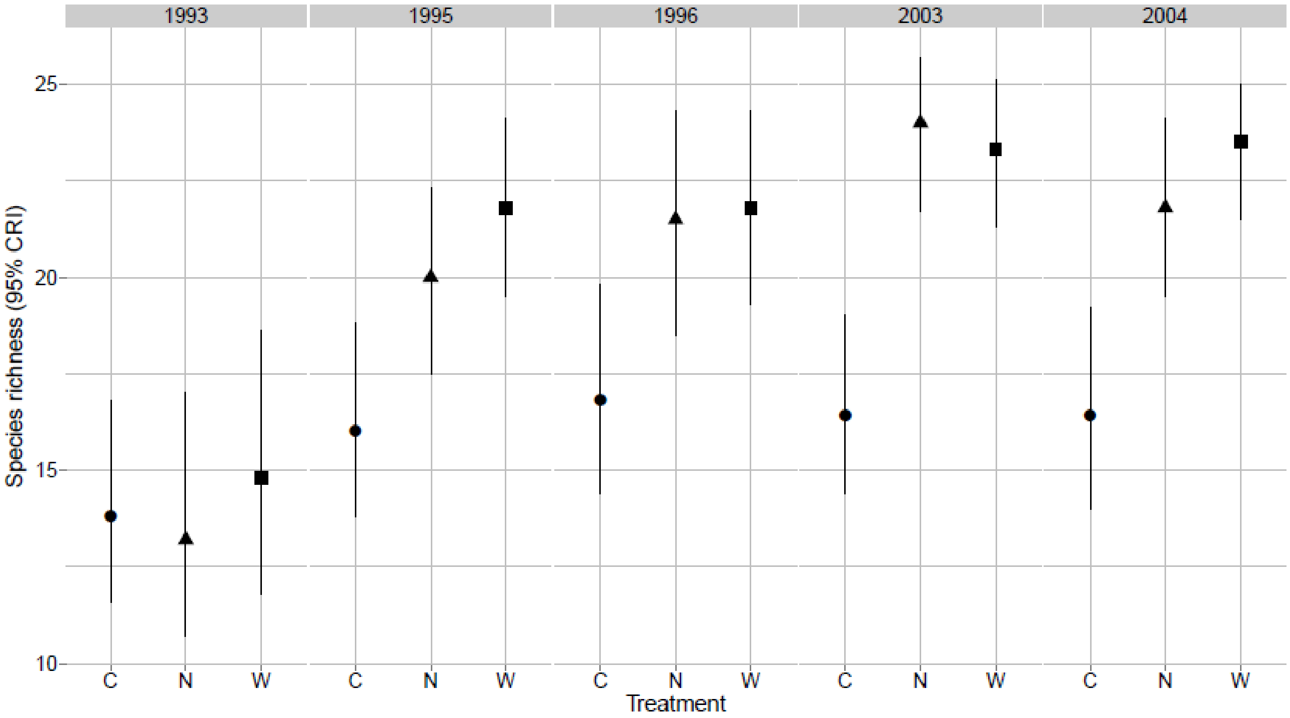


Figure 4. Estimated annual median species similarity (95% credible interval) by year and treatment (C, Control; N, Narrow; and W, Wide) in western Washington, USA, 1993 (pre-harvest), 1995-1996, and 2003-2004. Each treatment had 5 experimental units (n=15). Species similarity is an estimate of the percent of species shared by two treatments in a given year.

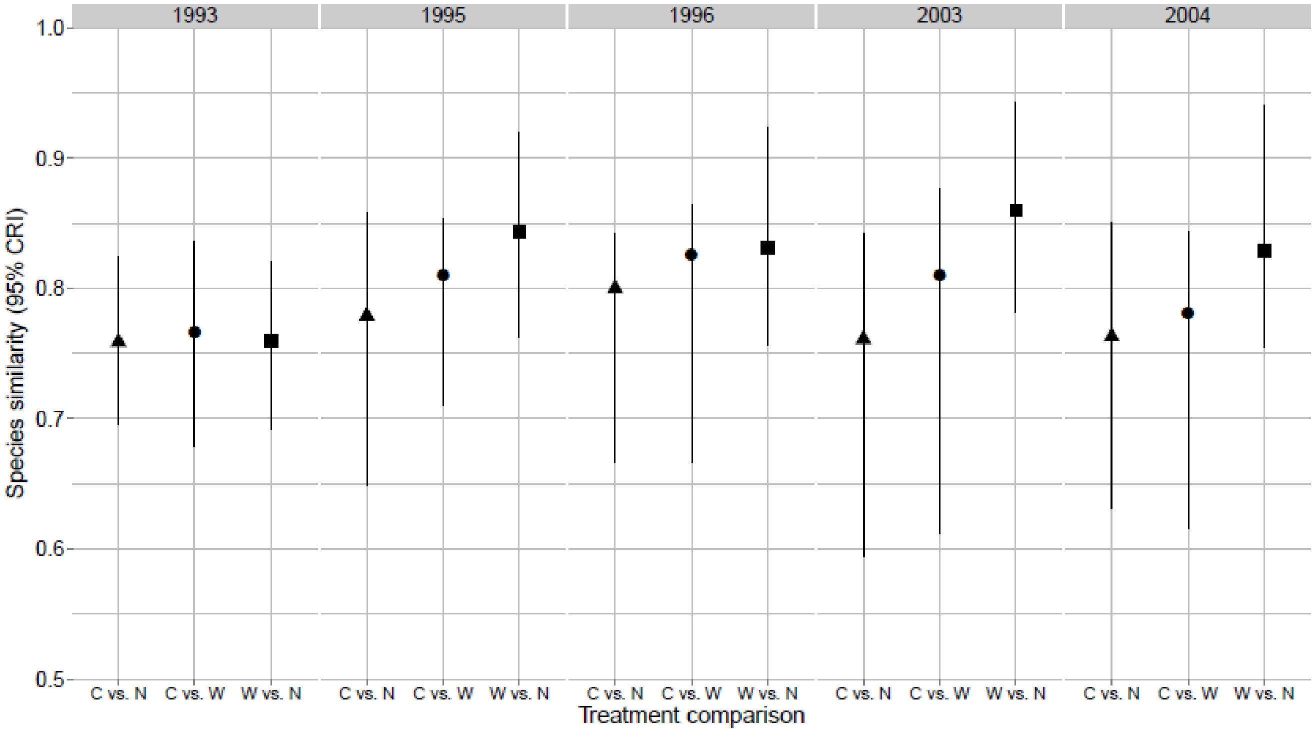


Figure 5. Estimates (95% credible interval) of local extinction and turnover probabilities between pairs of years by treatment (C, Control; N, Narrow; and W, wide) in western Washington, USA, 1993 (pre-harvest), 1995-1996, and 2003-2004. Each treatment had 5 experimental units (n=15). Turnover is the probability that a species selected at random from a treatment at time *t* is a "new" species. Local-extinction is the probability that a species that occupied a treatment in time t did not occupy the treatment in time *t* + 1.

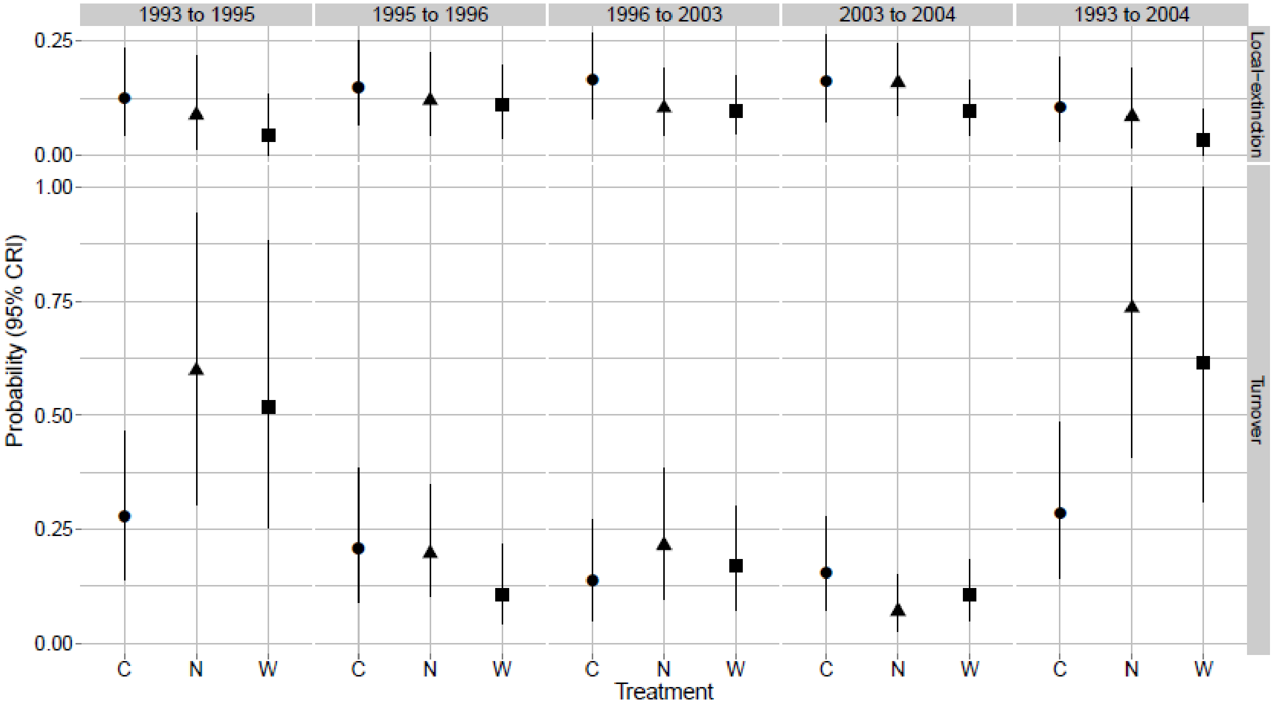


Figure 6. Contrasts (95% credible interval) in the probability of occupancy (top) and abundance (bottom) between the control and each treatment (wide and narrow forested riparian buffers) before harvesting, immediately following, and 10 years post in western Washington, USA, 1993(pre-harvest), 1995-1996, 2003-2004. A point estimate of 1 suggests that a given species has ~2.7 times greater odds to occupy the treatment as the control or is 2.7 times as abundant on the treatment than the control. A solid symbol indicates 95% CRI do not overlap 0; an open symbol indicates that the 95% CRI does include 0. Species acronyms are provided in Table 2.

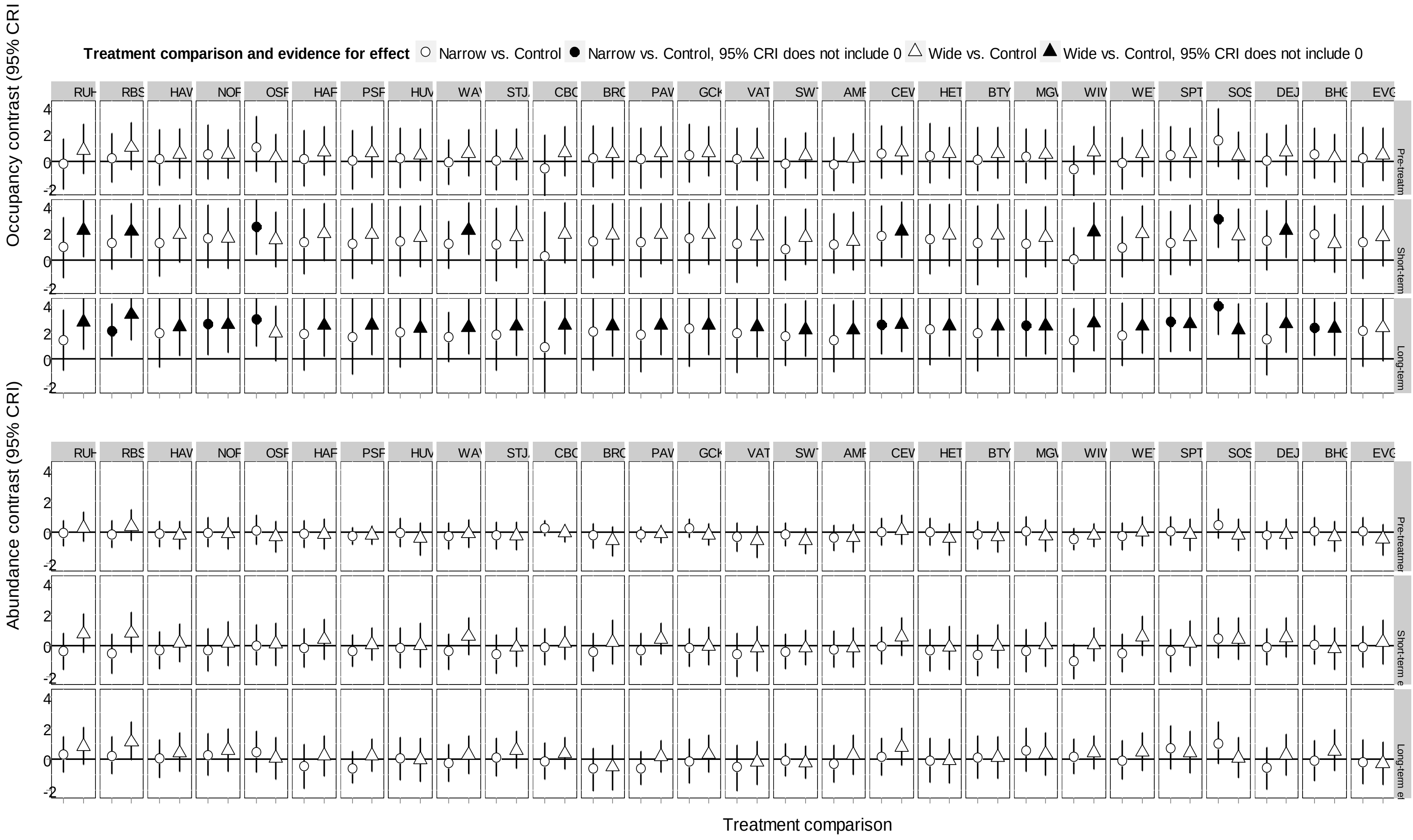


Figure 7. Average (95% credible interval) predicted effect (while holding the other 4 covariates at their mean values) of each vegetation (trees and shrubs) and buffer width covariate on species richness (A) and total bird abundance (B).

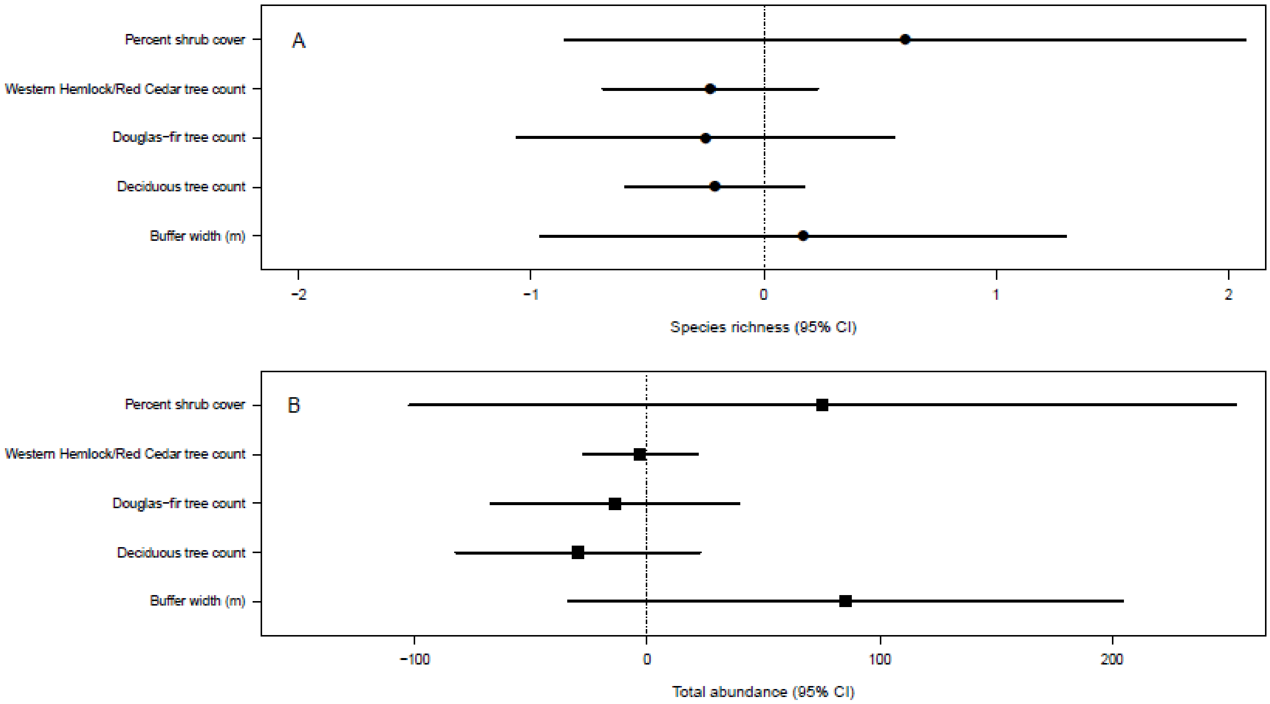


Figure 8. Effect (95% credible interval) of vegetation (shrub and tree abundance) and buffer width covariates on the probability of species occupancy (circles) and abundance (triangles). This analysis disregards treatment assignments and takes advantage of the variation in the covariates within and among the two buffer treatments to examine their relative effect on site level occupancy. A solid symbol indicates 95% CRI do not overlap 0; an open symbol indicates that the 95% CRI does include 0. Bird species acronyms are provided in Table 2.

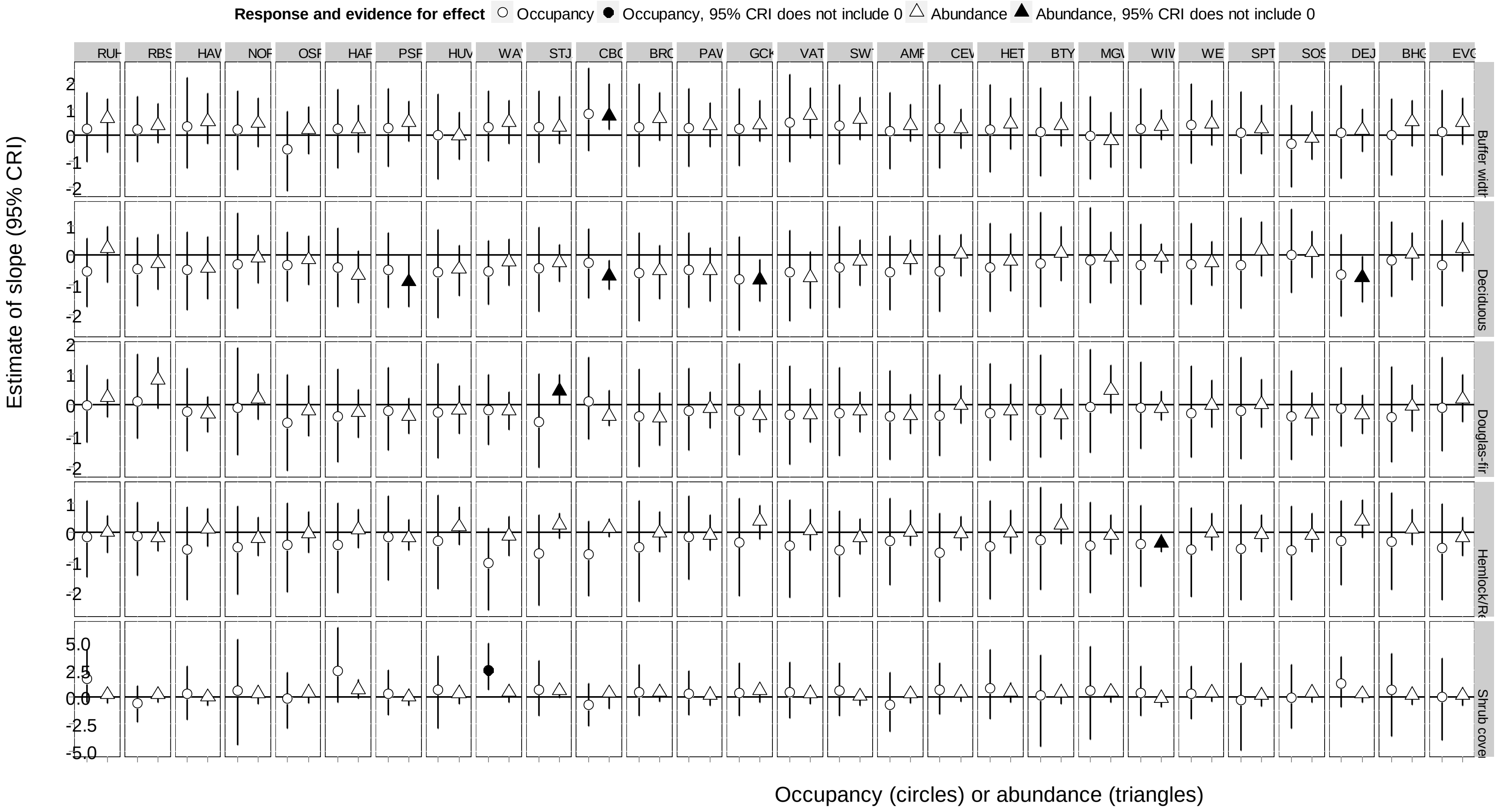


Figure 9. Estimates (95% confidence interval) of site level species richness (A) and total abundance (B) as functions of site specific buffer width. We used the variation in buffer width across sites to identify potential buffer width thresholds. Control site species richness and abundance are provided on the right sides (triangle) of both graphics. Estimates are calculated from the model based on the treatment design. We calculated mean richness values for each site and plotted these by buffer width. Intervals are not credibility intervals, but rather confidence intervals. Estimates for all sites were averaged across 1995-2004. Horizontal lines extending from the upper and lower bounds of the confidence intervals for the control sites are provided as reference lines.

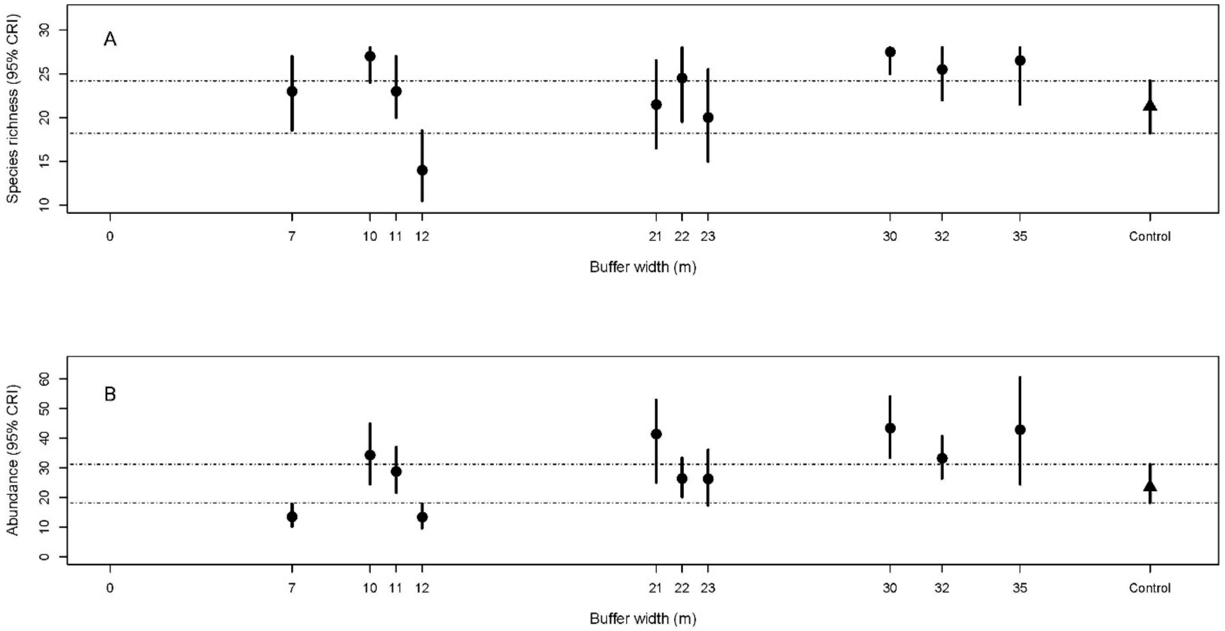
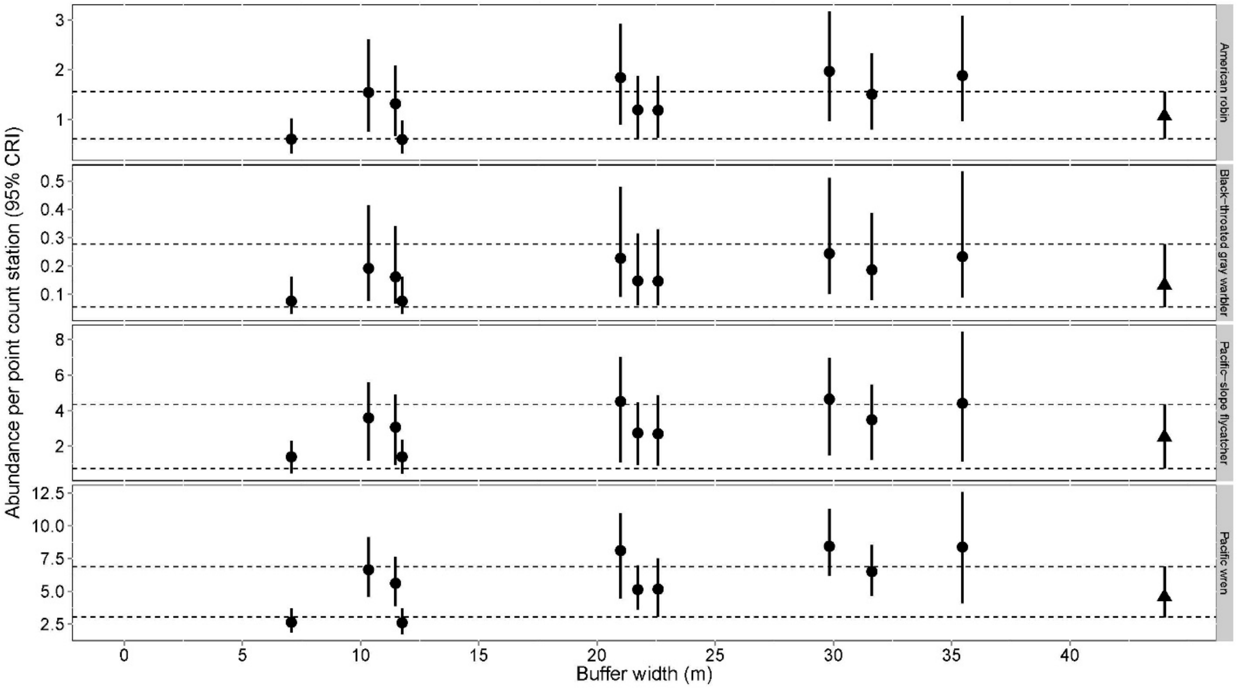


Figure 10. Site level abundance (95% confidence interval) for the four species previously identified in Pearson and Manuwal (2001) as riparian associates. We used the variation in buffer width across sites to identify potential buffer width thresholds. Control site species richness and abundance are provided on the right sides (triangle) of both graphics. Estimates are calculated from the model based on the treatment design. We calculated mean richness values for each site and plotted these by buffer width. Intervals are not credibility intervals, but rather confidence intervals. Estimates for all sites were averaged across 1995-2004. Horizontal lines extending from the upper and lower bounds of the confidence intervals for the control sites are provided as reference lines.



Supporting Information

Additional supporting information may be found in the online version of this article.

Text S1: R code and data for the MCMC implementation of the hierarchical community model and average predictive comparisons of species richness, western Washington, USA, 1993-2004.

Text S2: Posterior predictive checks (Bayesian p-values) to assess goodness of fit for Bayesian models, western Washington, USA, 1993-2004.

Table S3: Median effect (95% credibility interval) of three riparian buffer treatments on detection probabilities for 28 species, western Washington, USA, 1993, 1995-1996, and 2003-2004. Treatment effects were averaged across all 5 years.

Table S4: Median effect (95% credibility interval) of three riparian buffer treatments on capture probabilities for 28 species, western Washington, USA, 1993, 1995-1996, and 2003-2004. Treatment effects were averaged across all 5 years.