Assembly dynamics of a forest bird community depend on disturbance intensity and foraging guild

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Summary

1. Tree plantations occur globally and are often promoted as a strategy to supply wood products for an expanding human population while reducing pressure on natural forests. Herbicides can accelerate growth of crop trees by suppressing competing vegetation, but little information is available about potential trade-offs with early seral biodiversity resulting from more intensive management.

2. Using data collected over 5 years immediately following stand-replacing disturbance (clear-felling), we used a large-scale experiment to test how environmental filtering influences dynamics of avian community assembly. We evaluated avian responses to three levels of plant cover reduction (light, moderate and intensive herbicide applications) in relation to a control without herbicide. Under the environmental filtering hypothesis, we expected reduced avian species richness and higher turnover as broadleaf plant cover decreases with increasing management intensity. We predicted that the most intensive treatments would exert strong negative effects on leaf-gleaning insectivores, including several species of conservation concern due to long-term population declines.

3. Richness of leaf-gleaning bird species was reduced by 23–52% over the 5 years on moderate (standard practice) vs. control treatments, but effects were substantially smaller for the non-leaf-gleaner guild in years 1–4 (8–25%) and disappeared by year 5 (0%). Both leaf-gleaner and non-leaf-gleaner functional groups continued to colonize moderate and intensive treatments at higher probabilities than the control in Year 5 (range: 0·17–0·29), likely due to rapid vegetation recovery after herbicide applications ceased. Planted conifers were > 35% taller and > 70% larger in diameter in the two most intensive treatments, leading to substantially more wood volume produced per unit area than on stands without herbicide applications.

4. *Synthesis and applications.* Under current management regimes, stand-level trade-offs between conservation of avian diversity and production of wood commodities may be less severe than previously recognized. However, in landscapes where biodiversity conservation rather than wood production is the primary goal, managers can adjust the trade-off by making relatively small reductions in herbicide use that should have positive impacts on richness of leaf-gleaning insectivorous birds.

Key-words: Avian richness, community assembly, disturbance, environmental filtering, forest management, herbicides, hierarchical Bayes, presence–absence data, species pools, trade-offs

Introduction

Intensive Forest Management (IFM) produces more wood biomass per unit area than natural forests and provides more land for biodiversity conservation (Sedjo 1999; Edwards *et al.* 2014). However, negative effects of intensification, such as conversion from native forest types, fragmentation at stand and watershed scales, and species loss associated with the intensive practices themselves, may counteract benefits accrued by constraining area under management (Tittler, Messier & Fall 2012; Linden & Roloff 2013; Homyack & Kroll 2014). Given the prominent role of intensification in meeting global demand for forest products (Meyfroidt & Lambin 2011),

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experimental evaluations of IFM effects on biodiversity and other ecosystem services are of critical importance (Bennett, Peterson & Gordon 2009; Mace, Norris & Fitter 2012; Root & Betts 2016).

To meet demand for wood products, IFM regenerates stands rapidly after harvest in order to reduce rotation length. Herbicides are applied to control competing vegetation during stand establishment, thereby increasing crop-tree survival and growth rates (Fox, Jokela & Allen 2007; Vance, Maguire & Zalesny 2010). However, reduced structural and compositional diversity in the vegetation community can limit or eliminate nesting and foraging substrates for a range of taxa, including avian and invertebrate species (Hayes *et al.* 2005). In addition, IFM advances forest stands quickly from early seral stages to canopy closure, reducing temporal availability of early seral habitat even after initial herbicide effects dissipate (Franklin *et al.* 2002; Larson *et al.* 2008). Rapid succession to closed canopy plantations is a conservation concern both in the Pacific Northwest, USA, and globally, due to declines in early seral forest biodiversity (Thomas *et al.* 2006; Swanson *et al.* 2011). For example, several avian species, including leaf-gleaning and shrub-nesting birds, occurring in our study region have shown strong sensitivities to management intensity in correlative (Morrison & Meslow 1983; Kroll *et al.* 2007) and experimental studies (Betts *et al.* 2013).

Identifying sources of spatial and temporal variation in community structure is a fundamental problem in community and landscape ecology (Gotelli & McCabe 2002; Kraft *et al.* 2014). The environmental filtering hypothesis posits that site-level factors (i.e. the presence of appropriate local abiotic or biotic features) will determine the types of species available as colonists (Belyea & Lancaster 1999). Forest managers utilize a variety of practices (crop-tree density, vegetation control methods), each of which influences local-scale vegetation composition and complexity (Brandeis, Newton & Cole 2001; Kroll & Haufler 2010). If environmental filtering is an important process, local-scale management can exert a strong influence on community structure. However, factors besides site-level habitat quality and quantity, such as competition (Diamond 1975) and regional species pools (Ricklefs 1987), may determine how communities respond to management-induced disturbances (Loreau *et al.* 2001; Tilman, Isbell & Cowles 2014). Further, species traits may interact with habitat structure and composition to alter community assembly (McGill *et al.* 2006). As a result, management alone is unlikely to be the sole determinant of community assembly.

Unfortunately, hypothesized determinants of community structure may be confounded in the field and difficult to separate under non-experimental conditions (Kraft *et al.* 2014). For instance, due to spatial autocorrelation alone (caused by landownership patterns or regional policy), habitat features such as understorey vegetation and canopy cover may be similar at site, landscape and regional scales (Betts *et al.* 2006). Retrospective, non-experimental studies are often inadequate to test specifically for environmental filtering and create a need for experimental studies that control for landscape structure (Kraft *et al.* 2014).

We established a 5-year, randomized complete block experiment to quantify the role of environmental filtering on community assembly dynamics of passerine bird species during forest regeneration in Coast Range, OR, USA. We evaluated the size and duration of effects on avian community composition for control (no herbicide application) and three treatment levels: light (herbicide applied at reduced level compared to moderate); moderate (standard operational practice); and intensive (a treatment designed to control all vegetation except conifer crop). Unlike many previous studies (e.g. Rose, Rosner & Ketchum 2006), we designed our experiment at the scale of the entire forest stand (>10 ha). Within each study block, we placed treatments in relative close proximity (<5 km) to one another in relation to the scale of dispersal in passerines (Bowman 2003). As a result, we could test experimentally for filtering effects while holding landscape-scale variation (the species pool) constant. To our knowledge, this study represents one of the most spatially extensive and well-replicated IFM experiments in the world.

Under the environmental filtering hypothesis, we evaluated support for four predictions: (i) avian species richness will decrease as a function of treatment intensity due to reductions in plant community complexity caused by herbicides; (ii) species preferring open habitats will dominate the most intensively managed stands while leaf-gleaning and shrub-nesting species will dominate in control and light treatments due to availability of structurally and compositionally complex shrub communities; (iii) local-extinction probabilities will be low (<0·2) across control and light treatments given the broader range of niche availability from bare ground to high vegetation cover; alternatively, if competition drives community assembly, we would expect high local-extinction probabilities as heterospecific competition forces species displacement (Tilman 1982); and 4) turnover probabilities will increase with management intensity, as some species will be represented in low abundance by only a few colonists.

Maintenance of native species diversity is a critical aspect of sustainable forest management. Despite the broad-scale use of herbicides in timber plantations worldwide (Carnus *et al.* 2006), relatively few studies examine herbicide effects on alpha (species richness at the stand level) and beta-diversity (species turnover across forest stands). Also, studies are of insufficient duration to quantify temporal variation in responses (Bennett & Adams 2004; Marczak *et al.* 2010). As a result, managers possess only a 'snapshot' of biodiversity responses to management-induced disturbance. By quantifying changes in both avian community structure and tree growth as a function of experimentally imposed levels of forest management intensity, our results illuminate potential trade-offs

between two ecosystem services, biological diversity and wood production, in intensively managed forests.

Materials and methods

STUDY AREAS

In cooperation with private and state landowners, we established 32 study stands, 12–16 ha in size, in the Coast Range, Oregon, USA (Fig. S1, Supporting Information). We grouped study stands in eight blocks along a 100 km north to south axis. All blocks are in the western hemlock zone (Franklin & Dyrness 1973) and range in elevation from 210 to 850 m. The climate consists of cool, wet winters and mild, dry summers. Douglas fir (*Pseudotzuga menziesii*) saplings, with minor components of grand fir (*Abies grandis*), western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*), dominate tree plantations in this region. Common broadleaf species include California hazelnut (*Corylus cornuta* sub-spp. *californica*), ocean spray (*Holodiscus discolor*), vine maple (*Acer circinatum*), big-leaf maple (*Acer macrophyllum*), cascara (*Rhamnus purshiana*), salmonberry (*Rubus spectabilis*), red alder (*Alnus rubra*), *Vaccinium* spp., salal (*Gaultheria shallon*) and Oregon grape (*Mahonia nervosa*). Numerous native and non-native plants occur in stands, although swordfern (*Polystichum munitum*) and brackenfern (*Pteridium aquilinum*) are dominant species.

EXPERIMENTAL TREATMENTS

Stand selection followed a randomized complete block design with four treatment stands located in each of eight blocks. Operators commercially clear-felled all 32 stands in fall 2009 and planted Douglas fir in spring 2010. To reduce local variation and to hold the regional species pool constant, all stands within a block occurred within 5 km of each other. Our objective was to test the combined effects of the suite of herbicides and surfactants used in typical operations rather than to examine the effect of a particular chemical. Therefore, we applied a suite of chemicals to stands to create four levels of treatment intensity (Table 1). The moderate treatment is an approximation of current operational practices on millions of hectares of commercial forestland in both Oregon and Washington, USA (Maguire *et al.* 2009), and is designed to control woody vegetation, grasses and forbs. In contrast, the light treatment is a less effective control of woody vegetation and is thus less severe than the moderate treatment. The

Table 1. Timing of individual management activities for C = control, L = light, M = moderate and I = intensive treatments, respectively, Oregon Coast Range, USA, 2011–2015

Activity	Post-harvest year	Treatment			
		C	L	M	I
Site preparation (broadleaf vegetation spray)	0 (2010)			X	X
Planted at *c.* 1100 trees ha^{-1}	1 (2011)	X	X	X	X
Herbaceous spray	1 (2011)		X	X	X
Herbaceous spray	2 (2012)				X
Broadleaf release spray	2 (2012)		X		X
Herbaceous spray	3 (2013)				X
Broadleaf release (as required)	4 (2014)				X

intensive treatment is an experimental prescription (not deployed under current management scenarios) in which we attempted to suppress all vegetation except the conifer crop. Woody vegetation control occurred in late summer or early fall, and herbaceous vegetation control occurred in early spring of the year they were applied. Control stands had no woody or herbaceous vegetation control. Within a treatment, we applied the same amount and type of chemicals across all blocks (Appendix S1). Finally, we note that activities concluded on the light treatment in 2012; the moderate treatment in 2011; and continued to occur on the intensive treatment in 2015. Moderate and intensive stands had not yet been differentiated during the first year of data collection (Table 1).

SAMPLING

We selected three point count plots within the treated area of each stand using a stratified random approach to maximize the distance between survey locations and stand edge while sampling representative portions of the treatment area. At each of 96 point count locations, we sampled the avian community from 2011 to 2015. Each point was sampled four times during the breeding season (May 28–July 3). To avoid bias, we varied survey order, time of survey and observer throughout the season. We recorded data in a manner consistent with the point count survey guidelines described by Ralph, Droege and Sauer (1995) within a 10-min time interval. Censuses began at sunrise and were completed by 10 am. Technicians recorded all bird detections and associated behaviour and estimated first detection distances from the census point. We excluded detections that occurred >50 m. We totalled avian detections by species, functional group, treatment and year (Table S1).

Ocular estimates of broadleaf vegetation cover were recorded annually for all woody, non-coniferous plants by species within three 3-m-radius subplots each centred 20 m from avian census locations. The bearing to the initial subplot was selected randomly; remaining plots were separated at 120-degree intervals from other plots. Total cover for each plant species was based on the sum of measurements (sometimes overlapping) for the three 3-m-radius subplots (Ellis, Kroll & Betts 2012). We chose this method to quantify the three-dimensional nature of the woody vegetation. As a result, summed point-level cover totals across species could exceed 100%. We estimated per cent cover and species richness of woody vegetation by treatment and year (Fig. 1a,b).

Finally, to examine potential trade-offs between biodiversity and crop-tree growth, we sampled Douglas fir crop trees within 20, 5-m-radius plots in each stand using a systematic sampling design. We individually marked all trees in each plot to quantify individual survival. For all trees, we measured tree height and diameter at 15 cm from the base of the tree.

ANALYSIS

We fit a multispecies occupancy model (Dorazio & Royle 2005; Zipkin, DeWan & Royle 2009) within a Bayesian framework to estimate species-level treatment effects and community-level summaries, such as species richness and species similarity (proportion of overlap in species richness between two stands) between control and treatment stands (Dice 1945; Dorazio & Royle 2005; Giovanini *et al.* 2013). Also, we estimated associated dynamics,
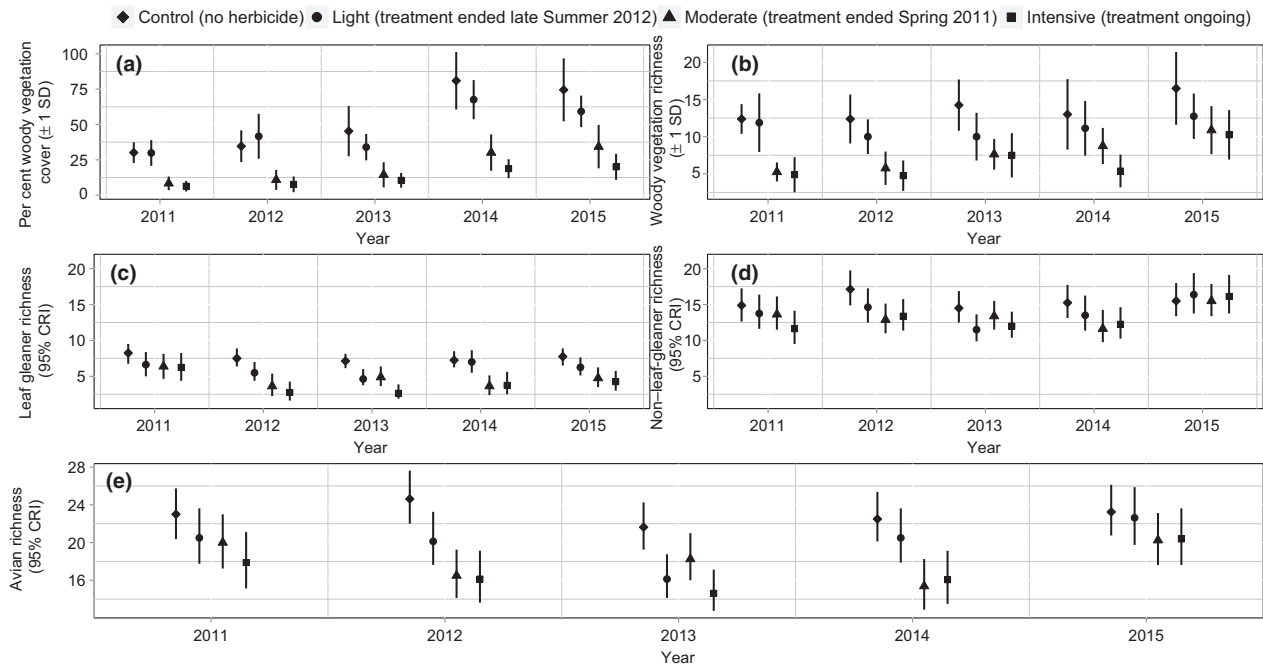
Fig. 1. Vegetation and avian responses to herbicide applications, Oregon Coast Range, USA, 2011–2015. Per cent woody vegetation cover (a), woody vegetation richness (b), leaf-gleaner richness (c), non-leaf-gleaner richness (d) and total avian richness (e) are displayed. Note that *y*-axis scales change between a, b, c/d, and e.

including species turnover (probability that a species that occurs at time *t* did not occur at time *t* − 1) and local extinction (Russell *et al.* 2009). We estimated occupancy for 40 species with ≥10 detections and which are known to occur as breeding populations in early seral stands (Kroll *et al.* 2012b). Species not included in the analysis were either incidental species (e.g. hawks) or species associated with mature forest stands (e.g. nesting in conifer canopy). Following previous examples (Linden, Roloff & Kroll 2012; Homyack *et al.* 2014), 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. We provided model description and notation, and details of model fitting, in Appendix S2.

To evaluate specific predictions about avian responses to herbicide treatments, we included a hyperprior in the model to distinguish leaf-gleaner and non-leaf-gleaner guilds (Gelman & Hill 2007; Pacifici *et al.* 2014; Homyack *et al.* 2016). Under the hierarchical community model, we assume species-specific effects for a given parameter are drawn from one of two common normal distributions, for example, $\alpha_{\text{Leaf−gleaner},i} \sim N(\mu_1, \sigma_1^2)$ for parameter $\alpha_{\text{Leaf−gleaner}}$ of species *i,* where the mean and variance of $\alpha_{\text{Leaf−gleaner},i}$ are population-level hyperparameters depending on whether species *i* is a leaf-gleaner species. These population-level distributions provide a summary of community response, both in terms of the mean behaviour and the variability in behaviour. 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 amount of information available for each species. For species with little information (i.e. those with low detection probabilities), estimates will tend to shrink towards the population mean value. The priors we used in the analysis are included with the R code for the model (Appendix S3). To assess consistency between our models

and data, we used posterior predictive checks (Gelman *et al.* 2004). We did not find any evidence of lack of fit in the model. We provide details and an example for the posterior predictive checks (Appendix S4).

Results

As expected, herbicide treatments had a strong influence on both woody and plant cover and diversity (Fig. 1a,b). Less intensively managed treatments (control and light) had 3·5 times more woody plant cover than the moderate treatment (standard operational prescription in western Oregon) in year 1, but these differences were reduced (2·2 and 1·7 times more, respectively) by year 5. Similarly, control and light treatments contained, on average, two to five more plant species than the moderate treatment in year 5 (Fig. 1b).

On average, planted Douglas fir seedlings were 35% taller and 68% greater in diameter in moderate than control stands (Table 2). Paired with increases in seedling density with treatment intensity (due to reduced seedling mortality; Table 2), herbicide use facilitated substantially more wood volume per unit area (range: 210–530%) in the two most intensively managed treatments compared to the less intensively managed treatments (control and light). The moderate treatment yielded volume gains of 210% and 390% vs. light and control treatments, respectively.

Overall, avian species richness was lower on all treatments with herbicide applications in years 2 and 3 (Fig. 1e), a result that supports the environmental filtering

Table 2. Average height, diameter and density of planted Douglas fir (*Pseudotzuga menziesii*; PSME) in four different herbicide treatments, Oregon Coast Range, USA, 2015

Treatment	PSME height (cm)	Standard deviation	PSME diameter (cm) (15 cm from base of tree)	Standard deviation	Density (PSME/100 m²)	Standard deviation
Control	145·0	61·8	2·2	1·0	5·6	1·2
Light	162·4	75·8	2·8	1·3	6·2	1·4
Moderate	195·2	82·1	3·7	1·6	6·6	1·4
Intensive	201·8	80·8	4·3	1·9	6·8	1·8

hypothesis and is consistent with our first prediction. Upon completion of herbicide treatments, differences were minimal (*c.* 2 species) between control and light treatments (years 4 and 5) and between the control and both moderate and intensive treatments (year 5). Differences in species richness in year 5 were due to ongoing treatment effects on the leaf-gleaner group (Fig. 1c) rather than the non-leaf-gleaner group (Fig. 1d), a result supporting our second prediction.

Effects of herbicide treatments were more pronounced for the leaf-gleaner than the non-leaf-gleaner group (Fig. 2), also supporting our second prediction. Median species occupancy was lower on treatments than controls for the leaf-gleaner group in all 5 years. However, differences in median occupancy between moderate and control treatments for the non-leaf-gleaner group declined from year 2 [−0·29, 95% credibility interval (CRI): −0·52, −0·03] to year 5 (0·01, 95% CRI: −0·27, 0·28). Median species occupancy probability tended to be higher for the leaf-gleaner than non-leaf-gleaner groups across all four treatments in year 1 (Fig. S2). Although leaf-gleaner occupancy probability remained higher in the controls across all 5 years, non-leaf-gleaner occupancy probability was higher in all three treatments in years 2 and 3. Once herbicide applications ceased and vegetation recovered on the light treatment in year 3, leaf-gleaner occupancy probability was either higher than, or similar to, non-leaf-gleaner occupancy in years 4 and 5 (Fig. S2). For the moderate and intensive treatments, non-leaf-gleaner occupancy probability was higher than or equivalent to leaf-gleaner occupancy probability in years 4 and 5.

Local-extinction probabilities were low for the non-leaf-gleaner group in all years and declined for the leaf-gleaner group during the study (Fig. 3), results which are generally consistent with our third prediction. Two exceptions included the response of the leaf-gleaner group in year 2, which may be related to the harvest of the experimental stands rather than to herbicide applications *per se*, and the moderate treatment in year 4. Turnover probabilities differed by functional group (Fig. 3) and species in the non-leaf-gleaner group continued to colonize stands in year 5. Turnover probabilities remained high, but were imprecise, for the leaf-gleaner group in the moderate and intensive treatments in year 5, providing some support for our fourth prediction. Evidence for an association between turnover and treatment intensity was inconsistent, with turnover probabilities in the moderate and intensive treatments higher than control and light treatments in some years (e.g. non-leaf-gleaner group in years 3 and 5) but not others (leaf-gleaner and non-leaf-gleaner groups in year 4).

Community composition was similar for treatment comparisons across the 5 years of sampling (Fig. 4). The largest difference in median species similarity between
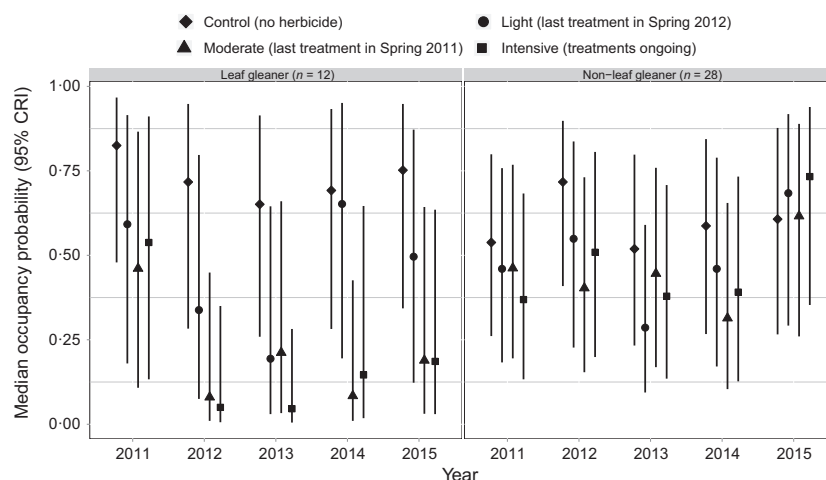
Fig. 2. Median (95% CRI) occupancy estimates by functional guild, treatment and year, Oregon Coast Range, USA, 2011–2015. Estimates are the average probability of a species within each guild occurring in a specific treatment × year combination.
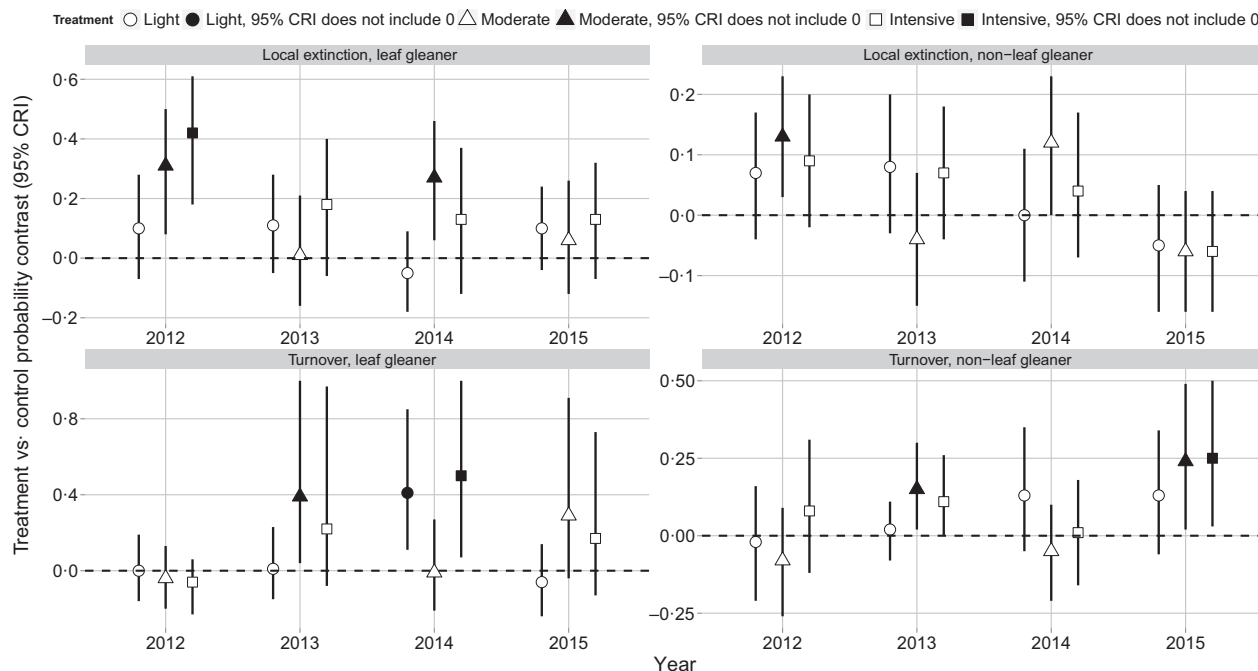
Fig. 3. Contrasts (95% CRI) with controls for local-extinction and turnover probability by guild, treatment, and year, Oregon Coast Range, USA, 2011–2015. Contrasts are on the probability scale. Note that *y*-axis scales change across panels. Open symbols indicate 95% credible intervals included 0; closed symbols indicate 95% credible intervals did not include 0. Treatments were concluded in late summer 2012 on the light treatment and spring 2011 on the moderate treatment. The intensive treatment continued through 2015.

control and treatments occurred in year 2; by year 5, median species similarity was nearly equivalent both within controls and between control and treatment stands.

Finally, we found substantial differences in species richness across blocks (Fig. S3) that likely reflected variation in the regional species pool. This underlying variation may have contributed to species similarity across treatments despite evidence for negative effects on leaf-gleaner occupancy due to environmental filtering.

Species-specific occupancy estimates (Fig. 5) suggested that effects of moderate and intensive treatments persisted for 5 of 12 (42%) leaf-gleaner species (MacGillivray's warbler *Geothlypis tolmiei*; orange-crowned warbler *Oreothlypis celata*; Swainson's thrush *Catharus ustulatus*; warbling vireo *Vireo gilvus*; and Wilson's warbler *Cardellina pusilla*). In contrast, negative treatments effects declined during the 5 years of observation for other species including American goldfinch *Spinus tristis*, black-headed grosbeak *Pheucticus melanocephalus*, song sparrow *Melospiza melodia* and western tanager *Piranga ludoviciana*.

Species-specific estimates of detection probability indicated substantial variation across species, treatments and years (Fig. S4). Importantly, detection probability was relatively high and precise for the leaf-gleaning species we expected to respond negatively to the treatments, including common yellowthroat *Geothlypis trichas*; MacGillivray's warbler; orange-crowned warbler; Swainson's thrush; and Wilson's warbler. Finally, we found a strong positive association between number of detections and detection probability for many species, including dark-

eyed junco *Junco hyemalis oregonus*; house wren *Troglodytes aedon*; MacGillivray's warbler; orange-crowned warbler; rufous hummingbird *Selasphorus rufus*; song sparrow*;* and white-crowned sparrow *Zonotrichia leucophrys* (Fig. S4 and Table S1).

Discussion

We present evidence from a manipulative experiment to support the environmental filtering hypothesis, as we found strong negative effects of both moderate and intensive experimental vegetation control on leaf-gleaner richness that persisted throughout the 5 years following initial disturbance (our first and second predictions). In contrast, initial negative impacts on total species richness dissipated during the study. Although treatments caused substantial reductions in woody vegetation cover and richness (an environmental filter), our experimental design did not allow us to separate effects of plant abundance and diversity from direct herbicide effects (toxicity) on the avian community. However, many of the species we detected are migrants (particularly leaf-gleaners) and therefore not present on stands during herbicide applications. Further, we consider a toxicity effect to be unlikely given how quickly herbicides dissipate (Newton *et al.* 1984; Lautenschlager & Sullivan 2004). Also, substantial differences in plant community structure and composition and leaf-gleaner species richness between the least and most intensively managed treatments suggest that negative treatment effects occurred through reductions in habitat amount and
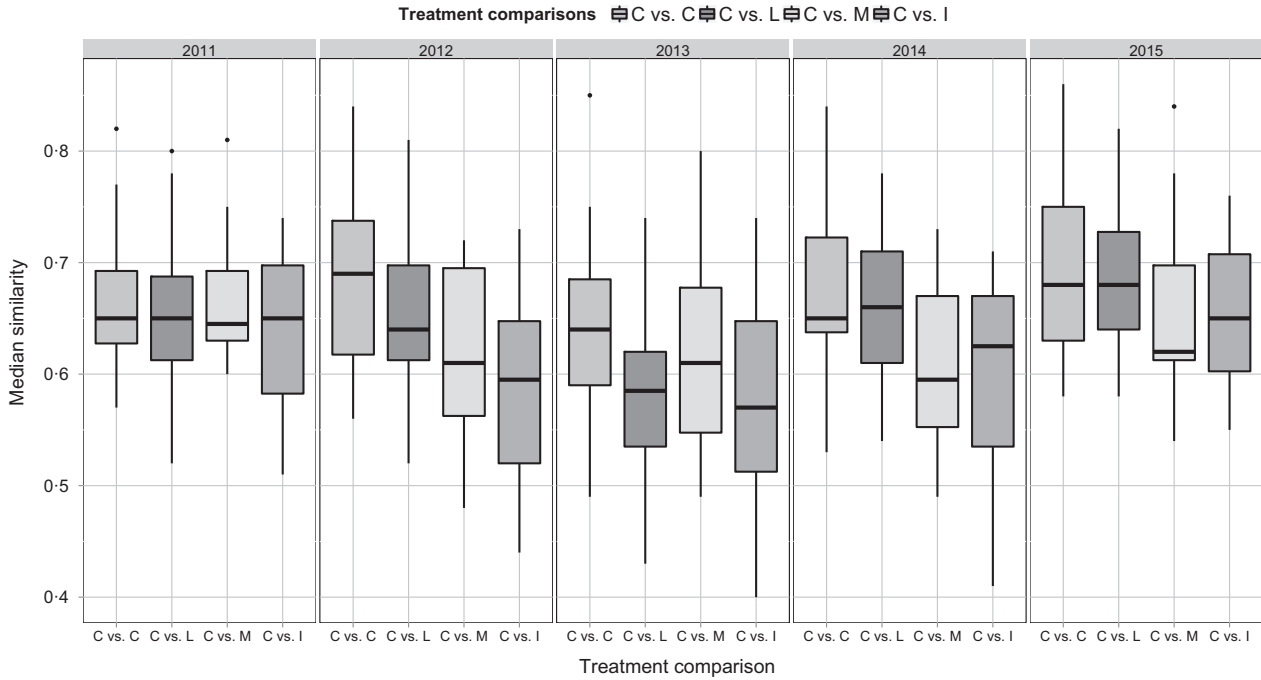
Fig. 4. Distribution of median similarity (overlap in avian species composition) among all plots, with comparisons by treatment and year, Oregon Coast Range, USA, 2011–2015. C = control, L = light, M = moderate, and I = intensive treatments, respectively. 0 indicates no overlap in species composition; 1 indicates complete overlap. Treatments ended in late summer 2012 on the light treatment and spring 2011 on the moderate treatment. The intensive treatment continued through 2015.
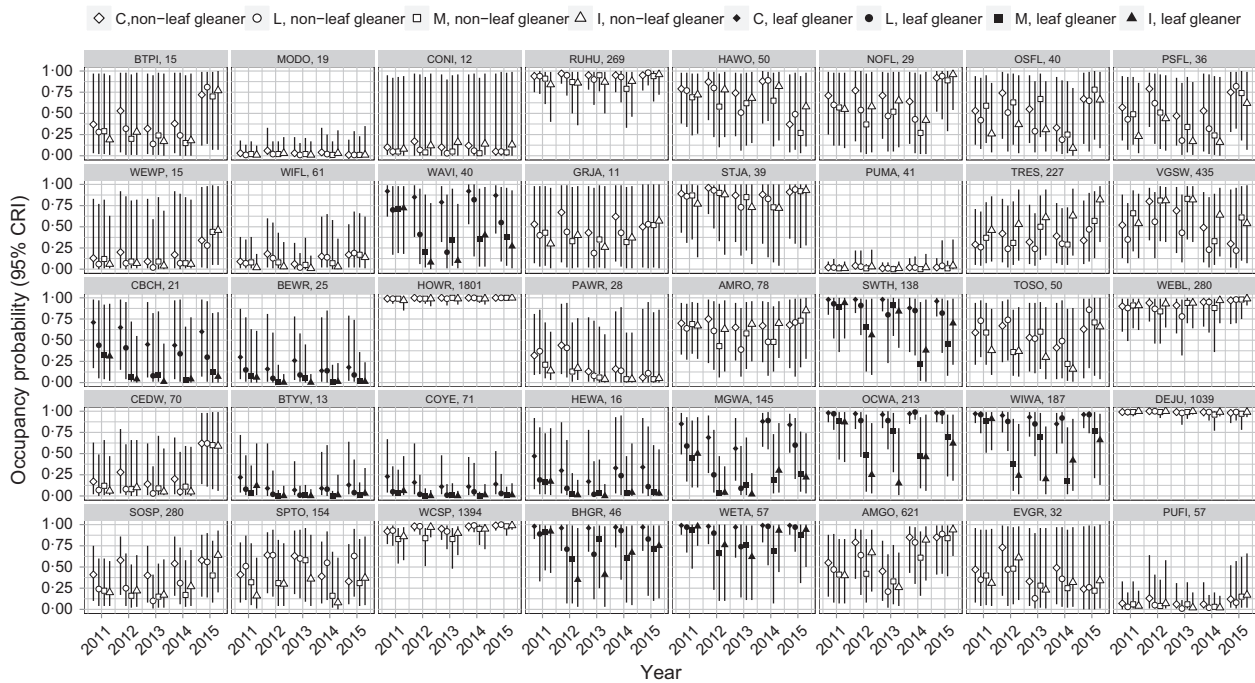
Fig. 5. Median (95% CRI) species occupancy probability by treatment and year, Oregon Coast Range, USA, 2011–2015. Total number of detections is shown next to each species code. C = control, L = light, M = moderate, and I = intensive treatments, respectively. Treatments were concluded in 2012 on the light treatment and 2011 on the moderate treatment. The intensive treatment continued through 2015. Symbols identify leaf-gleaner (closed) or non-leaf-gleaner (closed) species. Species are sorted by taxonomic order. Definitions for species codes are in Table S1.

quality (indirectly through herbicide effects on plants), and not through toxicity (directly through mortality to birds).

Counter to our expectations, avian species richness in the moderate and intensive treatments recovered substantially during the study. In addition, crop-tree volume on

moderate and intensive treatments was substantially higher than on either control or light stands. This result provides further evidence that IFM can meet growing demand for wood products on a reduced forest area (Rose & Rosner 2005). Given that the moderate treatment is analogous, in terms of herbicide application and subsequent vegetation control, to silvicultural activities common to private ownerships globally (and replicates a prescription applied to millions of hectares in the Pacific Northwest, USA), our results indicate that trade-offs between timber growth and avian diversity may be less severe than expected from shorter term studies (Jones *et al.* 2012; Betts *et al.* 2013). However, we emphasize that long-term data are required to quantify whether this potential benefit of intensive management remains until stand rotation. This research effort will continue to estimate avian species richness, along with associated dynamics, and tree growth to quantify biodiversity–wood production trade-offs during the 40- to 60-year rotation for Douglas fir.

Our results indicate similarity in avian community composition among and within control and treatment stands 5 years after we implemented prescriptions, suggesting spatial variation in species richness could not be explained by treatments alone. Unspecified variation could arise from multiple sources, including differences in regional species pools across our study landscape (Cornell & Harrison 2014; Mittelbach & Schemske 2015) and differences in landscape configuration and/or composition around experimental blocks (Kroll *et al.* 2012a, 2014; Tscharntke *et al.* 2012). We attempted to control variation due to factors other than the treatments by including block- and site-specific random effects in the statistical model. This result has important management implications, as community responses to a specific treatment at the local scale will depend on the regional and landscape species pool (Ricklefs 1987).

Evidence from a dynamic community model indicated avian colonization of treatment stands continued into the fifth year of our study, although we found only modest support for our fourth prediction that stated turnover would increase with management intensity. In contrast, local-extinction probabilities were low for most treatments in years 4 and 5 (in support of the third prediction), suggesting species retention even in the face of potentially lower densities for some species. Given the oft-noted relationship between occupancy and abundance (Yin & He 2014), we were not surprised to find evidence that avian communities continued to change 5 years after treatment implementation. In another study of avian community responses to forest disturbance in the same region, and using a similar analytical framework, Pearson *et al.* (2015) found that species continued to colonize riparian buffers 10 years after surrounding stands were harvested. We expect this dynamic to persist as additional species, unobserved to this point, will occupy harvest stands as the conifer crop matures and habitat diversity increases (Ellis & Betts 2011; Jones *et al.* 2012).

In our study, absolute estimates of richness may be biased low because we included only species with 10 detections or more. As a result, inference on community-level effects (e.g. species richness) may not reflect species with low prevalence or especially low detection probabilities. Species richness may change substantially if uncommon species increase sufficiently to be included in future analyses. In addition, although species richness may be relevant to ecosystem processes (Cardinale *et al.* 2006), occupancy may be a poor proxy for abundance at fine spatial scales (Bock, Jones & Bock 2007). Equivalent species richness across treatments does not necessarily indicate lack of population-level effects (which may be most relevant to conservation objectives; Phalan *et al.* 2011). Future studies should consider abundance across a gradient in IFM for a subset of species as well as demographic parameters such as nest success, survival and recruitment.

Using a multilevel model, we tested and found support for our second prediction that stated non-leaf-gleaner species would dominate the most intensively managed stands while leaf-gleaner species would occur in stands with diverse, broadleaf-dominated plant communities. We allowed responses to vary by functional group, which prevented ubiquitous species from dominating the 'mean' treatment response (Pacifici *et al.* 2014). For example, three non-leaf-gleaner species, dark-eyed junco, house wren and white-crowned sparrow, were detected most frequently and we did not find evidence of a treatment effect for these three species. Multispecies models can estimate responses for rare species, but a few hyperabundant species often dominate ecological communities and will shape the posterior distribution of the species-level 'random effect' if they respond similarly to a treatment (Gelman & Hill 2007; Giovanini *et al.* 2013).

Given that conifer survival and growth are often reduced without vegetation control (Rose & Rosner 2005; this paper), implementation of 'conservation' prescriptions, similar to the control or light treatments, would require active forest management over additional hectares to maintain wood production at similar levels. In contrast, the moderate treatment can likely maintain wood production on a smaller proportion of the landscape, leaving other forested areas available as conservation reserves. These allocations resemble those in land sharing vs. land sparing agricultural landscapes (Phalan *et al.* 2011; Gabriel *et al.* 2013). In our region, broad-scale conservation efforts emphasize late seral forest, with early and mid-seral stages occurring in production areas or as a result of natural disturbances. Our results indicate that intensive management reduces, but does not eliminate, habitat availability and that effects of reductions are of relatively short duration for most avian species using early seral forest. We cannot yet address whether contemporary habitat availability is sufficient at the landscape scale to maintain populations of early seral species, given current land-use allocations. This conservation question is complex and merits further research attention. However, in landscapes

where biodiversity conservation rather than wood production is the primary goal, managers can make relatively small reductions in herbicide use that should have positive impacts on richness of leaf-gleaning insectivorous birds.

Acknowledgements

Data accessibility

Avian and tree growth summary data are included in Appendix S5.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Distribution of treatment blocks and experimental units, IFM study, Oregon Coast Range, USA, 2011–2015.

Fig. S2. Boxplot summaries of species occupancy probability by foraging guild, treatment, and year, Oregon Coast Range, USA, 2011–2015.

Fig. S3. Block-specific estimates (95% CRI) of avian species richness by year, Oregon Coast Range, USA, 2011–2015.

Fig. S4. Median (95% CRI) species detection probability by treatment and year, Oregon Coast Range, USA, 2011–2015.

Table S1. Number of avian detections by species, year, and IFM treatment, Oregon Coast Range, USA, 2011–2015.

Appendix S1. Herbicide type and application rate, IFM experiment, Oregon Coast Range, USA, 2011–2015.

Appendix S2. Models to estimate avian occupancy and calculate community summaries, Oregon Coast Range, USA, 2011–2015.

Appendix S3. R code for Bayesian multilevel community occupancy model to estimate herbicide treatment effects for 40 avian species, Oregon Coast Range, USA, 2011–2015.

Appendix S4. Details of, and an example for, the posterior predictive checks for a multilevel avian community occupancy model, Oregon Coast Range, USA, 2011–2015.

Appendix S5. Avian and tree size and density data, Oregon Coast Range, USA, 2011–2015.