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Removal pattern mitigates negative, short-term effects of stepwise Russian olive eradication on breeding birds

JONATHON J. VALENTE,[1],† KELSEY B. MCCUNE,[2] RACHEL A. TAMULONIS,[3]
ELIZABETH S. NEIPERT,[4] AND RICHARD A. FISCHER[4]

[1]Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, Washington, D.C. 20013 USA
[2]Institute for Social, Behavioral, and Economic Research, University of California Santa Barbara, Santa Barbara, California 93106 USA
[3]Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331 USA
[4]Environmental Laboratory, U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi 39180 USA

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Abstract. Invasive species can have disastrous ecological consequences, and management is often required to control these invasions and mitigate the damage. Yet in many systems, biological invaders can serve critical ecological roles, particularly where they have been long-established or effectively replaced functionally similar native species. In such cases, eradicating invasions can have unintended consequences on other components of the ecosystem, and potential control measures must be viewed within an ecosystem-wide context to ensure they do not cause more harm than good. On the lower Snake River in eastern Washington, invasive Russian olive (*Elaeagnus angustifolia*) comprises 90% of the woody riparian vegetation in some areas. In this study, we experimentally removed half of the Russian olive from 0.5-ha plots using three configuration patterns that varied in the amount of interspersion of remaining vegetation ($n = 9$ replicates) to evaluate the short-term impact of a stepwise restoration strategy on breeding bird communities. We monitored plots for 5 yr and found that Russian olive removal on low interspersion treatments negatively affected occupancy rates for 50 of 52 species (96%) and significantly reduced richness by up to 2.41 (95% credible interval [CI] = 0.73, 4.14) species relative to control plots. These effects dampened with increasing interspersion, and occupancy rates of only 41 (79%) species decreased on high interspersion treatments, leading to non-significant richness reductions of only 0.99 (95% CI = −0.70, 2.75) species. Given the dominance of Russian olive in this region, removing it eliminates critical habitat for birds that require woody structure for nesting and foraging. Thus, we caution managers to consider the potential short-term negative impacts to the local fauna when planning invasive control efforts. However, we found that several riparian-dependent species known to breed in the region were noticeably absent from our study plots, and short-term losses in avian habitat may be tolerable where restoration of native vegetation supports greater diversity in the long term. In such restoration efforts, managers may be able to mitigate the negative effects of invasive shrub control by maintaining high interspersion among unmanipulated vegetation while waiting for native vegetation to re-establish.

Key words: avian diversity; breeding birds; community occupancy model; ecosystem perspective; *Elaeagnus angustifolia;* invasive plant control; Russian olive.

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† **E-mail:** Jonathon.J.Valente@gmail.com

Introduction

Invasive species can have wide-ranging effects on the structure and function of the areas they colonize (Pimentel et al. 2005, Simberloff 2011, Vilà et al. 2011). They can alter the physico-chemical environment of native systems (Ehrenfeld 2003, 2010), affect the evolutionary pathways of organisms they interact with (Mooney and Cleland 2001), and are a leading cause of biodiversity loss worldwide (Sala et al. 2000, Clavero and García-Berthou 2005, Butchart et al. 2010). The impacts of these invasions often come at great cost both financially and in terms of human well-being (Mooney 2005, Pimentel et al. 2005, Charles and Dukes 2007, Crowl et al. 2008, Pejchar and Mooney 2009). Thus, control of invasive plants and animals has become a significant conservation priority worldwide (Millennium Ecosystem Assessment 2005).

One of the major challenges facing control efforts is that, over time, invasive species can develop into entrenched components of an ecosystem, often serving critical functions (Zavaleta et al. 2001, Carroll 2011, Schlaepfer et al. 2011). While there are numerous examples of positive outcomes from eradications of invasive species (Simberloff 2009, Simberloff et al. 2011), such management can also have unintended consequences on other ecosystem components (Zavaleta et al. 2001, Bergstrom et al. 2009, Skurski et al. 2013, Buckley and Han 2014). For instance, invasive species control is linked with reduced abundance and diversity of native plants (Rinella et al. 2009, Zarnetske et al. 2010, Skurski et al. 2013), exacerbation of biotic invasions (Reid et al. 2009, Rinella et al. 2009, Skurski et al. 2013), and elimination of critical faunal habitat (Casazza et al. 2016, Packer et al. 2016, Tredick et al. 2016). Avoiding such potential pitfalls requires adopting an ecosystem-wide perspective to invasive species management (Zavaleta et al. 2001).

In the western United States, broad expansion of invasive woody plants throughout riparian zones (Friedman et al. 2005) has impacted hydrology (Tickner et al. 2001, Birken and Cooper 2006, Cleverly et al. 2006), nutrient cycling (Harner et al. 2009, Mineau et al. 2011, 2012), vegetation structure (Fleishman et al. 2003, Katz and Shafroth 2003), and faunal habitats (Knopf and Olson 1984, Zavaleta et al. 2001, Pendleton et al. 2011, Fischer et al. 2015). As a result, control and removal of these plants has become a major focus for managers of inland rivers and streams (Richardson et al. 2007, Shafroth and Briggs 2008, Collette and Pither 2015). Yet in many areas invasive trees are dominant components of the riparian system (Friedman et al. 2005), and management efforts could have negative impacts on native fauna. For instance, western riparian ecosystems support the preponderance of local avian abundance and diversity compared to uplands (Stevens et al. 1977, Hehnke and Stone 1979, Knopf et al. 1988), and substantial removal of dominant invasive riparian plants has the potential to dramatically alter floristic structure and cause concomitant declines in the avian community (Zavaleta et al. 2001, Fleishman et al. 2003, Sogge et al. 2008). In one prominent example, biological control of invasive Saltcedar (*Tamarix* spp.) resulted in up to 94% reductions in habitat for the federally endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*, Hatten 2016). Disturbance of wildlife habitat has thus become one of the major sources of conflict worldwide in decisions about whether to remove or control invasive trees (Dickie et al. 2014).

Russian olive (*Elaeagnus angustifolia*) is one such plant that has become a source of management controversy in western riparian systems. This large shrub is native to Eurasia but was introduced in the late nineteenth or early twentieth century for use in windbreaks, soil stabilization, shade, and wildlife habitat (Christiansen 1963, Katz and Shafroth 2003). However, Russian olive is a highly successful competitor due to its shade tolerance (Collette and Pither 2015), lack of herbivore predation (Katz and Shafroth 2003), and diverse dispersal capabilities (Shafroth et al. 1995, Pearce and Smith 2001). Further, its expansion has been exacerbated by the alteration of natural hydrologic processes such as dam construction and water withdrawals (Lesica and Miles 1999, Katz and Shafroth 2003, Stromberg et al. 2009). With its ability to thrive under a broad range of conditions (Shafroth et al. 1995, Pearce and Smith 2001), Russian olive has become naturalized in 37 U.S. states (Katz and Shafroth 2003) and is now the fourth most frequently occurring woody riparian plant in the western United States (Friedman et al. 2005). Though little is known about the impact of Russian olive invasions to native birds (Bateman and Paxton 2010), some species seem to show preference for the invasive shrub while others actively avoid it (Stoleson and Finch 2001).

Two components of vegetation structure can impact avian distributions. The first is *amount* of available habitat. In a recent study, Fischer et al. (2012) found that overall avian density and diversity peaked at 50–70% total woody vegetation cover in a riparian system nearly completely (i.e., ~90%) dominated by Russian olive. These results suggest a potentially straightforward remove-and-replace management approach for restoring such ecosystems. By reducing Russian olive cover to intermediate amounts, managers could maintain much of the structural complexity required by riparian birds while encouraging regrowth of native plants. Once the native vegetation reaches a point where it can provide necessary structure for nesting, foraging, and cover, the remainder of the Russian olive could be removed. Such stepwise management has been advocated to minimize the impacts of invasive plant removal on wildlife (Dudley et al. 2000, Lampert et al. 2014), yet to our knowledge, no study has tested the efficacy of such an approach.

The second component of vegetation structure is configuration, which is also known to influence avian distributions at both broad (Saab 1999, Villard et al. 1999) and fine (LaRue et al. 1995, Rehm and Baldassarre 2007) spatial scales. It is therefore critical to consider how the spatial pattern of removal could affect community response. For instance, removing all invasive riparian shrubs from one half of a river reach would result in an ecosystem structurally very different from one where every other invasive shrub was removed from the entire reach (Fig. 1). Further, species diversity is known to increase with habitat heterogeneity (Tews et al. 2004), which may vary among removal configurations. Thus, evaluating how the spatial arrangement of removed and remnant vegetation affects bird communities could help minimize potential negative impacts of control measures.

Here, we present results from a Russian olive removal experiment conducted along the lower Snake River in eastern Washington. In riparian habitats dominated by Russian olive, we compared avian communities between control and treatment plots where approximately half of the Russian olive was removed. Our study was designed to test two hypotheses regarding the impact of Russian olive removal on breeding birds during the earliest phases of riparian restoration (i.e., before regeneration of mature native plants). The first hypothesis is that the reduction of invasive shrub cover to intermediate levels will improve foraging and nesting habitat for breeding birds, as has been noted in previous observational work (Fischer et al. 2012). Secondly, by varying the interspersion of removed and remaining Russian olive, we test the hypothesis that increased diversity in vegetation structure enhances these habitat benefits. If our hypotheses are supported, we would expect occupancy rates and species richness to increase in removal sites compared to control sites and to increase with increasing interspersion. The results of this study will help inform riparian managers on how to mitigate impacts to biodiversity while controlling invasive woody plants and restoring native vegetation structure.

MATERIALS AND METHODS

Study sites and restoration treatments

The Walla Walla District of the U.S. Army Corps of Engineers (USACE) manages approximately 9650 ha of wildlife habitat in southeastern Washington on approximately 90 distinct habitat management units (HMUs). These HMUs were constructed and are maintained under the lower Snake River Fish and Wildlife Compensation Plan to address riparian habitat losses resulting from Corps dam construction (USACE 1975). Habitat management units were primarily sited along the margins of the lower Snake River, and in the 1980s, they were planted with woody riparian species such as serviceberry (*Amelanchier* spp.), hawthorn (*Crataegus* spp.), cottonwoods (*Populus* spp.), and Russian olive (USACE 1975). On approximately 20% of HMUs, USACE promotes growth of riparian vegetation using center-pivot irrigation systems consisting of numerous high-powered sprinkler heads that distribute water in a circular pattern over an area of approximately 0.5 ha. The resulting landscape on each irrigated HMU is characterized by

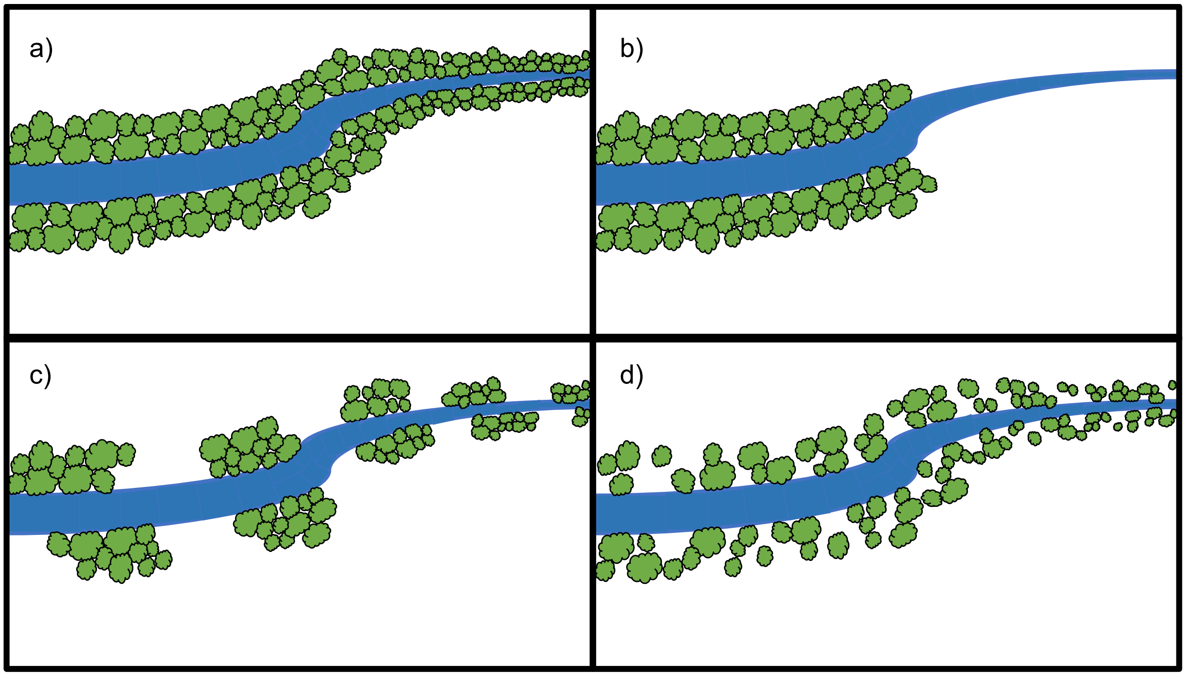

Fig. 1. In riparian areas heavily invaded by Russian olive (a, illustrated as green tree crowns bordering a blue stream), it may be beneficial to remove the invasive shrub in a stepwise fashion to retain vegetative structure throughout the restoration process. Evidence suggests that maintaining intermediate Russian olive cover could support high avian diversity during regrowth of native plants, though less is known about the best pattern of removal. For instance, reduction to 50% Russian olive cover could be done in such a way as to maintain low (b), medium (c), or high (d) levels of interspersion among removed and remaining vegetation, leading to variability in the horizontal and vertical complexity of the vegetation structure used by birds for shelter, nesting, and foraging.

grassy, upland shrub-steppe communities interspersed with dozens of dense, local, and circular concentrations of woody shrubs comprised of nearly 90% Russian olive (Fischer et al. 2012, Figs. 2, 3). Although these areas are artificially maintained, they are representative of regional riparian habitat, given that most of the natural riparian vegetation was lost to inundation during dam construction (USACE 2014). Thus, nearly all remaining riparian areas along the lower Snake River are heavily altered or managed (Carey and Clark 2013) and dominated by invasive shrubs (Dixon and Johnson 1999, Bailey 2008). Moreover, previous work has indicated these HMUs support a greater abundance and diversity of breeding and migrating birds than other riparian systems locally (Rocklage and Ratti 2000). We chose four of these irrigated HMUs for our study: Big Flat, Hollebeke, Fifty-five Mile, and Lost Island (Fig. 2).

Within our four HUMs, we chose 40 of the circular riparian plots as experimental units (mean size = 0.48 ha, standard deviation [SD] = 0.09). All plots were spaced ≥200 m apart to maintain spatial independence, and the number of plots chosen on each HMU was proportional to HMU size (Fig. 2). Because we were unsure how the bird community would respond, these relatively small and discrete sampling units (Figs. 2, 3) allowed us to test effects of Russian olive removal on a scale that was unlikely to substantially alter local populations. We chose 13 plots as controls; four were purposefully chosen because high concentrations of native shrubs prevented substantial manipulation, while the other nine control plots were chosen randomly. The other 27 plots were randomly assigned to receive one of three removal treatments (n = 9 plots per treatment). The three treatments were similar, in that approximately 50% of the Russian olive

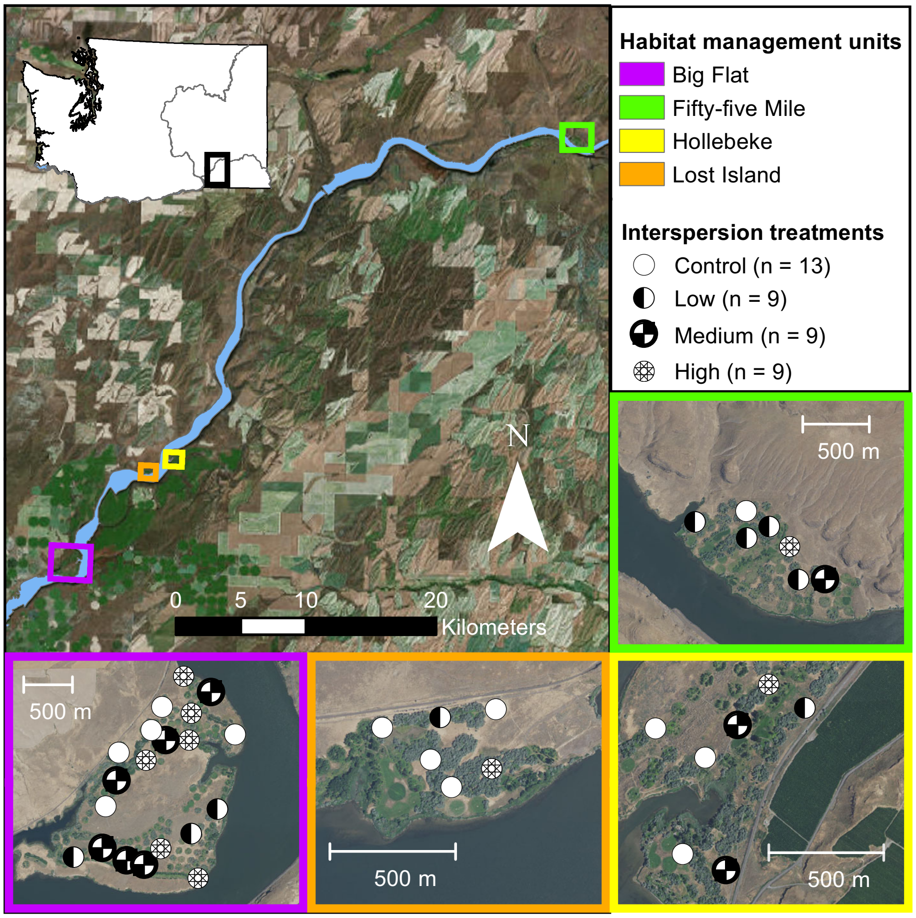

Fig. 2. We investigated impacts of Russian olive removal on bird communities using four habitat management units (HMU) along the lower Snake River in eastern Washington state (upper left). On each HMU, we randomly assigned plots dominated by Russian olive as controls (no management), or to receive one of three removal treatments (low, medium, and high interspersion). Approximately half of the Russian olive cover was removed on all treatment sites.

canopy cover was removed on each plot, but they differed in the degree of interspersion of the removed and remaining vegetation. The low interspersion treatment consisted of completely removing all Russian olive in a single block from half of the riparian plot (Fig. 3b), while the medium treatment involved dividing the plot into fourths and removing all Russian olive from two non-adjacent quarters (Fig. 3c). For the high interspersion treatment, we removed approximately every other Russian olive tree so that the remaining woody vegetation was roughly evenly distributed across the plot (Fig. 3d). Costs were roughly equivalent for all plots in terms of time (~16 man-hours) and money (~$3,000 USD), regardless of treatment type.

We used well-established methods to remove Russian olive from the 27 treatment plots (O'Meara et al. 2010). To avoid habitat disturbances to breeding and nesting birds, we mechanically removed Russian olive during winter 2014 using a Skid Steer Mulcher (FAE USA, Flowery Branch, Georgia, USA). Selected Russian olive trees in each plot were cut down by applying the mulching head to the tree trunk, and all portions of the felled tree then were chopped to a coarse mulch that was left in place. Each tree stump was then mulched to ground level and

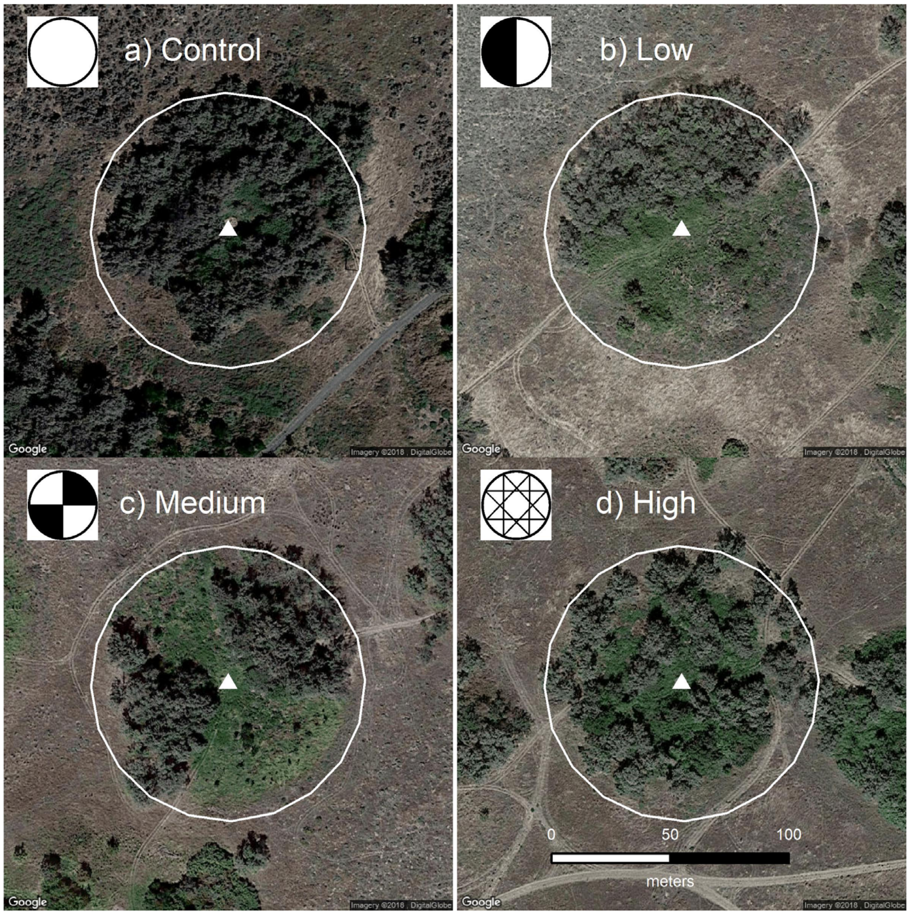

Fig. 3. Aerial images of plots used for assessing avian responses to Russian olive removal on the lower Snake River in eastern Washington state. Shrub cover on these plots was almost completely dominated by Russian olive. Thirteen plots received no management action (a), while we removed nearly half of the total Russian olive cover on other plots in three different interspersion patterns (low, medium, and high). Russian olive was removed from half of the plot in low treatments (b, $n = 9$), from non-adjacent quarters in medium treatments (c, $n = 9$), or throughout the plot in high treatments (d, $n = 9$). Avian point counts were conducted at the white triangles in the plot centers using a 40 m radius (white circle).

sprayed with Garlon 3A herbicide (Dow AgroSciences, Indianapolis, Indiana, USA) per label instructions. During subsequent years, any Russian olive re-sprouting on treatment plots was controlled by an application of Roundup herbicide (Scotts Miracle-Gro Company, Marysville, Ohio, USA). On each treatment plot, USACE also replanted native riparian saplings, including Black Cottonwood (*Populus trichocarpa*), Common Chokecherry (*Prunus virginiana*), Woods Rose (*Rosa woodsii*), Golden Currant (*Ribes aureum*), and Blue Elderberry (*Sambucus cerulea*).

We quantified total woody cover and Russian olive cover before and after treatments by digitizing aerial images from the National Agriculture Inventory Program (data available from the U.S. Geological Survey) in ArcMap 10.5 (ESRI, Redlands, California, USA). Pre-treatment images were collected in June 2013 (~6 months before treatment), and post-treatment images were collected in June 2015 (~18 months after treatment). With these 1-m-resolution images, Russian olive is easily distinguishable from native woody plants due to its silver-gray foliage color

(Hamilton et al. 2006). Prior to treatment, mean total woody cover was 85.50% (SD = 7.46) across plots and was comprised of an average of 90.49% (SD = 16.41) Russian olive. Post-treatment imagery indicated that the crowns of many remaining woody plants expanded following removal of proximate competitors (particularly in the high interspersion treatments). Thus, while we removed 50% of the Russian olive shrubs, imagery suggested slightly more subtle canopy cover reductions of 45.19% (SD = 9.32), 42.02% (SD = 8.65), and 37.05% (SD = 8.41), on low, intermediate, and high interspersion plots, respectively. After removal, mean total woody cover was 86.85% (SD = 8.10) on control plots and 49.87% (SD = 7.02) on treatment plots. After 5 yr, replanted native trees and shrubs were still low-growing saplings on our treatment plots. Thus, there was no substantial change in woody cover over the course of the study, and we emphasize that our results reveal nothing about the long-term benefits of regenerating native vegetation.

Bird surveys

We conducted three or four avian point counts per year (depending on logistical constraints) at the center of each riparian plot during the peak of the breeding seasons of 2014–2018 (5 yr). All counts in a single year were conducted within a two-week window (31 May and 15 June) to minimize the probability of intra-annual changes in site use and were separated by 1–4 d to ensure availability for sampling was independent on each occasion (Valente et al. 2017). Counts were only conducted in suitable weather conditions (i.e., low wind and no precipitation) between 04:30 and 09:00 hours to maximize bird detectability. During each 5-min point count, a trained observer recorded all birds seen or heard at any distance within 10 m distance bins. We did not record flyovers, as we could not be certain those birds were using our plots, and we rotated which observers visited which points, as well as the order in which points were visited, to minimize systematic sampling bias.

Statistical analyses

We compiled a list of all species (n = 79) detected during any of our point count surveys and removed those that were poorly sampled by our point count methods (e.g., raptors, swifts and swallows, nocturnal or crepuscular species, and waterbirds). For the 52 remaining species (Appendix S1: Table S1), we eliminated detections >40 m from the plot center so that our sampled area (0.50 ha) approximated the size of our management plots. We then fit temporally dependent, Bayesian community occupancy models to the recorded detection histories. This approach is an extension of traditional occupancy modeling (MacKenzie et al. 2002), where species-specific parameters are constrained to be related to one another through community-level hyperparameters (Kéry and Royle 2008, Zipkin et al. 2009). The full benefits of using such an approach are described elsewhere (Kéry and Royle 2008, Royle and Dorazio 2008, Zipkin et al. 2009, Iknayan et al. 2014), but we chose it because it allowed us to (1) model species-specific probabilities of site occupancy while accounting for imperfect detection (MacKenzie et al. 2002); (2) generate parameter estimates for rare species by borrowing information from more common species (Royle and Dorazio 2008, Zipkin et al. 2009, Iknayan et al. 2014); and (3) propagate detection error into estimates of species richness (Zipkin et al. 2009). We did not use data augmentation (Royle et al. 2007) because we felt our sampling effort over 5 yr was sufficient to identify all species that use these sites. However, to ensure we captured the entire potential community, we did include four species (Appendix S1: Table S1) in our analysis that were detected during a point count, but never on an actual riparian plot (i.e., within 40 m of the observer).

We fit two different community models, corresponding to our hypotheses. In the first, occupancy was simply modeled as a function of whether the plot was treated with Russian olive removal (hereafter cover model), and in the second occupancy was a function of removal configuration (hereafter interspersion model). In all models presented, s indexes species (1–52), i indexes site (1–40), j indexes year (1–5), and k indexes survey (1–4). The values of y represent observed detections (1 if detected, 0 otherwise), Z represents true occupancy state (1 if occupied, 0 otherwise), p represents detection probability, and ψ indicates occupancy probability. In both models, we assumed sites were closed to changes in use over the two-week sampling periods within a single year (likely reasonable for most species, Valente et al. 2017) and modeled detection probability as a function of standardized sampling time:

$$y_{s,i,j,k} \sim \text{Bernoulli}(Z_{s,i,j} \times p_{s,i,j,k})$$

$$\text{logit}(p_{s,i,j,k}) = \alpha 0_s + \alpha 1_s \times \text{TIME}_{i,j,k}$$

We then assumed

$$Z_{s,i,j} \sim \text{Bernoulli}(\Psi_{s,i,j})$$

and modeled $\psi_{s,i,j}$ as a logit-linear function of the main effects. In the cover model, the variable REM equals 1 if one of the removal treatments was applied to the site, and 0 otherwise; in the interspersion model, the variables HIGH, MED, or LOW similarly take values of 0 or 1 depending on whether they received high, medium, or low interspersion treatments, respectively. Thus, in the first year, the models were specified as:

Cover (j = 1)

$$\log\text{it}(\Psi_{s,i,1}) = \beta 0_s + \beta 1_s(\text{REM}_i)$$

Interspersion (j = 1)

$$\begin{aligned}\log\text{it}(\Psi_{s,i,1}) = {} & \beta 0_s + \beta 1_s(\text{LOW}_i) + \beta 2_s(\text{MED}_i) \\ & + \beta 3_s(\text{HIGH}_i)\end{aligned}$$

Because we anticipated that occupancy rates may change with time since Russian olive removal (e.g., due to time since disturbance), in subsequent years we also included linear and quadratic terms for years since removal. Further, because we resampled the same sites each year, we modified the intercept term so that site-specific occupancy probability was dependent on the site's occupancy state in the previous year (Tingley et al. 2016, Valente and Betts 2019):

Cover (j = 2, 3, 4)

$$\begin{aligned}\log\text{it}(\Psi_{s,i,j}) = {} & \delta 0_s + \delta 1_s(Z_{s,i,(j-1)}) + \beta 1_s(\text{REM}_i) \\ & + \beta 2_s(j-1) + \beta 3_s(j-1)^2\end{aligned}$$

Interspersion (j = 2, 3, 4)

$$\begin{aligned}\log\text{it}(\Psi_{s,i,j}) = {} & \delta 0_s + \delta 1_s(Z_{s,i,(j-1)}) + \beta 1_s(\text{LOW}_i) \\ & + \beta 2_s(\text{MED}_i) + \beta 3_s(\text{HIGH}_i) \\ & + \beta 4_s(j-1) + \beta 5_s(j-1)^2\end{aligned}$$

In these subsequent years, $\delta 1_s$ represents a species-specific auto-logistic parameter (Royle and Dorazio 2008), which allows the intercept to be adjusted if the site was previously occupied. We chose this model specification over a dynamic occupancy model (MacKenzie et al. 2003) because we were not explicitly interested in colonization and extinction rates. Note that we also fit models that included an interaction between the year terms and the main effects. However, we found little evidence (based on 95% posterior credible intervals [CIs]) that these main effects changed with time and focused on this more parsimonious model. Finally, we attempted to incorporate species-specific random HMU effects into the model to account for the uneven distribution of treatment types among the 4 HMUs that resulted from randomly assigning treatments to plots (Fig. 2). Unfortunately, the parameter estimates for this model did not converge, likely due to the large number of additional parameters (52 species times 4 HMUs). That said, the bird communities are unlikely to vary substantially across HMUs given they are all located on the Snake River within 50 km of one another and are similarly managed.

We assumed that species-specific parameters in these models came from a normal hyperdistribution with a parameter-specific mean and variance. That is

$$\begin{aligned}\theta_s & \sim \text{Normal}(\mu_\theta, \sigma_\theta^2), \theta \\ & = \alpha 0, \alpha 1, \beta 0, \beta 1, \beta 2, \beta 3, \beta 4, \beta 5, \delta 0, \delta 1\end{aligned}$$

where μ_θ represents the average parameter value for species in the community, and σ_θ^2 is the variance in parameter values among species. We fit all models in JAGS (Plummer 2003) using the jagsUI package (v. 1.4.4, Kellner 2016) in R (v. 3.4.0). We ran three MCMC chains for 200,000 iterations with a burn-in of 100,000 and a thinning rate of 50. We chose a vague normal prior (mean = 0, variance = 100) for the means of all hyperdistributions and a vague gamma prior (shape = 0.1, rate = 0.1) for the inverse of the hyperdistribution variances with one exception. The mean and variance of the detection intercept ($\alpha 0$) hyperdistribution was fixed based on data from the 21 most common species (representing 95% of detections) to prevent unreasonably large occupancy estimates for rare species (see Appendix S2 for details). To assess model convergence, we ensured the Gelman-Rubin statistic for all model parameters was less than 1.1 (Gelman et al. 2004) and visually inspected trace plots for interspersion among chains and signs of temporal autocorrelation within chains. Full model specification, including an assessment of model fit, can be found in Appendix S2.

We considered any parameter statistically significant if the 95% posterior CI did not overlap zero. To summarize the magnitude of the Russian olive removal treatments on each species on the probability scale, we calculated the percent change in occupancy probability as

$$\text{percent change} = 100 \times \left(\frac{(\text{treatment estimate} - \text{control estimate})}{\text{control estimate}}\right)$$

For simplicity, these estimates are based on occupancy from the first year (2014) because in subsequent years percent change differed depending on whether sites were previously occupied (see model specification above).

True species richness on any plot is a latent variable because all species are detected imperfectly. Rather than using the number of species detected as an index for richness, we compared predicted richness between control and removal (cover model) or treatments (interspersion model) by summing the expected occupancy probabilities for each species at each MCMC iteration (Zipkin et al. 2009, 2010, Valente and Betts 2019). This left us with a posterior distribution for expected richness in each site group, allowing us to infer differences by comparing the associated CIs.

Results

Over 5 yr, we conducted 17 or 18 point counts at each location, recording 4134 detections within our sampled areas. Full model results are presented in Appendix S1: Tables S2, S3. Contrary to our prediction, results from the cover model indicated that Russian olive removal had a negative effect on occupancy rates for 48 of 52 (92%) species (Fig. 4a). The percent change ranged from −47.67% (95% CI = −84.97%, 9.60%) in Yellow-rumped Warblers (*Setophaga coronata*) to 22.99% (CI = −3.43%, 69.79%) in Lazuli Buntings (*Passerina amoena*). However, most effect sizes tended to be small, as the absolute percent change was less than 30% for 42 (81%) species (Appendix S1: Table S4). Because our study had low statistical power to detect significance for such small changes (Appendix S3), the 95% CIs for the removal effect overlapped 0 for all species (Fig. 4a). That said, the average effect of removal across members of the community was significantly negative (estimate = −0.31, CI = −0.60, −0.06). Average occupancy among species peaked in 2016 and was estimated to be 0.13 (CI = 0.06, 0.22) at control sites and 0.09 (CI = 0.04, 0.16) at removal sites. Average occupancy was lowest in 2018, estimated to be 0.05 (CI = 0.02, 0.14) at control sites and 0.03 (CI = 0.01, 0.09) at removal sites. Further, because of the largely negative effects of removal on occupancy, expected richness was significantly lower in removal sites in all years (Fig. 5a and see Appendix S1: Table S5 for difference estimates).

The interspersion model indicated that while all removal treatments tended to negatively affect occupancy rates, the effects were mitigated by increased interspersion, yielding support for our second hypothesis. Comparing each treatment to the control sites revealed a negative effect of removal on 50 species (96%) in the low and medium interspersion treatments, but only 41 species (79%) in the high treatment (Fig. 4b–d). At the community level, average occupancy probability among species was significantly lower in the low interspersion treatment compared to the control, but not in the medium or high treatments. Following a similar pattern, expected species richness was significantly smaller in the low interspersion treatment in all years, but not in the medium or high interspersion treatments (Fig. 5b; Appendix S1: Table S5). The most extreme percent changes in occupancy ranged from −41.50% (CI = −79.97%, 2.34%) for House Finches (*Haemorhous mexicanus*) in the medium treatment to 21.09% (CI = −45.25%, 157.44%) for Spotted Towhees (*Pipilo maculatus*) in the high treatment (Appendix S1: Table S6). However, the effect sizes tended to be small here as well; of the 156 comparisons (52 species × 3 treatments) with control sites, the absolute percent change was less than 30% in 145 (93%) cases. Thus, the 95% CIs for the effects of removal overlapped 0 in all but one case (Fig. 4b–d); Bullock's

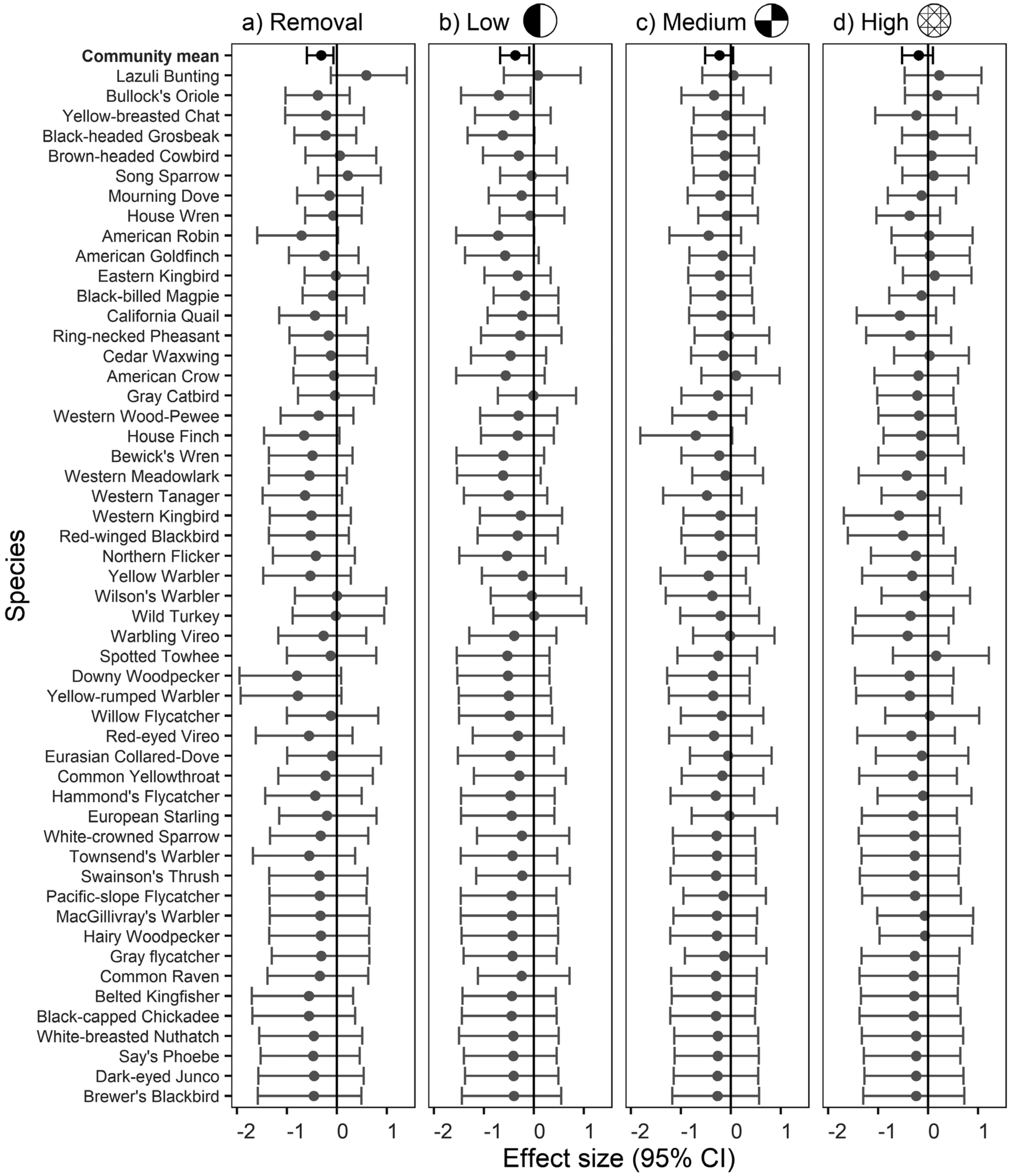

Fig. 4. Results from a vegetation cover model (a) suggest that removal of half of the Russian olive cover from riparian plots reduced occupancy probabilities for 48 of 52 species, and the average effect on the community was significantly negative. When the spatial configuration of removal was considered, occupancy probabilities tended to increase across the gradient from (b) low, to (c) medium, to (d) high interspersion removal treatments. Species are arranged from most common (top) to least common. Effect sizes are reported on the logit scale.

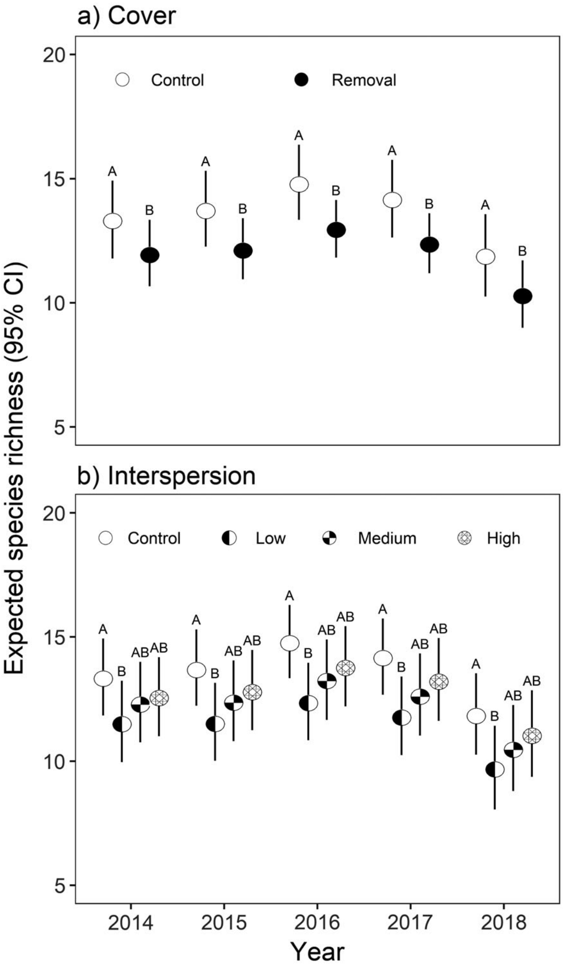

Fig. 5. A comparison of expected species richness (±95% credible intervals) of breeding birds between control and experimental riparian plots along the lower Snake River. Results from a cover model (a) indicated that removal of approximately half of the Russian olive cover significantly reduced species richness in all years. Results from an interspersion model (b) indicated that richness increased on removal plots with increasing interspersion among remnant and removed Russian olive. Within a given year, richness estimates that do not share the same letters (A or B) are significantly different from one another.

Orioles (*Icterus bullockii*) had significantly lower occupancy rates in the low interspersion treatment.

Comparing the interspersion treatments to one another revealed that occupancy rates were greatest in the high interspersion treatment and smallest in the low interspersion treatment for the overall community average and for 22 species (43%, Appendix S1: Fig. S1). Similarly, species richness was greatest in high treatments and smallest in low treatments in all years (Fig. 5b). Unfortunately, our statistical power for comparing individual treatments was low (Appendix S3), and none of these differences were significant except in 1 case (occupancy rates for Bullock's Orioles were significantly greater in high than in low treatments). Nonetheless, the patterns observed indicate that occupancy rates tended to increase with increasing interspersion and that the strong effects from the cover model were driven primarily by low interspersion removal treatments.

DISCUSSION

While removal of invasive species can restore the natural structure and function of ecosystems (Hartman and McCarthy 2004, Flory 2010, Baskett et al. 2011, Shields et al. 2014), it can also have unintended, and sometimes disastrous, consequences for native species (Bergstrom et al. 2009, Rinella et al. 2009, Skurski et al. 2013, Casazza et al. 2016, Hatten 2016). As such, it is critical to develop management approaches that meet the dual goals of invasive eradication and maintenance of native biodiversity (Zavaleta et al. 2001, Buckley and Han 2014, Dickie et al. 2014). Results from our manipulative experiment revealed that removal of Russian olive from riparian plots experiencing severe invasions reduced occupancy rates for most bird species, resulting in significant declines in species richness. These results also may imply a decrease in local abundance for these species given that occupancy rates tend to reflect abundance and dynamics of a population (Joseph et al. 2006, Noon et al. 2012). However, these findings were strongly influenced by low interspersion treatments, and the short-term negative effects of this stepwise remove-and-replace strategy were substantially reduced by maintaining high interspersion of remnant vegetation. Further, despite these negative impacts, we stress that there may be long-term benefits (i.e., 10–20 yr after replanting) to the avian community if the removed vegetation is ultimately replaced by mature, native woody plants with greater structural and functional diversity.

We originally predicted that occupancy rates would increase on these plots following Russian olive removal. We expected that this disturbance would create habitat heterogeneity that tends to positively affect diversity (Tews et al. 2004), and previous research in this system indicated avian abundance and diversity peaks at intermediate levels of woody cover (Fischer et al. 2012). However, because Russian olive has become entrenched in our study area and comprises approximately 90% of the woody vegetation, it provides the preponderance of the structure required by riparian breeders for nesting, foraging, and shelter. Removal of this invasive shrub is thus analogous to removal of habitat for many species because often it is the *only* vegetation structure available, which likely explains the declines we observed. It is unclear why results from our manipulative experiment differed so markedly from findings in previous observational work (i.e., that diversity peaks at intermediate woody cover levels, Fischer et al. 2012). One possibility is that the dramatic disturbance caused by manually removing Russian olive with heavy machinery affected avian communities beyond the simple effect of changes in woody cover (e.g., by compacting soils or altering arthropod communities). However, if this were true, we would expect to see the disparity in occupancy rates between treatment and control sites mitigated with time, which did not occur. Alternatively, only about 15% of sites used by Fischer et al. (2012) had >80% total woody cover, and it is possible that their sample size was insufficient to assess bird distributions at those higher cover levels. Regardless, our experimental approach provides strong evidence that Russian olive removal from heavily invaded plots has short-term negative impacts on the breeding bird community.

We note that there is one other explanation for our results stemming from the non-random selection of 4 of 13 control plots. These plots were chosen because high concentrations of native shrubs and trees prevented us from making substantial alterations to the amount of cover or interspersion of vegetation. Results from a Wilcoxon rank sum test ($W = 113$, $P = 0.07$) revealed a nearly significant difference in the proportion of the post-treatment shrub cover comprised of Russian olive on control (mean = 81.47%, SD = 25.27) and treatment (mean = 94.09%, SD = 7.52) plots, and thus, it is possible that occupancy rates were higher on control plots given the higher concentration of native vegetation. That said, when we eliminated the non-random control plots from the dataset and re-fit our models, results were qualitatively similar (Appendix S1: Fig. S2), suggesting the removal effects are driving observed patterns.

The detrimental removal effects on short-term occupancy were surprising to us given the relatively small spatial scale to which we applied treatments, and the small percentage of the overall woody cover on each HMU disturbed by our treatments (Big Flat = 8.66%, Fifty-five Mile = 7.74%, Hollebeke = 4.96%, Lost Island = 4.97%). For perspective, we compared the size of our management plots (~0.5 ha) with the maximum and minimum reported home range sizes for the species we analyzed (Rodewald 2015). These home range estimates encompassed or were smaller than 0.5 ha for only 20 of 41 (49%) species for which such data were available. For the remaining 21 (51%) species, home ranges were larger than our plots, and up to 10 times larger for 9 species (Appendix S1: Fig. S3). Thus, for more than half of our focal species, our plots would comprise a relatively small proportion of the breeding territory, and yet, our results suggest a significant decrease in use of Russian olive removal sites on average. Given we disturbed <10% of the available woody cover, individuals may have been able to shift their territories to unaffected areas, depending on densities of competitors. However, there could be population-level consequences if our approach were scaled up to entire riparian systems (Fig. 1).

To our knowledge, our study is one of the first to investigate how the spatial pattern of invasive species removal can alter wildlife responses, and we found some evidence that the short-term negative effects of Russian olive removal could be mitigated by increasing the interspersion of remnant and removed vegetation (Figs. 4, 5). The remnant woody vegetation on low and medium interspersion treatments was spatially concentrated in dense thickets (Fig. 2), which would likely necessitate individual birds nesting or foraging in close proximity during a time of year when they tend to be territorial. The habitable area is also effectively cut in half on these plots, which may reduce the number of territories that could be supported, particularly for species that utilize home ranges <0.5 ha (Appendix S1: Fig. S3). Conversely, the woody vegetation on high interspersion plots was more spatially dispersed, which may help minimize direct competition for resources. Additionally, high interspersion sites may be more favorable for species that prefer sparse woody cover. This is supported by the fact that many of the species with the most dramatic differences in occupancy rates between high and low interspersion treatments (e.g., Bullock's Oriole, Black-headed Grosbeak [*Pheuticus melanocephalus*], Eastern Kingbird [*Tyrannus tyrannus*], American Goldfinch [*Spinus tristis*], Cedar Waxwing [*Bombycilla cedrorum*]) tend to prefer nesting in open woodlands (Rodewald 2015) that would be most similar to our high interspersion treatments. Though the differences we observed among treatment types were not statistically significant (likely due to low power, Appendix S3), even small effects on occupancy could be critical for maintaining threatened or endangered species. Thus, we recommend that future studies evaluate whether and how spatial removal patterns could be used to mitigate negative effects of invasive species control on dependent wildlife (Sogge et al. 2008, Casazza et al. 2016, Tredick et al. 2016).

Results from our study imply two important considerations when implementing large-scale eradication of invasive woody vegetation. First, we join others (Zavaleta et al. 2001, Bateman et al. 2008, Hatten 2016) in cautioning managers to consider the potential short-term negative impacts to the avian community. While all species we examined are of no particular conservation concern according to the IUCN Red List (IUCN 2018) or Partners in Flight Watch List (Rosenberg et al. 2016), Breeding Bird Survey data suggest there have been significant declines in abundance for at least 11 species in the region over the last 50 yr (Sauer et al. 2017; Appendix S1: Table S1). Further, though artificially maintained, the riparian systems we sampled tend to be local hotspots of avian abundance and diversity because of a general lack of riparian habitat in the region (Rocklage and Ratti 2000). In arid riparian areas, total vegetation volume has been shown to be the strongest predictor of avian diversity even where invasive plants dominate, (Fleishman et al. 2003) and removal of invasive woody plants in heavily impacted systems may eliminate critical habitat (Sogge et al. 2008). Of course, we only examined effects on breeding birds, and there may be benefits to Russian olive removal for other species such as lizards and bats (Bateman et al. 2008), and certainly native plants. Where removal is implemented, negative impacts to the avian community could be minimized by maintaining well-interspersed woody cover during restoration.

Secondly, where invasive species control results in a substantial decrease in vegetation structure, it should be accompanied by restoration of native vegetation cover that can ultimately replace lost habitat. Our study only monitored avian communities in the immediate aftermath of Russian olive removal, and there are likely to be longer-term benefits to breeding birds if regeneration of native woody cover is successful and leads to increased abundance, diversity, or habitat quality (Brand et al. 2008, Van Riper et al. 2008). Comparing avian communities in riparian habitats dominated by Russian olive to those in native riparian vegetation was beyond the scope of our study. However, it is known that many species (particularly cavity nesters) seem to avoid Russian olive (Stoleson and Finch 2001), perhaps because it has a growth form that does not promote tree cavities or because it often supports higher densities of nest predators (Knight and Fitzner 1985, Gazda et al. 2002). To better understand the potential benefit of regenerating native habitat on avian community composition, we identified locally common riparian species by crossing 10 yr of eBird data with a list of riparian-dependent birds in the western United States (Rich 2002; Appendix S1: Table S7). Based on this list, several species were notably missing from our study area, including Black-chinned Hummingbird (*Archilochus alexandri*), Calliope Hummingbird (*Stellula calliope*), Lesser Goldfinch (*Spinus psaltria*), Orange-crowned Warbler (*Oreothlypis celata*), Veery (*Catharus fuscescens*), Fox Sparrow (*Passerella iliaca*), and Red-naped Sapsucker (*Sphyrapicus nuchalis*). Clearly, we cannot predict that these species will necessarily utilize habitat in our study areas in the future, though that is a hypothesis worth testing. If regeneration of native woody plants leads to a more natural or complete avian community in the long-term, managers may deem the small (<30%) reductions in occupancy we observed acceptable losses in the interest of restoring ecosystem structure and function.

Even with planting, invasive species control does not necessarily lead to regeneration of native plants (Reid et al. 2009, Rinella et al. 2009, Skurski et al. 2013), though most studies fail to track this (Kettenring and Adams 2011). We intend to continue monitoring these plots to evaluate the success of native tree and shrub restoration across treatments, and the resulting dynamics of the bird community. Our study adds to a growing body of research (Zavaleta et al. 2001, Sogge et al. 2008, Bergstrom et al. 2009, Casazza et al. 2016, Hatten 2016, Tredick et al. 2016) highlighting potential unintended consequences of invasive species control on native wildlife, at least in the short-term. However, careful consideration of removal configuration may help mitigate these impacts in the interest of long-term restoration goals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2756/full